MAXIMUM DIVING DEPTH AND DIVING PATTERNS OF THE GENTOO PENGUIN *PYGOSCELIS PAPUA* AT THE CROZET ISLANDS

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SUMMARY

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The diving behaviour of breeding Gentoo Penguins *Pygoscelis papua* was investigated at the Crozet Islands during October and November 1991. Results from 15 birds showed that the individual maximum dive depths ranged from 40-210 m. One continuous dive record from a data logger from one trip of 9.5 h made by a female involved 103 dives greater than 10 m. Two categories of dives were reported: shallow dives (less than 5 m), and "deep" dives, mostly flat-bottomed dives. The accumulated time spent shallow and flat-bottomed diving was 24.5 and 75.4% of the total time spent under water, respectively. Dive duration was positively related to maximum depth. There was a positive relationship between the time spent at the bottom and depth. Stomach flushing indicated that the prey was exclusively *Euphausia vallentini*. The pattern of diving and the maximum diving depth are compared with those obtained at more southerly localities.

INTRODUCTION

Penguins are highly specialized diving birds and as such, their ecology at sea has recently attracted much interest. Recent intensive studies on the foraging ecology of the Gentoo Penguin *Pygoscelis papua* and the two other congeners have examined depth utilization (Croxall *et al.* 1988, Naito *et al.* 1990, Wilson *et al.* 1991a,b, Williams *et al.* 1992). The Gentoo Penguin has a wide breeding range compared to other species of penguins, extending from the Crozet Islands (46° S) to the Antarctic Peninsula (65° S) (Woehler 1993). It is the least numerous penguin in the sub-Antarctic and the Antarctic, with a current population of about 300 000 pairs (Woehler 1993).

Most studies of Gentoo Penguin diving behaviour have been conducted at the southerly parts of the range (Trivelpiece *et al.* 1986, Croxall *et al.* 1988, Wilson *et al.* 1991a, Williams *et al.* 1992) where Antarctic Krill *Euphausia superba* is a plentiful food resource. Only one study reports information for populations north of the Antarctic Polar Front, conducted at Marion Island where Antarctic Krill is absent and food availability is much lower (Williams 1980, Adams & Wilson 1987).

We present information on maximum diving depths and diving patterns of Gentoo Penguins at the Crozet Islands and compare the results with those obtained at more southerly localities.

STUDY AREA AND METHODS

The study was carried out between October and November 1991 at the Chaloupe colony (120 pairs), in the eastern sector of Possession Island (46°30'S, 52°30'E). Possession is the largest of the Crozet Islands and has a Gentoo Penguin population consisting of about 1400 pairs (Bost 1991).

Maximum dive depths were determined by using capillary depth gauges (Burger & Wilson 1988) made from lengths (180 mm) of flexible plastic Tygon tubing (diameter 0.8 mm) coated internally with a thin layer of icing sugar. Water entering the open end of the capillary tube compressed the volume of air trapped in the tube. The maximum depth attained by the penguin during its foraging trip was indicated by the line between the dissolved and undissolved powder. The maximum compression and depth may then be calculated using Boyle's Law (Burger & Wilson 1988). This gauge has been used to provide information on diving capacities of free-living penguins (Adams & Brown 1983, Whitehead 1989, Wilson & Wilson 1990, Scolaro & Suburo 1991). These gauges are very small and light (<1 g) and errors in depth estimates are considered to be <10% for multiple immersions (Burger & Wilson 1988). Thirty-four Gentoo Penguins guarding chicks were fitted with depth gauges attached to the dorsal midline of the back using water-proof tape passed under a few feathers (Wilson & Wilson 1989). Birds were sexed by mass, bill and flipper lengths (Bost 1991) and were released near the colony. The procedure from capture to releasure took less than five minutes. After recapture, we read the length of disolved icing sugar in the gauges to the nearest 0.5 mm.

In addition, data loggers with a time-depth recorder were deployed on three penguins visiting the colony during the same period. The recorders were microprocessor-controlled (Driesen+Kern Gmbh: Postfach 1424, 24572 Bad Bramsted, Germany, c.f. Wilson *et al.* 1993). These units had an internal RAM with a capacity of 64 kB and were programmed and read out from a computer fitted with appropriate interface. The depth was set to be recorded at intervals of 10 s, with a minimal threshold of 2 m. The units were hydrodynamically shaped and measured 140 x 57 x 24 mm, and weighed 160 g. They were taped to the dorsal midline of the back in a manner similar to that of the capillary depth gauges.

