

## Sexual differences in the foraging behaviour of Magellanic Penguins related to stage of breeding

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**Abstract.** Understanding the foraging behaviour of seabirds and its plasticity is vital to establish their role in marine food webs and their use as indicators of change in the availability of prey. The foraging behaviour of penguins is known to differ with locality, sex, stage of breeding and between years. We studied the diving behaviour of breeding Magellanic Penguins (*Spheniscus magellanicus*), using time-depth recorders, during incubation and brooding in the 2003–04 and 2004–05 breeding seasons at Isla Martillo, Tierra del Fuego, Argentina. Foraging trips during the incubation period were longer than those during the brooding period for both sexes in both years of the study. Sex-related differences in foraging behaviour were observed during the incubation stage. During the incubation stage females performed longer foraging trips than males, foraging effort was lower, and did not dive as deep as males in both years. Foraging success was lower for females than males during incubation only in 2003. Our results suggest that sexual differences, expressed as differences in the foraging parameters of males and females, only develop when Fuegian Sprat (*Sprattus fuegensis*), the main prey in this locality, is not abundant close to the colony. Females may be extending the volume of water they can exploit by extending the duration of trips (horizontal distance), whereas males do so by diving deeper (vertical distance). Our results show the fundamental differences in foraging strategies between the sexes in Magellanic Penguin are a consequence of environmental conditions not morphological differences between sexes.

**Additional keywords:** Beagle Channel, diving behaviour, foraging ecology, foraging strategies, seabirds, sexual dimorphism, Tierra del Fuego.

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### Introduction

Seabirds are considered to be good indicators of temporal and spatial variation in the availability and distribution of resources (Cairns 1987; Trathan *et al.* 2006; Boersma *et al.* 2009). Changes in the foraging behaviour of seabirds can indicate variation in food availability (Cairns 1987; Wilson 1992; Bost and Le Maho 1993) because birds need to forage efficiently in order not to compromise breeding success. On the other hand, changes in the environment can be reflected in breeding parameters of seabirds (Kitaysky *et al.* 2000; Davoren and Montevecchi 2003; Boersma and Rebstock 2009). Furthermore, seabird foraging behaviour is known to vary with sex (Pütz *et al.* 2006; Thaxter *et al.* 2009), with stage of breeding (Raya Rey *et al.* 2007), between years (Walker and Boersma 2003) and, in particular, between colonies given the physical and biological characteristics of their foraging environment (Wilson *et al.* 2005; Boersma *et al.* 2009). In this context, understanding seabird foraging behaviour at a fine scale,

including the plasticity of foraging related to the species of bird, sex and site, is vital to establish the role of seabirds in marine food webs and their use as indicators of change in the availability of prey (Croxall and Lishman 1987; Bost and Le Maho 1993; Grémillet and Charmantier 2010).

Magellanic Penguins (*Spheniscus magellanicus*) breed on the Atlantic and Pacific coasts of South America, from 42°S on the eastern coast, around Cape Horn and north to 29°S on the Pacific coast; they also breed on the Falkland (Malvinas) Islands (Williams 1995; Gandini *et al.* 1996; Schiavini *et al.* 2005). The foraging ecology of Magellanic Penguins has been studied in continental Patagonian colonies (Walker and Boersma 2003; Wilson *et al.* 2005) as well as on some islands in the Strait of Magellan, Chile (Wilson *et al.* 1995; Radl and Culik 1999). During the breeding period, penguins are central place foragers and perform foraging trips of varying length, each of which comprise numerous dives (Croxall and Lishman 1987). The

duration of foraging trips, and hence the distance that can be travelled to foraging areas, varies between colonies (Wilson *et al.* 2005; Boersma *et al.* 2009) and stage of breeding (Walker and Boersma 2003; Boersma and Rebstock 2009). As a result, annual variation in breeding success of Magellanic Penguins can be associated with differences in foraging areas and variation in the quantity and quality of their prey (Boersma *et al.* 1990; Williams 1995; Boersma and Rebstock 2009). Even though Magellanic Penguins show slight sexual dimorphism (Gandini *et al.* 1992) and larger Magellanic Penguins perform deeper dives than smaller Penguins (Walker and Boersma 2003), sexual differences in diving parameters and trip characteristics have been shown in only one study (Scioscia *et al.* 2010).

