

Foraging distance affects reproductive success in Magellanic penguins

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ABSTRACT: Foraging distance affects reproductive success and other demographic parameters in seabirds and pinnipeds. We tracked breeding Magellanic penguins *Spheniscus magellanicus* at Punta Tombo, Argentina using satellite transmitters from 1996 to 2006 (n = 148 males, 57 females) to investigate the variability in foraging distance and its effects on reproductive success. The time a penguin was away from its nest predicted the distance it swam during all stages of the breeding season ($p < 0.005$); this relationship was linear during incubation and nonlinear during chick rearing. During incubation, penguins went 1.0 km farther from the colony for every additional hour they were away from the nest, and the distance penguins traveled predicted the mean colony reproductive success. When chicks were >30 d old, the probability of fledging 2 chicks was highest when penguins went less than 70 km from their nests. Penguins that went between 70 and 180 km from their nests were most likely to raise one chick, and the probability of losing both chicks increased with trip distance. Females and males made trips of similar distance. Foraging-trip distance varied within breeding season ($p < 0.005$). Penguins went farthest during incubation (411 ± 11.8 km), and stayed closest (61 ± 3.9 km) when chicks were <30 d old, requiring parents to guard them. When chicks were older, adults traveled 111 ± 5.0 km. Mean foraging-trip distance varied among years ($p < 0.005$) by factors of 1.5 to 1.8, and trips by an individual penguin varied by a factor of 22.

KEY WORDS: *Spheniscus magellanicus* · Magellanic penguin · Foraging-trip distance · Variability · Reproductive success · Satellite tracking · Argos · Argentina

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INTRODUCTION

Oceanographic conditions vary from year to year, affecting the foraging locations and breeding success of marine central-place foragers, such as seabirds and pinnipeds, that feed at sea but breed on land (Boyd et al. 1994, Kitaysky et al. 2000, Sydeman et al. 2001, Davoren & Montevecchi 2003). Foraging locations at sea, particularly distance to food, influence offspring feeding frequency (Pinaud et al. 2005), reproductive success (Inchausti et al. 2003), and adult energy balance (Shaffer et al. 2003). How central-place foragers use the ocean affects not only their breeding parameters, but also their conservation, because of increasing conflicts between human activities and wildlife (Boersma 2008). Our knowledge of where seabirds and pinnipeds forage has increased during the last decade because of remote-tracking devices (e.g. Burger &

Shaffer 2008). In many cases, we know mean foraging-trip distances, but little about how distances and foraging areas vary. Quantifying the variability in trip distance among years is necessary for a variety of reasons including understanding species' energy needs, reproductive success, recruitment, population dynamics, and determining ocean zoning and locations of protected areas for management and conservation.

For central-place foragers, distance to foraging areas is often related to trip duration and the frequency of offspring feeding (Shaffer et al. 2003, Boersma et al. 2007). Many seabirds and pinnipeds feed at particular oceanographic features (Hunt et al. 1999, Boersma et al. in press), and flying or swimming from breeding sites to the foraging areas make up a large percentage of the trip duration. Boersma et al. (in press) found a nonlinear relationship between trip distance and duration, with penguins spending more time in foraging

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areas farther from the colony. If foraging trips take longer, offspring will be fed less frequently, resulting in slower growth rates and lower weights at fledging or weaning (Kitaysky et al. 2000, Davoren & Montevecchi 2003). Longer travel distances also require increased energy expenditure that may affect adult body condition (Arnould et al. 1996) and the balance between food assimilated by the adult and that delivered to offspring (Weimerskirch et al. 1994, Ropert-Coudert et al. 2004). In the case of seabirds that share incubation and provisioning duties, long trip distances and durations may also affect the fasting mate's condition, eventually causing abandonment of the nest (Yorio & Boersma 1994, Numata et al. 2000, Tveraa & Christensen 2002).

In some seabird species, males and females have different foraging strategies during the breeding season (Clarke et al. 1998, González-Solís et al. 2008). This is often linked to sexual size dimorphism, but also occurs in species with males and females of similar size (Lewis et al. 2002). Male Magellanic penguins are slightly larger than females and are at sea a few weeks earlier during incubation (Boersma et al. 1990). Either of these differences may cause males and females to adopt different foraging strategies.

Trip distance often varies across the breeding season, reflecting different constraints (Weimerskirch et al. 1993, Guinet et al. 1997, Beauplet et al. 2004, Lescroël & Bost 2005, Phalan et al. 2007). Older chicks have greater food needs and greater storage capacity than younger chicks (Walker & Boersma 2003) which may both require and allow adults to go farther to forage when chicks are older. Seabirds can go farthest during incubation when there are no chicks to feed; they need to stay closest to the colony when chicks are small, have limited storage capacity (small stomachs and limited energy reserves), and require the attendance of a parent for protection and thermoregulation. Adults may go intermediate distances when chicks are larger and have increased storage capacity and energy needs. Additionally, prey distribution may change during the breeding season, resulting in changes in foraging-trip distance (Humphreys et al. 2006).

Interannual changes in prey distribution or availability may also cause foraging-trip distance to vary (Boyd et al. 1994, Sydeman et al. 2001, Inchausti et al. 2003). Longer foraging trips in years of low prey availability may cause increased investment in reproduction by adults (Boyd et al. 1994) and decreases in offspring growth rates (Davoren & Montevecchi 2003, Pinaud et al. 2005) and reproductive success (Inchausti et al. 2003). Climate fluctuations may affect species differently, depending on prey and foraging strategies (Kitaysky et al. 2000).

We present foraging-trip data from 11 years of satellite tracking the at-sea locations of over 200 breeding

Magellanic penguins *Spheniscus magellanicus* at Punta Tombo, Argentina. Using our large dataset we quantified the relationships between trip distance and duration, and between trip distance and reproductive success. We also tested whether foraging-trip distance differed between males and females, and quantified variability in trip distances within and among breeding seasons.

MATERIALS AND METHODS

Magellanic penguins breed at mainland and island colonies in Argentina, Chile and the Falkland (Malvinas) Islands (Williams 1995). They eat primarily small pelagic fish, hake *Merluccius hubbsi*, and squid (Williams 1995) that are often associated with oceanographic frontal systems (Hansen et al. 2001, Acha et al. 2004). We divided breeding into 3 stages: (1) incubation, when mates alternate long incubation periods with long-duration foraging trips, generally mid-October to late November; (2) early-chick rearing, when mates alternate every couple of days between attending the chicks and foraging, late November to late December; and (3) late-chick rearing, when both adults forage simultaneously and leave the chicks unattended, from late December until fledging in January or February (Boersma et al. 1990). During incubation, males generally take their longest foraging trip after egg laying, and females after the males return to relieve them. Males are typically at sea during October and females during November, with some overlap in late October and early November. (Boersma et al. 1990). We checked nests daily until both chicks hatched, and used chick age (<30 d or >30 d) to separate early-chick and late-chick period tracks. Year refers to the calendar year of the beginning of the breeding season, e.g. 2006 is the 2006–2007 season.

