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# Breeding biology of Magellanic Penguins (*Spheniscus magellanicus*) at the Beagle Channel: interannual variation and its relationship with foraging behaviour

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**Abstract** Interannual variation in seabird foraging or reproductive behaviour may reflect fluctuations in marine resources. In this study, we evaluated different foraging and breeding parameters of Magellanic Penguins (*Spheniscus magellanicus*) from Martillo Island in the Beagle Channel, and the relationships between these parameters at different stages within the season (incubation, early and late chick-rearing) over three consecutive breeding seasons (2006–2007, 2007–2008 and 2008–2009). In 2007, we observed greater adult foraging effort (longer foraging trip duration and vertical travel distance, VTD) and lower chick feeding frequency, together with a slower growth rate and later fledging date of chicks, which we suggest was linked to lower food availability near the colony that year. The increased foraging effort appeared to be compensated by enhanced feeding activity (e.g., number of wiggles per dive). However, this increase did not coincide with a larger amount of food load brought to colony, which may have been due to a change in the type or size of prey consumed by the penguins. Magellanic Penguins from Martillo Island showed great plasticity in foraging behaviour, as evidenced by changes in consumed prey type or increased foraging effort and feeding activity when the consumption of their main prey item, *Sprattus fuegensis*,

seemed to decrease. Moreover, during this particular breeding season, although the growth rate of chicks was lower, the breeding success remained constant throughout the study period, suggesting that the penguins managed to compensate for the apparent decrease in Fuegian sprat.

**Keywords** Seabirds · Reproductive parameters · Foraging effort · Feeding activity · Argentina

## Zusammenfassung

**Die Brutbiologie von Magellanpinguinen (*Spheniscus magellanicus*) im Beagle-Kanal: Variation zwischen Jahren und ihre Beziehung zum Nahrungserwerbsverhalten.**

Interannuale Variation im Nahrungserwerbs- und/oder Fortpflanzungsverhalten von Seevögeln könnte Schwankungen im marinen Ressourcenangebot widerspiegeln. In dieser Studie haben wir unterschiedliche Nahrungs- und Brutparameter von Magellanpinguinen (*Spheniscus magellanicus*) auf der Martillo-Insel im Beagle-Kanal sowie die Beziehungen zwischen diesen Parametern in unterschiedlichen Stadien der Brutsaison (Bebrütung, frühe und späte Kükenaufzucht) in drei aufeinanderfolgenden Brutsaisons (2006–2007, 2007–2008 und 2008–2009) ausgewertet. Im Jahr 2007 haben die Altvögel mehr Aufwand in die Nahrungssuche investiert (längere Nahrungstrips und längere vertikale Wegstrecken, VTD) und die Küken weniger häufig gefüttert, und die Küken wuchsen langsamer und flogen später aus. Wir schlagen vor, dass dies mit einer geringeren Nahrungsverfügbarkeit in der Nähe der Kolonie in diesem Jahr zusammenhängt. Der höhere Nahrungssuchaufwand wurde offenbar durch eine erhöhte Nahrungsaufnahme (z. B. Anzahl der Bewegungen

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pro Tauchgang) ausgeglichen. Dieser Anstieg stand jedoch nicht mit einer größeren zur Kolonie gebrachten Nahrungsmenge in Einklang. Dies könnte auf eine Veränderung des Typs und/oder der Größe der von den Pinguinen aufgenommenen Nahrung zurückzuführen sein. Magellanpinguine von der Martillo-Insel zeigen große Plastizität in ihrem Nahrungserwerbsverhalten. Diese offenbart sich anhand von Veränderungen des konsumierten Nahrungstyps und/oder der Steigerung des Nahrungssuchaufwands und der Nahrungsaufnahme, wenn der Verzehr der Hauptnahrung der Pinguine, *Sprattus fuegensis*, scheinbar abnimmt. Zudem blieb in dieser bestimmten Brutsaison der Bruterfolg über den gesamten Untersuchungszeitraum hinweg konstant, obwohl die Wachstumsrate der Küken niedriger war. Dies deutet darauf hin, dass die Pinguine den offensichtlichen Rückgang ihrer Hauptbeute ausgleichen konnten.

## Introduction

Changes in the foraging behaviour of seabirds due to fluctuations in food availability can affect their reproductive performance; as such, these interannual variations in foraging and breeding behaviour are used as indicators of local changes in marine resources (Montevecchi 1993; Piatt and Sydeman 2007; Boersma 2008). In penguins, for instance, trip duration determines how frequently parents deliver food to their chicks, which is considered an important factor for chick growth and survival (e.g., Boersma et al. 1990; Barlow and Croxall 2002; Takahashi et al. 2003; Ropert-Coudert et al. 2004; Hennicke and Culik 2005; Raya Rey et al. 2007).

At times of low food availability or quality, adults are faced with a choice between maintaining their own body condition and ensuring the survival of their brood (e.g., Watanuki et al. 1993). Watanuki et al. (1993) proposed two alternatives under such circumstances. One involved adults investing in maintaining their own body condition at the expense of the growth and survival of their offspring (e.g., Tremblay and Cherel 2003; Hennicke and Culik 2005; Croll et al. 2006). In the second scenario, in order to maintain their breeding success, adults compensate for fluctuations in food availability by increasing their foraging effort (e.g., Uttley et al. 1994). However, a third situation could occur if the adults were not able to completely offset a decrease in food resources by higher foraging effort, and thus the food delivered to chicks would nonetheless be reduced, affecting their growth, although a decrease in breeding success might not be observed.

To understand a predator's response to changes in the marine ecosystem, it is first necessary to understand the

trophic and breeding parameters of the species of interest and the relationships between these parameters on a local scale, as well as the behavioural changes within and among breeding seasons. Within a species, foraging behaviour parameters can vary across breeding sites (Radl and Culik 1999; Wilson et al. 2005; Boersma et al. 2009; Sala et al. 2012a, b, 2014). Therefore, choosing the parameters that best reflect the changes in marine resources can be very complex, involving several aspects of the predators' trophic or breeding behaviour (Reid et al. 2005).