RESULTS

Maximum depth

Fifteen penguins with capillary depth gauges were recaptured one to eight days after being equipped. These depth gauges appeared to function perfectly. More birds could not be recaptured during this period despite pre-dawn to post-dusk watches due to the penguins' timidity. Nine other penguins with depth gauges were recaptured 20 to 29 days after release. Measurements from these devices were ignored because prolonged deployment can lead to significant errors (Burger & Wilson 1988). The maximum dive depth recorded ranged from 40 m to 210 m, the mean being 77 m (S.D. 45 m). Maximum dive depths were nonrandomly distributed with two records less than 40 m, four between 40 and 60 m, three between 60 and 100 m, and six over 100 m. The maximum dive depth of 210 m was achieved by a male (mass 7100 g) caught eight days after release. A maximum dive depth of 180 m for a female (mass 6100 g) was recorded three days after release. However, no significant difference was found between the overall mean dive depth of males and females ($P>0.05$, $n=6$ for males and 6 for females). No significant correlation was found between duration of trip at sea and maximum depth recorded ($r=0.41$, $n=15$, $P>0.05$).

Patterns of diving

A continuous diving record from a data logger was available from one trip made by a female. The other two fitted birds did not visited again the colony during the study period. The female went to sea at 06h20, 10 minutes after sunrise, and came back the same day to the colony at 18h15, one hour before dusk, having been at sea for 9.6 h. Sixty percent of the foraging trip was spent underwater.

We estimated the distance between the colony and the foraging area from the time between departure to sea and the first "deep" dive of the bird (more than 10 m since maximum recorded depth from this trip was less than 40 m) and assuming that the penguin travelled in a straight line, with a mean speed of 4.5 km h^{-1} (Trivelpiece *et al.* 1986). This estimated distance was 1.9 km. Once at the presumed foraging area, the penguin dived continuously for 8.5 h (Fig. 1). The maximum dive depth recorded was 37 m and the maximum dive duration was 5.5 minutes.

We were able to distinguish two distinct categories of dives: "shallow dives" (less than 5 m) and "deep" dives (more than 10 m) (Fig. 2). A total of 103 deep dives was recorded. The mean depth of deep dives was 25.3 $\pm$ 6 m and their mean duration was 3.39 $\pm$ 0.56 minutes (n=103). Most of these deep dives (76%) had the pattern of flat-bottomed dives (FB dives). During these dives, the bird performed a rapid descent when it was in transit between the surface and the bottom, a bottom phase and an ascent phase. Twentytwo percent of the "deep" dives exhibited a succession of ascent and descent phases with an amplitude of more than 5 m.

The accumulated time spent during shallow dives and "deep dives" was 24.5% and 75.4%, respectively, of the total time spent underwater. The distribution of time spend per metre depth during deep dives shows a peak at 25-26 m (25%, Fig. 3). Eightyfour percent of the time spent in deep dives was recorded between 15 and 28 m. Dive duration was positively related to maximum depth ($r=0.73$, $n=79$, Fig. 4). The mean interval between dives exceeding 10 m was 1.06 $\pm$ 0.46 minutes (n=98). The dive duration was also positively related to the ensuing surface interval ($r=0.42$, $P<0.01$, $n=98$). During FB dives, the mean time spent at the bottom was 1.96 $\pm$ 0.5 minutes, i.e. 52 $\pm$ 12% of diving time. The mean amplitude at the bottom was 4.2 $\pm$ 2.5 m (n=80). The bottom duration was positively related to depth ($r=0.18$, $n=88$, Fig. 5). During deep dives, the time spent in ascent was shorter than for descent (0.99 $\pm$ 0.30 minutes and 1.15 $\pm$ 0.21 minutes, respectively, t-test for matched pairs $t=3.7$, $P<0.01$).

Depth utilization varied as a function of time of day (Fig. 1) with the penguin diving deeper as the day progressed ($r=0.98$, $n=9$ mean diving depths calculated during nine intervals of one hour). When recaptured at the colony the Gentoo Penguin was stomach-flushed (Wilson 1984). Stomach contents were almost entirely comprised of the euphausiid *Euphausia vallentini*. A total of 1293 individuals was counted amounting to 94 g of food.