There has been no detailed study on the diving behaviour of Magellanic Penguins at our study location in Tierra del Fuego, Argentina. The aim of our study was to examine the foraging trips and dives of Magellanic Penguins from Isla Martillo and to test for differences in these parameters between sexes, stage of breeding and years. We specifically tested the hypothesis of Walker and Boersma (2003) that male and female Magellanic Penguins will have different diving capabilities related to size dimorphism.

## Materials and methods

### *Study area and birds*

The study was conducted at the Magellanic Penguin breeding colony on Isla Martillo, Tierra del Fuego, Argentina (54°53'S, 67°34'W). The colony supports 3000 breeding pairs (A. Raya Rey and A. Schiavini, unpubl. data) and has been increasing since it was established 30 years ago (Schiavini *et al.* 2005). This island is part of a group of small islands located in the eastern section of the Beagle Channel, with the South Atlantic Ocean ~74 km to the east of the colony.

We studied the foraging trips and diving behaviour of breeding Magellanic Penguins during the incubation and brooding stages (chicks 1–20 days old) in the 2003–04 and 2004–05 breeding seasons (hereafter referred to as the 2003 and 2004 breeding seasons) by attaching time-depth recorders (TDR). Some individuals were studied in both stages or years – in 2003, seven Penguins were tagged for both stages, in 2004, four Penguins were tagged for both stages, and seven penguins were tagged in both years and stages. On Isla Martillo, incubation started immediately after laying on 10 October (G. Scioscia, unpubl. data), and the mid-date of the laying period is 26–28 October. The first deployments of TDRs began no earlier than the 29 October each year.

We captured breeding adult penguins by carefully removing them from their burrows using a hook attached to a rod (as described in Pütz *et al.* 2002). Penguins were weighed using a Pesola balance (to the nearest 100 g) and bill-depth and bill-length measured using calipers to determine sex of individuals (Gandini *et al.* 1992). At the time of capture, males were significantly heavier than females (males,  $n = 18$ ,  $4.32 \pm 0.35$  kg; females,  $n = 19$ ,  $3.66 \pm 0.37$  kg;  $t = 5.76$ ,  $P < 0.001$ ). Sexual differences in bill-length and bill-depth for males were  $5.76 \pm 2.2$  and  $2.44 \pm 1.1$  cm, and for females were  $5.32 \pm 2.2$  and  $2.1 \pm 1.1$  cm. We checked the nests every 3 days to determine the stage of breeding (incubation or brooding).

We attached a time-depth recorder (TDR; MK9, Wildlife Computers, Redmond, WA, USA) along the midline of each Penguin's back, as close as possible to the tail without impairing the bird's access to the preen gland, using black tape (Tesa, Beiersdorf AG, Hamburg, Germany) and a two-component neoprene glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany), as described by Wilson *et al.* (1997). The devices were then covered with a layer of quick-drying epoxy glue (Loctite 3430, Loctite Deutschland GmbH, München, Germany) to prevent the birds from removing the tape with their bills. The whole process took less than 20 min per bird.

The fitted TDRs weighed ~30 g, which is <1% of the mean body mass of a Magellanic Penguin (see above), and the maximum dimensions of the fitted TDR were  $67 \times 17 \times 17$  mm, corresponding to ~2% of a Penguin's cross-sectional body area (Stokes *et al.* 1998). The TDRs were programmed with MK9HOST (Wildlife Computers), with a measurement interval of 2 s to allow us to determine details in dive parameters. Data were stored in 64-Mb non-volatile flash memory, which could store 8–16 million samples (sensor readings). TDRs were each equipped with a pressure sensor, a light sensor and a temperature sensor. A saltwater switch prevented data being recorded while the TDR was not submerged (i.e. when Penguins on the surface). The pressure sensor recorded depth of dives between 0 and 350 m, with an accuracy of 0.5 m (depths of 0–20 m), 1 m (depths of 20–200 m) or 5 m (depths of 200–350 m). The temperature and light measurements were not considered in this study.