Satellite tracking. We tracked Magellanic penguins at Punta Tombo, Argentina (44° 2.7' S, 65° 13.4' W) using satellite transmitters and the Argos system (Argos 2006). From the late-chick stage of 1996 through the 2006 season, we attached transmitters to 148 adult males and 57 adult females in a total of 268 deployments (Table 1). We tracked 49 penguins more than once (43 males and 6 females) but in different years. For 52 penguins transmitters did not start until the penguin was far at sea, or failed prematurely, resulting in incomplete trips that we did not use. We attached the devices to feathers with fast-setting epoxy or tape (Wilson & Wilson 1989) and epoxy. We reduced drag on the devices by centering them low (6.6 ± 1.5 cm above the uropygial gland, $n = 219$) on the penguin's back (Bannasch et al. 1994) and positioning feathers over the leading edge.

Table 1. *Spheniscus magellanicus*. Satellite transmitters deployed (n = 268) on Magellanic penguins at Punta Tombo from the 1996 breeding season through the 2006 season. Numbers in parentheses in 'No. males' and 'No. females' columns represent the deployments (n = 216) with nearly complete trips, which were used to calculate trip distances. Inc = incubation; EC = early chick; LC = late chick. See 'Materials and methods' for definitions. Deployment dates are dates transmitters were attached; transmitters were left on for 30 to 90 d. Mean weight is at time of deployment

Year	Stage	Deployment dates	No. males	Mean weight ± SE (kg)	No. females	Mean weight ± SE (kg)	Transmitter type(s)
1996	LC	15 Dec 1996–18 Jan 1997	5 (3)	4.44 ± 0.207	0		ST-10
1997	Inc	13–19 Oct 1997	3 (2)	4.11 ± 0.176	3 (3)	3.76 ± 0.185	ST-10
	LC	23–31 Dec 1997	5 (5)	4.89 ± 0.231	0		ST-10
1998	Inc	5–18 Oct 1998	4 (3)	4.30 ± 0.120	4 (2)	3.36 ± 0.063	ST-10
	EC	8–17 Nov 1998	6 (6)	4.44 ± 0.114	6 (6)	4.41 ± 0.158	ST-10
1999	LC	26 Dec 1998–12 Jan 1999	6 (5)	4.24 ± 0.159	5 (5)	3.44 ± 0.070	ST-10
	Inc	9–22 Oct 1999	5 (4)	4.04 ± 0.165	5 (1)	3.13 ± 0.078	ST-10
	EC	22–27 Nov 1999	5 (3)	4.17 ± 0.199	5 (3)	3.64 ± 0.173	ST-10
2000	LC	5–18 Jan 2000	4 (3)	4.33 ± 0.198	2 (2)	3.80 ± 0.400	ST-10
	Inc	7–28 Oct 2000	17 (13)	4.00 ± 0.110	6 (0)	3.63 ± 0.162	ST-10 & Kiwisat
	EC	27 Nov–9 Dec 2000	6 (4)	3.88 ± 0.154	6 (5)	3.47 ± 0.119	ST-10
2001	LC	5–13 Jan 2001	7 (6)	4.44 ± 0.118	5 (4)	3.50 ± 0.085	ST-10
	Inc	8–19 Oct 2001	6 (5)	4.08 ± 0.096	6 (2)	3.27 ± 0.129	ST-10
	EC	13–19 Nov 2001	4 (4)	4.43 ± 0.138	4 (4)	4.18 ± 0.165	ST-10
2002	LC	26–31 Dec 2001	8 (8)	4.47 ± 0.182	6 (6)	3.49 ± 0.260	ST-10
	Inc	15–25 Oct 2002	12 (4)	4.07 ± 0.130	0		ST-10
2003	LC	26 Dec 2002–2 Jan 2003	12 (12)	4.33 ± 0.096	0		ST-10
	Inc	9–15 Oct 2003	10 (9)	4.26 ± 0.070	0		ST-10
2004	LC	21 Dec 2003–1 Jan 2004	7 (7)	4.44 ± 0.189	0		ST-20 & ST-10
	Inc	3–10 Oct 2004	12 (9)	4.24 ± 0.069	0		ST-20 & ST-10
2005	LC	27 Dec 2004–8 Jan 2005	13 (12)	4.38 ± 0.059	0		ST-20 & ST-10
	Inc	8–13 Oct 2005	12 (11)	4.24 ± 0.091	0		ST-20
2006	LC	26 Dec 2005–7 Jan 2006	12 (12)	4.53 ± 0.107	0		ST-20
	Inc	9–20 Oct 2006	12 (12)	4.13 ± 0.071	0		ST-20
2006	LC	19–30 Dec 2006	12 (11)	4.74 ± 0.127	0		ST-20
	Totals		205 (173)	4.30 ± 0.028	63 (43)	3.61 ± 0.058	

We used 3 types of transmitters (Table 1): ST-10s and ST-20s transmitted every 45 s every day, Kiwisat transmitters were programmed to transmit every 60 s for 12 h out of each 48 h (12 h on:36 h off). ST-20 and Kiwisat transmitters were higher power (0.5 W) than ST-10s (0.25 W) and provided more frequent and higher-quality locations (authors' unpubl. data).

Track processing. We used only Argos locations calculated from 4 or more messages received during each satellite pass (location class 0-3). Argos estimates 1 SD of errors in latitude and longitude of Class 1 to 3 locations to be within 1000 m, while Class 0 locations have no estimate of error (Argos 2006). We applied 4 filters to the data (authors unpubl.). The first filter removed locations closer together than 45 min, to make the samples more evenly spaced. The second and third filters were the speed filters of Austin et al. (2003) and McConnell et al. (1992). The 4th filter removed locations that were far off the penguin's track, but were not rejected by the speed filters because they were far apart in time (authors' unpubl.).

We calculated trip distance as the straight-line distance from Punta Tombo to the farthest point of each trip (Boersma et al. in press). This is less than the total distance traveled by the penguins, because they often

make looping trips with meanders. During incubation, we used the longest trip recorded that began after the first egg was laid for each bird. In 24 cases, we used incomplete trips (those in which transmission began or ended at sea but close to the colony relative to the trip distance; $13.2 \pm 12.6\%$ mean \pm SD) for distance calculations but not for estimating trip duration. During the chick-rearing periods, we generally recorded more than one trip per penguin. We defined a trip as at least 3 consecutive points that were at least 5 km from Punta Tombo with at least one point preceding and following within 5 km of Punta Tombo (Boersma et al. in press). We used nest attendance data to determine when penguins returned to the colony, and if returns were not recorded in the Argos data, we used the trips to calculate distance but not duration.