DISCUSSION

Patterns of diving

Despite a limited data set, this study suggests that patterns of diving of Crozet Gentoos Penguins differ from those described for other localities with regard to depth utilization. We report here only two distinct categories of dives: shallow dives and (relatively) deep dives, which were mostly flat bottomed dives (Wilson 1989, Wilson *et al.* 1991a, Williams *et al.* 1992). Shallow dives have been interpreted as travelling dives (Trivelpiece *et al.* 1986, Wilson & Wilson 1990, Williams *et al.* 1992), used on penguins commuting between the colony and the foraging area (Wilson *et al.* 1991b). The short distance travelled is consistent with the inshore-foraging habits of the Gentoo Penguin at the Crozet Islands

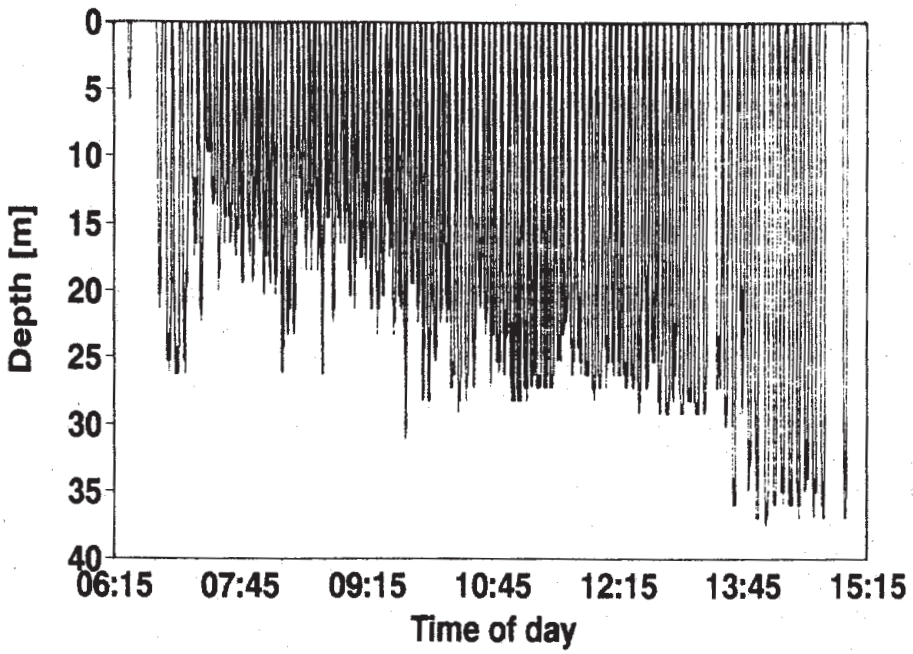

Figure 1

Time-compressed diving patterns of a data logger-fitted Gentoo Penguin during a foraging trip (17 October 1991).

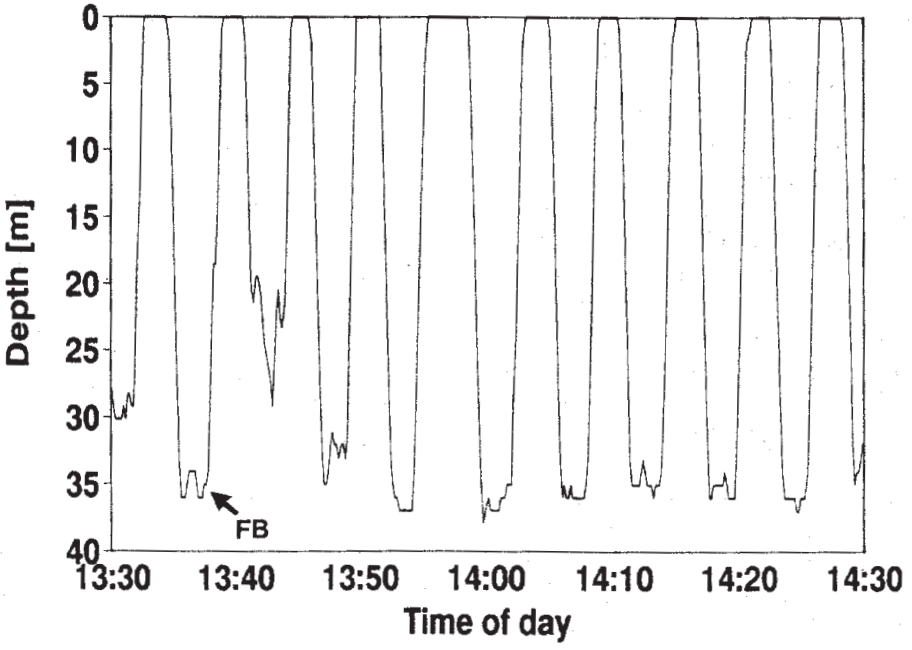

Figure 2

Enlarged section of a diving record for an individual Gentoo Penguin showing types of dives profiles obtained (FB dives).