Breeding parameters for Magellanic Penguins differ among localities along the Patagonian coast (Scolaro 1984; Boersma et al. 1990; Frere and Gandini 1996; Frere et al. 1998; Yorio et al. 2001). Sala et al. (2012a, b, 2014) found differences in foraging behaviour among colonies as well, likely related to differences in prey type and abundance at each locality. Some authors have suggested that interannual variations in foraging behaviour (Boersma and Rebstock 2009), breeding success (Radl and Culik 1999) and other breeding parameters such as chick growth rate and fledging weight and age (Boersma et al. 1990) are related to fluctuations in food availability or the quality of prey consumed near the colony (Forero et al. 2002). The associations among different aspects of foraging behaviour, breeding success and population rates have been studied throughout the Patagonian coast (Boersma and Rebstock 2009; Sala et al. 2012a, 2015), but none have examined the simultaneous effect of foraging behaviour on other breeding parameters (e.g., fledging weight). In order to assess population trends, it is important to consider other breeding parameters since, for example, fledging weight can influence juvenile survival and recruitment to the colony (Cimino et al. 2014). Furthermore, the potential use of these parameters as indicators of population health and of changes in marine resources requires the assessment of their variation over time at the same locality (Wilson et al. 2015). In Tierra del Fuego, the southern limit of the geographic distribution of Magellanic Penguins, several studies have investigated their foraging behaviour (Scioscia et al. 2009, 2010; Raya Rey et al. 2010, 2012; Sala et al. 2012a), with one in particular showing a relationship between parental body size and clutch quality (Scioscia et al. 2010). However, there is little information on the breeding biology and its relationship to other aspects of foraging behaviour. Importantly, differences have been found in this colony in certain parameters of foraging behaviour between sexes and different breeding stages and seasons (Scioscia et al. 2010; Raya Rey et al. 2012). Therefore, the objectives of this study were (1) to describe and analyze the interannual variation of different breeding and trophic (diet and foraging behaviour) parameters of Magellanic Penguins from Martillo Island over three consecutive years, taking into account sex and breeding stage,

and (2) to assess the relationship between breeding and foraging parameters. We tested the hypothesis that lower foraging effort and/or higher feeding activity demonstrated by parents will be associated with higher growth rates, fledging weight and survival of their chicks.

## Materials and methods

The study was conducted at the Magellanic Penguin breeding colony on Martillo Island, Beagle Channel, Tierra del Fuego, Argentina (54°53'S, 67°34'W). At the time, the colony held approximately 4000 breeding pairs (Raya Rey et al. 2014).

Research was conducted during pair establishment (late September to early October) and incubation (late October to early November), and during early (chicks 1–30 days old, late November to December) and late chick-rearing stages (chicks >30 days old, early January) in the 2006–2007, 2007–2008 and 2008–2009 breeding seasons (hereafter referred to as the 2006, 2007 and 2008 years, respectively).

At the beginning of each breeding season, by the time of pair establishment (late September to early October), nests were marked and monitored every 7–15 days until egg laying was completed or the chosen nest was deserted by the pair, and the number of eggs was recorded. During incubation, from about 30 days after the first egg laying was recorded, nests were checked every 1–3 days, and hatching date and number of eggs hatched were recorded. Then, during the chick-rearing stages, nests were checked 2–3 times per week, and the number of chicks and their weight were recorded until fledging occurred.

A total of 267 nests were sampled (84, 65 and 118 during the 2006, 2007 and 2008 years, respectively). Chicks were weighed using a 1-kg or 5-kg Pesola balance (to the nearest 10 or 50 g, respectively), depending on the stage of breeding, and the first chick that hatched was marked with a small cut in the interdigital membrane of the left foot to identify hatching order. Moulting state was also recorded (i.e., quantity and part of the body with down, *see above* for more detail).

Hatching success was calculated as the number of eggs hatched per nest where two eggs were laid (eggs/N), and breeding success was the number of fledged chicks per nest (Ch/N). A chick was considered fledged when it presented an advanced state of moulting (with small patches of down only on its back, nape and/or axils), it was seen alive after 7 January (chicks older than 50 days), it was not found dead later in the season, and it weighed at least 2 kg at the time it was last seen (adapted from Boersma et al. 1990). The age and weight of fledging chicks were recorded the last time the chick was seen in the nest with its advanced moulting.

Breeding penguins were captured by carefully removing them from their burrows and were weighed using a 10-kg Pesola balance (to the nearest 100 g). To determine the sex of individuals, flipper length (from the joint between the humerus bone and radius-ulna to the tip) and foot length (from the bend in the tarsus to the end of the middle toenail) were measured with a ruler to the nearest 1 mm, and bill depth and length were measured using a caliper (to the nearest 0.02 mm) (Gandini et al. 1992). Adults were identified with implanted glass-encapsulated microchips 23 mm long and 3.9 mm in diameter, with individual identification numbers (TIRIS™ Transponders in radio frequency identification and tracking device, 23 mm; Texas Instruments Incorporated, Dallas, TX, USA), following Raya Rey et al. (2007), which were detected by passing an antenna connected to a handheld reader (Ges-reader 2S, Rumitag Argentina Sistemas de Identificación Electrónica) over the penguin's back.

A total of 126 adults of marked nests as detailed above were equipped with time-depth recorders (TDRs) to study their foraging behaviour. The recorders (TDR-MK9; Wildlife Computers Inc., Redmond, WA, USA), which were attached along the midline of each penguin's back according to Wilson et al. (1997), were programmed with MK9Host software (Wildlife Computers Inc.), with a measurement interval of 2 s, following Raya Rey et al. (2012). To study the penguins' diet, reproductive birds were captured on their way to their nests as they returned to the colony after foraging at sea. Individuals sampled for diet were not the same as the instrumented birds. Stomach contents were collected using a water-offloading technique (Wilson 1984). Diet samples were processed following Scioscia et al. (2014).

Diving data were analyzed 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 due to waves, currents, tides, etc.). A dive was deemed to have occurred if the maximum depth was >3 m (after Chappell et al. 1993; Tremblay and Chérel 2000, 2003; Schiavini and Raya Rey 2004). The bottom phase was defined as the time the animal had a vertical speed of ≤0.3 m/s while diving (detection criteria for the existence of a bottom phase was “Normal” in MultiTrace, with an ad hoc fixed “threshold bottom”). For each dive, we registered onset, total duration, pre-dive interval (from which we calculated the post-dive interval), bottom time, maximum depth and the number of wiggles, which are phases of short ascending and descending movement (amplitude > 1 m, i.e., wiggles of lower amplitude were ignored; modified from Bost et al. 2007; Raya Rey et al. 2012) during the bottom phase.

Based on these data, to estimate foraging effort, we calculated the following: foraging trip duration as the sum

of the durations of all dives and intervals between dives (considering that a foraging trip finished when the temperature sensor stopped recording data, as it was programmed to register when in salt water); percentage of time diving as the sum of the durations of all dives divided by foraging trip duration; 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); percentage of bottom time as the sum of bottom time duration for all dives divided by foraging trip duration; and feeding frequency as the number of trips made by adults to the colony as function of the days they were equipped with TDRs (assuming that chicks were fed during each visit to the colony).

Wiggles are a behavior associated with the pursuit or capture of prey, and have been used to assess the number of prey caught per dive (e.g., Simeone and Wilson 2003; Bost et al. 2008; Hanuise et al. 2010; Sala et al. 2012b). Thus we calculated the feeding activity index as the number of wiggles per dive.

