DIVING BEHAVIOUR OF HUMBOLDT PENGUINS *SPHENISCUS HUMBOLDTI* IN NORTHERN CHILE

GUILLERMO LUNA-JORQUERA[1,2] & BORIS M. CULIK[1]

[1]*Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany*
[2]*Current address: Departamento Biologia Marina, Facultad Ciencias del Mar, Universidad Catolica del Norte, Larrondo 1281, Coquimbo, Chile*
(gluna@nevados.cecun.ucn.cl)

SUMMARY

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The Humboldt Penguin *Spheniscus humboldti* is an endangered species whose population is decreasing over its whole distributional range. In support of conservation efforts, systematic studies are being conducted on the ecology and behaviour of these birds at sea. Time-depth recorders were used to investigate the foraging behaviour of Humboldt Penguins at Isla Pan de Azúcar (26°S, 72°W), northern Chile, during the breeding seasons of 1994/95 and 1995/96. A four-channel logger (MK6, Wildlife Telemetry) equipped with speed, depth, temperature and light-intensity sensors was used to obtain information from 20 foraging trips of 12 penguins, amounting to a total of 301 hours of swimming consisting of 11 011 dives. Birds departed from the colony between 06h00 and 09h00 and returned mainly between 15h00 and 23h00. Distance travelled was strongly correlated with total time spent at sea. Maximum dive depth was 53 m around mid-day when light intensity was maximal. At night maximum depth attained was 12 m. Maximum dive depth was positively correlated with dive duration ($r = 0.80$), as well as with descent and ascent angle ($r = 0.78$), and descent and ascent rate ($r = 0.86$). Dives to between 0.5 and 3 m were interpreted as travelling dives and had a mean depth of 1.6 m. All dives deeper than 3 m were regarded as foraging dives with a mean depth of 11.5 m. Mean dive durations during travelling and foraging were 18.4 s and 47.9 s, respectively. Mean swim speed during travelling was 1.7 m.s^{-1}. Overall speed during foraging dives (descent, bottom and ascent) was 1.9 m.s^{-1}.

INTRODUCTION

The Humboldt Penguin *Spheniscus humboldti* breeds in the region influenced by the cold Humboldt Current, with colonies between Isla Foca (5°S), Peru, and Chiloé (42°S), Chile (Williams 1995). This species is considered vulnerable (Ellis *et al.* 1998) with the population decreasing along its distributional range (Williams 1995). Reasons considered to have contributed to the decline are exploitation of guano for fertiliser, the collapse of Anchovy *Engraulis ringens* stocks due to over-fishing, incidental catch of birds in gill nets, human impact due to industrial activities near breeding colonies and tourism (Hays 1984, Guerra *et al.* 1986, Williams 1995). In addition, Hays (1984) estimated that 9264 Humboldt Penguins were exported to zoos within a period of 32 years. This does not include birds which died during capture and transport. Finally, Humboldt Penguins were strongly affected by the El Niño of 1982/83 (Duffy *et al.* 1988) and 1997/98. Although the pre-1982 population was estimated to total around 16 000–20 000 birds (Araya & Todd 1987), it decreased dramatically by 72–76% in Chile and 65% in Peru after 1983. Since 1986 some recovery has been observed (Hays 1986, Araya & Todd 1987). In 1996 the population was estimated at around 13 000 birds (Ellis *et al.*1998).

Several aspects of the biology of Humboldt Penguins have been poorly studied (Williams 1995). Most information comes from captive birds (Drent & Stonehouse 1971, Kojima 1978, Manton 1978, Schmidt 1978, Hui 1985, 1987, Merrit & King 1987, Scholten 1987, 1989a,1989b), or concerns distributional and demographic aspects (i.e. Hays 1984, 1986, Guerra *et al.* 1986, Duffy 1987). Although the foraging ecology of other penguin species has been frequently investigated (Trivelpiece *et al.* 1986, Chappell *et al.* 1993, Pütz 1994, Kooyman & Kooyman 1995), only two published studies on the behaviour of *Spheniscus* penguins at sea include data for Humboldt Penguins (Wilson & Wilson 1990, Wilson *et al.* 1995a) and most aspects of their diving behaviour and foraging ecology remain to be clarified. As has been suggested for the African Penguin *S. demersus*, also a species with a decreasing population, the elucidation of its foraging ecology is a key issue for the conservation of the species (Frost *et al.* 1976) if interactions with fisheries are to be understood. Modelling indicates that seabirds in several ecosystems consume 20–30% of the annual pelagic fish production (Furness 1984).

Humboldt Penguins feed principally on Anchovy (Wilson & Wilson 1990, Williams 1995), which generally occurs in dense schools predominately in the top 50 m of the water column where the amount of sunlight required for photosynthesis is highest and, consequently, the phytoplankton fed on is most abundant (Arntz & Farhbach 1991). We speculate that Humboldt Penguins adjust their behaviour to that of their prey and do not dive deeper than 50 m. Here we present data on the swimming and diving behaviour of free-living Humboldt Penguins equipped with time-depth recorders in northern Chile.

MATERIALS AND METHODS

Fieldwork was conducted at Isla Pan de Azúcar (26°09'S), northern Chile, between 13–26 November 1994 and 5–20 November 1995. In total, 12 breeding Humboldt Penguins were equipped with time-depth recorders (TDRs). TDRs employed were MK6 instruments (Wildlife Computers, 20630 N.E. 150th Street, Woodinville, WA 98072, USA) equipped with a salt-water switch and 128 Kbytes of memory. The units had a depth sensor, a light intensity sensor, a temperature sensor, and a Flash Electronics speed sensor consisting of a turbine. They had a mass of 110 g, corresponding to 2.5% of penguin body mass; dimensions were $73 \times 55 \times 36$ mm. The cross-sectional area of 1640 mm^2 of the loggers corresponds to 6.1% of the bird's cross-sectional area (*c*. 27 060 mm^2 in the similar-sized Gentoo Penguin *Pygoscelis papua*, Oehme & Bannasch 1989).