For each stage of the breeding season, we calculated the maximum and mean trip distances for each penguin in each year. No penguin was tracked in more than one period in the same year; hence we used one value per individual except where the same penguin was tracked in multiple years (n = 32). For incubation, maximum and mean trip distances were the same since we used one trip per penguin (per year).

Foraging trip distance and duration. We previously reported a positive relationship between trip distance and duration for female penguins at Punta Tombo (Boersma et al. 2007). Here we refined the relationships using both males and females. The trip distances differed from those used in the earlier paper (Boersma et al. 2007), because we used only Argos locations of Class 1 to 3 in the earlier regressions; in the present analysis we also included Class 0 and filtered all 4 location classes. Retention of Class-0 locations resulted in more trips and sometimes longer trips in the current analysis.

Graphs of trip distance as a function of duration by individual penguins during the chick-rearing stages indicated that slopes and intercepts might differ by individual. We fitted mixed-effects models (random-intercept models, allowing the intercept to vary among penguins as in the previous study) and mixed-effects random-coefficient models (allowing both intercept and slope to vary among penguins) (Rabe-Hesketh & Skrondal 2005). We included duration squared to test for nonlinearity, since some curves appeared to flatten out for longer trips. We included year, sex, and the interaction between sex and duration as factors.

For incubation, we had a maximum of 3 trips (in different years) for any penguin. We calculated robust SEs, with degrees of freedom equal to the number of individual penguins, to account for the lack of independence when the same bird was tracked in more than one year (Long & Freese 2006). For incubation, we only used the higher-power ST-20 transmitters, deployed in 2004–2006 on males only, because we had few complete incubation trips from ST-10 transmitters and we could not estimate trip duration for the intermittent Kiwisat transmitters. For chick-rearing stages, we ran regressions for the years 1998 to 2001, when we tracked males and females, and all years for the late-chick stage (1996 to 2006).

Foraging trip distance and reproductive success. We measured reproductive success yearly in 2 areas within the colony separated by about 320 m. We checked all nests (mean \pm SD = 173.5 \pm 36.4 nests with eggs per year) within the 2 study areas every 1 to 10 d from prior to egg laying until fledging. We counted chicks as fledged if they were last seen after 10 January, weighed \geq 1800 g, and had not lost weight during the last few measurements (Boersma et al. 1990). Reproductive success was calculated as the number of chicks fledged per nest with eggs, with a maximum of 2. We tested the effect of mean distance from the colony that penguins swam during incubation and the late-chick stage on mean reproductive success using multiple linear regression. We did not test for an effect when chicks were <30 d old because we only had 4 years of data. We included precipitation as a covariate because heavy rain can cause nests to flood or collapse, killing embryos and

small chicks (Boersma et al. 2004, Boersma 2008). We measured rainfall daily with an on-site rain gauge, except in 2005, when we used data collected at the La Regina Estancia, about 25 km from Punta Tombo. We used total rainfall between 16 October and 15 December, when eggs and chicks are most vulnerable to weather. The Estancia data for 2005 covered 1 October to 31 December and although this was a longer period, the total rainfall in 2005 was lower than what affected reproductive success in the other years (Boersma 2008). We removed the 3 years with heaviest rainfall from 16 October to 15 December (>50 mm) and regressed reproductive success on mean trip distance during incubation and late-chick stages.

We also compared the number of chicks fledged by each penguin that carried a transmitter during each stage of the breeding season with the mean trip distance for that penguin using a multinomial logistic regression. We used only penguins that still had 2 chicks when we attached the transmitters (28 of 33 penguins when chicks were small and 79 of 100 penguins when chicks were older). All years were combined and robust SEs were calculated to account for the lack of independence in trips by the same penguin. Following the regression, we modeled the predicted probability of each outcome for each mean distance (Long & Freese 2006).

We used an index based on the first principal component of bill, wing, and foot measurements (Yorio & Boersma 1994, Hood et al. 1998) to evaluate the body condition of 3 females that made unusually long trips during late-chick stages of 1998 and 2001. Because of small sample sizes in 1998 and 2001, we used all females weighed and measured between 16 December and 15 January 1983 to 2006 to develop the index ($n = 473$). We also compared an egg-volume index (length \times width²) for 2 of the females to the means for 1998 ($n = 538$ 1st eggs, 508 2nd eggs), as lower clutch volumes reflect poor female body condition at egg laying (Moreno et al. 2002). Egg size has little influence on nesting success but it does reflect parental quality in Magellanic penguins (Reid & Boersma 1990).

Variation between sexes, within and among seasons. We used multiple regression to test for effects of stage of the breeding season, year, and sex on trip distances. We included year as a categorical factor rather than a continuous variable because we expected inter-annual differences in prey availability but not necessarily a linear trend. In addition to regressions for 1996 to 2006, we ran separate tests for 1997 to 2001, the only years in which we tracked females (Table 1). We also ran regressions for 1998 to 2001, the only years in which we tracked during the early-chick stage (both sexes). We also included start date of incubation trip instead of sex in one set of regressions because date may be more important than sex, and variability in trip

timing within males and females may mask the effects of date.

Regression models were run in Stata 9.2 (StataCorp LP). Examination of the residuals did not indicate problems with any of the regression fits. Means are presented ± 1 SE.

RESULTS

Foraging-trip distance and duration

Trip distance was positively correlated with trip duration, although the details of the relationships varied over the breeding season (Table 2). Trip distance depended linearly on duration during incubation (26 trips by 23 penguins, males only, $F_{3,22} = 23.65$, $p < 0.005$, $R^2 = 0.74$; coefficient for duration: $t = 8.01$, $p < 0.005$) but not on year ($p = 0.41$ and 0.75). Duration squared was not significant ($p = 0.84$), indicating the relationship was linear. Penguins went 1.0 ± 0.13 km farther from the colony for every hour they were away from the nest.

Distance depended nonlinearly on duration when penguins had small chicks (152 trips by 33 penguins): both duration ($Z = 16.0$, $p < 0.005$) and duration squared ($Z = -7.19$, $p < 0.005$) were significant (Table 2). The relationship between distance and duration also varied significantly with year ($p < 0.005$): slopes were steeper in 2000 and 2001 when penguins went farther from the colony than in 1998 and 1999 when they stayed closer to their nests. Penguins generally swam farther in 2000 and 2001 than in the first 2 years, but trip durations were not proportionately longer. Sex ($Z = -1.27$, $p = 0.20$) and the interaction between sex and duration ($Z = 1.28$, $p = 0.20$) were not significant. Trips by different penguins had similar slopes: the random-coefficient model was not significantly better than the random-intercept model (likelihood-ratio test: $LR \chi^2(2) = 1.82$, $p = 0.4$). Moreover, correcting for the conservative nature of the likelihood-ratio test (Rabe-Hesketh & Skrondal 2005) gave similar results. Results of a linear

Table 2. *Spheniscus magellanicus*. Relationship between foraging-trip distance and duration during 3 stages of the breeding season. Relationships were nonlinear if duration squared was included in the best model. Only males were used in the regression for incubation. Slopes by individual penguin could not be tested for incubation because we used only 1 trip per penguin (per year). N/A: not applicable

	Incubation	Early chick	Late chick
Linear	Yes	No	No
Years differ	No	Yes	No
Sexes differ	N/A	No	No
Slopes differ	N/A	No	Yes

regression run without duration squared were similar to those of Boersma et al. (2007), after excluding a female that went almost 300 km after her chicks died: in both analyses the slope was 0.87 ± 0.07 .