For feeding success indicators, we used calculations of the food load brought to the colony (average stomach load mass per average foraging trip duration by sex, breeding stage and season) and prey biomass (average reconstituted biomass of the main prey items consumed per average foraging trip duration, by sex, breeding stage and season). We assumed that the average stomach load mass and average reconstituted biomass for the main prey items, *Sprattus fuegensis*, *Munida gregaria* and *Loligo gahi*, represented the amount of food consumed by the Magellanic Penguin population from Martillo Island (Scioscia et al. 2014). The average reconstituted biomass of the main prey items was calculated as the sum of the biomass of each item consumed by individuals, divided by the number of individuals studied, by sex, breeding stage and season.

## Data analysis

Hatching and breeding success and the fledging age and weight of chicks were compared among the three breeding seasons using one-way ANOVA or Kruskal–Wallis (*H*) tests in cases of a lack of normality and when variances were not homogeneous (Sokal and Rohlf 1995). To assess fledging weight, nests with two chicks were used, including both first and second chicks, since we found no differences between siblings (paired Student *t* test; 2006:  $t = 0.11$ ,  $P = 0.91$ ,  $n = 25$ ; 2007:  $t = -0.59$ ,  $P = 0.56$ ,  $n = 68$ ; 2007:  $t = -1.26$ ,  $P = 0.22$ ,  $n = 22$ ). These statistical analyses were performed using InfoStat software (Di Rienzo et al. 2009).

Growth curves for the chicks were determined using nonlinear mixed effects models (Pinheiro and Bates 2000; Crawley 2007) fitted by maximum likelihood. The growth

model that best described the weight of each chick (*W*) as a function of its age (*x*) was a logistic equation in the form:

$$W = \frac{a}{[1 + b * \exp(-cx)]}$$

where *a* refers to the final weight (asymptote) achieved, *b* indicates a constant which translates the time axis such that time *t* is equal to zero at the inflection point where  $b = 1$  for the logistic equation, and *c* is the constant of growth, which is proportional to the overall growth rate (Ricklefs 1968; Richner 1989). We evaluated differences in the growth constant (*c*) among years and between the first and second chicks using a likelihood ratio test (Pinheiro and Bates 2000; Crawley 2007). We conducted one test with both variables as factors, and we also analyzed the variation in the growth constant between first and second chicks separately for each year. These analyses were performed using the package 'nlme' in the open-source statistical package R version 2.9.1 (R Development Core Team 2009).

A body size index was calculated for breeding adults as the first factor extracted from principal component analysis on measurements of bill length, bill width and flipper length. This first factor explained 74 % of the variance. The residuals for the mass  $\times$  body size index regression ( $\text{mass} = 4.2 + 0.149 * x$ ) were then used as indices of body condition. Only adult mass values recorded during incubation (between ca. 3 and 27 days from incubation) were used to assess body condition. Differences in indices of body condition between years and sexes (as well as their interaction) were assessed using two-way ANOVA (Sokal and Rohlf 1995).

The effect of sex, breeding season and stage (incubation and early chick-rearing stage), as well as their interactions, on the different foraging trip parameters were analyzed using generalized linear mixed effects models (GLMM) fitted by restricted maximum likelihood with a Gaussian distribution of errors and identity link function (Pinheiro and Bates 2000; Crawley 2007). Sex, year and breeding stage were included as fixed factors and bird identity as a random factor to avoid pseudoreplication (Hurlbert 1984). Multiple comparisons (Fisher's least significant difference [LSD]) were performed when these were suitable. When appropriate, data were square root- ( $\sqrt{\quad}$ ) or log-transformed to fulfil the criterion of normality (Kolmogorov–Smirnov; Sokal and Rohlf 1995, MINITAB). Feeding frequency was compared among years by sex for each chick-rearing stage (early and late chick-rearing stages) using Kruskal–Wallis and Mann–Whitney tests. All statistical analyses were performed using InfoStat software (Di Rienzo et al. 2009) linked with the R statistical package. Means are presented together with standard deviations (SD).

Sample sizes differed between analyses due to loss of devices or breeding failure of pairs. Late chick-rearing was

**Table 1** Body measurements of female and male Magellanic Penguins at Martillo Island across all breeding stages and seasons (2006, 2007 and 2008)

Variable	Female		Male		Female vs. male		
	Mean (SD)	<i>n</i>	Mean (SD)	<i>n</i>	<i>t</i> value	DF	<i>P</i>
Weight (kg)	4.09 (0.56)	275	4.76 (0.49)	262	-14.87	533	<0.0001
Bill length (mm)	53.22 (2.16)	254	57.56 (2.24)	244	-21.95	496	<0.0001
Bill width (mm)	21.01 (1.09)	254	24.4 (1.08)	244	-34.99	496	<0.0001
Flipper length (mm)	178.3 (7.6)	234	186.4 (6.5)	222	-12.21	450	<0.0001
Foot length (mm) <sup>a</sup>	29.4 (5.5)	19	30.4 (4.8)	21	-0.63	38	0.5346

DF degrees of freedom

<sup>a</sup> Only for the 2006 year

excluded from GLMM analysis, because during chick-rearing of 2007, some individuals did not return on time, and thus we lost the devices and consequently recorded data on foraging behaviour from only two females, which were not representative for performing further analysis.

## Results

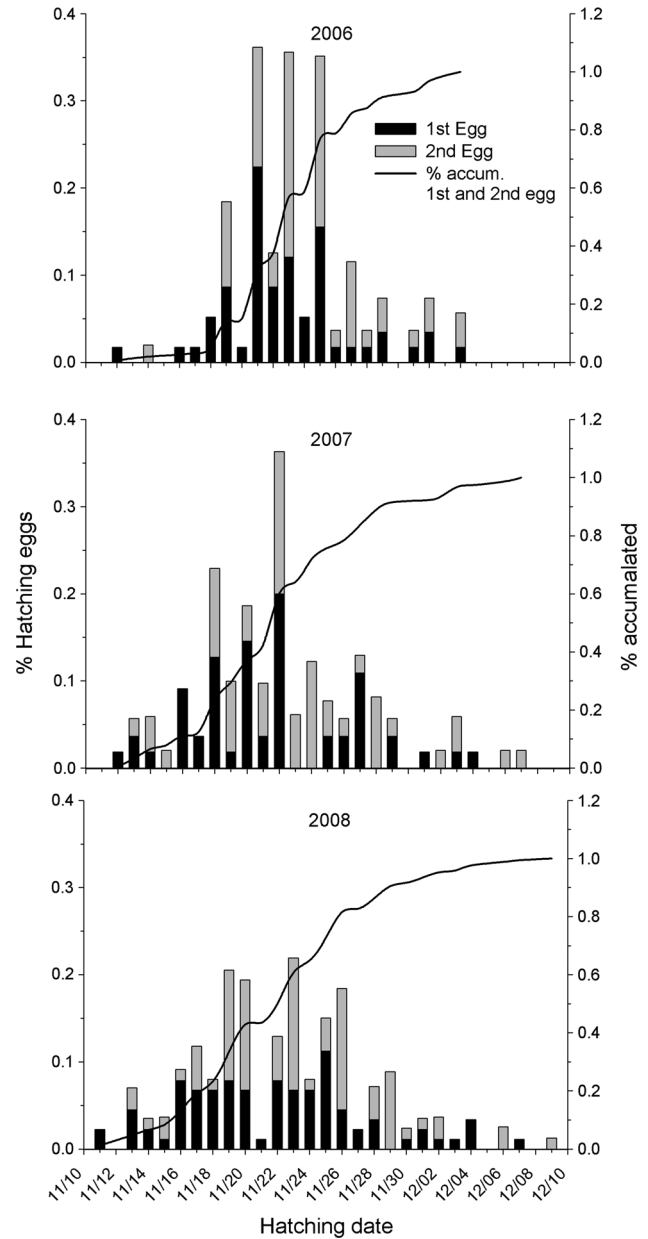
### Adult measurements and body condition