The birds were captured at the nest site using an anaesthetic (Ketamine hydrochloride) in order to minimise stress (Luna-Jorquera *et al.* 1996). The devices were attached to the feathers with tape (Tesa tape, Beiersdorf, Hamburg, Germany) as described by Wilson & Wilson (1989), along the mid-line of the birds' lower backs (Bannasch *et al.* 1994). In the 1995 season, before attachment of the loggers, body mass of adults and chicks was recorded to the nearest 25 g using a spring-balance. When the penguins returned to the nests, the loggers were removed and the birds were reweighed. This procedure was not adopted in 1994 because of concern about stress effects.

All sensors were calibrated in the laboratory, except for the swim-speed sensors, which were calibrated on three Humboldt Penguins swimming in a 20-m long water channel (Luna-Jorquera & Culik in press). The speed sensor was designed by the manufacturer to be used with the water inflow of the speed-sensing turbine facing forward. However, hydrodynamic considerations (Culik *et al.* 1994a) indicated that the device would impose less drag on the penguins if rotated by 180°. Six experiments were conducted to yield 272 speed measurements on birds swimming with the loggers back to front. After calibration a linear relationship was obtained between the readings of the loggers and penguin swim speed ($r = 0.80$, $P < 0.0001$). Loggers were programmed to start readings the moment the penguins went to the sea (using the salt-water switch) and to record data at 5-s intervals. Depth resolution of the pressure transducer was 1 m and accuracy, tested by submerging devices to known depths, was directly equivalent to true values.

Loggers were recovered when the penguins returned to their nests, again using Ketamine hydrochloride to tranquilise the animals (Luna-Jorquera *et al.* 1996). After recovery of the TDRs, dive parameters were analysed using the program ANDIVE 7.0 (Jensen Software, Lammertzweg 19, D-24235 Laboe, Germany). This program assesses data on dive depth and swim speed and calculates for each dive the time at which it occurred, total dive duration, descent duration, bottom duration, ascent duration, descent angle (the angle between the bird's trajectory and the surface), bottom angle, ascent angle, vertical descent and ascent rate, absolute swim speed during the descent, bottom and ascent phases of the dive, maximum depth attained and the amplitude of the bottom phase of the dive.

Using a threshold of 0.5 m, a total of 11 011 dives was analysed and all the parameters derived from ANDIVE were collated to produce files of one or more particular dive parameter for all birds. In order to be able to analyse the data statistically, the files were reduced to a random data set using specially designed software for some dive parameters that comprised no more than 1500 measurements. All data were statistically treated using SYSTAT for Windows. Data were tested for normality and homoscedasticity before applying parametric or non-parametric tests as appropriate.

Pan de Azúcar Island forms part of the Pan de Azúcar National Park admiinistered by the Corporación Nacional Forestal, CONAF III Región, Chile. This study was conducted with permission of CONAF and in accordance with its regulations to protect penguins and other resources.

RESULTS

Light intensity

Light intensity measured by penguins equipped with devices was related to both dive depth and time of day (Fig. 1). At the surface, light intensity was maximum at midday (local time) when the sun was directly overhead (51 800 Lux). Light intensity diminished to *c*. 5 Lux at dusk and to 0.5 Lux at midnight. At midday, light intensity diminished with increasing depth to a minimum of *c*. 300 Lux at 50 m (Fig 1). Minimum light intensity of 0.15 Lux was registered at 4 m at night (24h00).

Water temperature

Despite the fact that temperatures measured by the loggers showed great variability, water temperature was related to dive depth (Fig. 2). The variability in logged data is probably caused by a delay in temperature equilibration of the sensor at different depths due to the dampening effect of the logger body. Variability will also result from different water masses occurring in the penguin foraging area, as indicated by the large range in sea surface temperatures. Water temperature at the surface ranged between 13 and 18°C with a mean of 14.6°C (SD = 0.76). Minimum water temperature experienced by the birds was 12–13°C.
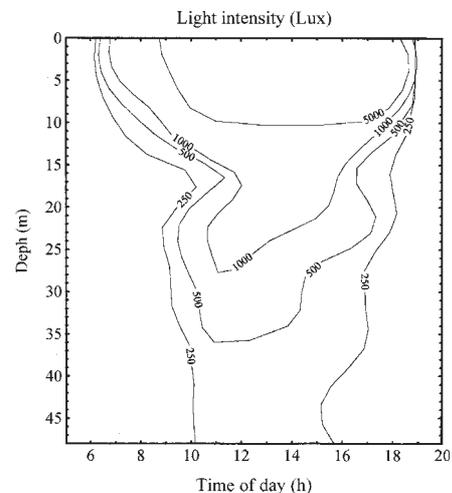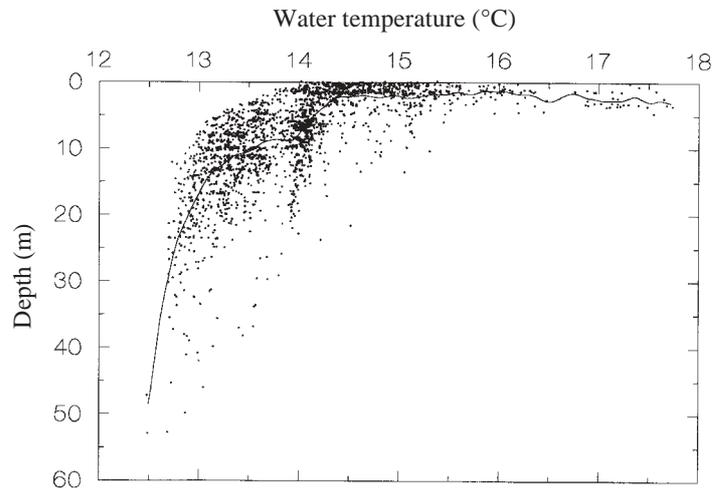

Fig 1. *Light intensity (Lux) measured by breeding Humboldt Penguins equipped with time-depth recorders as a function of time of day and dive depth. Data were obtained from 12 birds during 20 foraging trips in November 1994 and November 1995.*

Fig 2. Water temperature at depth as measured by 12 Humboldt Penguins equipped with time-depth recorders. The line shows the predicted value at each depth fitted by the method of least squares.