The non-linear relationship between distance and duration of penguin foraging trips was also apparent when penguins had large chicks (191 trips by 37 penguins): duration ($Z = 15.84$, $p < 0.005$) and duration squared ($Z = -7.36$, $p < 0.005$) were significant (Table 2). The relationship between trip distance and duration did not depend on year ($p = 0.15$ to 0.70), sex ($p = 0.93$), or the interaction between sex and duration ($p = 0.69$). However, individual penguins had different slopes ($LR \chi^2(2) = 61.33$, $p < 0.005$). Results from a linear regression were similar to those reported in Boersma et al. (2007) for females: in both cases, penguins went 0.87 ± 0.04 km farther from the colony for each hour they were gone.

Foraging-trip distance and reproductive success

As foraging-trip distance increased, mean reproductive success of the colony decreased. Rainfall between 16 October and 15 December negatively affected reproductive success ($F_{1,8} = 33.1$, $p = 0.0004$, adjusted $R^2 = 0.78$, RMSE = 0.136) (Fig. 1). Adding mean trip distance during incubation as a covariate improved the fit ($F_{2,7} = 22.96$, $p = 0.0008$, adjusted $R^2 = 0.83$, RMSE = 0.120). However, adding mean trip distance during late chick did not improve the fit (rain only: adjusted $R^2 = 0.77$, RMSE = 0.147; rain + trip distance: adjusted $R^2 = 0.75$, RMSE = 0.152). With the 3 years of heaviest rainfall removed, reproductive success depended on

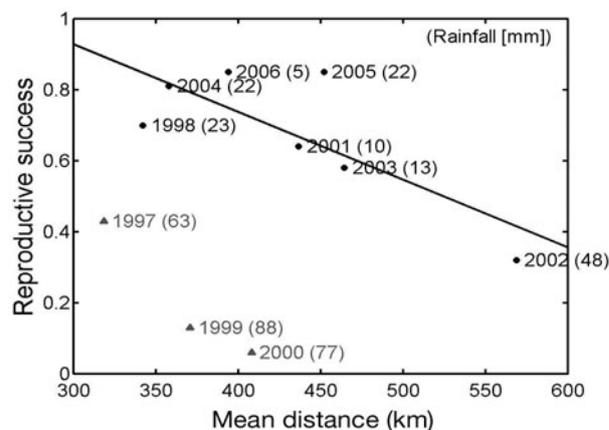


Fig. 1. *Spheniscus magellanicus*. Mean reproductive success (number of chicks fledged per nest with eggs) in 2 areas of the colony as a function of the mean distance penguins traveled from the colony during incubation. Points are labeled with year and total rainfall (parentheses, in mm) between 16 October and 15 December. (●) years with < 50 mm rain; (▲) > 50 mm rain; (Line) least-squares regression excluding 3 years with > 50 mm rain (reproductive success = $1.5 - 0.002 \times$ mean distance; adjusted $R^2 = 0.51$)

trip distance during incubation ($F_{1,5} = 7.28$, $p = 0.04$, adjusted $R^2 = 0.51$, $n = 7$) (Fig. 1), but not during late chick ($F_{1,6} < 0.1$, $p = 0.96$, $n = 8$).

Foraging-trip distance also predicted individuals' reproductive success (Fig. 2). The multinomial logistic regression of number of chicks fledged on mean trip distance for transmitter-equipped birds with chicks older than 30 d was significant (Wald $\chi^2 = 5.96$, $p = 0.015$). The probability of fledging 2 chicks was high (>0.5) for penguins that made the shortest trips (<70 km) and decreased with increasing distance to <0.01 (Fig. 2). The probability of fledging zero chicks was low (~ 0.01) for birds making very short trips but increased with increasing distance to ~ 0.8 . The probability of fledging one chick peaked at intermediate foraging distances (~ 70 to 180 km) and was lower at short and long distances. There was no relationship between number of chicks fledged and mean trip distance during incubation (Wald $\chi^2 = 0.69$, $p = 0.71$) or when chicks were small (Wald $\chi^2 = 1.45$, $p = 0.48$).

Variation between sexes

Males and females traveled similar distances during incubation (all years and 1997 to 2001: $p \geq 0.46$) (Fig. 3). Foraging-trip distance was not related to trip start date ($p \geq 0.36$), suggesting the prey distribution was similar throughout incubation. When chicks were small, males and females also traveled similar distances (mean and maximum distance: $p \geq 0.67$). When chicks were >30 d old, maximum but not mean distance was greater for females than for males (all years

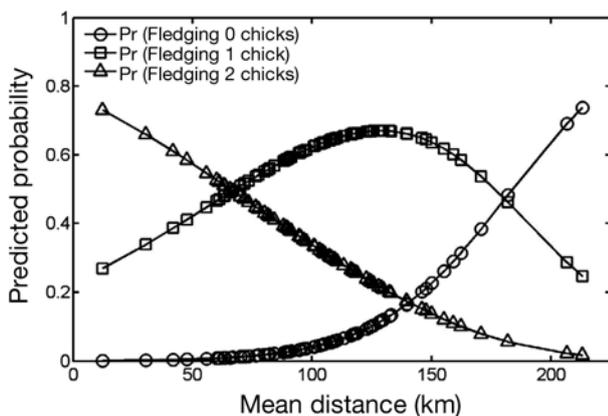


Fig. 2. *Spheniscus magellanicus*. Predicted probability of Magellanic penguin fledging success (0, 1, or 2 chicks) calculated from the multinomial regression of chicks fledged against mean foraging-trip distance during the late-chick stage ($n = 78$). Predicted fledging probabilities are plotted against actual mean distances. One female that traveled >300 km was excluded. Each penguin tracked had 2 chicks 30 d of age or older when the transmitters were attached in late December or early January 1996–2007