All morphological measurements except foot length differed between sexes (Table 1). Body condition did not differ among years but differed between sexes (2006: 0.07 SD = 0.7; 2007: -0.05 SD = 0.7; 2008: -0.08 SD = 0.82; two-way ANOVA: year:  $F_2 = 2.35$ ,  $P = 0.10$ ; sex:  $F_1 = 189.82$ ,  $P < 0.0001$ ; year  $\times$  sex:  $F_2 = 1.17$ ,  $P = 0.31$ ). Body condition was higher for males (0.56 SD = 0.42) than females (-0.61 SD = 0.41).

### Breeding parameters

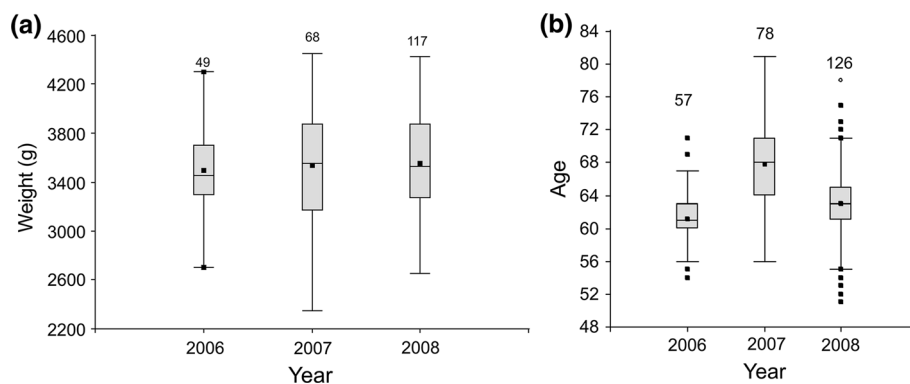
On Martillo Island, incubation began immediately after egg laying, between 7 and 10 October, when 29–36 % of the nests had one egg and 10–12 % of the nests had two eggs. Hatching began on 10–12 November and continued for 22, 25 and 28 days in 2006, 2007 and 2008, respectively. In 2006, the median hatching date was 23 November, and in 2007 and 2008 it was 22 November (Fig. 1).

There was no significant difference among years in hatching success (2006: 1.75 eggs/N, SD = 0.56,  $n = 83$ ; 2007: 1.59 eggs/N, SD = 0.75,  $n = 63$ ; 2008: 1.61 eggs/N, SD = 0.72,  $n = 97$ ; Kruskal–Wallis:  $H_2 = 0.94$ ,  $P = 0.42$ ) or breeding success (2006: 1.52 Ch/N, SD = 0.75,  $n = 46$ ; 2007: 1.28 Ch/N, SD = 0.86,  $n = 65$ ; 2008: 1.43 Ch/N, SD = 0.83,  $n = 99$ ; Kruskal–Wallis:  $H_2 = 2.07$ ,  $P = 0.25$ ). Similarly, no differences were found in fledging weight among years (ANOVA  $F_2 = 0.46$ ,  $P = 0.63$ ; Fig. 2a), and fledging chicks reached an average weight of 3536 g (SD = 387.3, rank 2350–4450 g,  $n = 234$ ). In contrast,



**Fig. 1** Timing of hatching of first and second eggs of Magellanic Penguins at Martillo Island over 3 consecutive years

**Fig. 2** **a** Fledging weight **(a)** and age **(b)** of Magellanic Penguin chicks at Martillo Island over 3 consecutive years. Grey boxes indicate 25th and 75th percentiles, vertical lines 1 SD, black dot mean, horizontal line median, and dots outside the boxes correspond to values outside of the percentiles. Numbers above the bars or boxes indicate sample sizes



**Table 2** Growth constant estimates from the logistic growth model (*c*: mean, SD) for Magellanic Penguin chicks during 2006 (*n* = 64), 2007 (*n* = 98) and 2008 (*n* = 152)

Year	2006		2007	
	<i>c</i>	<i>t</i> value	<i>t</i> value	<i>P</i>
2006	0.101 (0.004)			
2007	0.082 (0.002)	7.75		<0.0001
2008	0.098 (0.003)	-1.28	11.30	<0.0001

Degrees of freedom = 2731

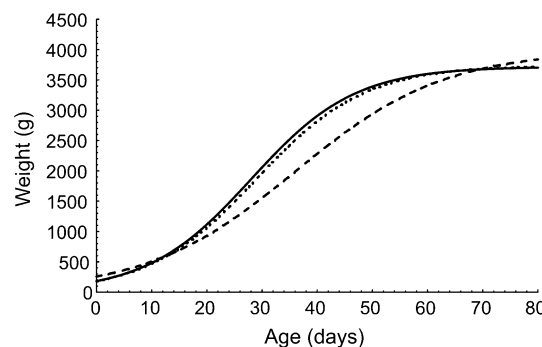
differences were observed among years in fledging age (ANOVA:  $F_2 = 40$ ,  $P < 0.0001$ ; Fig. 2b), with the oldest fledging age recorded in 2007 and the youngest in 2006 (Tukey test,  $P < 0.05$  all comparisons).

The growth constant (*c*) of chicks for the logistic growth model differed among years ( $\chi^2_3 = 118.3$ ,  $P < 0.0001$ ), with the lowest in 2007 (Table 2; Fig. 3). First and second chicks demonstrated a similar growth constant value for all years together ( $\chi^2_1 = 2.4$ ,  $P = 0.12$ ). However, when analyzing differences between (first and second) chicks within each year, we recorded a lower growth constant value for the second chick only during 2007 ( $t_{1028} = -2.23$ ,  $P < 0.05$ ).