The time of sunrise and sunset for the mean date of deployment of TDRs in 2003 (28 November was 0434 and 2124 hours (local time = GMT – 3 h), giving a solar daylength of 16 h 50 min. Using the nautical definition of dawn and dusk (i.e. when the sun is 12° below the horizon), for the same day, dawn was at 0222 hours and dusk at 2400 hours. Thus, the combined period of twilight (dawn and dusk together) was 4 h and 48 min and night lasted 2 h and 22 min.

To measure breeding success we marked nests from which adults were taken using a plastic pole and checked the contents of nests (number of eggs) at the mid-date of the laying period (26–28 October) and re-checked the nests during the late chick-rearing period (chicks 50–60 days old, 6–8 January). Breeding success was calculated as the number of fledged chicks per breeding pair ( $n = 39$  breeding pairs in 2003, 109 in 2004).

### *Data analyses*

We analysed diving data using MULTITRACE (Jensen Software Systems, Kiel, Germany). Data were first corrected for a drifting surface level (i.e. to correct the surface level for differences for waves). A dive was deemed to occur when the maximum depth of a dive was  $\geq 3$  m (after Chappell *et al.* 1993; Tremblay and Cherel 2000, 2003; Schiavini and Raya Rey 2004). The duration of a foraging trip was calculated as the sum of all diving times and intervals between dives. We considered a foraging trip finished when the period without a dive exceeded 3 h, with the end of the foraging trip calculated to the end of the last dive recorded. For each dive we calculated: total duration, onset, maximum depth, post-dive interval, bottom time (time spent at 75% of maximum dive depth attained during the dive; after Cherel *et al.* 1999; Tremblay and Cherel 2000, 2003), rate of descent (from

beginning of dive to start of bottom phase), rate of ascent (from end of bottom phase to end of dive), and the number of wiggles, which are phases of short ascents and descents (>2 m) during the bottom phase. As a measure of foraging effort, we calculated percentage of time spent underwater (sum of dive duration divided by foraging trip duration), rate of diving (number of dives divided by foraging trip duration), and vertical travel distance (VTD), which is defined as twice the sum of the maximum dive depth for all dives performed during each trip (Horning and Trillmich 1997). In penguins, wiggles are generally considered to be indicative of prey pursuit (e.g. Rodary and Wienecke 2000; Simeone and Wilson 2003). Thus, as an index of foraging success we calculated a wiggle-rate as the number of wiggles divided by the duration of bottom time in minutes (modified from Zimmer *et al.* 2010). Data from successive dives are partially autocorrelated, as the maximum depth of a dive is influenced by the previous depths attained (Tremblay and Cherel 2000). To overcome this we followed the method of Tremblay and Cherel (2003) and performed a partial autocorrelation analysis, which verified that maximum dive depth failed to correlate after six successive dives. Thus, only one dive out of six was selected to reduce the autocorrelation, and from these dives 50 per bird were randomly selected for graphical display.

#### Statistical analyses

We analysed the effect of sex, year and breeding stage (as well as their interactions) on the different foraging trip and dive parameters using generalised linear mixed effects models (GLMM) fitted by restricted maximum likelihood with a Gaussian distribution of errors and identity link function. Sex, year and breeding stage were included as fixed factors and bird identity as a random factor to avoid pseudoreplication (Hurlbert 1984). When appropriate, data were log-transformed to fulfil the criterion of normality. We used likelihood ratio tests to evaluate the significance of the inclusion of individuals as a random factor. This analysis was performed using the open source statistical package R version

2.9.1 (R Development Core Team 2009). All mean values are presented as  $\pm$ s.d., and differences tested considered statically significant when  $P < 0.05$ .

