

DIVING BEHAVIOUR OF TWO GALÁPAGOS PENGUINS *SPHENISCUS MENDICULUS*

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SUMMARY

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The foraging behaviour of two Galápagos Penguins *Spheniscus mendiculus* was studied from June to September 1994 on two islands within the Galápagos Archipelago, Ecuador. Diving occurred exclusively during daylight hours, with birds departing land between 05h30 and 06h30 and returning between 18h00 and 18h30, with short intervals on land throughout the day. The maximum dive depth and duration recorded was 32 m and 3 min 10 s, respectively. Dive depth and duration averaged 4±4 m and 25±22 s from the Fernandina Island record, and 2±1 m and 9±9 s from the Bartolomé Island record. The foraging behaviour of this species appears to consist of mostly shallow dives of short duration and to be concentrated relatively close inshore.

INTRODUCTION

Little is known about the foraging behaviour of the Galápagos Penguin *Spheniscus mendiculus*, the most northerly breeding penguin species. The Galápagos Penguin is endemic to the Galápagos Archipelago, Ecuador, and within this area it has a restricted distribution. Approximately 90% of the penguin population inhabits the two westernmost islands of Fernandina and western Isabela (Mills & Vargas 1997), which coincide with the main path of the Cromwell Current (Houvenaghel 1978). This eastward-flowing undercurrent upwells as it meets the edge of the submarine slope, making these the richest waters of the area (Houvenaghel 1978, 1984, Feldman 1986). The remaining 10% of the penguin population is distributed among several of the central islands, including Bartolomé, Santiago, Sombrero Chino, Rábida, and Floreana, a southern island (Mills & Vargas 1997). This central region is surrounded by warmer, shallower water than the western islands (Houvenaghel 1978). Herein I report information on the diving behaviour of two Galápagos Penguins; one from the western island of Fernandina and the other from the centrally located island, Bartolomé.

STUDY AREA AND METHODS

The study took place on two islands within the Galápagos Archipelago, on Fernandina Island and Bartolomé Island (Fig. 1). I spent 58 days at Cape Douglas, the north-western corner of Fernandina Island, and 21 days on Bartolomé Island. Data were gathered between June and August 1994 on Fernandina, and August and September 1994 on Bartolomé. Records from a time-depth recorder (TDR) were obtained from two penguins, one from each of the two islands. The TDR was deployed for six days on the Fernandina penguin (11–17 July 1994; total number of dives: 1243) and for 13 days on the Bartolomé penguin (22 August–4 September 1994; total number of dives: 3898).

A Mark IV time-depth recorder (Wildlife Computers, Wood-

ville, WA, USA) with 128 KBytes of memory was used for data collection. The TDR used had a depth range of 0 to 125 m, a depth resolution of 0.5 m, and contained a conductivity switch to determine whether the penguin was on land or at sea. The dimensions of the TDR used in this study were 67 × 37 × 15.5 mm and the mass 38 g. The TDR was programmed to take depth readings at intervals of five seconds for the Fernandina penguin and three seconds for the Bartolomé penguin. Before deployment, the TDR was shaped hydrodynamically to reduce drag and was placed on the penguins' lower back with fast-setting epoxy. Both penguins on which the TDR was deployed were identified as non-breeding adult males according to sexual dimorphic characteristics as described by Boersma (1974). The Fernandina penguin weighed 2.35 kg and the Bartolomé penguin weighed 2.13 kg. I used non-breeding individuals because at the time there were very few breeding pairs present, and also because I was concerned about disturbing breeding attempts, given that the penguin population is very small.

In addition to the deployment of the TDRs, I recorded sea-surface temperatures (SST) at both sites. SST was taken daily at 07h00 from an exposed section of shore with a mercury thermometer at approximately 50-cm depth. The SST reading that was recorded for the day was the average of three separate readings taken consecutively. I did not take into account variations in SST according to the tide cycle since I was consistent in the time I recorded the SST so that I sampled at different tides.