### Trophic parameters

All foraging effort parameters and the feeding activity index showed variation between incubation and early chick-rearing stages, as well as among years (Tables 3, 4, except for feeding frequency, see below). During incubation, all foraging effort parameters and the feeding activity index were higher during 2007 and 2008 than during 2006 ( $P < 0.05$  all multiple comparisons; Tables 3, 4; Figs. 4, 5).

During early chick-rearing, the percentages of time diving and bottom time were higher during 2007 and 2008 than 2006, whereas trip duration and VTD were highest in 2007. Moreover, VTD was higher in 2008 than 2006



**Fig. 3** Growth curves for Magellanic Penguin chicks at Martillo Island during 2006 (solid line, logistic equations:  $Weight(W) = 3717.842/[1 + 19.42 * \exp(-0.106x)]$  *n* = 315); 2007 (dashed line,  $W = 3985.028/[1 + 14.418 * \exp(-0.074x)]$  *n* = 1199); 2008 (dotted line,  $W = 3738.013/[1 + 19.315 * \exp(-0.102x)]$ , *n* = 1534) years

( $P < 0.05$  all multiple comparisons; Tables 3, 4; Fig. 4). The feeding frequency was lower in 2007 than in 2006 for both sexes (males: 2006: 0.8, SD = 0.3; 2007: 0.4, SD = 0.3; 2008: 0.6, SD = 0.1;  $H_2 = 10.4$ ,  $P < 0.01$ ; females: 2006: 0.7, SD = 0.3, 2007: 0.6, SD = 0.5, 2008: 0.7, SD = 0.1;  $H_2 = 6.7$ ,  $P < 0.05$ ; multiple comparisons:  $P < 0.05$ ; Fig. 4). During late chick-rearing, there were no differences in feeding frequency between 2006 and 2008 (males: 2006: 0.7, SD = 0.2; 2008: 0.8, SD = 0.1;  $W = 50$ ,  $P = 0.27$ ; females: 2006: 0.7, SD = 0.2; 2008: 0.8, SD = 0.1;  $W = 47$ ,  $P = 0.50$ ).

With regard to the feeding activity index, the number of wiggles per dive was higher in 2007 than in the other years ( $P < 0.05$  all multiple comparisons; Tables 3, 4; Fig. 5).

Males and females showed similar foraging effort and feeding activity indices, except for trip duration and VTD during incubation. Females performed longer foraging trips than males only during incubation, and males had higher VTD than females (Tables 3, 4; Fig. 4).

With regard to feeding success indicators, the food load brought to the colony per day by males and females during early chick-rearing in 2007 was approximately one-third



**Table 3** Foraging effort parameters (except feeding frequency, *see* text) and feeding activity index of Magellanic Penguins at Martillo Island during incubation and early chick-rearing stages in 2006, 2007 and 2008

Stage	Incubation					
	2006		2007		2008	
Year						
Sex	Female ( <i>N</i> = 15)	Male ( <i>N</i> = 12)	Female ( <i>N</i> = 7)	Male ( <i>N</i> = 6)	Female ( <i>N</i> = 5)	Male ( <i>N</i> = 4)
Number of trips	43	28	11 <sup>a</sup>	9 <sup>a</sup>	7	6
Trip duration (days)	1.6 (1.5)	1.4 (1.6)	5.0 (4.4)	2.4 (1.1)	3.7 (1.7)	3.1 (1.7)
Time diving (%)	28.4 (8.4)	25.8 (7.4)	32.2 (9.2)	34.6 (8.4)	34.2 (9.6)	35.5 (10.2)
VTD (m/h)	529.6 (188.2)	550.6 (197.5)	729.9 (397.3)	865.0 (199.4)	812.6 (273.9)	905.1 (327.5)
Bottom time (%)	10.7 (4.7)	9.1 (3.3)	12.3 (3.2)	12.8 (4.6)	13.4 (6.3)	13.2 (4.1)
Wiggles per dive	0.9 (0.2)	1.0 (0.3)	1.4 (0.5)	1.4 (0.3)	1.5 (0.7)	1.4 (0.3)
Stage	Early chick-rearing					
	2006		2007		2008	
Year						
Sex	Female ( <i>N</i> = 16)	Male ( <i>N</i> = 15)	Female ( <i>N</i> = 9)	Male ( <i>N</i> = 9)	Female ( <i>N</i> = 6)	Male ( <i>N</i> = 6)
Number of trips	72	79	36 <sup>b</sup>	31 <sup>c</sup>	42	37
Trip duration (days)	0.5 (0.2)	0.5 (0.2)	2.3 (4.6)	1.2 (0.7)	0.6 (0.4)	0.6 (0.4)
Time diving (%)	31.0 (10.8)	34.3 (10.3)	46.6 (10.2)	41.4 (9.5)	42.0 (14.5)	37.8 (13.5)
VTD (m/h)	655.9 (252.5)	822.5 (274.5)	1224.1 (350.1)	1196.4 (383.7)	905.3 (361.3)	866.6 (356.8)
Bottom time (%)	11.3 (5.2)	12.4 (5.2)	19.0 (5.3)	15.2 (4.5)	17.7 (9.0)	15.2 (7.7)
Wiggles per dive	1.0 (0.3)	1.2 (0.5)	1.4 (0.5)	1.5 (0.5)	1.3 (0.5)	1.0 (0.3)

Means are presented together with standard deviations (SD)

*N* number of birds, *VTD* vertical travel distance

For trip duration: <sup>a</sup> 14, <sup>b</sup> 43, and <sup>c</sup> 36 trips analyzed

**Table 4** GLMM to analyze the factors affecting the foraging effort parameters and feeding activity index (except feeding frequency, *see* text) of Magellanic Penguins at Martillo Island during incubation and early chick-rearing stages in 2006, 2007 and 2008

Foraging effort		Intercept	Year	Stage	Sex	Year × stage	Stage × sex
Trip duration (days)	<i>F</i>	2.2	19.0	110.5	1.0	6.6	4.1
	<i>P</i>	0.1	<0.0001	<0.0001	0.3	<0.005	<0.05
Time diving (%)	<i>F</i>	8475.8	19.3	21.7	0.0	0.7	0.2
	<i>P</i>	<0.0001	<0.0001	<0.0001	1.0	0.5	0.6
VTD (m/h)	<i>F</i>	6758.8	37.2	37.8	4.2	3.9	0.1
	<i>P</i>	<0.0001	<0.0001	<0.0001	<0.05	<0.05	0.8
Bottom time (%)	<i>F</i>	4319.7	17.1	12.8	0.5	0.3	0.2
	<i>P</i>	<0.0001	<0.0001	<0.0005	0.5	0.7	0.7
Feeding activity index							
Wiggles per dive (no.)	<i>F</i>	9.4	17.4	5.1	3.4	6.2	0.0
	<i>P</i>	0.0	<0.0001	<0.05	0.1	<0.005	0.8