#### Results

We recorded 515 foraging trips from 15 female and 17 male Magellanic Penguins during the incubation and brooding periods over the two breeding seasons at Isla Martillo. Breeding success did not differ significantly between years, with  $1.51 \pm 0.64$  chicks per breeding pair in the 2003 season and  $1.61 \pm 0.69$  in the 2004 season (Mann–Whitney test,  $W = 2677$ ,  $P = 0.3$ ).

#### Characteristics of foraging trips

The mean foraging parameters and statistical analysis are listed in Tables 1 and 2 respectively. The inclusion of individuals as a random effect was significant ( $P < 0.001$ ) for all the analysis with the different dependent variables. The interpretation of these results is complex but several key patterns can be identified.

The mean duration of foraging trips varied with year, sex and stage of breeding (Fig. 1). For both sexes, trips were significantly longer during incubation than the brooding period in both years. Females performed longer trips than males only during the incubation period. Accordingly, both males and females made more overnight trips during incubation than during the brooding period (57 v. 16% in 2003, 91 v. 17% in 2004). Most departures occurred between 0400 and 0800 hours (50%,  $n = 252$  foraging trips) with a peak at 0500 hours (27%,  $n = 85$ ). Time of return was widely distributed, between 0800 and 0100 hours, with a peak at 2100 hours but only accounting for 8% of the arrivals.

In terms of foraging effort, the time spent underwater was significantly lower for females during incubation compared with females during brooding and males during incubation and brooding; diving rates of females were lower during incubation than brooding in 2004; and the vertical distance covered was lower for females during incubation compared with the other groups. The number of wiggles per minute of bottom time was

**Table 1. Summary of the characteristics of foraging trips and dive parameters for female and male Magellanic Penguins during the incubation and brooding periods of the 2003 and 2004 breeding seasons**

All means are presented  $\pm$ s.d.

	2003				2004			
	Female		Male		Female		Male	
	Incubation	Brooding	Incubation	Brooding	Incubation	Brooding	Incubation	Brooding
Number of birds (number of trips)	10 (50)	5 (87)	8 (61)	8 (81)	5 (20)	7 (101)	4 (13)	9 (102)
Duration of trips (h)	39.9 $\pm$ 30.1	11.0 $\pm$ 6.0	23.1 $\pm$ 17.8	11.9 $\pm$ 5.9	88.2 $\pm$ 85.8	11.0 $\pm$ 5.5	52.5 $\pm$ 38.6	11.2 $\pm$ 7.7
Proportion of time spent underwater (%)	24 $\pm$ 9	39 $\pm$ 14	34 $\pm$ 11	40 $\pm$ 12	25 $\pm$ 8	37 $\pm$ 12	36 $\pm$ 12	31 $\pm$ 11
Number of dives per hour	17.5 $\pm$ 5.3	19.9 $\pm$ 6.1	20.7 $\pm$ 7.1	19.0 $\pm$ 5.3	13.9 $\pm$ 4.2	21.2 $\pm$ 5.9	16.2 $\pm$ 3.3	18.2 $\pm$ 5.7
Mean depth of dives (m)	12.9 $\pm$ 4.9	27.9 $\pm$ 7.7	19.6 $\pm$ 6.2	31.0 $\pm$ 10.0	20 $\pm$ 3.1	23.0 $\pm$ 7.5	27.7 $\pm$ 8.3	23.9 $\pm$ 7.7
Mean duration of dives (s)	50.2 $\pm$ 9.5	70.1 $\pm$ 12.3	60.7 $\pm$ 12.8	76.9 $\pm$ 14.5	63.4 $\pm$ 5.6	62.4 $\pm$ 11.8	77.7 $\pm$ 14.1	61.0 $\pm$ 13.0
Mean bottom time (s)	20.2 $\pm$ 4.9	37.6 $\pm$ 11.4	28.0 $\pm$ 7.9	38.2 $\pm$ 10.3	28.8 $\pm$ 3.2	29.0 $\pm$ 8.7	36.7 $\pm$ 10.3	27.7 $\pm$ 8.8
Rate of descent ( $\text{m s}^{-1}$ )	0.8 $\pm$ 0.2	1.4 $\pm$ 0.2	1.0 $\pm$ 0.2	1.3 $\pm$ 0.2	1.0 $\pm$ 0.1	1.1 $\pm$ 0.2	1.1 $\pm$ 0.2	1.1 $\pm$ 0.2
Rate of ascent ( $\text{m s}^{-1}$ )	0.7 $\pm$ 0.2	1.4 $\pm$ 0.3	0.9 $\pm$ 0.2	1.3 $\pm$ 0.3	1.0 $\pm$ 0.2	1.1 $\pm$ 0.2	1.0 $\pm$ 0.2	1.1 $\pm$ 0.3
Vertical distance per hour ( $\text{m h}^{-1}$ )	453 $\pm$ 229	1113 $\pm$ 394	810 $\pm$ 433	1144 $\pm$ 388	560 $\pm$ 194	973 $\pm$ 377	924 $\pm$ 406	892 $\pm$ 471
Wiggle-rate (wiggles $\text{m}^{-1}$ )	1.4 $\pm$ 0.4	1.9 $\pm$ 0.6	1.6 $\pm$ 0.4	1.8 $\pm$ 0.6	2.2 $\pm$ 0.4	1.7 $\pm$ 0.5	1.6 $\pm$ 0.4	1.8 $\pm$ 0.5