Continuous observations were made from shore between 07h00 and 18h00 to determine penguin distances offshore, penguin participation in seabird feeding aggregations (see Mills 1998), and general behaviour of both penguins at sea and on land. The distance offshore of actively foraging penguins was estimated to the nearest 50 m based on several landmarks of known distance. In addition, I snorkelled daily at both locations to record observations on the foraging behaviour of the penguins and fish availability. I slowly approached feeding penguins and remained at a distance of about 5–10 m from

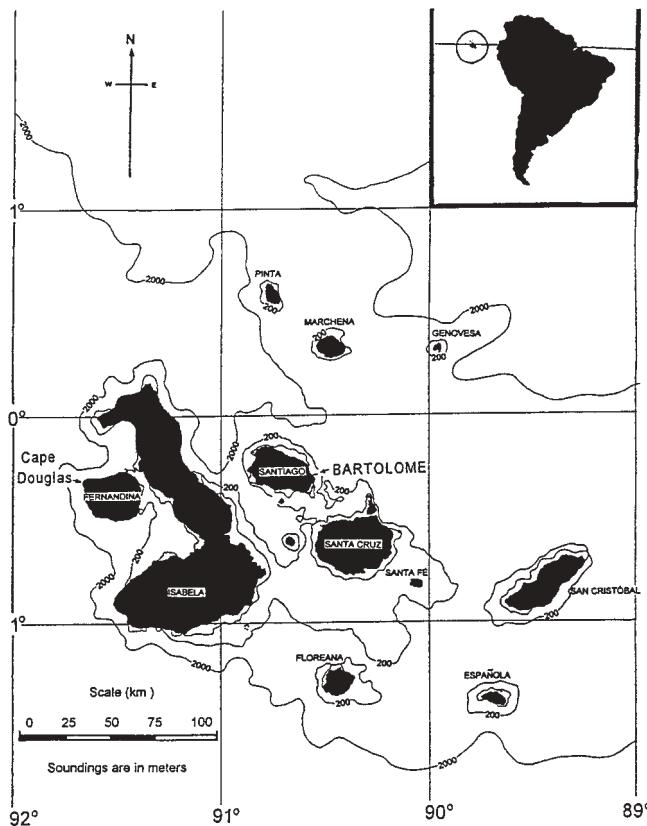


Fig. 1. The Galápagos Archipelago showing bathymetry.

where they were foraging. In general, penguins appeared more curious than disturbed when I was snorkelling, although they were still very cautious. However, when penguins were actively feeding, they seemed indifferent to my presence if I stayed at a minimum distance of approximately 5 m.

Data analysis

The dive record from the Fernandina penguin encompasses six days, although the bird did not enter the water on 14 July (day three of deployment) and therefore no dives were recorded for that day. The TDR was deployed on the Fernandina penguin at night. The total time the penguin spent in the water the day after deployment did not appear to differ from the other days and therefore day one was included in the analyses. However, for the Bartolomé penguin record, the first and last days were not used in the analyses because the first day (the day the TDR was deployed) showed erratic dives, which were most likely a result of disturbance to the animal following its early-morning capture. The last day of the record was excluded because the memory of the TDR was filled and it had stopped recording the morning that the instrument was recovered.

Dive data were analyzed by first running the record through the Zero-Offset Correction (ZOC ver. 1.25) software program from Wildlife Computers. This program manually compensates for drift of the pressure transducer from the zero depth line. The corrected data were then analyzed with the DIVE ANALYSIS (DA ver. 4.08) program (Wildlife Computers) and dive depth, dive duration, time since last dive, bottom time, and descent and ascent rates were extracted from the record.

Data on maximum depths, duration of dives, time since last dive, and bottom time were not normally distributed, even after

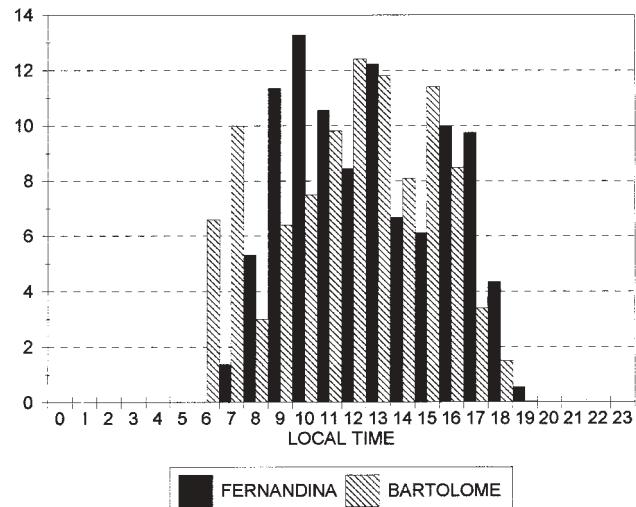


Fig. 2. Percent dives by time of day for the Fernandina and Bartolomé Galápagos Penguins.

log-transformation. However, because the sample sizes were large, I assumed that the sample means were normally distributed even though the variable was not (Sokal & Rohlf 1981). Because of this, the untransformed data were analyzed using parametric statistics. Both STATISTICA (ver. 5.0) and SYSTAT (ver. 5.0) statistical software programs were used to analyze the data. Means are reported with their standard deviations, and the level of significance used was 0.05. A Student-*t* test was used to test for differences of SST between islands and Pearson correlations were used to test for associations among diving parameters.