At-sea activity

We recorded a total of 20 foraging trips from the 12 Humboldt Penguins equipped with time-depth recorders, amounting to 301 hours of swimming and diving including 11 011 dives (Table 1). Although some parameters used to describe the dives were significantly different between individuals, we found no significant differences in the time spent at sea, distance travelled, time spent foraging and time spent at the surface (ANOVA, $P > 0.05$). Inter-individual variability in dive parameters has been reported for other penguin species but analyses have been made with pooled data in order to describe the species' behaviour (Wilson *et al.* 1995a). To describe Humboldt Penguin behaviour we have also combined data from all individuals.

From our data we could not determine the direction in which Humboldt Penguins from Pan de Azúcar travelled and the areas where they foraged. However, we calculated the distance covered by each penguin from the time it spent swimming at a given speed. The distance swam per foraging trip was obtained by summing all products of speed and duration.

TABLE 1

Summary of recorder deployments on Humboldt Penguins from Isla Pan de Azúcar, northern Chile. All adults were guarding chicks. The total number of dives includes travelling and foraging dives. Total distance travelled and total time at sea are the sum of these values obtained per foraging trip (all day of attachment).
A = Attachment. R = Recovery. * = Speed sensor defective

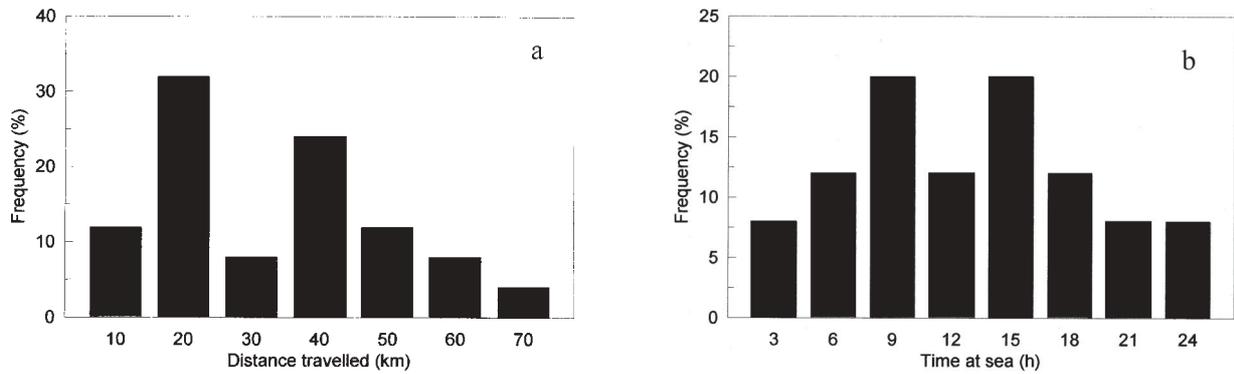| Bird No.	Date of attachment and recovery	Body mass (g)						Total dives	Total time at sea (h)	Total distance travelled per day (km d^{-1})
		Adults		Chicks						
				1st		2nd				
		A	R	A	R	A	R			
1	10–13.11.94	–		–		–		869	36.77	53.20
2	10–13.11.94	–		–		–		625	12.56	26.10
3	10–14.11.94	–		–		–		457	15.85	27.10
4	19–22.11.94	–		–		–		820	13.06	*
5	19–26.11.94	–		–		–		895	17.49	66.40
6	22–26.11.94	–		–		–		1248	27.39	61.20
7	05–09.11.95	3975	3875	425	650	300	250	1887	44.44	119.40
8	05–08.11.95	4525	4225	975	975	850	840	756	15.86	43.23
9	08–11.11.95	4300	4900	925	1025	–	–	1429	51.00	123.29
10	11–13.11.95	4975	4450	100	125	–	–	436	13.46	39.23
11	15–17.11.95	4000	4000	1200	1225	500	600	519	12.18	31.00
12	17–20.11.95	4000	3875	1225	1375	600	575	1070	41.07	72.60
Mean		4295.8	4220.8	808.3	895.8	562.5	566.3	917.6	25.1	60.30
SD		397.9	400.4	451.0	450.7	228.7	242.3	432.8	14.4	34.00
Total								11011	301.13	662.75

Fig. 3. *Frequency distribution of **a.** the distance travelled per day and **b.** the time spent at sea during foraging trips by breeding Humboldt Penguins.*

Thus, distance travelled includes the horizontal, vertical (during diving) and non-directional components of swimming. The mean distance travelled was 26.5 km.d^{-1} (SD = 16.99, n = 25, range 8.1–68.7 km). The frequency distribution of the distance travelled per day had modes at 20 km (32%) and 40 km (24%) (Fig. 3a). The time spent at sea during each foraging trip was also bimodal (Fig. 3b), with maxima at 09h00 and 15h00.