**Table 2. Statistical analyses (GLMM) of the factors affecting the trip characteristics and diving parameters of Magellanic Penguins**  
The numerator (1) and denominator (435) for the degrees of freedom are the same for all cases except sex (denominator: 31)

		Intercept	Year	Sex	Stage	Year × Sex	Year × Stage	Sex × Stage	Year × Sex × Stage
Duration of trip	<i>F</i>	1428.6	21.7	5.3	102.6	1.6	23.5	8.1	0.02
	<i>P</i>	<0.0001	<0.001	0.01	<0.001	0.2	<0.001	0.005	0.9
Time spent underwater	<i>F</i>	14132.3	6.3	7.4	24.7	6.5	0.7	8.8	1.2
	<i>P</i>	<0.0001	0.01	0.01	<0.001	0.01	0.4	0.003	0.3
Diving rate	<i>F</i>	10897.5	4.0	0.4	6.5	2.1	13.5	5.2	2.1
	<i>P</i>	<0.0001	0.04	0.5	0.01	0.1	0.0003	0.02	0.1
Mean depth of dives	<i>F</i>	6965.3	7.6	21.5	36.2	5.8	59.9	5.2	2.6
	<i>P</i>	<0.0001	0.01	0.001	<0.001	0.02	<0.001	0.02	0.1
Mean duration of dives	<i>F</i>	2532.3	5.2	14.2	19.7	5.0	58.6	0.6	0.1
	<i>P</i>	<0.0001	0.02	0.001	<0.001	0.03	<0.001	0.4	0.7
Mean bottom time	<i>F</i>	11835.3	8.0	10.2	24.4	4.2	59.7	3.7	1.9
	<i>P</i>	<0.0001	0.005	0.003	<0.001	0.04	<0.001	0.1	0.2
Rate of descent	<i>F</i>	1441.1	64.9	10.0	41.6	0.7	42.9	4.6	4.5
	<i>P</i>	<0.0001	<0.001	0.004	<0.001	0.4	<0.001	0.03	0.03
Rate of ascent	<i>F</i>	926.6	50.6	6.9	39.4	1.0	50.6	2.0	10.0
	<i>P</i>	<0.0001	<0.001	0.02	<0.001	0.3	<0.001	0.2	0.002
Vertical distance	<i>F</i>	25870.9	7.6	16.7	48.3	7.0	8.3	12.5	0.0
	<i>P</i>	<0.0001	0.02	0.0003	<0.001	0.01	0.004	0.001	1.0
Wiggle-rate	<i>F</i>	992.1	0.8	0.8	0.07	2.5	12.7	0.05	11.5
	<i>P</i>	<0.0001	0.3	0.4	0.8	0.1	<0.001	0.8	<0.001

lower for incubating females in 2003 compared with the other groups (Fig. 1).