Vertical travel distances were calculated by multiplying the sum of all the maximum depths of dives by two. This value gives an estimate of the total distance covered by the penguin while diving, and therefore a rough estimate of the diving effort. However, this value only incorporates vertical displacement (i.e. dives) and does not include horizontal displacement (i.e. travelling at the surface).

RESULTS

The mean SST was significantly colder on Fernandina than on Bartolomé ($18.9 \pm 1.0^\circ\text{C}$, $n = 54$ and $21.6 \pm 1.3^\circ\text{C}$, $n = 21$, respectively; $t_{66} = 8.1$, $P < 0.001$). Galápagos Penguins spent most of the day at sea, entering the water between 05h30 and 06h30, and returning to land between 18h00 and 18h30 (Fig. 2). Based on observations of penguins and on time-depth recorder data, penguins have brief resting periods on land throughout the day. Once at sea, the penguins dove almost continuously, travelling parallel to the coastline, with short pauses between dives. Based on my observations of the penguins with data-loggers and other penguins in the area, the mean maximum distance offshore at which penguins were observed was 36 ± 25 m ($n = 192$) for Fernandina Island and 60 ± 86 m ($n = 865$) at Bartolomé Island. The maximum distance penguins were observed was 100 m from the Fernandina coast and 300 m from the Bartolomé coast.

The record obtained from the Fernandina penguin includes 3192 dives in six days (144 h). The record from the Bartolomé penguin includes 8742 dives, covering a time span of 11 days (264 h). The total number of dives per day was greater for the

TABLE 1

Summary statistics of dives made by the Fernandina and the Bartolomé Galápagos Penguins

Parameter	Fernandina		Bartolomé	
	Mean	SD	Mean	SD
Mean no. dives per day	638.0	79.0	795.0	259.0
Mean vertical travel dist./day (m)	5234.0	968.0	3102.0	1863.0
Mean dive duration (s)	5.2	21.6	9.0	8.7
Mean max. dive depth (m)	4.1	3.9	1.9	1.0
Dive frequency (dives/h)	27.0	13.0	33.0	31.0
Proportion (%) of time diving	19.0	NA	8.0	NA
Overall max. dive depth (m)	32.0	NA	11.5	NA
Overall max. dive duration (min)	3.1	NA	1.9	NA

NA = not applicable.

Bartolomé penguin, although the vertical travel distance per day was greater for the Fernandina penguin. This is most likely a result of the Fernandina penguin undertaking deeper dives of greater duration than did the Bartolomé penguin. Furthermore, the Fernandina penguin spent more than twice as much time diving as did the Bartolomé penguin but had fewer dives per hour (Table 1). Although both diving records show that dives were mostly shallow, the Fernandina penguin had a greater number of deeper dives, with 27% of all recorded dives deeper than 5 m (Fig. 3). In contrast, only 3% of the Bartolomé penguin dives were deeper than 5 m.

There was a significant positive correlation between dive depth and duration for both penguins (Fernandina: $r = 0.76$, $P < 0.001$; Bartolomé: $r = 0.46$, $P < 0.001$). There was no statistically significant relationship between the time since the last dive (surface interval) and the depth of the previous dive for either the Fernandina or the Bartolomé records. Nevertheless, my results indicate a significant positive correlation between time spent at maximum depth and the depth of the

dive (Fernandina: $r = 0.4$, $P < 0.001$; Bartolomé: $r = 0.2$, $P < 0.001$). The dive profiles of the two records were similar in the shape of the dives, but differed in the overall number and the maximum depth of dives (Figs 4a,b).

Observations made while snorkelling close to feeding penguins indicated that penguins made repetitive dives at the periphery of a fish school and dove to the bottom of the school, approaching from the bottom and feeding on the way up. These observations were mostly made in water that was approximately 10-m deep, and within 30 m from shore. In several multi-species feeding aggregations that I observed on Fernandina, penguins were seen feeding on large schools of Pacific Sardines *Sardinops sagax*, which were fairly abundant in the inshore waters of Fernandina. In contrast, few schools of sardines were observed near Bartolomé. Penguins at this site were observed mostly chasing unidentified single fish or fish in small schools, many times cornering the fish against the beach and in very shallow water.