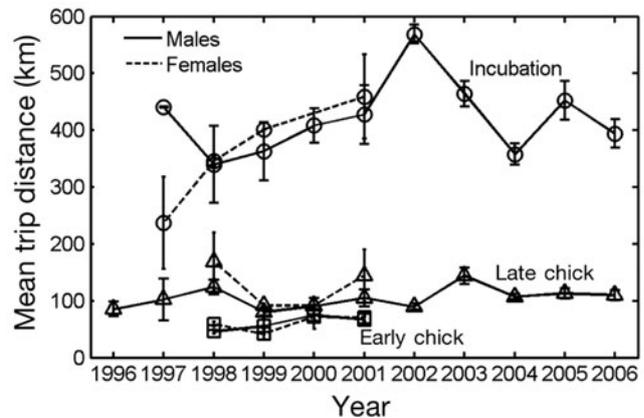


Fig. 3. *Spheniscus magellanicus*. Mean trip distance by stage of the breeding season, year, and sex for Magellanic penguins breeding at Punta Tombo, Argentina. Error bars are 1 SE. See Table 1 for sample sizes. (O) incubation; (□) early chick; (Δ) late chick; (—) males; (---) females. Distance varied by stage and year, but not sex

and 1998 to 2001, maximum distance: $p = 0.03$ and 0.04; mean distance: $p \geq 0.21$).

The difference between the sexes in maximum foraging-trip distance during late chick was driven by 3 females (2 in 1998, 1 in 2001) that took trips of 275, 307, and 372 km with durations of 23, 19.5, and 18.2 d, respectively (see Fig. 6f). Excluding these 3 trips there were no significant differences between the sexes, nor was the interaction between sex and breeding stage significant (Table 3). The mean trip duration for late chick, excluding the 3 females, was 2.9 d; the 3 females made trips 6 times the mean duration. The longest trip by any other penguin was 10.8 d. The female that made an unusually long trip in 2001 of 18.2 d had the lowest body condition index in our dataset ($n = 473$). The 2 females that made unusually long trips in 1998 were also in poor condition (negative index), but did not have lower index values than other females we tracked. However, they both laid at least one small egg (1st eggs: 219.9 and 232.1 cm^3 ; 2nd eggs: 213.0 and 218.0 cm^3) compared to the mean egg size for 1998 (1st eggs: $231.7 \pm 0.9 \text{ cm}^3$, $n = 538$; 2nd eggs: $228.8 \pm 1.0 \text{ cm}^3$, $n = 506$), indicating that they were in poor body condition when they laid eggs. All 3 females returned to their nests before the end of the season, and 2 of the 3 bred in subsequent years. Males were seen at the nests 2 to 15 times while the females were at sea and were able to compensate in part for the females' absence, as 2 of the 3 pairs fledged one chick. The third pair had one chick that was still alive but weighed <1.8 kg (our criterion for fledging) when last seen on 3 February, >2 wk after the return of the female. A few males made trips >275 km from the colony, but none made trips with duration >11 d during chick rearing.

Table 3. *Spheniscus magellanicus*. Multiple regressions of maximum and mean trip distance on stage of the breeding season, year (as a categorical variable), sex, and the interaction between sex and stage. Foraging-trip distance depended on stage of the breeding season and year. The significant coefficients for sex (for maximum distance only) and the interaction between sex and stage were driven by 3 females that made anomalous trips (see 'Results'). Statistics for sex and the interaction excluding those 3 females are also shown. Inc: incubation; LC: late chick; EC: early chick

Response variable or predictor variable	F for regression or t for predictor variables	p	R ²
Maximum distance	44.2 _{15,171}	<0.005	0.79
Inc (vs. LC)	15.33	<0.005	
EC (vs. LC)	-5.36	<0.005	
Year (1996–1999 and 2001–2006 vs. 2000)	3.73–0.06	<0.005–0.95	
Sex	1.94	0.05	
Sex, excluding 3 females	0.80	0.42	
Sex × Stage	-2.15	0.03	
Sex × Stage, excluding 3 females	-1.57	0.12	
Mean distance	52.9 _{15,171}	<0.005	0.84
Inc (vs. LC)	19.74	<0.005	
EC (vs. LC)	-3.21	0.002	
Year (1996–1999 and 2001–2006 vs. 2000)	2.77–0.05	0.006–0.96	
Sex	1.38	0.17	
Sex, excluding 3 females	-0.51	0.61	
Sex × Stage	-2.05	0.04	
Sex × Stage, excluding 3 females	-1.31	0.19	

Variation within the breeding season

Penguins traveled farthest during incubation (411 ± 11.8 km, $n = 80$) (Table 3, Figs. 3 & 4), and stayed closest to the colony when chicks were small (mean trip distance = 61 ± 3.9 km, mean maximum trip distance = 92 ± 6.5 km, $n = 35$) (Fig. 5). During the late-chick period when chicks had a larger storage capacity, distances were intermediate (mean trip distance = 111 ± 5.0 km, mean maximum trip distance = 176 ± 5.9 km, $n = 101$) (Fig. 6). Distances among all 3 stages of the breeding season were significantly different (Table 3). The direction penguins swam from the colony, generally northeast, varied little among stages or years (Figs. 4–6). No penguins used the extensive areas south or southeast of the colony when breeding.

Variation among years

Trip distances during incubation increased from 1997 through 2002, and then declined, though not to the level of the earlier years (Table 3, Fig. 3). In the first

5 yr of tracking (1997 to 2001), 3 of 35 penguins (8.6%) traveled more than 500 km (Fig. 4a–c). In the last 5 yr (2002 to 2006), 13 of 45 penguins (28.9%) traveled >500 km ($G = 5.49$, $p = 0.02$) (Fig. 4d–f). The mean trip distance for 1997 to 2001 was 386 ± 18.7 km, and in 2002 to 2006 the mean trip distance increased to 431 ± 14.7 km ($t_{69} = -1.86$, $p = 0.07$). In 2002, all penguins swam >500 km from the colony ($n = 4$) (Fig. 4d). Two of the males that we tracked in 2002 took the first incubation shift, and therefore did not leave their nests when the transmitters were attached. Males rarely incubate first but will when females are in poor body condition (Yorio & Boersma 1994).

Distances to foraging locations during chick rearing were variable among years but overall increased with year (Figs. 3, 5 & 6). When chicks were small, both mean (simple linear regression: $F_{1,32} = 10.83$, $p = 0.002$, $R^2 = 0.13$) and maximum distances ($F_{1,32} = 9.55$, $p = 0.004$, $R^2 = 0.17$) increased over 4 yr (Figs. 3 & 5). When chicks were older, maximum distances (simple linear regression: $F_{1,84} = 5.98$, $p = 0.02$, $R^2 = 0.07$), but not mean distances ($F_{1,84} = 2.37$, $p = 0.13$) increased over 11 yr (Figs. 3 & 6).