#### Characteristics of dives

The maximum depth and duration of dives were observed in the brooding period in 2003, for both sexes (males, 112 m and 192 s; females, 96 m and 164 s). Almost all dives were during daylight hours, with <5% of dives between 2400 and 0200 hours (data not shown). Mean depth of dives was evenly distributed during daylight hours, mostly between 15 and 40 m (Fig. 2a, b). Mean depths of dives were significantly lower during incubation than during the brooding period for both sexes in 2003, and higher for males than females during the incubation period in both years. The lowest mean depth of dives was recorded during incubation in 2003, when 90% of dives by males and females were to depths of <30 m. Mean duration of dives was significantly lower during incubation than the brooding period in 2003 for both sexes (Fig. 1). Bottom time and rates of descent were significantly lower during incubation than the brooding period for both sexes in 2003 and it was lower for females than males during the incubation period in both years. For both sexes, rates of ascent were significantly higher during the brooding period than during incubation only in 2003.

#### Discussion

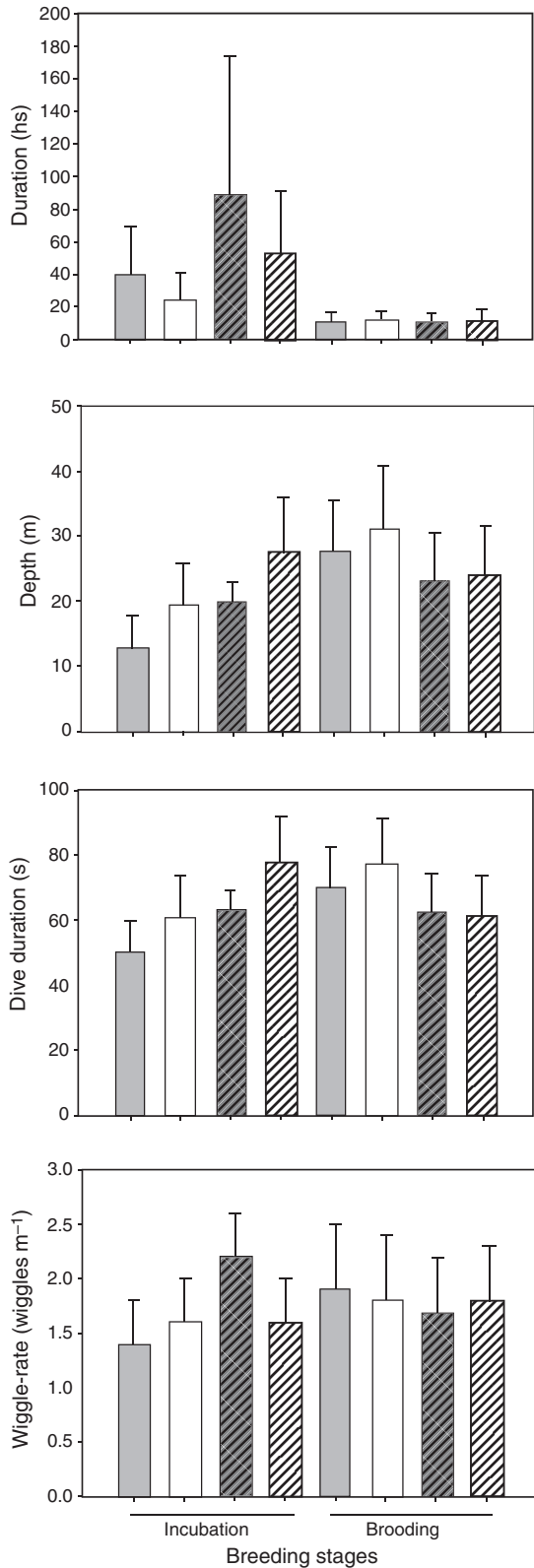
Our results are consistent with previous studies of the diving behaviour of breeding Magellanic Penguins at other breeding colonies (e.g. Radl and Culik 1999; Walker and Boersma 2003) but, more importantly, reveal some sex-related differences, in particular during the incubation period.

