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Foraging behaviour and reproductive success in Magellanic penguins (*Spheniscus magellanicus*): a comparative study of two colonies in southern Chile

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Abstract During the breeding season 1996/97 we compared the foraging and diving behaviour of adult Magellanic penguins (*Spheniscus magellanicus*), growth rates of their chicks and their breeding success at two colonies in the south of Chile. One of the colonies is located on Magdalena Island in the Strait of Magellan, where a commercial fishery existed several years ago; the other, on the shores of the yet unexploited Otway Sound. Thirty adult Magellanic penguins were equipped with time–depth recorders (TDR) to investigate their behaviour at sea. In each colony 15 adults returning from the sea were stomach flushed to analyse dietary composition. Chicks of TDR-nests and of 12 additional control nests were weighed regularly. Foraging effort was significantly higher at Magdalena than at Otway. The Magdalena-birds usually remained at sea overnight and foraged with a mean duration of 18 h, whereas the penguins of Otway Sound foraged during 1-d trips with a mean duration of only 9 h. Compared to Magdalena, penguins at Otway dived shallower (mean depth 14.9 vs 16.5 m), shorter (mean duration 57.8 vs 64.3 s) and showed more searching and feeding as opposed to travelling activity (on average 69 vs 55%) during the foraging trips. Compared to other breeding locations both colonies were characterised by high chick growth rates, high fledging body masses (>3 kg) and early fledging date (after 70 to 80 d), and a very high reproductive success of >1.75 chicks per breeding pair. Comparison of the diet (almost exclusively sprats) with former investigations suggests for both areas an unchanged food structure over the last decade. The results in both colonies indicate ample food availability in the season 1996/97. However, compared to the much smaller Otway colony, penguins on Magdalena have to cope

with more competition for food. Therefore, future prey limitation, through resumed fishery operations or effects of El Niño, might affect the penguin population on the island more negatively than in Otway Sound.

Introduction

As top-predators, penguins prey mainly on fish, cephalopods and crustaceans, and some of their prey species are of commercial importance. Reproductive success in penguins and other seabirds depends on food availability (Crawford and Dyer 1995), a parameter which is related to natural conditions as well as fishery activities. Fluctuations in seabird populations and seasonal reproductive failure have previously been associated with overfishing (Brown and Nettleship 1984) or El Niño events (Duffy et al. 1987). Data on dietary composition and population parameters of seabirds such as breeding success or growth rates and fledging weight of the chicks can therefore be used as bioindicators in monitoring the marine environment (Cairns 1987; Furness and Camp-huysen 1997). However, all aspects of the predators' foraging and breeding biology, e.g. the complexity of the marine food web (Lavigne 1996), opportunistic feeding possibilities (Crawford 1987) or different interpretations of parameters such as chick growth (discussed by Williams and Croxall 1990) must be considered. Recently, behavioural observations of the foraging and diving activities of breeding seabirds were used in monitoring studies (Le Maho et al. 1993; Monaghan et al. 1996). Because of their easy handling, penguins are particularly suitable for such investigations.

The use of data loggers, radio- and satellite-telemetry has increased our knowledge of penguin behaviour at sea (e.g. Culik and Luna Jorquera 1997; Culik et al. 1998). Using this methodology, information was gained about the diving behaviour of the birds, such as timing and organization of foraging trips and location of foraging areas (summarized by Wilson 1995). Behavioural investigations on diving and foraging activities exist for

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almost all penguin species (among others for Magellanic penguins, Scolaro and Suburo 1991; jackass penguins *Spheniscus demersus*, Wilson and Wilson 1995; king penguins *Aptenodytes patagonicus*, Pütz 1994; Gentoo penguins *Pygoscelis papua*, Williams et al. 1992; macaroni penguins *Eudyptes chrysolophus*, Croxall et al. 1993), but only a few of these studies deal with ecological variabilities between different habitats (see e.g. Kirkwood and Robertson 1997, for emperor penguins *Aptenodytes forsteri*). The same is valid for possible competition of penguins with commercial fisheries and the resulting consequences for their foraging behaviour (see Culik and Luna Jorquera 1997).

The Magellanic penguin breeds in colonies along the southern coasts of South America: from 29°S down the Pacific Ocean coast, around Tierra del Fuego and on the Atlantic coast north to 42°S, including the Falkland Islands (Williams 1995). This species, the most abundant penguin in South America, is affected by many human and natural impacts like commercial fisheries, use as bait for king crab fishery, tourism, oil pollution and unfavourable oceanographic conditions (Boersma et al. 1990). The reproductive success of Magellanic penguins is highly variable (Boersma et al. 1990), but the relationships between reproductive success, foraging behaviour and local effects have not yet been investigated.

Our aim was to compare (I) the diving behaviour of breeding Magellanic penguins, (II) dietary composition, (III) growth of the chicks and (IV) the breeding success in two colonies near Punta Arenas, Chile. Both sites differ with respect to several parameters, such as commercial use of the marine environment, effects of tourism on individual penguins and whole colonies, colony size and interspecific competition for nesting grounds and food. On the basis of our investigations, we try to explain how local environmental conditions affect the foraging biology and reproductive outcome of the penguins.

Materials and methods

This study was conducted in southern Chile on Magdalena Island (52°55' S; 70°34' W) in the Strait of Magellan and Otway Sound (52°58' S; 71°12' W) between 29 November 1996 and 21 February 1997. Field work alternated between both colonies on a weekly basis. Sixteen adult Magellanic penguins at Magdalena and 14 penguins at Otway were equipped with streamlined time-depth recorders (TDR) attached with black waterproof tape (TESA-Beiersdorf, Hamburg, Germany; Wilson et al. 1997) to feathers on the mid-line of the birds' lower backs, according to Bannasch et al. (1994). Devices were removed after 2 to 10 d, after the penguins had carried out at least one foraging trip. All equipped penguins were breeding birds with two chicks.

TDRs (Wildlife Computers Mk 5 and Mk 6, Redmond, Washington, USA) contained 512-kilobyte memories. The Mk 5 weighed 50 g, measured 65 × 36 × 16 mm and had a frontal area of 580 mm², which corresponds to 2.1% of the bird's cross-sectional area (measured on a similar-sized Gentoo penguin, Oehme and Bannasch 1989); the Mk 6 weighed 130 g, measured 72 × 56 × 36 mm and had a frontal area of 1700 mm² (6.3% of the penguin's cross-sectional area). Both types of TDR had channels to

record depth (through a pressure transducer: Mk 5, 0 to 70 m; Mk 6, 0 to 125 m), temperature and light; the Mk 6 could additionally record swimming velocity (0 to 5.0 m s⁻¹). Both TDRs also had a salt-water switch to differentiate between the presence of birds on land and at sea.

We programmed the TDRs to record data in 5-s intervals. Depth threshold for dive analysis was 3 m, allowing us to filter out the shallower travelling dives. Recorded data were transferred to a PC via interface, and translated into readable form with the software PROCMM (Datastorm Technologies Inc., Columbia, Missouri, USA) and 3M (Wildlife Computers). Dive parameters were analysed using the programme ANDIVE 8.0 (Jensen Software Systems, Laboe, Germany). This software assesses dive depth and swimming speed, and calculates parameters like total dive duration; duration of descent, bottom and ascent phases; angle of descent, bottom and ascent phases (relative to the surface, only TDR Mk 6); vertical descent and ascent rates; absolute swimming speed during each phase (only Mk 6); and maximum dive depth per dive as well as bottom amplitude (difference between maximum and minimum depth during a bottom phase). These parameters can be calculated for each dive and for each programmed time interval (e.g. every 10 s). Dives are displayed on the computer screen (depth plotted against time) for visualization by the user before being stored. To save computer memory, we used a 10-s interval for data analysis, which was sufficient for analysing all parameters, especially the identification of different dive profiles (discussed by Wilson et al. 1995a). Parallel to depth and swimming speed, the TDRs recorded relative light-levels under water in units not specified by the manufacturer. Therefore the light intensity sensor was calibrated using a portable lux-meter. These data were used to compare oceanographic conditions in the areas of both colonies and their impact on the penguins' behaviour. Only when the TDR Mk 5 recorded extended periods at a depth of 70 m (maximum depth record of the Mk 5 pressure sensor) was extrapolation of correlated light and depth data used to calculate the "real" depth of these dives.