Fig 4. *Pattern of time of departure and time of return of Humboldt Penguins to the colony. The line shows the percentage of penguins at sea.*

Time of departure from the colony was variable (Fig. 4). In 70% of the cases the birds left the island between 06h00 and 09h00. Time of return to the colony occurred mainly (90%) between 15h00 and 23h00. Most birds were at sea around midday. Maximum dive depths were reached between 07h00 and 19h00 (Fig. 5). During this time the penguins performed 84% of all recorded dives. A further 7% were detected between 20h00 and 24h00, 5% at dusk (19h00–20h00) and 4% at sunrise (06h00–07h00).
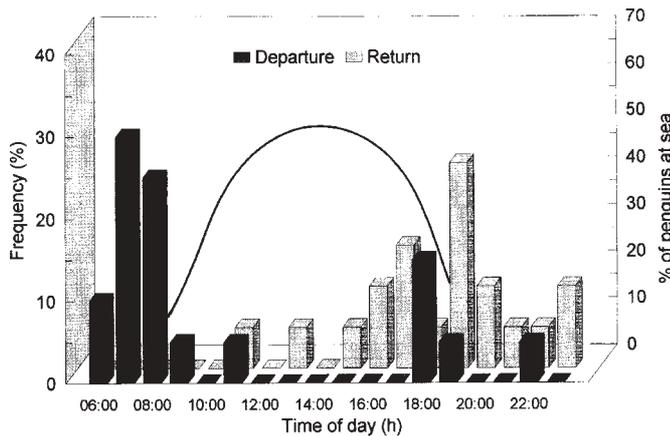
Dive profiles

Dives of Humboldt Penguins are principally of three types: either V, U or a W- shaped (Wilson 1995). In V-shaped dives (33% of all dive events) the penguins descended the water column at a fixed angle to a particular depth before returning immediately to the surface. In U-shaped dives (16%), the descent and ascent phases were similar to those of V dives, but the birds remained near the point of maximum depth for extended periods. In W-shaped dives (51.4%), penguins in the bottom phase moved up and down by a few metres in a series of irregular undulations.

The maximum depth attained during V-shaped dives had a mode at 3 m, whereas for U and W-shaped dives the mode was between 5 and 9 m (Fig. 6). For U and W-shaped dives shallower than 3 m the amplitude of the undulations during the bottom phase was <1 m.
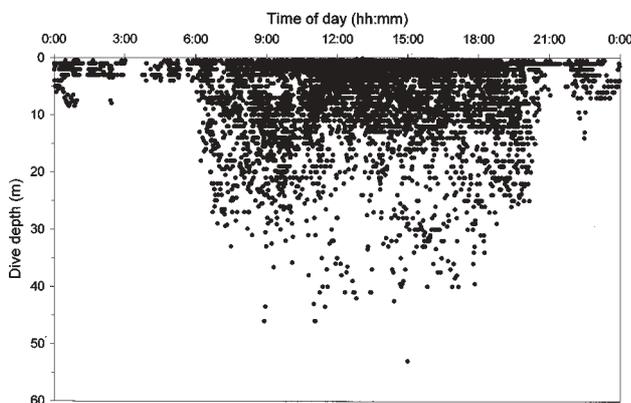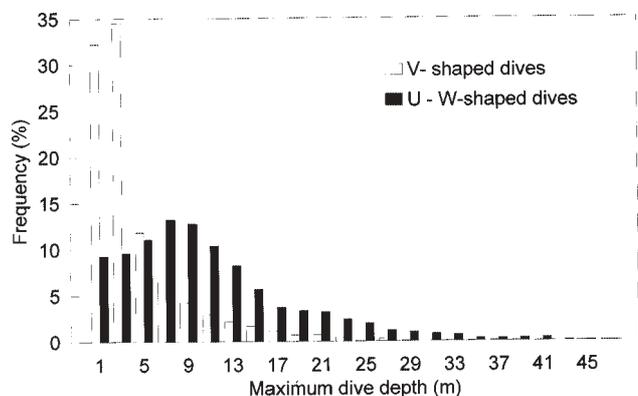

Fig 5. *Maximum dive depths as a function of the time of day. Data are from 12 Humboldt Penguins equipped with time-depth recorders and summarise a total of 11 011 dive events.*

Fig 6. *Frequency distribution of the maximum dive depths reached by breeding Humboldt Penguins.*

TABLE 2

Relations between selected dive parameters (dependent variable) and maximum dive depth (in metres) in Humboldt Penguins

Parameter	Type of equation	Constant (a)	Slope (b)	Correlation coefficient	P	n
Dive duration (seconds)	$y = a + b\,x$	18.91	2.43	0.80	$\ll 0.001$	8184
Bottom time (seconds)	$y = a + b\,x$	11.17	1.24	0.61	< 0.001	791
Descent angle (degrees)	$y = a + b\,x$	−8.83	−1.06	0.78	< 0.001	447
Ascent angle (degrees)	$y = a + b\,x$	15.88	0.48	0.40	< 0.05	679
Descent rate (m s^{-1})	$\log y = \log a + b\,\log x$	0.179	0.58	0.87	< 0.001	1319
Ascent rate (m s^{-1})	$\log y = \log a + b\,\log x$	0.183	0.57	0.85	< 0.001	1316

Consequently, all V, U- and W- dives between 0.5 and 3-m depth were interpreted as travelling dives with a mean depth of 1.6 m (SD = 0.77, n = 3688). All dives deeper than 3 m were interpreted as foraging-dives, with a mean depth of 11.5 m (SD = 7.32, n = 6849, range = 3–53 m).

Dive depths

Maximum dive depth reached by Humboldt Penguins was 53 m around mid-day when light intensity was highest (Figs 1 & 5) and was significantly correlated with several parameters of the dive (Table 2). Ninety-five percent of all dives classified as foraging were to depths between 3 and 27 m. That means that Humboldt Penguins mainly foraged in that part of the water column where light intensity at midday was between 1000 and 50 000 Lux (Fig. 1). Foraging dives started when light intensity was >250 Lux and most (91%) took place between 07h00 and 20h00. Diving activity was still detected, however, at night when maximum dive depth was 12 m.