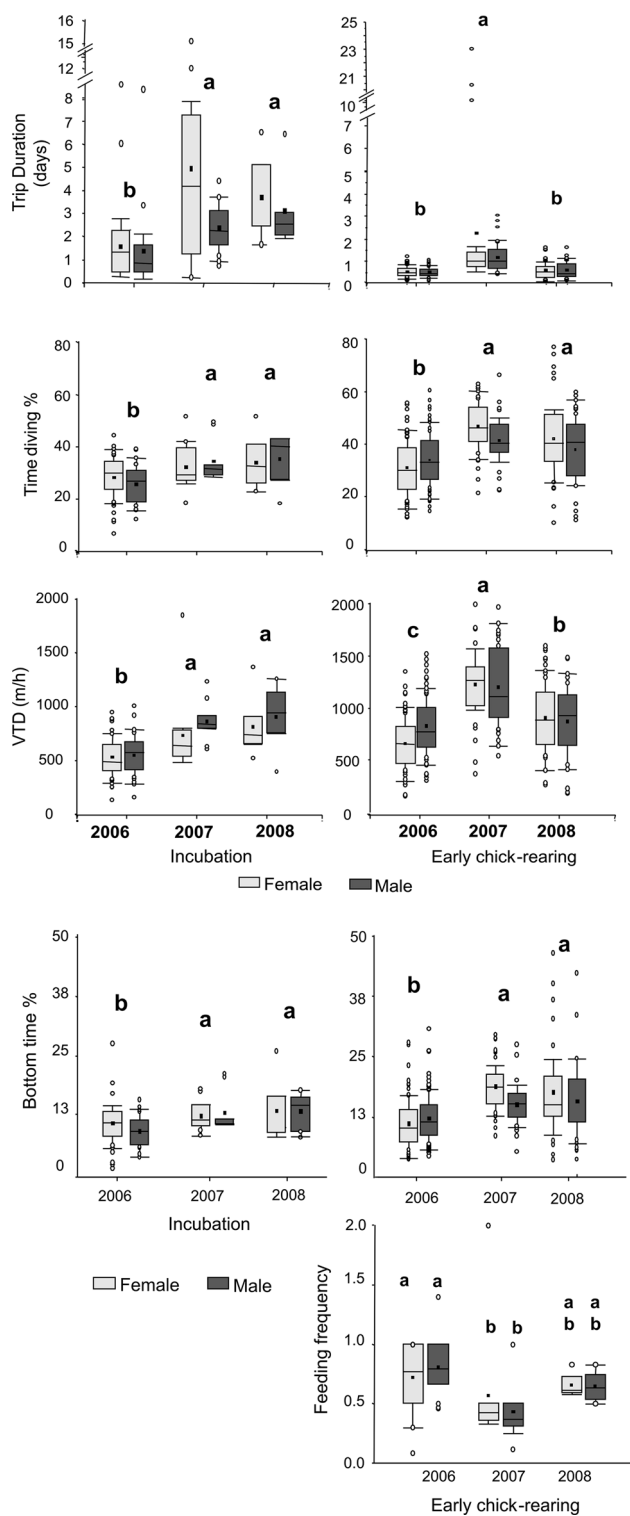
*Note:* The numerator (numDF: 1) and denominator (denDF: 306) for the degrees of freedom are the same for all cases except “year” and “year × stage” (numDF: 2) and “year and sex” (denDF: 87). For trip duration, the denDF is 320 except for year and sex (denDF: 93)

*GLMM* generalized linear mixed model, *VTD* vertical travel distance

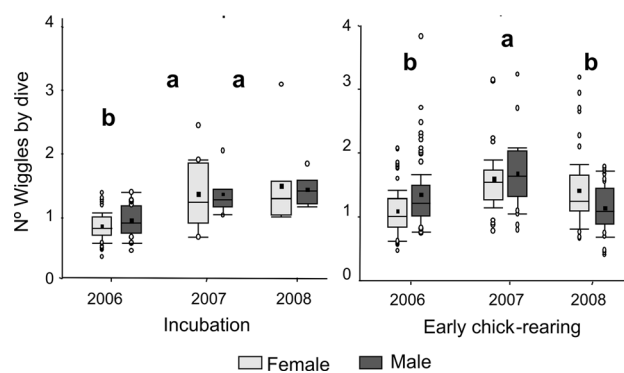
that brought during the same stage in 2006. In turn, during incubation, this was about half in 2007 compared to 2006 (Fig. 6a). During 2008, food load was also low during incubation, but in contrast, during early chick-rearing this quantity was almost twice that in 2007 and slightly lower

than in 2006 (Fig. 6a). During late chick-rearing, females brought more food in 2006 than in 2008, while males brought more food in 2008 than in 2006.

Considering the consumed biomass per day of each prey item (Fig. 6b), the prey that contributed most to the



**Fig. 4** Foraging effort of male and female Magellanic Penguins at Martillo Island during incubation and early chick-rearing stages in 2006, 2007 and 2008. Grey boxes indicate the 25th and 75th percentiles, vertical lines 1 SD, black dot mean, horizontal line median, and dots outside the boxes correspond to values outside of the percentiles. Letters above boxes indicate significant differences ( $P < 0.05$ ) between years



**Fig. 5** Feeding activity index of male and female Magellanic Penguins at Martillo Island during incubation and early chick-rearing stages in 2006, 2007 and 2008. Grey boxes indicate the 25th and 75th percentiles, vertical lines 1 SD, black dot mean, horizontal line median, and dots outside the boxes correspond to values outside of the percentiles. Letters above boxes indicate significant differences ( $P < 0.05$ ) between years