In both colonies, we determined chick growth rates and fledging success. The chicks of all TDR-equipped penguins were weighed regularly until fledging, if possible two times a week. In addition, we regularly weighed the chicks of 12 other nests in both colonies, to control any influence of the devices on reproductive success. The adults of all investigated nests were also weighed, but less often. Mass of stomach contents at the moment of weighings was unknown. All penguins were weighed in a black synthetic bag, using a spring balance (± 10 g for chicks, ± 50 g for adults; Salter Weigh-Tronix, West Bromwich, GB). Body mass of adults was the only parameter used to identify their sex (cf. Scolaro et al. 1983). The age of previously hatched chicks at their first weighing was calculated using data interpolation based on the few chicks, for which the hatch date had been determined during daily nest checks. Third degree polynomial functions were used to model chick growth. A chick was considered to have fledged successfully if it was alive when the first fledgling left the colony, and if the last time it was seen it weighed at least 2000 g.

In both colonies 15 adult penguins obviously returning from a foraging trip were stomach flushed according to Wilson (1984) to collect diet samples. The penguins were selected at random; therefore, the breeding status (breeders or non-breeders) was unknown. Birds were water-flushed several times until the water was clear, suggesting an empty stomach. Samples were stored in alcohol prior to examination. Fish fractions could be identified via otoliths. Cephalopods were identified by examination of their lower beaks (Clarke 1986). Singular beaks were assumed to have been enriched in the stomach prior to the most recent meal before sampling. They were used to determine the size-classes of the squid consumed.

Data were analysed statistically with STATISTIKA 5.0 (Stat-Soft Inc., Tulsa, Oklahoma, USA). All means are presented ± 1 standard deviation. Comparisons between the colonies with respect to foraging and diving behaviour were made with Student's *t*-test following Kolmogorov–Smirnov/Lilliefors test for normality.

Comparisons with respect to chick growth were made using a paired *t*-test. The Kruskal–Wallis ANOVA *H*-test was used to examine the individual differences of the penguins. Significance was tested at the $\alpha = 0.05$ level.

Results

At Magdalena Island 27 foraging trips were recorded from 15 Magellanic penguins equipped with TDRs for a total of 65 d. One penguin did not return to its nest site, so its TDR could not be recovered. At Otway Sound the 14 penguins equipped with TDRs for a total of 66 d did forage on 46 different trips. In total, 10 412 and 12 123 dives to depths of more than 3 m were recorded at Magdalena and Otway, respectively. Statistical parameters of foraging trips and dives are shown in Table 1.

Foraging trips

Penguins at Magdalena made significantly longer foraging trips compared to penguins at Otway (Table 1). All foraging excursions in both colonies were 1- or 2-d trips. At Magdalena 19 foraging trips lasted overnight (70%). At Otway most penguins finished their foraging trips before midnight; only one trip lasted overnight (2%). In both colonies foraging trip duration did not correlate with chick age or mass (Magdalena: $n = 27$, $r^2 = 0.016$, $t = 0.646$, $p = 0.524$; Otway: $n = 43$, $r^2 = 0.058$, $t = -1.588$, $p = 0.120$).

Foraging trip duration (of the 1-d trips) and departure time correlated well at Otway: the later the penguins departed from the colony, the shorter their foraging trips ($n = 45$, $r^2 = 0.641$, $p < 0.001$; Fig. 1). At Magdalena no such correlation was found. Most of the penguins at Magdalena Island departed from the colony in the afternoon between 12:00 and 18:00 hrs (63%), and another peak of departure was around 4:00 hrs in the morning (19%). At Otway more foraging trips started in the first half of the day between 2:00 and 10:00 hrs (52%), but the afternoon hours were also important for departure. Returning time (defined independently of 1- or 2-d trips) was between 9:00 and 18:00 hrs for most of the penguins at Magdalena (70%), while at Otway all recorded foraging trips ended in the second half of the day, often late in the evening between 20:00 and 1:00 hrs (41%).

Diving activity was significantly lower at Magdalena compared to Otway, as were the number of dives per foraging trip hour. On the other hand, the total number of dives per foraging trip was significantly higher at Magdalena than at Otway (see Table 1).

Diving behaviour

Mean dive depth (for dives in excess of 3 m) was significantly deeper at Magdalena compared to Otway (Table 1); shallow dives (<10 m) dominated the frequency distribution with 53 and 59%, respectively. In

Table 1 *Spheniscus magellanicus*. Comparison of foraging and diving parameters between the colonies on Magdalena Island and Otway Sound. For statistical analysis, Student's *t*-test was used after testing for normality with Kolmogorov–Smirnov/Lilliefors test

Parameter	Magdalena Island				Otway Sound				<i>t</i> -test		
	<i>N</i>	Mean	SD	Range	<i>N</i>	Mean	SD	Range	<i>df</i>	<i>t</i>	<i>p</i>
Foraging trips											
Duration (h)	15	17.7	5.9	4.0–26.6	14	9.2	3.1	5.1–16.0	27	4.821	<0.001
Diving activity (%)	15	54.5	8.6	40–64	14	68.8	12.6	44–87	27	-3.572	<0.005
Dives trip ⁻¹	15	393	162.8	118–739	14	268	80.7	101–401	27	2.571	<0.02
Dives h ⁻¹ trip ⁻¹	15	22.3	5.5	14.3–32.7	14	29.9	7.1	17.5–39.9	27	-3.256	<0.005
Surface											
Swim velocity (m s ⁻¹)	22 859	1.40	0.76	0.51–5.10	15 086	1.66	0.86	0.51–6.90	37 943	-31.089	<0.001
All dives											
Max. depth (m)	10 412	16.5	15.6	3.3–91.5	12 123	14.9	14.4	3.3–77.9	22 533	7.967	<0.001
Duration (s)	10 412	64.3	29.2	20–160	12 123	57.8	24.8	20–160	22 533	17.834	<0.001
Descent (V, U)^a											
Swim velocity (m s ⁻¹)	2 388	1.37	0.53	0.42–3.65	2 048	1.99	0.69	0.42–4.99	4 434	-33.697	<0.001
Ascent (V, U)^a											
Swim velocity (m s ⁻¹)	2 481	1.13	0.41	0.42–3.13	2 038	1.74	0.66	0.42–4.05	4 517	-37.705	<0.001
V-shaped dives^a											
Descent angle (°)	1 131	20.4	13.9	3–79	1 102	14.6	10.5	3–83	2 231	11.050	<0.001
Ascent angle (°)	1 125	24.3	15.7	3–88	1 096	17.4	11.7	3–82	2 219	11.687	<0.001
U-shaped dives^b											
Bottom time (s)	2 774	21.2	11.7	10–90	2 460	17.8	8.9	10–50	5 232	11.435	<0.001
Amplitude (m)	2 774	1.7	2.4	0–22.2	2 460	1.0	1.6	0–19.8	5 232	12.030	<0.001