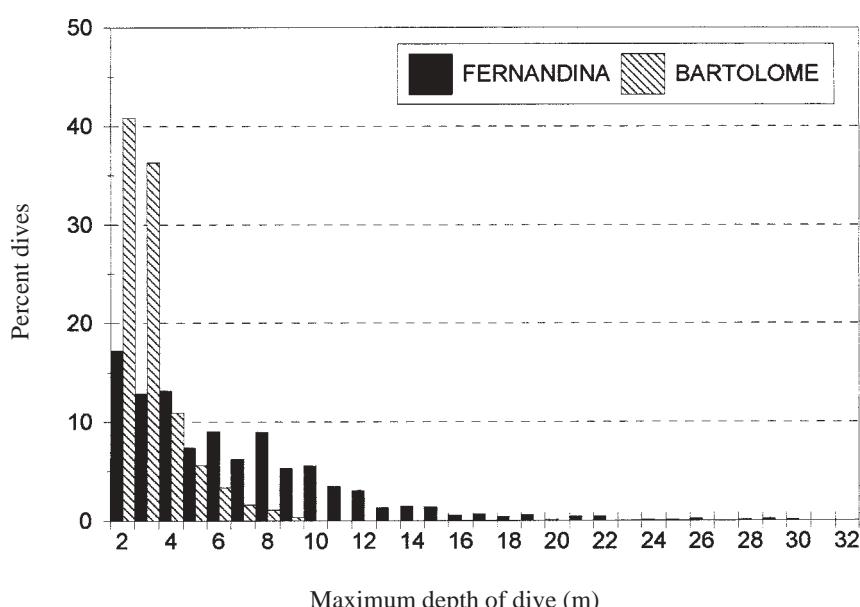


Fig. 3. Distribution of maximum diving depths for the Fernandina and Bartolomé Galápagos Penguins.

DISCUSSION

Instrument effects

Despite the fact that instruments such as TDRs have expanded our knowledge of the behaviour of animals that feed at sea, there is the potential that the instrument itself alters the behaviour of the animal because of the increase in drag caused by the instrument, or discomfort to the animal. Bannasch *et al.* (1994) found that turbulence caused by the device was reduced when the instrument was in the most caudal position on the animal and that shaping the instrument hydrodynamically could reduce drag. Unless one performs a comparative study between instrumented and non-instrumented animals and compares foraging trip numbers and duration, frequency of chick feedings and nest attendance, it is difficult to know the specific effect that an instrument has on a particular species. I attempted to reduce the effect of the instrument on the penguin by using the smallest and lightest TDR possible and by shaping the TDR hydrodynamically and placing it in the most caudal position. Nevertheless, I do not have data that demonstrate how these devices influenced the diving behaviour of the birds that I sampled.

Adding to the uncertainty of whether the difference in foraging behaviour between the two penguins in this study is due to individual variation is that the different sampling intervals of the TDRs may have accentuated differences that might have initially existed. Diving information is lost with an increase in

the sampling interval of the TDR (Boyd 1993, Wilson *et al.* 1995). These studies reveal that the number of dives increases with a shorter sampling interval, and that dive duration and surface intervals decreased with shorter intervals. The Bartolomé penguin record shows a greater number of dives and shallower dives than the Fernandina record. Since the TDR deployed on the Bartolomé penguin was programmed to sample depth every three seconds, and the Fernandina penguin sampled every five seconds, the results were biased toward recording more shorter and shallow dives at Bartolomé than at Fernandina. However, the differences in the recording intervals would not have affected the reading of deep dives, which were almost exclusive to the Fernandina penguin. My observations of the diving behaviour parallel the diving records. I often observed penguins on Bartolomé pursuing fish in very shallow water, and several times penguins actually dove within centimetres of the surface while pursuing fish. This behaviour was never observed in the Fernandina penguins, which were seen pursuing fish at greater depths and away from the shore.

I observed penguins at both sites porpoising quite often, especially when they had encountered a school of fish and were actively foraging. The sampling intervals at which the TDRs were programmed at both sites would not have had enough temporal resolution to record these brief surfacings and this would erroneously result in dives of greater duration at both sites.