The annual mean maximum distances during incubation, early-chick, and late-chick stages varied by factors of approximately 1.8, 1.6 and 1.9, respectively. Annual mean trip distances during early-chick and late-chick stages varied by factors of 1.5 and 1.7, respectively. However, individual trips varied more, with trip distances ranging from 94 to 605 km during incubation, 6 to 182 km during early chick, and 7 to 372 km during late chick (Figs. 4–6). One penguin made trips ranging from 8 to 182 km during early chick and another made trips ranging from 17 to 289 km during late chick. During incubation, the mean difference between the shortest and longest trips within years was 253 ± 35.1 km (Fig. 4). The shortest difference in trip distance during incubation within a year was 69 km in 2002; the longest was 456 km in 2000. When chicks were small, the mean difference among trips within years was 137 ± 19.2 km, and when chicks were large, 241 ± 21.5 km (Figs. 5 & 6).

DISCUSSION

Foraging-trip distance varied within and among years, as well as among penguins and among trips by the same penguin (Figs. 3–6). Magellanic penguins feed along fronts and in areas of high productivity (Boersma et al. in press). Many seabirds forage primarily in productive oceanographic features (Hunt et al. 1999), but some variability among years is probably the rule, as oceanographic features vary in strength

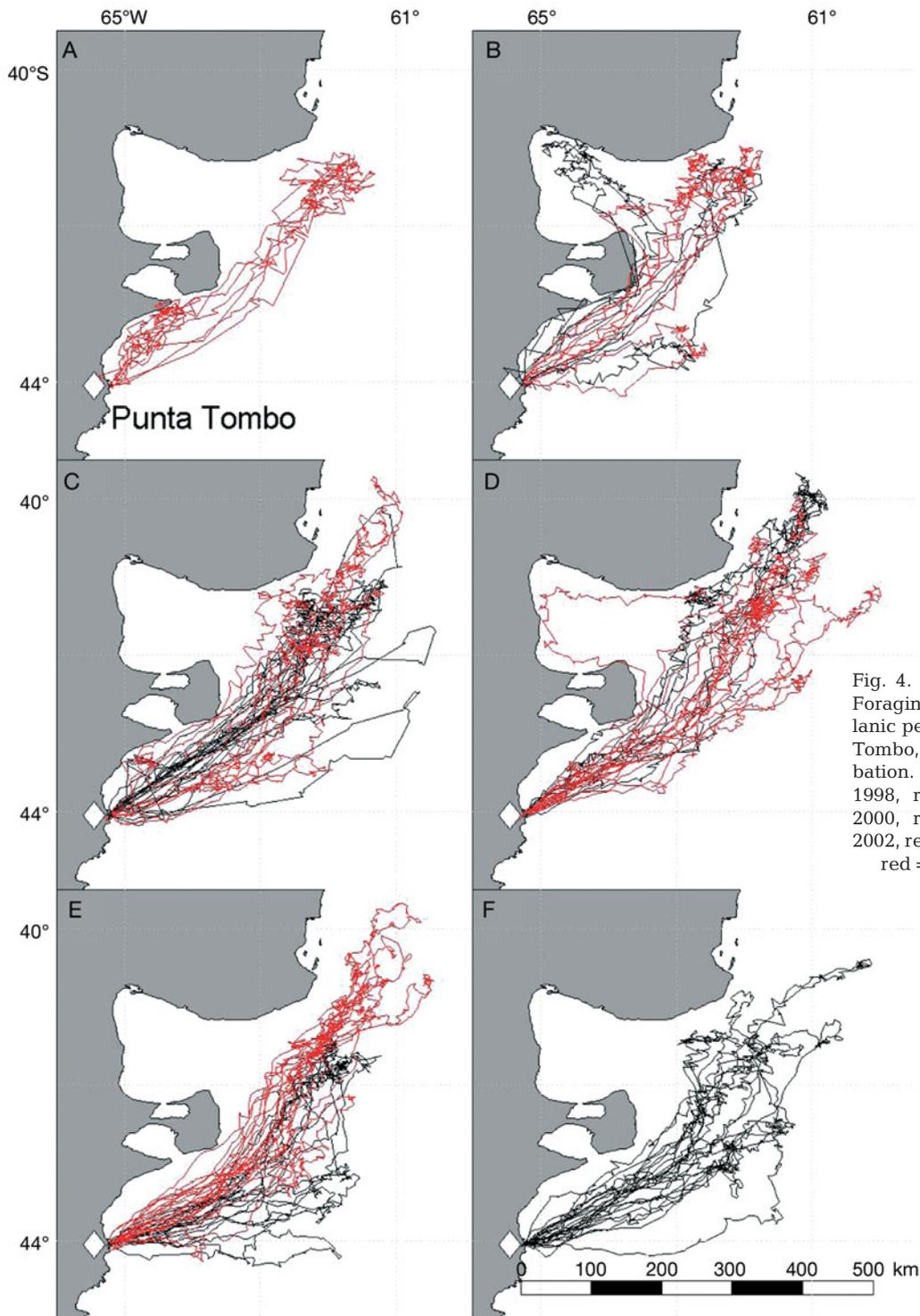


Fig. 4. *Spheniscus magellanicus*. Foraging trip tracks for Magellanic penguins breeding at Punta Tombo, Argentina, during incubation. (A) red = 1997, (B) black = 1998, red = 1999, (C) black = 1998, red = 2000, red = 2001, (D) black = 2002, red = 2003, (E) black = 2004, red = 2005, (F) black = 2006

from year to year and those that are not fixed bathymetrically move. Differences in foraging-trip distance or duration within species among years are common in multi-year studies and likely reflect changes in prey availability (e.g. Kitaysky et al. 2000, Ballard et al. 2001, Boersma et al. 2002, Lescroël & Bost 2005). Vari-

ability among individuals from the same colony is probably common as well (Ballard et al. 2001), reflecting factors such as age, experience, body condition, and number and size of chicks. Variability in foraging trips among individuals and among years is seldom accounted for in modeling studies (e.g. Green et al.