Dive duration

Mean dive duration during travelling (dives < 3 m) was 18.4 s (SD = 12.5, n = 3688, range 8–165 s), and during foraging (dives > 3m) was 47.9 s (SD = 21.85, n = 6848, range 9–135 s). Frequency distribution showed a mode at 40 to 50 s for foraging dives and at 10 s for travelling dives (Fig. 7). Maximum dive duration was 165 s during travelling. Dive duration dur-
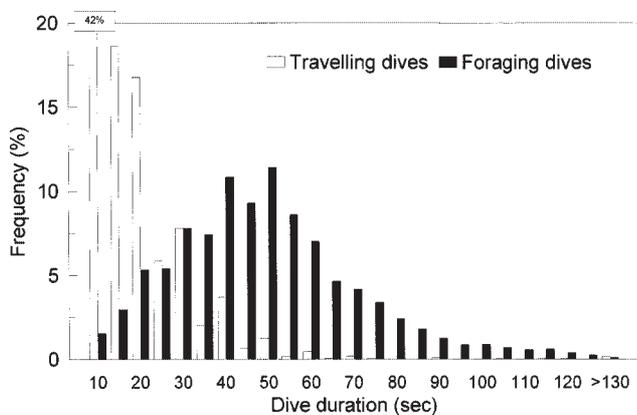
ing foraging was strongly correlated with maximum depths reached during the dive (Fig. 8 & Table 2). In total, 64% of the variation in dive duration is explained by dive depth, yet several outliers are observed. These outliers are most evident in shallow dives and were, presumably, derived from travelling dives or are due to recording mismatch (see Wilson *et al.* 1995b). Foraging dives were followed by a mean surface duration of 18.8 s (SD = 7.53, n = 4091, range 5–36 s). Frequency distribution of this parameter had modes at 15 and 21 s.

Ascent and descent angles

Descent angle was significantly correlated with maximum dive depth (Table 2) having a rate of change equal to 1.06°.m^{-1} (range 13–44° for depth from 3 to 50 m, respectively). Ascent angle was also significantly correlated with maximum depth, with a rate of change of +0.48°.m^{-1} (range 14–40° for depths from 3–50 m, respectively). The swim angle adopted during the bottom phase of U and W-dives was not related to maximum dive depth ($r = 0.074$, $P > 0.05$, n = 7421) and had a mean value of 0.1°.

Vertical speed

Vertical speeds of ascent and descent were significantly correlated with maximum dive depth, the relationships being best

Fig 7. *Frequency distribution of dive duration of Humboldt Penguins. Travelling dives are between 0.5 and 3 m, whereas foraging dives correspond to all dives deeper than 3 m.*
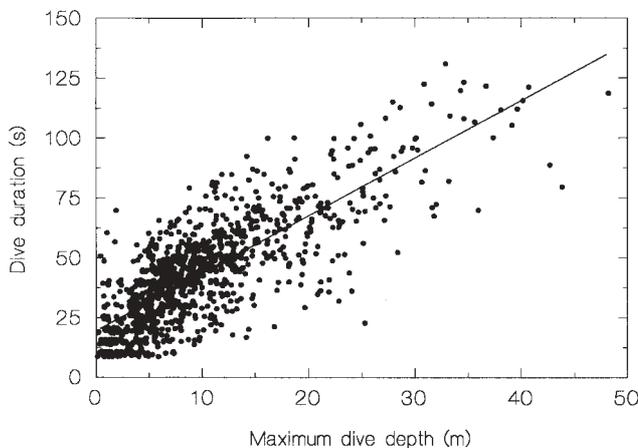

Fig 8. *Relation between maximum dive depths and dive duration in foraging Humboldt Penguins. The relationship was best fitted by the equation: y = 18.91 + 2.43x (r = 0.80, P < 0.001, n = 8184).*
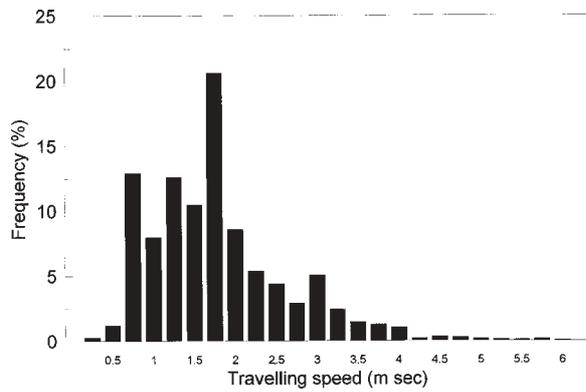
Fig 9. *Frequency distribution of underwater travelling speed of Humboldt Penguins.*

described by logarithmic equations (Table 2). Rates of descent and ascent (range 0.34–1.70 m.s⁻¹ for depths of 3 and 50 m, respectively) of Humboldt Penguins were similar throughout the water column.

Swim speed

Mean swim speed of Humboldt Penguins during travelling dives was 1.7 m.s⁻¹ (SD = 0.87, n = 3878). However, the frequency distribution of the travelling speed showed that Humboldt Penguins had a modal speed of 1.8 m.s⁻¹ (Fig. 9). Maximum travelling speed was 6.5 m.s⁻¹. Frequency distributions of swimming speeds during foraging-dives showed slight differences for the three phases of the dive (descent, bottom and ascent phases; Table 3). We tested for significant differences in the mean values among the three groups (Kruskal-Wallis one way analysis of variance on ranks; normality test failed with $P < 0.0001$) and rejected the hypothesis of equal speeds ($H = 1369.7$ with two degrees of freedom; $P < 0.0001$). Differences between groups were significant (Dunn's test, $P < 0.05$ for samples of different size, Zar 1984). Mean swim speed during descent was 1.65 m.s⁻¹ (SD = 0.687, n = 6126), during bottom phase 2.04 m.s⁻¹ (SD = 0.629, n = 5341) and during ascent was 1.97 m.s⁻¹ (SD = 0.833, n = 6167). Overall mean foraging speed during the three phases was 1.9.m s⁻¹ (SD = 0.75, n = 17691).