Characteristics of foraging trips and diving parameters varied extensively with year, stage of breeding and sex. Differences between sexes and years were only evident during the incubation period, when both sexes performed longer foraging trips, which

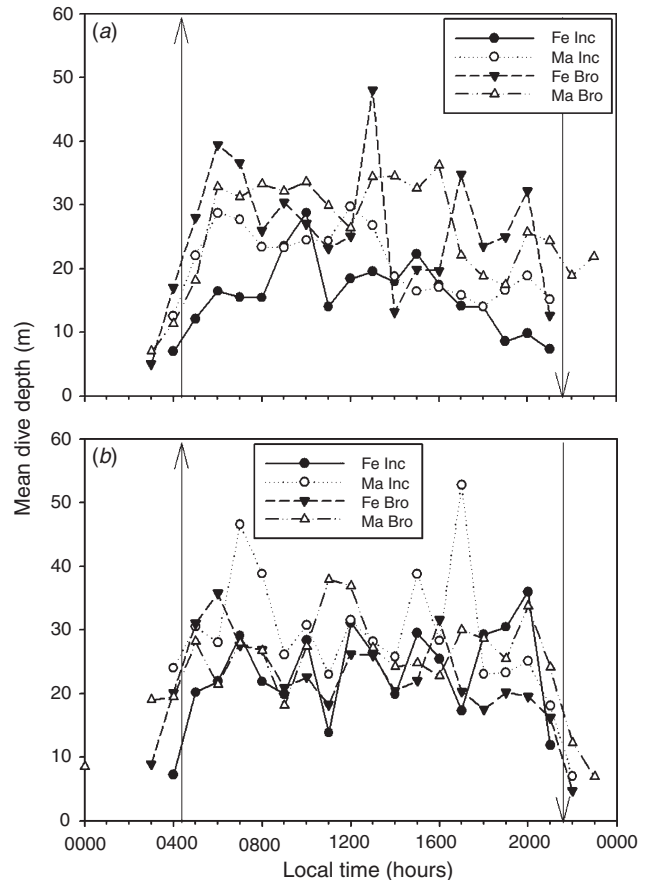
was the general pattern found at other colonies (Boersma *et al.* 1990; Walker and Boersma 2003). One of the reasons for longer trips during incubation could be that adult birds need to regain energy lost from fasting after settlement, courtship and laying while not yet having to provision their chicks regularly with food (Yorio and Boersma 1994; Hood *et al.* 1998; Taylor *et al.* 2002). Another factor known to affect the duration of trips is the availability and distribution of prey close to the breeding sites (Wilson *et al.* 2005; Boersma *et al.* 2009). Magellanic Penguins from Isla Martillo preferentially feed on Fuegian Sprat (*Sprattus fuegensis*) and, to a lesser extent, Lobster Krill (*Munida gregaria*) (Schiavini *et al.* 2005; G. Scioscia, A Raya Rey and A Schiavini, unpubl. data). Recent surveys confirmed that high concentrations of Sprats are found closer to the colony as summer progresses (Lloris and Rucabado 1991; Hansen *et al.* 2004; Scioscia *et al.* 2009). Since, in Magellanic Penguins, the distance travelled per trip was positively correlated with duration of the trip (Boersma and Rebstock 2009), the differences in duration of trips found in our study between breeding stages may reflect the changes in distribution of prey near the colony during the course of the breeding season.