^a Only dives recorded with Mk 6-loggers

^b Only dives with maximum depth between 10 and 70 m

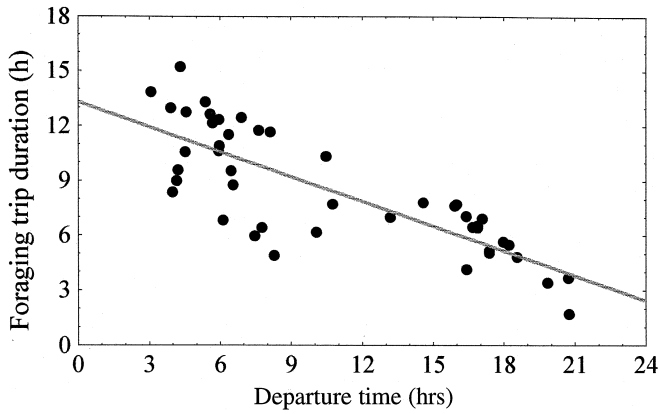


Fig. 1 *Spheniscus magellanicus*. Correlation of departure time and foraging trip duration in penguins of the Otway colony. Only 1-d foraging trips are included. The relation was best fitted by the linear equation: $y = 13.306 - 0.453x$ ($n = 45$, $r^2 = 0.642$, $p < 0.001$)

general, a decrease in dive frequency with increasing depth was recorded, except for small increases between 40 and 50 m at Magdalena and between 30 and 40 m at Otway (Fig. 2). Three penguins at Magdalena and two penguins at Otway dived deeper than 70 m.

During foraging trips, penguins of both colonies only dived deeper than 30 m during daylight, between 4:00 and 23:00 hrs. Maximum dive depth was obviously dependent on light levels, and at night the penguins rarely dived deeper than 10 m (Fig. 3).

Mean dive durations (minimum 20 s) were significantly longer at Magdalena than at Otway (Table 1). In both colonies we recorded dives between 20 and 160 s

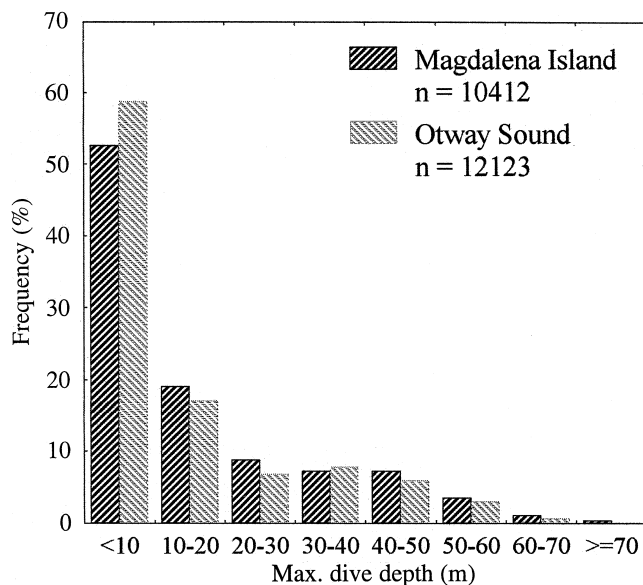


Fig. 2 *Spheniscus magellanicus*. Frequency distribution of maximum dive depths reached by penguins at Magdalena Island ($n = 10412$) and Otway Sound ($n = 12123$). Only dives deeper than 3 m were evaluated

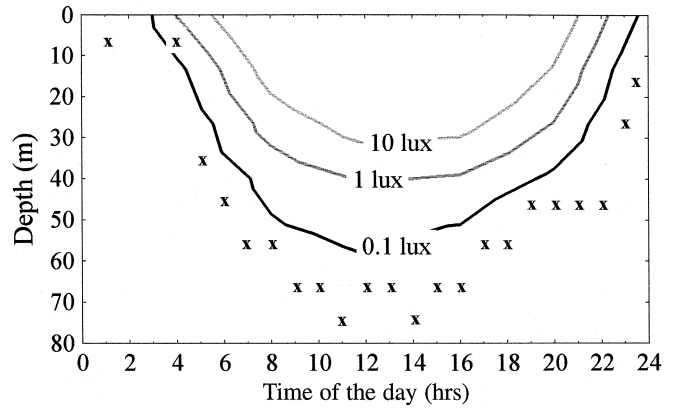


Fig. 3 *Spheniscus magellanicus*. Isolines of light levels at depth (10, 1 and 0.1 lux) and the maximum dive depth of penguins at Otway Sound (shown as "x"), both with respect to time of day (hrs). Light measures were calculated in lux after calibration of the TDR light sensors. Light levels were recorded during three foraging trips between 9 and 11 December 1996; cloud covering and particle concentration in the water during this period were unknown

duration (Fig. 4). Most of the dives lasted between 40 and 60 s (46% at Magdalena, 55% at Otway). Mean dive duration increased with maximum dive depth in both colonies. Penguins of Magdalena dived significantly longer in all depth-classes (10-m intervals) between 10 and 70 m, than penguins of Otway (Wilcoxon-test for paired comparisons, $n = 8$, $T = 0$, $z = 2.521$, $p = 0.012$, two-tailed; Fig. 5).

Dive profiles were classified as V- and U-shaped, following Wilson (1995). In V-shaped dives the penguins returned immediately to the surface after reaching their

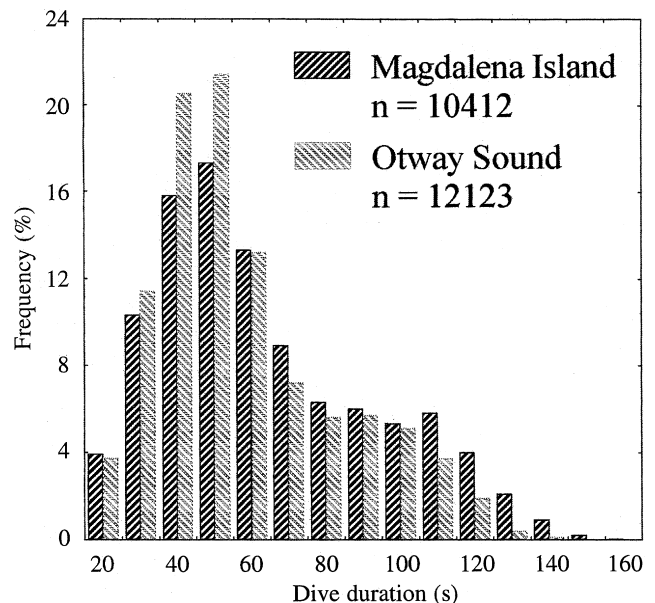


Fig. 4 *Spheniscus magellanicus*. Frequency distribution of the dive durations at Magdalena Island ($n = 10412$) and Otway Sound ($n = 12123$). Because of the time interval used for analysis (10 s), the minimum dive time recorded was 20 s