DISCUSSION

Device effects

In several studies it has been demonstrated that devices can affect penguin behaviour at sea (see for example Wilson & Culik 1992). Externally attached devices alter the streamlined shape of the penguin's body, thus increasing the amount of energy the birds expend during swimming (Culik & Wilson 1991). Culik *et al.* (1994a) conducted a study on Adélie Penguins *P. adeliae* swimming in a water channel to measure the energy expenditure of the birds with and without a device. The loggers used in their experiment (dimensions $150 \times 57 \times 37$ mm) had a cross-sectional area of 2100 mm² and a mass of 200 g, representing 10.5% of the birds' cross-sectional area and 5% of penguin body mass. Adélie Penguins swimming with these loggers expended 8.8% more energy and swam 7.7% slower than those without devices. The cross-sectional area of our loggers was 22% lower and their mass 45% lighter than the device tested by Culik *et al.* (1994a). Consequently, their deleterious effect on penguin swimming energetics was presumably lower than that reported by Culik *et al* (1994a). This is further supported by the fact that during experiments on Humboldt Penguins carried out in the 1995 season, adults showed no significant change in body mass between the dates of deployment and recovery (Paired *t*-test $_{0.05\,(2),\,5}$ = 0.485, $P = 0.65$, see Table 1). In addition, we examined body mass variation of the chicks to test for significant differences between the first and the last foraging trip recorded for each penguin during the 1995 season. Here we assumed that increase in chick mass represents a relative measure of the efforts of the parents to cover both their own food requirements and those of their chicks. Increase in body mass was not significant in the second hatched chicks (paired *t*-test$_{0.05\,(2),\,3}$ = −0.481, $P = 0.663$), probably due to:

1. a slower growth rate in siblings (Seddon & van Heezik 1991),
2. an insufficient time between sampling to detect for significant change, or
3. the small sample size (only four nests had two chicks).

However, in all the first-hatched chicks (including those from one-chicks nests), the positive change found in body mass was

TABLE 3

Mean swimming speeds of *Spheniscus* penguins in relation to different activities

Species	Activity	Speed (m.s⁻¹)			Source
		Mean	*SD*	**n**	
S. humboldti	Travelling	1.89	0.33	11	Wilson & Wilson (1990)
S. magellanicus	Travelling	2.11	0.36	10	"
S. demersus	Travelling	2.02	0.14	87	"
"	Porpoising	3.42	0.64	7	"
"	Travelling	1.86	0.47	20	Wilson (1985)
S. humboldti	Travelling	1.70	0.87	3878	This study
"	Foraging:				
"	overall	1.90	0.75	17634	"
"	during descent	1.65	0.68	6126	"
"	bottom phase	2.04	0.63	5341	"
"	during ascent	1.97	0.83	6167	"

statistically significant (paired t-test$_{0.05\,(2),\,5}$ = −2.94, P = 0.032). In other words, chicks increased in body mass between dates of deployment and recovery interspaced by one to four foraging trips made by one of the parents.

Distance travelled and time at sea

During the breeding season, Humboldt Penguins are central place foragers since they must return to their nests between foragings trips (Orians & Pearson 1979). Due to flightlessness their foraging range is limited by comparison with other birds (Wilson 1995). Whereas flying birds can explore a greater surface area to find food, penguins compensate for this by being more proficient divers (Furness & Monaghan 1987).

It has been pointed out that the distance that penguins can swim during each foraging trip depends on the time spent by the birds at sea (Wilson 1995). Humboldt Penguins conform to this prediction (Fig. 10) since daily distance travelled by our birds correlated well with time spent at sea (r = 0.80, F-Ratio = 38.225, P < 0.001). Mean distance travelled during foraging trips was 26.5 km (SD = 16.99, n = 25), with a minimum and maximum distance of 8.1 and 68.7 km, respectively. This compares well to the results reported by Wilson (1985) for African Penguins, where mean distance travelled was 40.2 km and where most foraging birds remained within 20 km of their breeding islands. With the use of satellite transmitters Culik & Luna-Jorquera (1997) determined that Humboldt Penguins foraging from Pan de Azúcar Island showed no preference for any particular marine sector and that 90% of the birds remained within 35 km of their breeding islands.

Light intensity, foraging rhythms and dive depths

As expected, Humboldt Penguins showed a marked diurnal foraging rhythm as a result of the daily cycle of light intensity (Ferrer *et al.* 1994). Breeding birds left the colony at about dawn and returned in the late afternoon or early morning (Fig. 4) but not necessarily on the same day. The pattern of time of departure and time of return to the colony was similar to that observed for non-breeding penguins from the same colony, where at midday c. 50% of birds were at sea (Luna-Jorquera 1996). This daily activity pattern is also similar to that observed by Wilson & Wilson (1990) for a colony of Humboldt Penguins at Algarrobo (33°30'S), in central Chile and is also comparable to that reported for nesting and non-nesting African Penguins (Frost *et al.* 1976, Cooper 1977, Wilson & Wilson 1990).

Martin & Young (1984) state that the Humboldt Penguin is probably a visual hunter, being well adapted to the spectral qualities of its aquatic environment (Bowmaker & Martin 1985), which explains why these birds are most active during the day. However, we found that Humboldt Penguins also dive at night reaching depths of up to 12 m (Fig. 5). In 24% of cases birds did not return to the colony in the afternoon. Whether Humboldt Penguins continue foraging or only travel at night remains to be clarified. During the night Anchovies rise close to the surface (Arntz & Farhbach 1991), thus becoming more readily available to the birds. However, although almost all penguins species studied to date dive at night, relatively few actually feed, and those that do feed ingest little (Wilson *et al.* 1993 and references therein). It has been suggested that night dives are generally associated with travelling, because night dives have a much greater horizontal than vertical component which would, necessarily, lead to a greater horizontal displacement, again a factor tending to indicate travel (Wilson 1995).
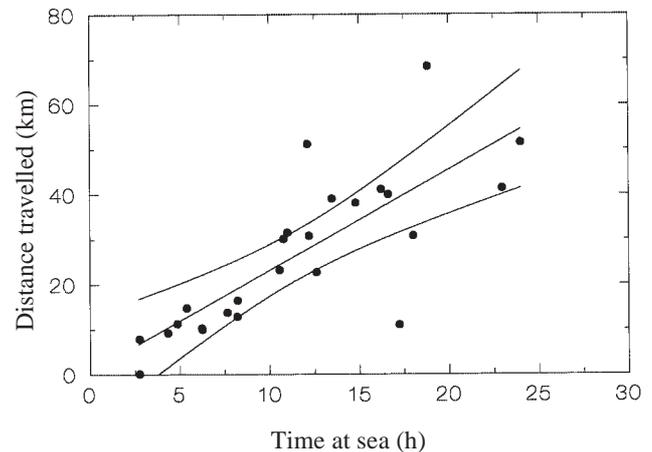