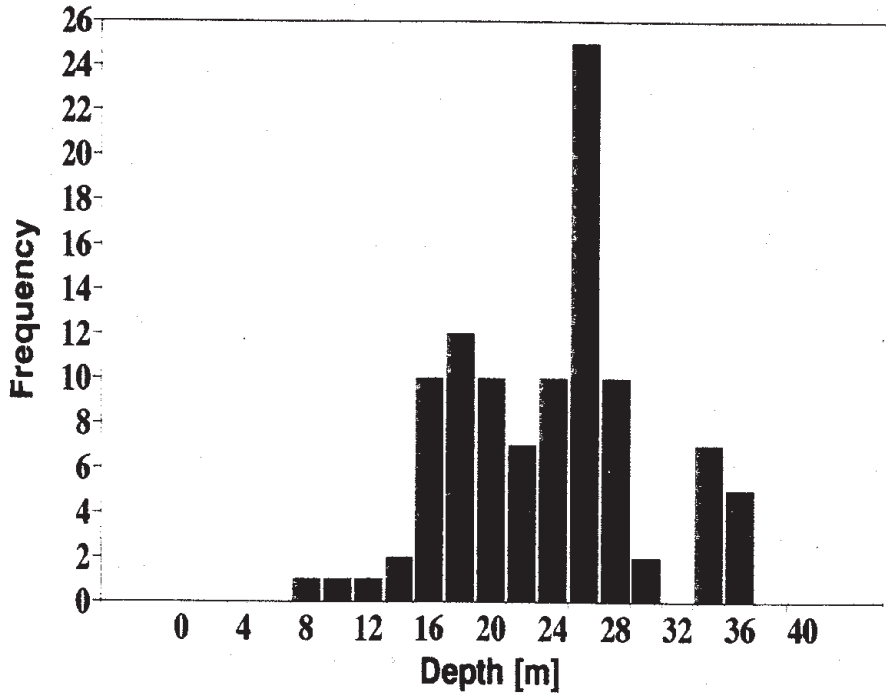

Figure 3

Frequency distribution of dive depth in Gentoo Penguin at the Crozet Islands.

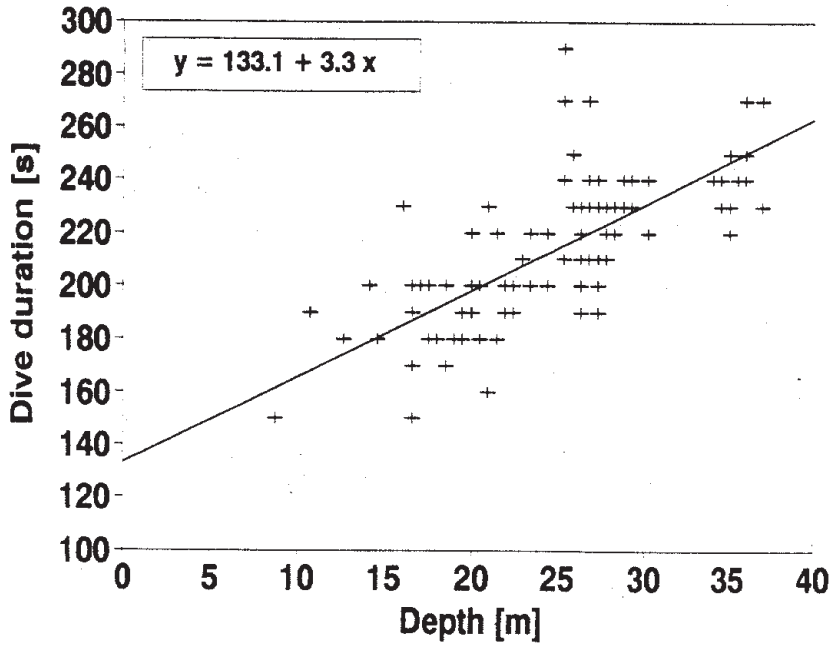

Figure 4

Relationship between maximal depth of dives and dive duration in the Gentoo Penguin (P=0.73).