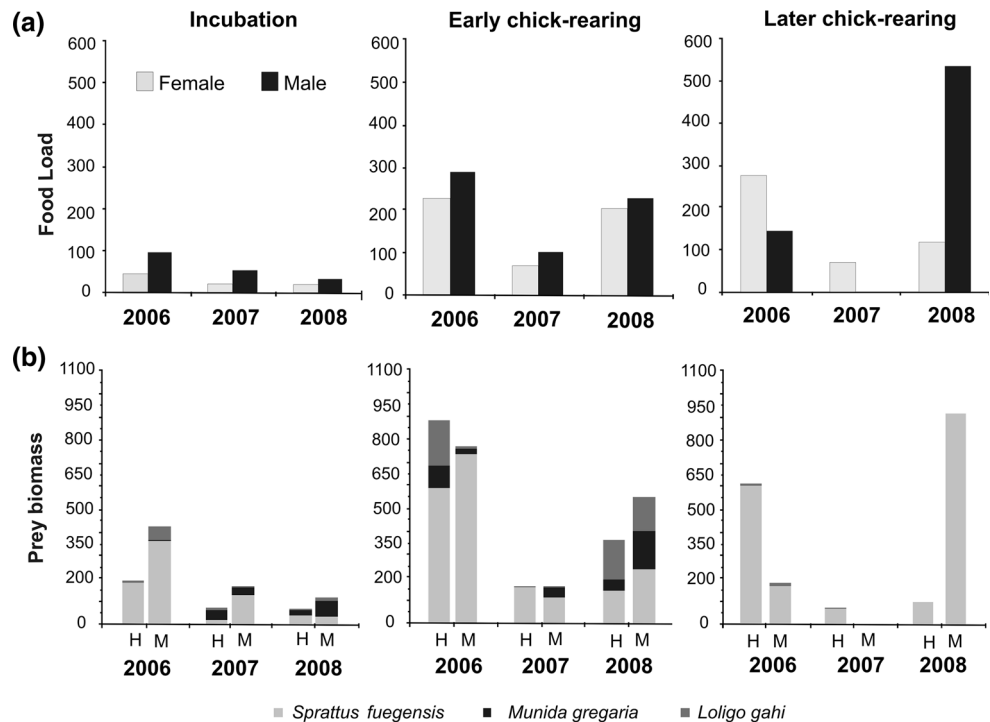
Magellanic Penguin diet was the Fuegian sprat (*Sprattus fuegensis*). The consumed biomass of this prey during incubation decreased throughout the years studied. During early chick-rearing, the consumption of Fuegian sprat was highest in 2006 and lowest in 2007. Unlike the pattern observed for the food load brought to the colony per day, the Fuegian sprat biomass consumed per day in 2008 was almost as low as that in 2007 (Fig. 6b). During early chick-rearing in 2008, increased consumption of squat lobster (*Munida gregaria*) and Patagonian squid (*Loligo gahi*) biomass was observed for both sexes, although mainly for males.

## Discussion

### Breeding biology

In this study, the breeding biology of Magellanic Penguins at the southern limit of their geographical distribution is described for the first time. As in other colonies (Boersma et al. 1990; Frere et al. 1996; Yorio et al. 2001), adults at Martillo Island showed differences in morphological measurements, body weight and body condition between males and females, but not among years. Egg laying began in early October and was relatively synchronous, and most nests contained two-egg clutches within a period of 2 to 3 weeks. Although median laying date cannot be calculated, egg-laying peaks seemed to occur a week later than those at the Cape Virgenes colony (Frere et al. 1996). As Frere et al. (1996) suggested, the delayed laying date may be related to the later start of favourable weather conditions for reproduction at higher latitudes. However, more

**Fig. 6** Feeding success indicators of male and female Magellanic Penguins at Martillo Island during all stages and years studied. **a** Food load brought to the colony (g/day); **b** prey biomass (g/day)



intensive sampling early in the season would be necessary to accurately estimate the median laying date and, thus, to enable a better comparison with other localities and among different years at the colony.

Contrary to studies conducted at colonies in Argentine Patagonia and at the Malvinas (Falkland) Islands (Boersma et al. 1990; Frere et al. 1998; Stokes and Boersma 1998; Clausen and Pütz 2002), hatching and breeding success did not show interannual variation. Variations in breeding parameters among years were mainly reflected in slower chick growth and, consequently, in later fledging.

The breeding success recorded at Martillo Island was higher than that at other colonies, and is comparable only to the breeding success reported for southern Chile (Radl and Culik 1999). At the Punta Tombo colony, the high interannual variation observed in breeding success was related to low food availability (Boersma et al. 1990). As a consequence, the main cause of chick mortality at these colonies was starvation (Boersma et al. 1990; Scolaro 1990), with nest predation, extreme weather conditions, and nest type and location within the colony as other factors affecting breeding success (Scolaro 1990; Frere et al. 1992, 1998; Gandini et al. 1997). At Martillo Island, the absence of terrestrial predators and the building of most nests in deep burrows should increase the likelihood of breeding success. Thus food availability during the breeding season would be a key factor determining breeding success at this colony. Nonetheless, it is important to assess whether there are other factors influencing

breeding performance during the non-breeding season (e.g., individual physiological and body condition at the start of breeding season).

The growth rates and fledging weight of chicks were also considerably higher at Martillo Island than at colonies in Argentine Patagonia and the Malvinas (Falkland) Islands, where fledged chicks did not reach weights above 3 kg (Boersma et al. 1990; Frere et al. 1998; Yorio et al. 2001; Otley et al. 2004). In the present study, most chicks fledged at a weight between 3 and 4 kg, which is comparable to fledging weights of chicks in southern Chile (Radl and Culik 1999).

Slower chick growth has been linked to longer rearing periods (Frere et al. 1998), and differences in growth rates and weight between siblings are considered indicative of poor nutritional conditions (Radl and Culik 1999; Yorio et al. 2001). At Martillo Island, the chick growth rate during 2007 was lower than during 2006 and 2008; rates also differed between siblings, and chicks fledged later than in 2006 and 2008. In addition, the smaller food loads brought to the colony and the decreased Fuegian sprat biomass consumed per day by penguins suggests that food availability during 2007 was lower. During 2008, the chick-rearing period was longer, but the chick growth rate was similar to that of 2006, and there were no differences between siblings, suggesting that levels of food availability differed among the three breeding seasons. These potential differences in prey availability across years would also be supported by the observed variation in foraging parameters

such as foraging trip duration, among other parameters discussed in detail below. Trip duration is particularly important in that respect, because it is related to the distance to the foraging area (Boersma et al. 2009; Sala et al. 2012a). Using the relationship between trip duration and maximum distance from the nest (MDN or foraging range) reported for Magellanic Penguins from Martillo Island (trip duration =  $0.67 \times \text{MDN} + 1.84$ ; Sala et al. 2012a) and the mean trip duration during early chick-rearing (2006: 12 h, 2007: 55.2 h, and 2008: 14.4 h) we estimated that the distance to foraging areas was 15.16, 79.64 and 18.75 km in 2006, 2007 and 2008, respectively. Taken together, and comparing the three seasons studied, 2006 could be considered a “good” year, with high food availability; 2007 a “poor” year, with low food availability; and 2008 an “intermediate” year, but with enough available prey to sustain adults’ feeding demands and allow them to raise their chicks successfully.

### Relationship between trophic and breeding parameters

Changes in food availability near breeding sites can be indirectly inferred by evaluating several aspects of penguin foraging behaviour (e.g., trip duration), together with certain reproductive parameters (e.g., breeding success, growth rate) (Montevecchi 1993; Irvine et al. 2000; Hennicke and Culik 2005). For instance, foraging trip duration, as mentioned earlier, apart from its relationship with the distance to the foraging areas (Boersma et al. 2009; Sala et al. 2012a), is a key factor modulating breeding success and rates of population change (Sala et al. 2012a). In order to determine which of these parameters reflect changes in the marine environment, one must have an understanding of how the foraging behaviour and breeding parameters of Magellanic Penguins are related (Radl and Culik 1999; Boersma and Rebstock 2009; Sala et al. 2012a, 2014, 2015).