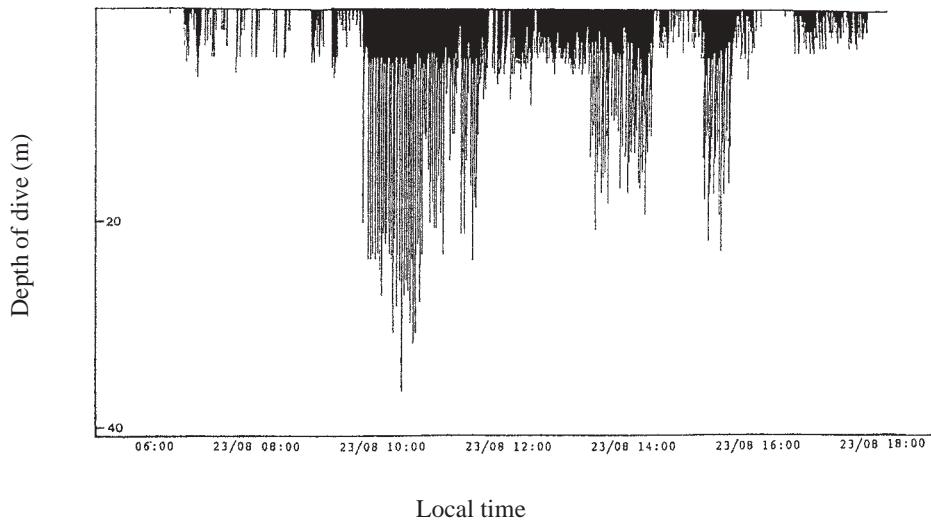


Fig. 4a. Time-compressed diving patterns of the Fernandina Galápagos Penguin for 15 July 1994.

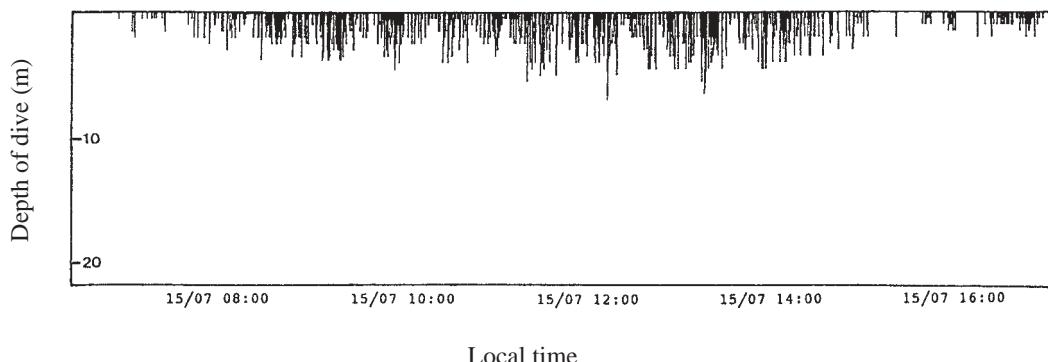


Fig. 4b. Time-compressed diving patterns of the Bartolomé Galápagos Penguin for 23 August 1994.

The extreme temperature differences between the air and the water found in the Galápagos Islands caused a large drift of the pressure transducer. This resulted in erroneous depth readings, overestimating diving depth following periods at the surface when the sun had warmed the recorder. To a certain degree, the ZOC software program was able to correct for this drift, but an unknown amount of error in depth estimation occurred after prolonged periods at the surface. It is unlikely that the differences in the diving records are a result of this drift since both records were obtained using the same instrument and therefore subjected to similar environmental conditions.

Comparison between records

The diving patterns of the two penguins in this study differ from each other in the depth and duration of the dives, frequency of dives, and the time spent at maximum depth. However, because records were obtained from only one penguin at each island and because of the difference in the sampling rates of the TDRs, I cannot determine if the recorded differences in diving behaviour reflect distinct foraging strategies typical of penguins in separate habitats, or if they are simply a result of individual variation. Also, because the sampling was not done simultaneously, the differences I found could also have been the result of seasonal differences or differences due to different stages within their breeding cycle. Oceanographic conditions and bathymetry differ between Fernandina and Bartolomé Islands, and it is possible that the differences in foraging behaviour that these two records indicate are a result of habitat differences. Fernandina penguins seldom ventured more than 100 m from the shore, and thus fed in water that was approximately 50 m or less in depth. At Bartolomé, penguins were foraging in water that was approximately 40 m deep, well beyond the depth to which the record indicates foraging by that penguin. Hence, it appears that the difference in the depth to which the penguins dove was not limited by the local bottom topography. It is possible that the fish communities differ between the two islands as a result of different ocean conditions, although this has not been determined. However, if this is the case, the penguins at the two sites may feed on different prey, which may be an explanation of their different foraging patterns.

The results obtained from these first dive records for the Galápagos Penguin support the conclusion that the species feeds on prey that occurs close to shore and at relatively shallow depths. A greater number of dive records are needed from the Galápagos Penguin to be able to make a generalization about the diving behaviour of this species and to be able to compare it with other penguin species.

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