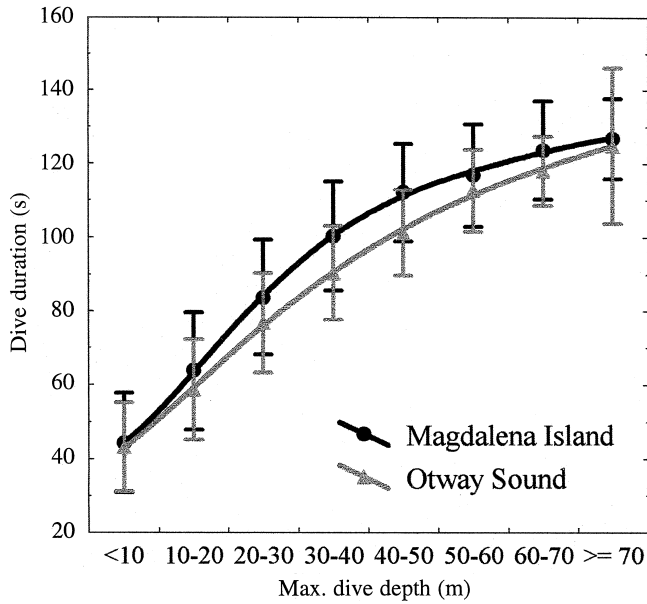


Fig. 5 *Spheniscus magellanicus*. Comparison of mean dive duration (\pm SD) for varying depth-classes between penguins of Magdalena Island ($n = 10412$) and Otway Sound ($n = 12123$). Depth and duration thresholds were 3 m and 20 s, respectively

maximum depth. These dives seem to represent prey-searching behaviour. In U-shaped dives the birds remained at the maximum depth for an extended period, the so-called bottom time, indicating prey capture (cf. Wilson et al. 1996). If the penguins moved up and down the water column during the bottom phase, the result was an irregular U-shaped or W-shaped dive, which for reasons of simplification were also considered U-shaped dives in the present study.

With regard to dive profiles, only dives between 10 and 70 m were considered, resulting in 4889 dives at Magdalena and 4999 dives at Otway. At Magdalena 57% of these dives were U-shaped with the highest proportion between 30 and 60 m (Fig. 6), resulting in a significant difference in the frequency distribution of both dive types against the depth-classes ($\chi^2 = 92.603$, $n = 6$, $p < 0.001$). The mean depth of U-shaped dives was 29.6 ± 15.0 m ($n = 2774$). At Otway 49% of the dives were U-shaped, and the ratios between V- and U-shaped dives were regularly distributed in all 10 m depth-classes, with no significant difference ($\chi^2 = 4.662$, $n = 6$, $p > 0.05$; Fig. 6). Mean depth of U-shaped dives was 28.4 ± 14.7 m ($n = 2460$).

Bottom phases of dives were classified with respect to bottom duration (Fig. 7). At Magdalena the penguins had U-shaped dives with a bottom time between 10 and 90 s, and the summation of the total bottom time represented 14% of the total dive time for all dives between 10 and 70 m. At Otway bottom phases lasted only between 10 and 50 s, resulting in a total bottom time representing 11.2% of the total dive time between 10 and 70 m. Mean bottom time at Magdalena was significantly longer than at Otway (Table 1).

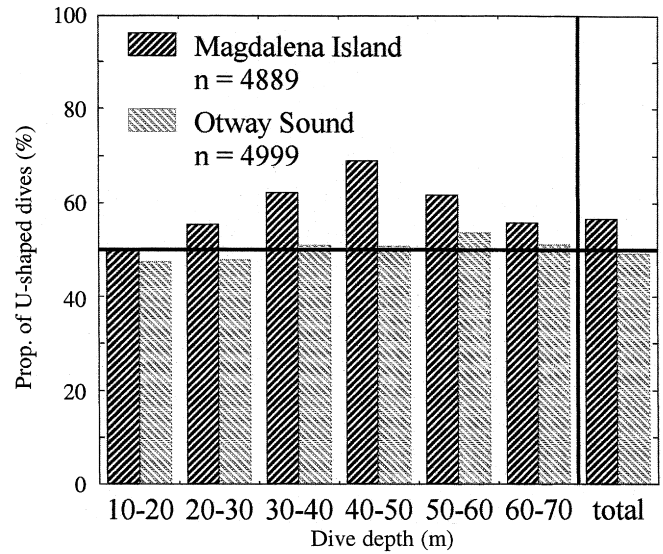


Fig. 6 *Spheniscus magellanicus*. Proportion of U-shaped dives, shown by depth-class at Magdalena Island ($n = 4889$) and Otway Sound ($n = 4999$); the upper limit of the depth-classes is excluded. The higher frequency, especially between 30 and 60 m, suggests a higher feeding activity at these depths at Magdalena as opposed to Otway, where V- and U-shaped dives were regularly distributed over all depth-classes. Further explanations for the classification of different dive types are given in “Results – Diving behaviour”

Depth amplitude during bottom phases of W- and U-shaped dives correlated with dive depth in both colonies (Table 2). The amplitudes were significantly larger at Magdalena than at Otway (Table 1). In very few cases bottom amplitude was larger than 6 m.

Descent and ascent angles of all V-shaped dives in both colonies were highly correlated with maximum dive depth (Table 2). Descent angles were significantly

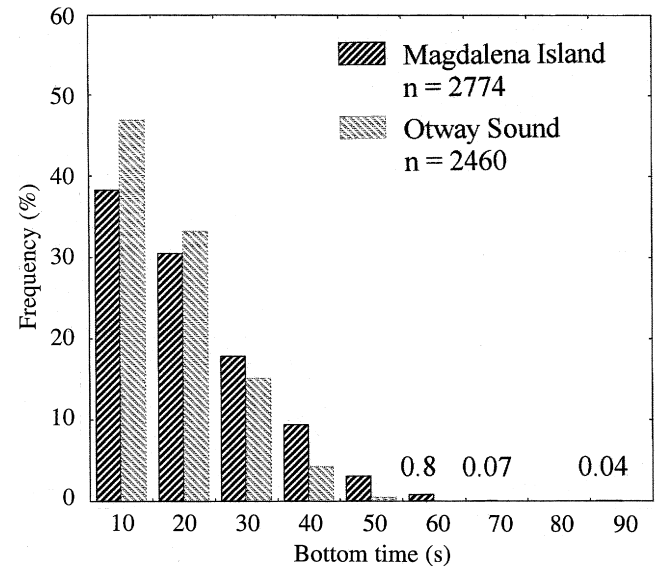


Fig. 7 *Spheniscus magellanicus*. Frequency distribution of bottom times in U-shaped dives with a maximum depth between 10 and 70 m, at Magdalena Island ($n = 2774$) and Otway Sound ($n = 2460$)

Table 2 *Spheniscus magellanicus*. Relations between selected dive parameters (dependent variable) and maximum dive depth (m) in penguins at Magdalena Island and Otway Sound. Descent and ascent angles refer to V-shaped dives, bottom amplitudes to U-shaped dives. Angles were calculated from dive depth, duration and velocity as recorded via Mk 6-loggers; type of equation used for all calculations: $y = a + bx$

Colony, parameter	Constant <i>a</i>	Slope <i>b</i>	Correl. coeff. r^2	<i>p</i>	<i>n</i>
Magdalena Island					
Descent angle (°)	12.371	0.596	0.285	<0.001	1131
Ascent angle (°)	17.055	0.528	0.180	<0.001	1125
Bottom amplit. (m)	0.670	0.035	0.049	<0.001	2774
Otway Sound					
Descent angle (°)	8.300	0.471	0.299	<0.001	1102
Ascent angle (°)	11.562	0.423	0.205	<0.001	1096
Bottom amplit. (m)	0.367	0.023	0.043	<0.001	2460

shallower than ascent angles, both at Magdalena (*t*-test, $n = 1131, 1125, t = -6.191, p < 0.001$) and at Otway (*t*-test, $n = 1102, 1096, t = -5.798, p < 0.001$). Both angles were significantly steeper at Magdalena than at Otway (Table 1).