During incubation of 2007 and 2008, the higher foraging effort (trip duration, percentage of time diving and VTD) and the lower amount of food load brought to the colony would indicate that food availability near the colony was lower at the beginning of both breeding seasons compared to 2006. However, this lower food availability would have been offset by a higher foraging effort, as hatching and breeding success did not vary between years. This may be related to a relatively constant body condition in parents throughout the studied years, and thus no significant change in their success, contrary to observations recorded in Magellanic Penguins at the Punta Tombo colony by Yorio and Boersma (1994a, b). However, the small differences found between hatching and breeding success suggest that the greatest reproductive failure occurs during the incubation stage.

During early chick-rearing of 2007, penguins demonstrated a greater foraging effort in terms of trip duration, VTD, and percentages of time diving and bottom time. The chick growth rate was also slower during this year, and chicks fledged at an older age, which could be related to the lower feeding frequency and smaller amount of food delivered to chicks, as previously described (food load brought to colony). This is similar to data reported for Adelie Penguins (*Pygoscelis adeliae*, Takahashi et al. 2003), Humboldt Penguins (*Spheniscus humboldti*, Hennicke and Culik 2005) and Magellanic Penguins at Punta Tombo and Southern Chile (Boersma et al. 1990; Radl and Culik 1999). These studies as well as our own suggest that the longer foraging trips—likely as a result of the low food availability near the colony—reduce the feeding frequency, which in turn slows the rate of chick growth. However, the lower feeding frequency at Martillo Island was not reflected in reduced breeding success as was reported for other colonies of Magellanic and Rockhopper Penguins (*Eudyptes chrysocome*) (Boersma et al. 1990; Walker and Boersma 2003; Otley et al. 2004; Raya Rey et al. 2007).

We suggest that food availability might have improved during the 2008 season, because food load brought to the colony was higher than in 2007, and penguins also showed lower foraging effort and higher feeding frequency during early chick-rearing. Boersma et al. (1990) found that an improvement in the food supply late in the season did not completely compensate for poor food conditions early in the season, given that body size (i.e., bill size) of fledging chicks was smaller despite reaching a weight similar to or greater than that observed in good years (Boersma et al. 1990). At both Martillo Island and the Punta Tombo colony, chicks’ weight at fledging was similar between years, although we did not take morphometric measures of those chicks. However, the increase in adverse conditions early in the season was reflected in older fledging age. Furthermore, during early chick-rearing of 2008, even though food load brought to the colony increased, the proportion of higher-lipid-content prey such as sprat was reduced, and less digestible and energy-rich prey such as squat lobsters and squids became a more common food source (Scioscia et al. 2014), likely resulting in late fledging age of chicks during this season.

### Parameter selection

Feeding activity can be inferred by the number of wiggles in the diving depth profile, an index widely used in studies of penguin foraging behaviour (Wilson 2003; Simeone and Wilson 2003; Takahashi et al. 2004; Bost et al. 2007; Hanuise et al. 2010, Wilson et al. 2010, 2011; Sala et al. 2012b). In our study, the number of wiggles per dive was the highest in the year that individuals had lower food loads

(2007). One possible explanation is that most or all of the higher food intake was needed to satisfy the adults' energy demands. Another reason might be the energy content and wet mass of the type of prey consumed (Sala et al. 2012b): if the quality of the consumed prey is lower, in order for penguins to obtain the required energy, they must eat more individual prey items, thus increasing their feeding activity index. One study found that different prey type consumed by Magellanic Penguins from four colonies in Patagonia, Argentina, were associated with several foraging parameters used as estimators of prey consumption (e.g., wiggles per dive, Sala et al. 2012b). Even prey size can be reflected in diving parameters (Elliot et al. 2008, 2009; Sala et al. 2012b). Chinstrap Penguins (*Pygoscelis antarctica*), for example, demonstrate a higher number of wiggles in their dive profiles (Takahashi et al. 2004) than do Magellanic Penguins, and feed mainly on krill (*Euphausia superba*), which is considerably smaller than the Fuegian sprat consumed by Magellanic Penguins. Researchers have estimated that Magellanic Penguins capture one individual prey per wiggle (Simeone and Wilson 2003). The higher number of wiggles reported in our study may be related to increased consumption of other prey such as squat lobster or juvenile nototheniids, and lower intake of Fuegian sprat, which has been reported at Martillo Island during the past 2 years (Scioscia 2011; Scioscia et al. 2014). However, since there is no direct analysis of a relationship between the size and type of prey and the number of wiggles in Magellanic Penguin dive profiles, inferences of a direct relationship between feeding activity indices and breeding parameters should be made with caution (but cf. Sala et al. 2012b). Other diving parameters that have been used for foraging effort, such as bottom time (Bost et al. 2008) and percentage of time diving, showed no obvious relationship with chick growth rate in our study, similar to results reported for Adélie penguins (Takahashi et al. 2003).

In conclusion, Magellanic Penguins from Martillo Island showed great plasticity in foraging behaviour, comparable to that observed in other colonies along Argentina's Patagonian coast (Sala et al. 2014), and evidenced by changes in prey type or increased foraging effort and feeding activity. Greater foraging effort was observed in particular when the availability of their main prey, Fuegian sprat, appeared to decrease (measured indirectly by prey biomass consumed by adults), with penguins exploring waters in both horizontal and vertical dimensions and increasing their feeding activity. These patterns in turn negatively affected the growth rates and fledging age of chicks. However, at least during the 3 years of the study, the penguins managed to compensate for the apparent decrease in Fuegian sprat, as their breeding success remained constant. Thus, our proposed hypothesis was partially corroborated, depending on the trophic and

breeding parameters evaluated and the environmental conditions at the colony. The trophic parameters related to slower chick growth rates included higher VTD, longer foraging trip duration and lower feeding frequency. In contrast, and counter to our expectations, in years in which feeding activity of Martillo Island penguins increased, their reproductive performance did not increase. As mentioned earlier, this higher feeding activity may have been due to a change in the type or size of prey consumed by penguins, or because much of the food consumed was used by adults to restore or maintain their own body condition, as the food load brought to the colony was not higher that year (2007).

Food availability is clearly an important factor affecting the Magellanic Penguin population at Martillo Island. At Beagle Channel, the major prey item of the penguins is Fuegian sprat, as reflected in its contribution to their diet in biomass and its importance as a source of energy (Scioscia et al. 2014). With this in mind, it would be interesting to assess whether changes in the abundance and distribution of Fuegian sprat in the oceanic environment surrounding the colony is a key factor in modulating population trends at this breeding site.

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