Most variation in foraging parameters between sexes was recorded during the incubation period, with no significant differences between sexes during the brooding period. A lack of difference between sexes in the characteristics of foraging trips and foraging areas during the brooding period had previously been reported for the same colony (Raya Rey *et al.* 2010). Males were found to dive deeper than females, as proposed by Walker and Boersma (2003), but only during the incubation period. Differences in diving depth, in accord with sexual dimorphism, have been reported for Macaroni Penguins (*Eudyptes chrysolophus*) (Green *et al.* 2005). During incubation, male Magellanic Penguins dive deeper, for longer and more often, and stay longer at the bottom and travel greater vertical distances per hour than females, but both sexes have similar rates of ascent and descent





**Fig. 1.** Mean ( $\pm$ s.d.) duration of trips, depth and duration of dives, and wiggle-rate for female (grey) and male (white) Magellanic Penguins during the incubation and brooding periods. Unhatched bars are date for 2003 and hatched bars for 2004.



**Fig. 2.** Mean depth of dives in relation to local time for female and male Magellanic Penguins during incubation and brooding in the (a) 2003 and (b) 2004 breeding seasons at Isla Martillo. Arrows indicate time of sunrise and sunset. Fe Inc., female incubation; Ma Inc., male incubation; Fe Bro, female brooding; Ma Bro, male brooding.

and similar wiggle rates. However, this cannot be explained by differences in diving capabilities between sexes, as females reach similar depths to males during the brooding period. A possible explanation is that females could be excluded by direct competition for food with the larger males around the colony during a period of food shortage. Another explanation, not mutually exclusive, could be that both sexes targeted different prey. However, a 3-year study of diet during incubation, and early and late brooding periods, observed no significant differences in prey of males and females (Scioscia 2011). Females would therefore have to go further to find food during incubation. As a consequence, they would have to perform more travelling dives (<5 m), and this would be reflected in a lower dive rate and time spent underwater during incubation than males. Given our results, and knowing that the availability of sprats close to Isla Martillo is lower during incubation than during the brooding period (Lloris and Rucabado 1991; Hansen *et al.* 2004; Scioscia *et al.* 2009), we suggest that females may be extending the volume of water they can exploit by extending the duration of trips (horizontal distance), whereas males do the same by diving deeper (vertical distance). This hypothesis also helps explain some of the inter-annual variation in diving parameters in the context of differential

availability of food, although this is speculative as we did not measure abundance of prey. Our results indicate the behavioural plasticity of Penguins.

In other studies, the duration of trips proved to be a good indicator of maximum foraging distance and was also related to breeding success (Walker and Boersma 2003; Boersma and Rebstock 2009). The duration of foraging trips of birds from Isla Martillo was short compared with those undertaken at other breeding localities, where foraging trips, especially during the beginning of the incubation period, lasted several days or even weeks (Wilson *et al.* 2005; Boersma and Rebstock 2009). Reproductive success varies considerably at different locations but is lower in general where foraging trips are longer. At two colonies in Chile, where foraging trips were also short (9.2 h during brooding), Magellanic Penguins fledged 1.79 and 1.96 chicks per nest (Radl and Culik 1999), similar to the breeding success in this study. In spite of the differences in duration of trips during incubation in different years in our study, breeding success did not differ significantly among years. This highlights the need to take into account the entire breeding period and not only incubation when correlating breeding success with duration of trips, and also indicates the behavioural plasticity of seabirds (Grémillet and Charmantier 2010).

Comparison of the diving parameters calculated in our study with those obtained from Magellanic Penguins at other breeding sites revealed differences according to locality (Peters *et al.* 1998; Radl and Culik 1999; Walker and Boersma 2003). It thus appears that Magellanic Penguins adapt their diving behaviour in relation to the local environmental conditions to a much larger extent than previously thought, and studies on diving behaviour together with diet and availability of prey need to be conducted in order to understand better their foraging ecology at the various breeding sites.

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