Fig 10. *Relation between the time spent at sea and the distance travelled by breeding Humboldt Penguins. The relation was best fitted by the equation: y = 0.692 + 2.241x (r = 0.80, P < 0.001, n = 25). The equation line with 95% confidence intervals is shown.*

There is also evidence that pygoscelid penguins feeding on krill are light dependent in their foraging patterns. For example, in Adélie Penguins from Ardley Island, South Shetlands, dive depth is most related to light intensity irrespective of whether prey are being ingested (Wilson *et al.* 1993). However, prey behaviour must also be taken into account because differences in prey acquisition rates between day and night can also be explained by changes in prey distribution. Evidence presented by Pütz & Bost (1994) shows that King Penguins *Aptenodytes patagonicus* ingest only 17% of their daily food mass at night. Pütz (1994), stated that the dispersion of myctophid fish close to the surface at night negatively affects prey capture rates of King Penguins. This is supported by results obtained from Gentoo Penguins where Bost *et al.* (1994) concluded that dive depths in these birds also reflect the distribution of their prey.

According to Wilson (1995), maximum dive depth in penguins is related to bird body mass and can be calculated from the equation suggested by Pütz (1994). A 4.3-kg penguin (Table 1) should theoretically dive to a maximum depth of 127 m. Humboldt Penguins should therefore perform deeper dives than the maximum observed here (53 m). Because our data shows that light intensity and its penetration in the water column might not be a limiting factor (Fig. 1), it is possible that dive depths of Humboldt Penguins from Pan de Azúcar are determined by the ecology of their prey and only secondarily by light intensity. Thus, dives deeper than 53 m might be disadvantageous due to scarcity of potential prey. In a sonar survey of the area around Isla Pan de Azúcar (unpubl. data) we only obtained reflections from pelagic targets at depths between 5 and 30 m, with 81% of all targets at depths between 5 and 20 m.

Travelling speed

Humboldt Penguins engaged in two main types of dives (travelling and foraging), as derived from the analysis of dive profiles. Mean underwater swimming speed during travelling (1.70 m.s^{-1}) is 10% lower than reported by Wilson & Wilson (1990) of 1.89 m.s^{-1}. However, these differences may have no biological significance and may result from differences in measurement techniques. For the African Penguin an under-

water speed of 1.86 m.s^{-1} has been reported (Wilson 1985), yet a mean of 2.02 m.s^{-1} was found in a later study (Wilson & Wilson 1990).

From our data we could not determine if Humboldt Penguins porpoised during travelling as do Adélie Penguins (Trivelpiece *et al.* 1986). African Penguins porpoise when swim speed is > 3.4 m.s^{-1} (Wilson and Wilson 1990; see also Heath & Randall (1989) for travelling speed of African Penguins indicating porpoising). In our study, *c.* 5% of travelling speeds were ≥3.5 m.s^{-1} , thus porpoising in Humboldt Penguins seems possible. We occasionally saw Humboldt Penguins porpoising in the morning when they entered the water, perhaps to generate heat before travelling to a foraging area or for preening purposes. On one occasion we observed a group of *c.* 10 birds at a distance of < 50 m. A pair of birds started to porpoise round the group and did so for 10 minutes before leaving the colony and heading away. Porpoising has been interpreted as a direct response to the threat of predators (Hui 1985, Wilson 1995), but in this case predator evasion was rejected because the rest of the group remained calm and was engaged in preening activities.

Foraging speed

The U and W-shaped dives can be interpreted as feeding dives, in which the penguins ingested prey (Wilson 1995). In these dives the initial speed and angles are similar to those of search dives, possibly because feeding dives start out as search dives (Wilson & Wilson 1995). Mean swimming speed showed significant differences between all three phases of the foraging dives (Table 3). High swimming speeds during ascent are probably due to buoyancy caused by air trapped in feathers (Wilson *et al.* 1992). Variable swimming speeds during the bottom phase of the dive (associated to undulations in dive depths) can be explained as a function of prey capture. To capture Anchovies the penguin must swim faster than its prey, at least over short distances. Mean swimming speed at the bottom was 2.0 m.s^{-1}. The maximum swimming speed for the Anchovy has not been determined, but a mean swimming speed of 0.3 m.s^{-1} has been reported (Villavicencio & Muck 1983). Analysis of stomach contents of Humboldt Penguins revealed that Anchovies consumed by adults ranged in length from 83–143 mm (mean = 109 ± 15 mm) (Wilson *et al.* 1995a). Assuming that these data were normally distributed,
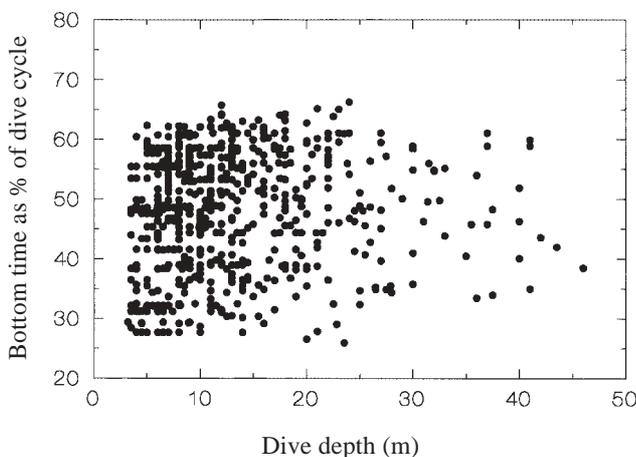

Fig 11. *Foraging efficiency (as % bottom time of dive cycle) in relation to dive depth. The correlation was not significant (P > 0.05).*

in approximately 68% of the cases the penguins preferred prey between 94 and 124 mm. Using the equation suggested by Blaxter & Dickson (1959), a swimming speed of 0.62 m.s^{-1} and 0.81 m.s^{-1} is expected for these fish, considerably lower than foraging swimming speeds of Humboldt Penguins.