Mean surface swimming speeds (depths 0 to 3 m) and mean swimming speeds during descent and ascent were significantly faster at Otway than at Magdalena (Table 1). In general, swimming velocities during all dives between 3 and 70 m were significantly faster during descent than during ascent, both at Magdalena (*t*-test, $n = 2388, 2481, t = 17.634, p < 0.001$) and at Otway (*t*-test, $n = 2048, 2038, t = 11.899, p < 0.001$).

Variances of diverse foraging and diving parameters in individual penguins were tested against intercolonial differences of the same parameters between Magdalena and Otway. For statistical reasons, only penguins with at least three foraging trips were included. At Magdalena individual penguins did not differ significantly in any of the investigated parameters. In contrast, at Otway they differed with respect to foraging trip duration, number of dives per foraging trip and per hour of foraging, maximum dive depth and maximum dive duration (Kruskal–Wallis *H*-test, Table 3).

Dietary composition

At Magdalena stomach contents were exclusively composed of sprats (*Sprattus fuegensis*). No seasonal differences in dietary composition were observed. Most of the samples were thoroughly digested. At Otway all samples contained *Sprattus fuegensis*, but in two samples (one each from December and January) additional, non-digested adult cephalopods of the genus *Loligo* (probably *Loligo gahi*) were found. In addition, these two samples contained almost non-eroded beaks of the upper ($n = 25$) and lower ($n = 24$) jaw of *Loligo*, suggesting that they had been ingested only a few days earlier (U. Piatkowski, IfM Kiel, Germany, personal commu-

Table 3 *Spheniscus magellanicus*. Kruskal–Wallis ANOVA *H*-test for variances of foraging and diving parameters in individual penguins. Significant individual variation should be considered in the assessment of observed intercolonial variation between Magdalena and Otway

Colony, parameter	<i>H</i>	<i>p</i>	Sign. individual differences?
Magdalena Island			
Foraging trips			
Duration (h)	3.974	>0.05	no
Diving activity (%)	6.692	>0.05	no
Dives trip ⁻¹	1.513	>0.05	no
Dives h ⁻¹ trip ⁻¹	7.000	>0.05	no
Dives			
Max. depth (m)	2.776	>0.05	no
Max. duration (s)	6.286	>0.05	no
Otway Sound			
Foraging trips			
Duration (h)	17.531	<0.05	yes
Diving activity (%)	14.662	>0.05	no
Dives trip ⁻¹	17.490	<0.05	yes
Dives h ⁻¹ trip ⁻¹	18.488	<0.05	yes
Dives			
Max. depth (m)	19.911	<0.02	yes
Max. duration (s)	24.985	<0.01	yes

nication). The determination of the size-classes of *Loligo* from the lower beaks resulted in a mean mantle length of 100.5 ± 16.8 mm and a mean mass of 68.8 ± 18.8 g.

Chick growth and breeding success

Chick growth curves (body mass against age) in both colonies indicated a slow mass gain during the first 10 d after hatching, a higher growth rate until Day 50, and finally a slower growth rate or even a slight mass loss until fledging. Mean net mass gain per day was about 40 g for the chicks in both colonies during their first 10 d, followed by 60 to 80 g during the phase of maximum growth and less than 40 g after Day 50. Chick growth between the second and eighth week of age was almost linear. It is apparent from steeper gradients of the linear regressions that chicks at Otway grew faster than at Magdalena during that time (Fig. 8). Body masses of the first hatched chicks (of equal age) in two-egg nests were significantly higher at Otway, especially during the second month (3-d age-classes, 1 to 60 d, paired *t*-test, $n = 20, t = 3.122, p = 0.006$). The same is valid for the second hatched chicks (paired *t*-test, $n = 20, t = 2.568, p = 0.019$). At Magdalena first chicks were not significantly heavier than second hatched chicks (paired *t*-test, $n = 20, t = 1.821, p = 0.084$), but at Otway they were (paired *t*-test, $n = 20, t = 3.762, p = 0.001$). Some chicks in both colonies reached body masses of more than 4000 g, but the mean maximum body mass of Otway chicks older than 50 d was 3390 ± 280 g ($n = 32$), and slightly less (3310 ± 470 g, $n = 37$) at Magdalena; this difference was not significant (*t*-test, $n = 69, t = -0.874$,

$p = 0.385$). In some chicks fledging masses were about 5% less than maximum masses.

Of the 28 nests observed at Magdalena, 50 chicks were found to have fledged successfully, resulting in a breeding success of 1.79 (± 0.42) chicks per breeding nest. Two chicks fledged in 22 nests, and in six nests only one chick survived. Four eggs did not hatch, and two chicks died during the first week. Differences in breeding success were significant between TDR (1.94 ± 0.25 , $n = 16$) and control nests (1.58 ± 0.51 , $n = 12$; t -test, $df = 26$, $t = 2.409$, $p = 0.023$). At Otway, 24 nests were observed, and 47 chicks fledged successfully, which resulted in a breeding success of 1.96 (± 0.20) chicks per pair. One chick died during the second week. No significant difference in breeding success was observed between the TDR (1.92 ± 0.29 , $n = 12$) and control nests (2.0 ± 0 , $n = 12$; t -test, $df = 22$, $t = -1.000$, $p = 0.328$). Breeding success was not significantly different between both colonies (t -test, $df = 50$, $t = -1.842$, $p = 0.071$).

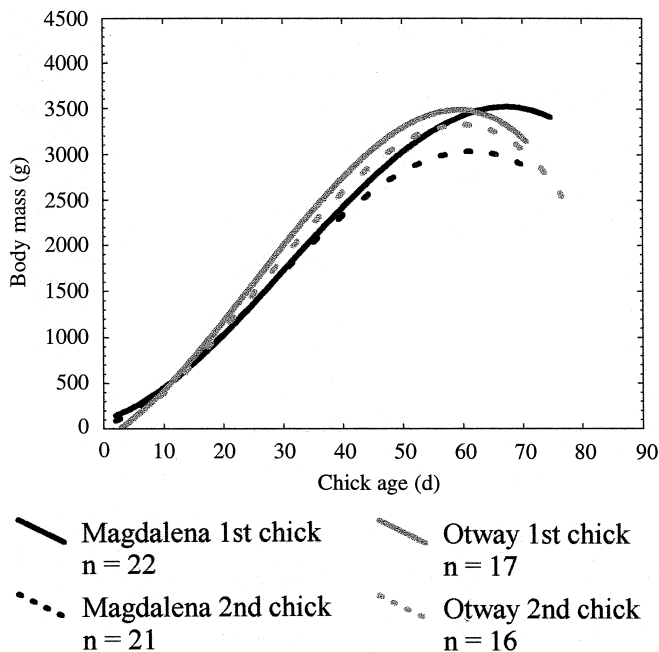


Fig. 8 *Spheniscus magellanicus*. Growth curves of first and second hatched chicks from two-egg nests at Magdalena Island and Otway Sound in the breeding season 1996/97. At Otway, first chicks reached their maximum body masses ca. 10 d earlier than at Magdalena. Second hatched chicks had higher maximum body masses at Otway. In both colonies first chicks showed slightly better growth than their siblings, but this was only significant at Otway. Growth curves are best fitted by the following equations:

$$\text{Magdalena Island 1st chicks: } y = 96.355 + 20.627x + 1.659x^2 - 0.018x^3,$$

$$\text{Magdalena Island 2nd chicks: } y = 23.344 + 29.549x + 1.427x^2 - 0.018x^3,$$

$$\text{Otway Sound 1st chicks: } y = -113.638 + 38.290x + 1.770x^2 - 0.023x^3,$$

$$\text{Otway Sound 2nd chicks: } y = -76.573 + 30.574x + 1.835x^2 - 0.023x^3$$

Discussion

Device effects

Data loggers have become an indispensable tool for investigations of the diving and foraging behaviour of seabirds (Wilson et al. 1993a). However, when using them, hydrodynamic problems and stress reactions of the animals must be considered and minimized. Externally attached devices alter the shape of a diving penguin (Bannasch et al. 1994). A decrease of swimming speed by 8.3% and an increase of transport costs by 13.7% were found by Culik et al. (1994) for Adélie penguins equipped with a streamlined data logger, with negative effects on foraging parameters. The probability of prey encounter depends on foraging range (Wilson and Culik 1992). Therefore penguins carrying external devices have to increase their foraging effort to obtain the same amount of prey. However, other diving parameters such as dive depth are influenced as well (discussed in Culik et al. 1994). By minimizing size, mass and cross-sectional area of the devices, while optimizing streamlining and attachment, these unwanted effects could be reduced (Bannasch et al. 1994).