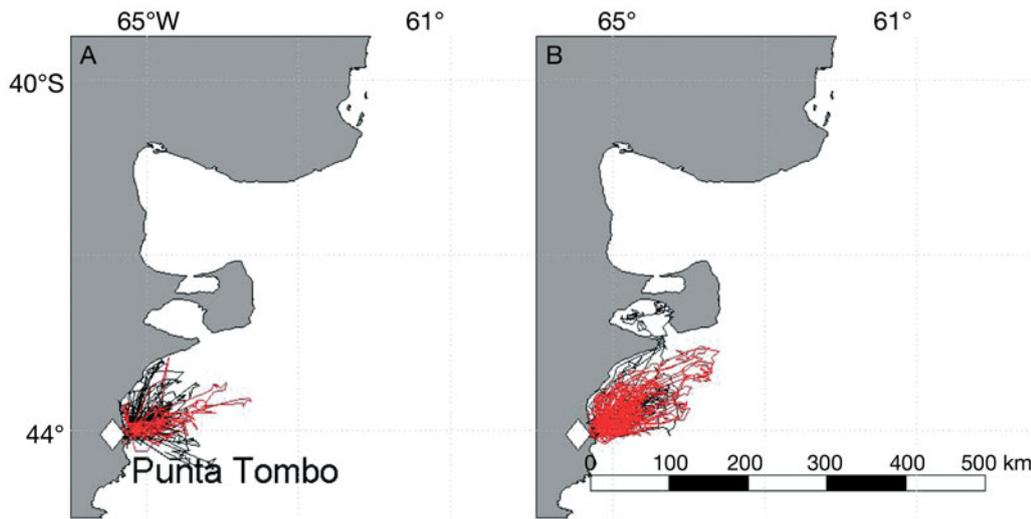


Fig. 5. *Spheniscus magellanicus*. Foraging trip tracks for Magellanic penguins breeding at Punta Tombo, Argentina, during early chick (chicks < 30 d old). (A) black = 1998, red = 1999, (B) black = 2000, red = 2001

2007), but it is large and affects adult and offspring energy balances as well as demographic parameters such as reproductive success and recruitment. It is also an important consideration for management and conservation. Marine protected areas and ocean zoning must take variability in trip distance into account to protect penguins in all their foraging areas, particularly when human and penguin uses of an area conflict.

Foraging-trip distance and duration

A positive relationship between trip distance and duration is known for several penguin species (e.g. Petersen et al. 2006, Boersma et al. 2007), but how that relationship varies is unknown. Our large dataset allowed us to refine the relationship for Magellanic penguins, and determine that it is linear during incubation and nonlinear during chick rearing. When chicks are older the relationship varies by individual penguin. Variation among penguins likely reflects luck as well as the foraging ability and experience of the individual and leads to variation in the reproductive outcome of mating pairs. The simple linear relationship between distance and duration was robust, suggesting that (1) duration is a good predictor of how far penguins travel, and (2) choice of filtering methods, at least for some analyses, may make little difference.

Penguins that traveled the farthest from the colony stayed away longer than predicted by a linear relationship. Boersma et al. (in press) found that penguins that go farther from the colony remain in the foraging area longer, probably because they need to replenish the extra energy required to swim greater distances. Our

findings are consistent with this hypothesis: additional time spent in the foraging area on longer trips increases trip duration but not trip distance.

Foraging-trip distance and reproductive success

Trip distance influenced reproductive success at 2 levels. At the colony level, the mean distance penguins with satellite transmitters traveled during incubation each year was reflected in mean annual reproductive success. If a penguin is away from the nest too long during incubation, the incubating mate may abandon the eggs to forage for itself, or the chicks may hatch and starve before the foraging parent returns with food (Yorio & Boersma 1994, Boersma & Stokes 1995, Otley et al. 2004). During chick rearing, longer trips mean less frequent feeding of chicks, slower growth, and higher risk of starvation or low fledging weights (Davoren & Montevecchi 2003). The major cause of mortality for Magellanic penguin chicks is starvation (Boersma & Stokes 1995), and lone chicks grow more rapidly than chicks with siblings, suggesting that food is limited for Magellanic penguins (Boersma 1992). We did not detect a significant relationship between mean trip distance during late chick and mean colony reproductive success, perhaps because the penguins we tracked in that stage were not representative. We selected only penguins that had healthy chicks >30 d old for tracking in late chick. However, the mean reproductive success in the colony included many penguins that had already lost both eggs or chicks by that time. The penguins we selected to track during late chick may have been better foragers than average, since many chicks starve before reaching 30 d (Boersma & Stokes 1995). Reproductive