Dive duration and foraging efficiency

Dive duration is a function of maximum dive depth (Fig. 8). Mean dive duration of Humboldt Penguins from Isla Pan de Azúcar during travelling (18.4 ± 12.5 s) and during foraging (47.9 ± 21.8 s) are 128% (14.4 ± 6.7 s) and 64% (75 ± 5 s) of previously reported values (Wilson & Wilson 1990) for penguins from Isla Chañaral. These differences are probably due to different measurement methods, as well as to different localities and time of year (Chappell *et al.* 1993). For example, data from two different colonies of Humboldt Penguins in Chile show significant differences in mean dive depths: at Isla Chañaral the mean was 62.2 m whereas at Algarrobo the mean was 27.3 m (Wilson *et al.* 1995a). These authors also found that at Isla Chañaral, penguins preferred mostly garfish *Scomberesox* spp. whereas in Algarrobo the main prey was Anchovy. We believe that the foraging ecology of Humboldt Penguins is quite flexible, particularly with regards to foraging depths. Variability may derive from:
1. competition with Magellanic Penguins *Spheniscus magellanicus* south of Pan de Azúcar Island (Wilson *et al.* 1995a);
2. environmental and oceanographic characteristics, and
3. prey species or prey depth distributions.

Frequency analysis of dive duration shows that 95% of all dives were shorter than 90 s (Fig. 7). The maximum length of time that a penguin can dive depends on the total amount of oxygen available while under water. The aerobic dive limit (ADL) is the time the penguin can remain underwater before oxygen stores are fully depleted and anaerobic metabolism begins to take place. Assuming that Humboldt Penguins have similar oxygen stores to Adélie Penguins (58.6 ml.kg^{-1}, Culik *et al.* 1994b), and also utilize oxygen while diving at a similar rate, ADL would be 110 s (Culik *et al.* 1994b). This may be the reason why analysis of dive and surface durations of Humboldt Penguins to determine the behavioural ADL (Pütz 1994) did not yield a result. Our calculated mean surface times (18.8 s), compared well with those reported by Wilson & Wilson (1990) for African Penguins. The use of aerobic metabolism during most dives would allow Humboldt Penguins to maximise the proportion of time spent under water and the calculated mean surface time is probably sufficient to allow the penguins to fully replenish their oxygen reserves.

It is possible to hypothesise that the amount of food ingested is a function of number of dives per foraging trip, because penguins apparently encounter many small prey patches in order to become satiated (Wilson 1995). Humboldt Penguins preying on small, randomly distributed prey schools, may have a greater prey encounter rate than when preying on a large school. The reason for this is the greater surface to volume ratio of small schools (Alcock 1989). Anchovy school size is highly variable (Arntz & Fahrbach 1991), but around Isla Pan de Azúcar, inside the 35-km foraging range determined by Culik & Luna-Jorquera (1997), Anchovy occurs in small widely scattered schools (unpubl. data).

Using the equation of Ydenberg & Clark (1989) it is possible to obtain a non-dimensional estimate of foraging efficiency. This parameter has been defined in terms of the bottom time

over dive cycle time (bottom time/ (dive duration + time at surface required for recovery), if only the bottom duration is regarded as profitable. Foraging efficiency decreases as depth increases because of the increase in transit time, but at any depth efficiency is highest if bottom time and duration are maximised. For Adélie and Emperor Penguins, whose dive durations are near their ADL, Chappell *et al.* (1993) and Kooyman & Kooyman (1995), respectively, found that with increasing dive depth, foraging efficiency diminished due to the increase in transit time and reduction in the time at the bottom. Our data on Humboldt Penguins do not agree with these results (Fig. 11), because bottom time increases with dive depth, leading to a percentage of bottom time that remains constant irrespective of depth. In addition, if Anchovies occur in dense schools between the surface and 50-m depth, the foraging efficiency may not be determined by the bottom time alone but also by dive duration because Humboldt Penguins may capture prey during their descent and ascent; prey can be swallowed underwater while the penguins swim (Wilson & Wilson 1990, Chappell *et al.* 1993). Another, but related, explanation is that dive duration in Humboldt Penguins may be kept short in order to minimise duration of the surface interval. This would allow penguins to reduce the time between leaving the prey school and returning to it, and hence increase the probability of relocating mobile prey.

As a pelagic predator, the Humboldt Penguin is highly dependant on predictable food resources in coastal waters near its nesting sites. Our data show that the dives are relatively short and shallow compared to other penguin species of similar body mass. Similarly, it seems that Humboldt Penguins are adapted to an essentially aerobic metabolism that reduces the total surface time and maximises foraging efficiency. A large number of dives compensates for shallow dive depths and allows penguins to exploit their prey efficiently.

Since the 1960s, the Anchovies that comprise the most significant prey item for guano birds, including the Humboldt Penguin, have been heavily over-fished. In Chile the exploitation still continues, with landings of Anchovies doubling from $1.2·10^6$ t in 1992 to $2.7·10^6$ t in 1994 and plumeting to $0.5·10^6$ t in 1998 (SERNAP 1992, 1994, 1998). Because Pan de Azúcar Island is one of the largest Humboldt Penguin colonies in Chile, it is important to protect the birds from over-fishing in areas that overlap with the fisheries, especially during El Niño events.

ACKNOWLEDGEMENTS

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