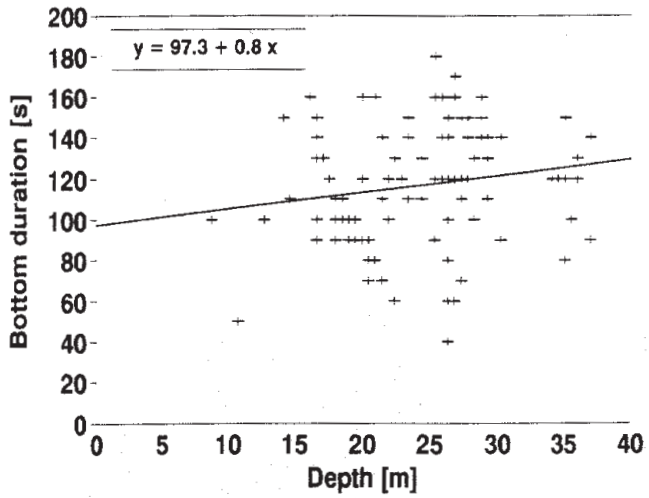

Figure 5

Relationship between time spent at the bottom and depth of dives in the Gentoo Penguin (P=0.18).

as it is for southern populations (Trivelpiece *et al.* 1986, Croxall *et al.* 1988, Bost & Jouventin 1990). At South Georgia, three types of dive profile have been distinguished from a total of 110 birds-days: "V", "U" (similar to flat-bottomed dives) and "W" dives. In our data set, the distinction between FB dives and "W" dives was not well pronounced. A succession of ascent and descent phases occured during bottom time, probably resulting from the bottom topography (Wilson 1990). Our bird spent 75% of its diving time between 5 and 37 m. By contrast, South Georgia Gentoo Penguins exhibit a strong bimodal diving pattern, with birds spending usually 71% of their total diving time in depths deeper than 30 m, with an average depth of 80-90 m at midday (Williams *et al.* 1992). Because the continuous diving activity of our fitted penguin was limited at depths less than 40 m, this raises the potential effect of the device on foraging behaviour (Wilson *et al.* 1986). However, we believe that this pattern of diving reflected prey distribution (euphausiids) rather than being a device-induced effect. Firstly, some Gentoos Penguins fitted during the same period with the capillary depth gauges did not exceed 40 m despite being caught again three days later. Secondly, swarms of *Euphausia vallentini* generally occur in the top 50 m of the water column (S. Razouls pers. comm.). This corresponds to the depth range of our fitted bird. Flat-bottomed dives seem to be related to the localization and the capture of prey (Wilson *et al.* 1991 a,b). It is probable that the euphausiids were caught during the extended flat-bottomed phase of the dive recorded which represented half of the diving time.

The foraging success of our fitted bird was low, with an stomach mass of less than 100 g. Substantial quantities of food may be digested by the time foraging penguins return to the colony (Wilson *et al.* 1989, Wilson *et al.* 1992). However, the small meal brought back by the studied bird was about three time less than the meal size usually carried by Gentoo Penguins to their chicks during this period (C.A. Bost unpubl. data). In addition, 23% of Gentoo Penguins

stomach contents may contain only crustaceans during this period of the year (V. Ridoux pers. comm.). This suggests that this trip may well not have been a typical foraging trip.

Maximum depth

Our study indicates that Gentoo Penguins at the Crozet Islands can dive to very deep depths. Among seabirds, only King *Aptenodytes patagonicus* and Emperor Penguins *A. forsteri* have been recorded as diving to greater depths (Kooyman *et al.* 1971, 1992). The Gentoo Penguin appears to have a highly variable maximum diving depth which depends on locality, as for some other penguins (Wilson & Wilson 1990, Wilson *et al.* 1991 a,b). Dives at the Crozet Islands can exceed 200 m whereas at Marion dives of more than 40 m seem unusual (Adams & Brown 1983). At the Kerguelen Islands, the maximum diving depth can reach 120 m (C.A. Bost unpubl. data). A depth of 156 m has been recorded at South Georgia (Williams *et al.* 1992) and more than 150 m in the Antarctic Peninsula (Wilson 1989).

Maximum depths reached at the Crozet Islands by Gentoo Penguins were greater than those recorded at other localities. Among penguins, maximum diving depth varies allometrically with body mass (Burger 1991). The Crozet Gentoo Penguins have the largest body size of all populations, being 10% larger than the South Georgia birds (Bost & Jouventin 1990). This confers to Gentoo Penguins an increased foraging niche due to the limited accessibility of shallow waters at the Crozet Islands, the 100 m isobath lying 2-3.5 km off the coast of Possession Island (from bathymetric data of Terres Australes et Antarctiques Francaises). Intensive studies using remote-sensing techniques during different periods of the year are necessary to understand better variation in depth utilization by Gentoo Penguins in relation to local oceanographic features.

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