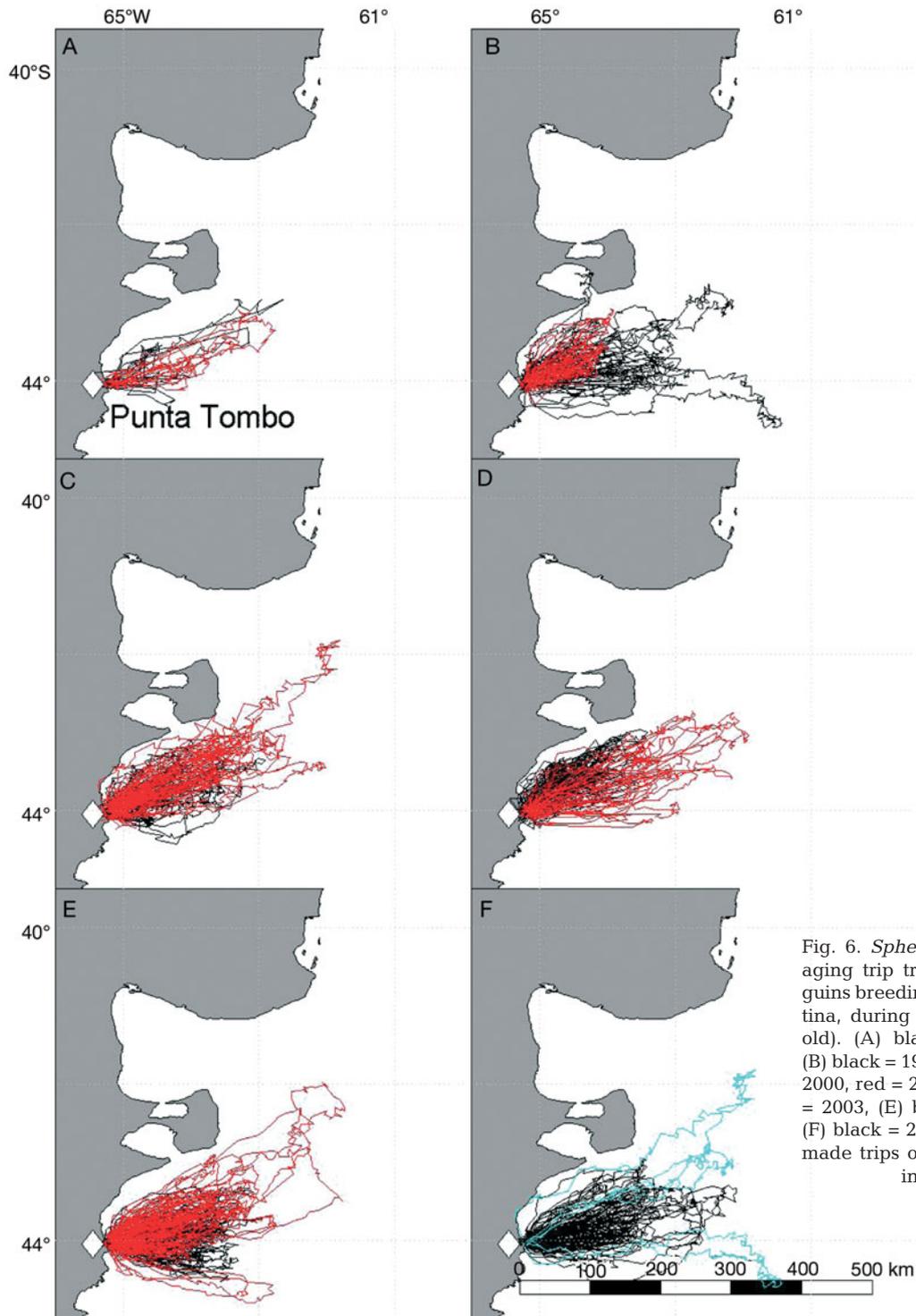


Fig. 6. *Spheniscus magellanicus*. Foraging trip tracks for Magellanic penguins breeding at Punta Tombo, Argentina, during late chick (chicks > 30 d old). (A) black = 1996, red = 1997, (B) black = 1998, red = 1999, (C) black = 2000, red = 2001, (D) black = 2002, red = 2003, (E) black = 2004, red = 2005, (F) black = 2006, blue = 3 females that made trips of unusually long duration in 1998 and 2001

success approached one chick per nest with eggs in only one of 25 years in our long-term study of this colony, and average reproductive success is usually less than half a chick per nest with eggs (Boersma 2008).

The number of chicks fledged was negatively related to an individual's mean trip distance during late chick

(Fig. 2). Penguins that swim too far during foraging trips may not be able to deliver meals frequently enough to keep a chick alive, however, those that find food very close to the colony (<70 km) may fledge both chicks. Penguins that travel intermediate distances (70 to 180 km) may be able to keep one chick alive, but not

both. Magellanic penguins feed the larger chick more than the smaller chick (Boersma 1992), so the smaller chick may not get enough food to keep it alive until the next feeding. These data show that the average distance a penguin forages for its chicks is an important determinant of reproductive success.

During incubation and early chick there was no relationship between the number of chicks fledged and trip distance. Many eggs and young chicks were lost to predators, obscuring the relationship between trip distance and reproductive success. In addition, if chicks fledged at lighter weights when trips were longer, trip distance could have an effect on future recruitment as well as current reproduction (Mougin et al. 2000, McClung et al. 2004).

Variation between sexes

We expected males to make longer trips than females during incubation, when males are at sea earlier than females. Seasonal coastal fronts form (Rivas et al. 2006) and spawning schools of anchovy *Engraulis anchoita* move south (Sánchez & de Ciechowski 1995) during this period. Hence prey may be more abundant or available farther north when males make their long incubation foraging trips and farther south when females make their trips. However, we found no evidence that females and males consistently swam different distances from the colony during any stage of the breeding season. Three females with chicks >30 d old were away from their nests for 18 to 23 d, longer than any males. We tracked about 5 times more males (84) than females (17) during late chick, but only females made these long trips. We were unable to tell if these females had abandoned their breeding attempts, but all 3 returned to their nests and their chicks were still alive when they returned. These long trips likely serve to replenish body condition and may be particularly important for females. Females are smaller than males, have a more limited storage capacity, and a less favorable surface-to-volume ratio, and hence are more likely to be in poor condition after their fast (see below) than males (Hood et al. 1998). Magellanic penguins are opportunistic foragers and prey on whatever they can find. Thus, individual differences as we found are likely more important than differences between the sexes.

Variation within the breeding season

Spawning aggregations of anchovy, a primary prey of Magellanic penguins (Frere et al. 1996, Wilson et al. 2005), are found north of Punta Tombo in October

(Sánchez & de Ciechowski 1995). Magellanic penguin adults in good condition can fast for at least a month, allowing the foraging mate to reach these aggregations during incubation and recover weight lost during settlement, courtship, and incubation (Boersma et al. 1990). Chlorophyll *a* concentrations peak in November in coastal waters on the Patagonian shelf at 43° S (Rivas et al. 2006). By November and December, when chicks hatch and need to be fed frequently, coastal fronts have formed (Rivas et al. 2006) and anchovy aggregations are near Punta Tombo (Sánchez & de Ciechowski 1995), allowing penguins to make much shorter trips during early chick than during incubation.

Variation among years

Variability in trip distance among years likely reflects environmental conditions and prey availability. Magellanic penguin foraging locations depend on local productivity and oceanographic fronts (Boersma et al. in press), so trip distances may reflect prey distribution and abundance. Magellanic penguins eat highly mobile pelagic prey such as anchovy that aggregate in fronts. Strength and location of fronts, and associated anchovy distributions, vary among years (Hansen et al. 2001), therefore penguin foraging-trip distances vary as well.

Penguins went farther from the colony during incubation in 2002 than in any other year. Foraging-trip distances were less variable in 2002 than in other years, in spite of having the highest mean; no penguins were able to find food close to the colony. Food was apparently scarce in 2002, as fewer penguins returned to the colony to breed, egg laying was delayed, and penguins that did breed were in poorer body condition than usual (P.D.B. unpubl. data). These factors, along with the unusual situation of males taking the first incubation shifts, indicated low food availability both prior to the breeding season and during incubation. However, during late chick 2002, penguins did not swim especially far compared to other years, indicating either that conditions had improved by January, or that penguins that still had chicks in January were very good at finding food.

Toxic algal blooms sometimes kill penguins (Shumway et al. 2003) and may also have affected the penguins in 2002. Four penguins carrying tags did not return from their incubation trips and were not seen again, suggesting they died, which is rare during the breeding season. It is possible they starved, but it seems unlikely because, in general, penguins return after their first incubation foraging trip in good condition. In 2000, 9 breeding penguins that we tracked appeared healthy right before they left on foraging

trips; these penguins failed to return and were not seen again, coincident with a toxic algal bloom and large seabird mortality event in the region (Shumway et al. 2003). Besides the 9 penguins in 2000 and 4 in 2002, only 3 other tracked penguins failed to return from incubation trips, 2 in 1999 and one in 2001.

Since 2002, significantly more penguins traveled farther during incubation than in 1997 to 2001, suggesting changes in prey availability. In addition, trip distances during early chick increased linearly over 4 yr, and mean maximum trip distance increased over 11 yr during late chick. These longer distances may indicate a longer-term shift in prey distribution or availability reflecting climate variation.

CONCLUSIONS

Foraging distance is closely related to the time a penguin is away from the nest and is an important determinant of reproductive success. Understanding the variability in animal use of the marine environment is critical for effective management, conservation, and reserve design. Marine reserves or zones need to be large or flexible enough to meet the needs of the species of interest throughout the annual cycle and among years with different prey availability. Our data show that the ocean habitat requirements of Magellanic penguins are large and variable. Management of the South Atlantic ecosystem should take this variability into account to conserve penguins as well as other seabirds and marine mammals in the area.

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