The data loggers Mk 5 and Mk 6 used in the present investigations were smaller in size and mass than loggers mentioned in the literature above. Consequently, effects on penguin swimming energetics (and therefore dive parameters) were presumably lower than reported. Previously, Mk 6-data loggers were used on the closely related Humboldt penguin (*Spheniscus humboldti*), and transport costs increased by 11% (Luna Jorquera 1996). However, our data show that chick mass gain and fledging success were only marginally, if at all, affected by our study.

Foraging trip duration, foraging rhythm and range, and diving activity

In penguins, foraging trip duration depends among other things on the stage of breeding (incubation or chick rearing) and chick size (e.g. Heath and Randall 1989; Williams et al. 1992). Because the food demands of chicks rise continually with age (Culik 1994), trip durations of feeding adults have to be lengthened, if catch per unit time is constant. Provided penguins maintain constant swimming speed, the amount of prey encountered is proportional to the distance travelled or to foraging trip duration, if prey is distributed regularly (Wilson and Wilson 1990). In older chicks with higher energetic requirements, Boersma et al. (1990) observed longer intervals between the feedings. On the other hand, Scolaro and Badano (1986) assumed an increase in the number of foraging trips with chick age, and therefore a decrease in feeding intervals. The crucial point seems to be the amount of food passed to the chicks. Other factors influencing this parameter are prey

availability and intraspecific regional differences (for Magellanic penguins see Williams 1995).

Mean trip duration at Magdalena Island of almost 18 h compares well to results of ca. 1.5 d in the nearby Cabo Virgenes colony (Williams 1995) and at San Lorenzo on Península Valdés (Scolaro and Suburo 1994) during the chick rearing period. Foraging trips lasting only 9 h as at Otway Sound (with some trips even shorter than 4 h) are a noticeable exception. Distinct clusters of diurnal and overnight foraging trips, corresponding to the differences between Magdalena and Otway, are recognizable in Fig. 9 (cf. Jansen et al. 1998). Short foraging trips like the ones at Otway are only possible, when prey availability near the breeding grounds is sufficiently high and travel distances therefore small. For this reason differences in trip length suggest differences in food availability near the investigated areas.

The non-existence of a correlation between trip duration and chick age (only nests with two chicks tested; Magdalena: $n = 26$, $r^2 = 0.037$, $t = 0.965$, $p = 0.344$; Otway: $n = 43$, $r^2 = 0.058$, $t = -1.586$, $p = 0.120$) suggests stomach content masses independent of foraging trip duration (i.e. varying catch per unit time), if the higher food demands of older chicks are to be met. Also, foraging trips were not significantly longer after the guard phase (chicks older than 30 d, averaged per nest, $n = 13$) than before ($n = 30$, data only available at Otway; t -test, $df = 41$, $t = 0.682$, $p = 0.499$).

For *Spheniscus* spp. penguins, Wilson and Wilson (1990) reported that birds left their colonies at dawn and

returned to their nest in the evening. In a former investigation on Magellanic penguins at Otway, Wilson et al. (1995b) determined departure peaks at dawn and return peaks in the early morning and just before dusk. Scolaro and Suburo (1994) reported similar results for Magellanic penguins at San Lorenzo, Argentina. Departure and arrival activity seemed to be restricted to hours of darkness. Both at Magdalena and Otway, the penguins differed from this pattern, showing that no universally valid rhythm in the foraging activities of Magellanic penguins exists. At Magdalena almost two-thirds of the birds departed in the afternoon, especially those staying at sea overnight, and returned without any preference in time. At Otway two departure peaks were found, one in the morning, the other in the afternoon. All penguins returned in the second half of the day. The different departure and return rhythms are clearly recognizable as clusters in Fig. 9. The correlation between late departure times and reduced foraging trip durations at Otway (Fig. 1) indicates easily exploitable feeding grounds near the colony. Another factor important to mention in this context is the synchronization of the mates (cf. Jansen et al. 1998), especially during the guard phase, i.e. the first 4 weeks after chick hatching. If prey availability allows a foraging penguin to shorten its trip started at sunrise, its nest mate is able to carry out another foraging trip before the following night. No parallel data of the nest mates were available for any nest, but it is possible, that two chick feedings per 24 h are carried out at Otway, at least by some breeding pairs. If, like at Magdalena, foraging trips had to be longer to reach adequate feeding grounds, an overnight trip becomes inevitable at least for one mate, resulting in only one feeding event per day. After the guard phase, when chicks are guarded only irregularly (but in Magellanic penguins chicks are not grouped in "crèches" as in other penguin species), feeding frequencies are independent of foraging trip duration, because both mates do not have to be synchronized.

By calculating trip distance using mean swimming speeds Wilson et al. (1995c) determined a foraging range per trip of ca. 30 km for Magellanic penguins. At Otway Wilson et al. (1995b) determined a mean foraging range of 24.8 km. We calculated the maximum distance travelled during foraging by multiplying surface time (total foraging trip duration minus total dive time of dives deeper than 3 m) by the surface swimming speed, neglecting the horizontal component during dives. Total distances were between 27 and 95 km at Magdalena and between 3 and 66 km at Otway. Maximum foraging range is at most half the total travel distance, therefore 47 and 33 km at Magdalena and Otway, respectively. We could not determine travel direction nor foraging grounds from the recorded data. However, it is almost certain, that penguins of both colonies did not leave the regions of the Strait of Magellan and Otway Sound. In both colonies the first deep diving bouts (>20 m) of foraging penguins started about 80 min after departure; this corresponds to feeding grounds ca. 7 to 8 km away

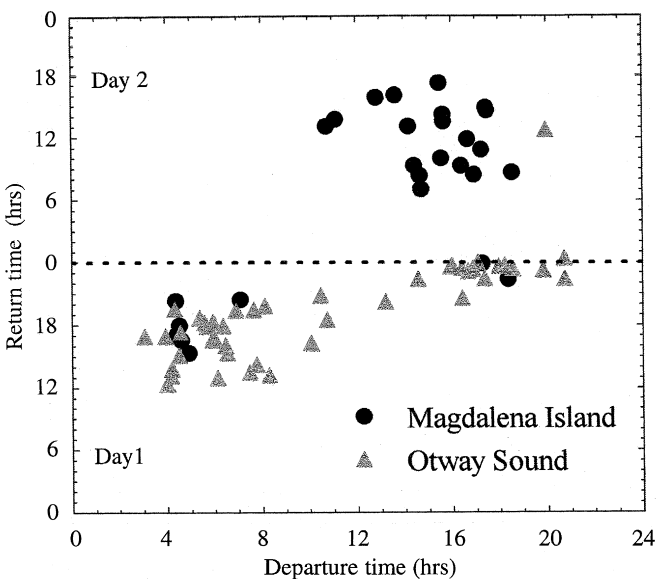


Fig. 9 *Spheniscus magellanicus*. Individual foraging trips, characterized by departure on Day 1 and return time on Day 1 or 2. Foraging trips are distinguished between the colonies of Magdalena Island ($n = 27$) and Otway Sound ($n = 46$) during the breeding season 1996/97. The dotted line separates 1- and 2-d foraging trips. For each colony two distinct clusters can be differentiated: at Magdalena Island 1-d and overnight foragers, at Otway Sound early and late departures

from the colonies, considering the recorded travelling speeds of 5 to 6 km h⁻¹.

In the present work we defined surface intervals of at least 5 min duration without dives deeper than 3 m as recovery periods during a foraging trip. Not only resting but also travelling dives (which usually are shallower than 3 m) are included in the recovery periods. Total foraging trip duration minus recovery periods was determined as activity. The higher activity rates at Otway (69%) than at Magdalena (59%) again suggest shorter travel distances to feeding grounds, but this has to be confirmed by locating the penguins during their varying diving activities (i.e. travelling, searching, feeding) by radio- or satellite-telemetry in combination with TDRs.

Comparable data for diving activity are given as underwater activity in jackass penguins (90, 40 and 30% for large, medium-sized and small chicks, respectively) by Wilson and Wilson (1990) or as total diving time in Humboldt penguins (50 to 70% of foraging trip duration) by Culik and Luna Jorquera (1997).

Diving behaviour

A decreasing dive frequency with increasing depth is valid for Magellanic penguins (Scolaro and Suburo 1991), as it is for other penguin species, e.g. little (*Eudyptula minor*, Gales et al. 1990), macaroni (Croxall et al. 1993) and emperor penguins (Kooyman and Kooyman 1995). Small increases in the frequency distribution at 30 to 40 m (Otway) and 40 to 50 m (Magdalena) suggest a higher foraging effort at these depths. It is apparent from the absolute maximum dive depths of 91.5 m (Magdalena) and 77.9 m (Otway) that topography was not a limiting factor in either area.

There is reason to believe that the diving behaviour of penguins depends on the vertical distribution of their prey (Kooyman et al. 1992). However, the opposite case is also possible: the diving behaviour of the predator, determined by extrinsic factors like light conditions under water, could lead to a typical vertical distribution of the prey (Wilson et al. 1993b). On the Argentine coast Scolaro and Suburo (1991) found another relationship between the diving behaviour of Magellanic penguins and their prey *Engraulis anchoita*. Not the vertical distribution, but the shoal behaviour of the fishes seemed to play an important role: during daylight, anchovies swam in compact shoals, which are easy to handle for penguins, at depths between 35 and 100 m, whereas at night they were found in layers near the surface in more disperse shoals. Unfortunately, nothing is known about the shoaling behaviour of *Sprattus fuegensis*.

The coherence of dive depth and light conditions underwater is obvious in both colonies (Fig. 3). Penguins are visual foragers, and their eyes are adapted both to terrestrial and aquatic life (Sivak et al. 1987). Activity patterns like foraging rhythms and diving behaviour are closely linked with light conditions (Wilson et al. 1989, 1993b). Examples for dive depths coinciding with light

conditions exist, among others, for the deep diving king and emperor penguins (Pütz 1994; Kirkwood and Robertson 1997). We can assume that the shallow, night dives of all penguins equipped with devices in the present study were not foraging dives, but travelling dives.

Dive duration depends on dive depth, dive profile, swimming velocity and dive angle. However, the main limiting factor for dive duration are the physiological abilities of the diving animal. Penguins and other lung breathers have an aerobic dive limit (ADL), which depends on metabolism and the utilization rate of O₂-stores (Kooyman and Davis 1987). Exceeding the ADL results in a substantially longer recovery at the surface to restore blood and muscle chemistry to pre-dive concentrations of lactic acid (Williams 1995). In good feeding conditions this could be achieved after several dive bouts, in which the penguin inevitably has to cope with an O₂-debt. For Magellanic penguins no data are available, but for the similar-sized Humboldt penguin Kooyman and Davis (1987) determined an ADL of 2.5 min, assuming an activity metabolism three times the resting metabolism. Based on swimming metabolism data, Luna Jorquera (1996) calculated an ADL for the same species of 115 s. At Magdalena only 3.2% of all dives were longer than 120 s, at Otway just 2.4%. We can assume, therefore, that, all things being equal, Magellanic penguins in both colonies usually dived within their ADL.

The different purpose of dive profiles is evident when dive bouts are investigated. Frequently foraging penguins start with a row of increasingly deeper V-shaped

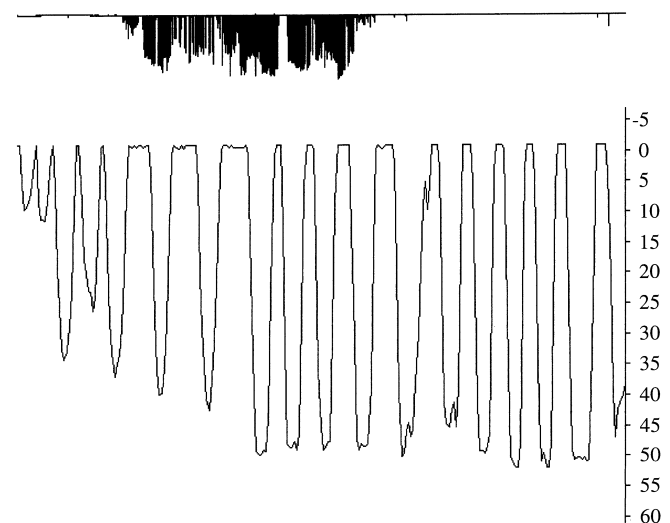


Fig. 10 *Spheniscus magellanicus*. Dive bouts from Magdalena Island during a foraging trip, displayed with the software ANDIVE 8.0. *Upper graph*: profile of the whole foraging trip. *Lower graph*: detail of ca. 45 min of the foraging trip against depth (scale in metres on the right). In this dive sequence the penguin started with increasingly deeper V-shaped dives, followed by numerous U-shaped dives (some of them with a clear amplitude during the bottom phase). Surface time between the deep V-shaped dives is remarkably longer than between the U-shaped dives

dives, and, presumably when successful in finding prey, a row of similarly deep U-shaped dives follows (Fig. 10). Usually the bottom amplitude was small (<2 m), therefore within the hystereses of the loggers' pressure sensor. Possibly the undulations in the bottom phase show a higher vertical and horizontal activity of the penguins during feeding within a fish shoal. Penguins of the genus *Spheniscus* attack their prey from below (Wilson and Wilson 1990). At Magdalena we determined a higher rate of U-shaped dives compared to Otway, especially at the middle depths of 30 to 50 m (Fig. 6). This is coherent with the longer mean dive duration at these depths (Fig. 5), suggesting a higher foraging effort at Magdalena. Assuming equal amounts of food passed on to the chicks in both colonies (chick growth was similar), these factors also indicate a lower catch per feeding dive and therefore a lower prey availability in the Strait of Magellan compared to Otway Sound. Besides this, no information is available about prey density. A coherence between dive profile and food intake could be investigated with stomach temperature-loggers, but this method is tainted with problems (discussed by Wilson et al. 1995d).

In Gentoo penguins, Williams et al. (1992) found mean bottom phases of about 50 s, representing approximately 30% of the total duration of U-shaped dives. In emperor penguins bottom durations of as much as 150 s were recorded, corresponding to 20–30% of total dive duration, depending on maximum dive depth (Kooyman and Kooyman 1995). Magellanic penguins (present study, Fig. 7) had mean bottom durations of 15 to 25 s (increasing with depth), which amount to approximately 25% of dive duration in shallow dives and less than 20% in deep dives. Compared to the total dive time during entire foraging trips at Magdalena and Otway, bottom time represented only 8.8 and 6.3%, respectively. Ultimately, this is the time used by the penguins for food uptake, if no feeding action happened during the descent and ascent phases (Wilson and Wilson 1995).

Dive angles usually depend on maximum dive depth: the deeper the dive, the steeper descent and ascent (Wilson 1995). By varying dive angles and velocities, penguins of both colonies seemed to develop two different strategies for an economical use of limited aerobic dive time: steeper and slower dives at Magdalena, but faster and less steep dives at Otway. Systematic measurement errors can be excluded, because the same loggers were used in both colonies. Energetic considerations associated with varying foraging strategies are an interesting point for further studies on the diving behaviour of penguins.

Dive parameters and penguin size

Maximum dive depth, maximum dive duration and dive angles depend on the size of the penguin species (Wilson 1995). Maximum depth recorded for little penguins,

Eudyptula minor (1 kg), was 69 m (Montague 1985). They usually dive no longer than 60 s (Gales et al. 1990). Maximum dive depth reported for emperor penguins (26 kg) was 534 m, with dive durations of more than 15 min (Kooyman and Kooyman 1995). It could be hypothesized that the correlation between size and dive performance should also be valid intraspecifically. Interestingly, statistical analysis of several foraging and diving parameters showed that individual differences were sometimes larger than intercolonial differences. However, for Magellanic penguins from Magdalena no significant correlation between body mass and maximum dive depth was found, but there was a significant correlation between body mass and dive duration (only Mk 5-logger; dive depth: $n = 11$, $R_s = 0.515$, $t = 1.801$, $p = 0.105$; dive duration: $n = 11$, $R_s = 0.645$, $t = 2.533$, $p = 0.032$). At Otway the correlation between body mass and dive depth was nearly significant, whereas it was not significant between body mass and dive duration (dive depth: $n = 11$, $R_s = 0.588$, $t = 2.179$, $p = 0.057$; dive duration: $n = 11$, $R_s = 0.382$, $t = 1.241$, $p = 0.246$). Dive angles to comparable depths are less steep in penguins of bigger size (Wilson 1995). During descent to 50 m, angles of 65° were recorded for jackass penguins (3 kg; Wilson 1995), but only 19° for king penguins (13 kg; Pütz 1994). In the present study we recorded mean descent angles to these depths of 42° at Magdalena and 32° at Otway for the medium-sized Magellanic penguins.

Dietary composition

The importance of *Sprattus fuegensis* as the main food item of Magellanic penguins has already been noted in previous investigations, both at Magdalena (Venegas and Sielfeld 1981) and at Otway (Venegas and Almonacid 1994; Wilson et al. 1995b). More than 90% of the samples consisted of this small fish species. Other prey were cephalopods like *Loligo* sp. or, rarely, other fish species like *Patagonotothen wiltoni*. In other regions the composition of prey for Magellanic penguins is different and highly variable, spatially, seasonally or interannually (see Thompson 1993, for the Falkland Islands). Opportunistic feeding allows Magellanic penguins to react flexibly to varying conditions. This is valid for other penguin species as well (e.g. jackass penguins, Randall and Randall 1986). However, variable food composition has consequences for chick growth and breeding success. The high fat content of fish is of higher energetic value for growing chicks than the protein richness of cephalopods, whereas crustaceans seem to be absolutely indigestible for Magellanic penguin chicks (Thompson 1993). The constant prey composition at Magdalena and Otway in all studies to date and throughout breeding seasons suggests constant food conditions in these areas for many years. Sprats are a high-quality food for penguins, from which they would only change, if supply did not cover demand. No data

are available about the distribution (both spatial and seasonal) of sprats and cephalopods in the investigated regions. However, according to fishermen, cephalopods do not occur in the Strait of Magellan before February. Therefore, it is possible that they play a more important role as food for moulting adult penguins at the end of the season.

Chick growth and breeding success

Chick growth rates depend on the feeding interval, and therefore on the foraging trip duration of their parents (Boersma et al. 1990), which again depends on food availability. When food conditions are poor, growth of first chicks is clearly better than that of their sibling, suggesting food amount as a limiting factor for reproductive success (Boersma 1991). The same is valid for lone chicks, which grow faster than chicks with a sibling, especially in the late breeding season, when food demand of the chicks is highest (Boersma 1991). Investigations with respect to chick growth and body mass in Magellanic penguins have to date only been conducted in Argentina. Boersma et al. (1990), in Punta Tombo, and Scolaro (1987), in Punta Clara, determined growth rates, which were considerably lower than in the present study. Fledging chicks in these Argentinian colonies usually were lighter than 3 kg. At Magdalena as well as at Otway most of the chicks reached 3.5 to 4.0 kg before fledging. Compared with the results at Punta Tombo (Boersma et al. 1990), feeding intervals at both Magdalena and Otway were shorter. In both colonies first chicks had slightly higher growth rates than their sibling (Fig. 8). However, in most investigated nests the development of second hatched chicks was even better than for first chicks at Punta Tombo, indicating good feeding conditions in Chilean waters. It is important to mention, that Magdalena and Otway differ with respect to colony size (ca. 50 000 breeding pairs at Magdalena Island, 2500 at Otway Sound) and food competition of other species. Magdalena Island also is an important breeding ground for other seabirds such as kelp gulls (*Larus dominicanus*), skuas (*Catharacta chilensis*) and cormorants (*Phalacrocorax magellanicus*). At nearby Marta Island breeding colonies of sea lions (*Otaria byronia* and *Arcotophalus australis*) are found.

The most important reasons for chick mortality are starvation and predation (Scolaro 1990; Boersma 1991). Higher mortalities are seen in the first week after hatching, during moult and shortly before fledging, when the chicks are unsupervised (Scolaro 1990). Depending on food conditions, reproductive success in Magellanic penguins is highly variable, e.g. in Punta Tombo between 0.02 chicks per breeding pair in 1984/85 (Boersma et al. 1990) and 1.4 in 1988/89 (Frere et al. 1992). Other factors determining breeding success are the fitness of the adults at the beginning of the season (Reid and Boersma 1990), location of the nests in the colony (Frere et al. 1992), nest density (Scolaro 1990)

and weather. Especially heavy rain can cause problems for slope-located nests (Scolaro 1990). Fledging age of the chicks differs between breeding colonies: at nearby Cabo Virgenes the chicks fledge after 60 to 70 d (Frere 1993), in Punta Tombo some of the chicks do not fledge before they are 120 d old (Williams 1995).

Both at Magdalena and Otway, chicks reached their maximum body masses after 60 to 70 d and fledged about 2 weeks later, i.e. end of January or beginning of February. No difference was observed between colonies. Interestingly some chicks did not complete moulting before they fledged. No information is available about the mechanism(s) behind fledging, be it hormonal or body mass controlled. Most of the investigated nests had two successfully fledging chicks.

Nest density was lower at Otway than at Magdalena, and the majority of nests were very deep, therefore protected against predators (like the Patagonian fox *Dusicyon griseus griseus*) and rain. All these factors contribute to the slightly higher reproductive success at Otway than at Magdalena. In both colonies the high reproductive success of more than 1.75 chicks per breeding pair in the season 1996/97, as opposed to other locations around South America (e.g. only one chick per breeding pair on the Falkland Islands, M. Bingham, personal communication) indicates very good food availability and a low rate of mortality due to predation or weather.

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