

Flexible foraging for finding fish: variable diving patterns in Magellanic penguins *Spheniscus magellanicus* from different colonies

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Abstract Seabirds have to deal with environmental variability and are predicted to modulate foraging behavior to maximize fitness, with particularly strong selection pressure for optimal behavior during chick provisioning when energy demands are high. We reported data from 42 breeding birds equipped during the early chick-rearing period with depth recorders at four different colonies [Punta Norte (42°S), Bahía Bustamante (45°S), Puerto Deseado (47°S) and Puerto San Julián (49°S)] in Patagonian Argentina. Although Magellanic penguins are purported to show little flexibility in foraging behavior, we discovered marked inter-colony differences in diving behavior. Even though the southern marine ecosystems, in general, and the area exploited by Magellanic penguins from the studied colonies, in particular, are usually characterized by their stability, we cannot entirely exclude that interannual differences may have also affected our results. The colonies located in the center of the breeding distribution, Bahía Bustamante and Puerto Deseado, showed the

greatest diving and foraging effort with Bahía Bustamante penguins having the deepest and longest dives of all birds and requiring the longest post-dive recovery durations at the surface. Puerto Deseado had the birds with the highest values of diving effort parameters. Penguins from both colonies also had the highest descent and ascent rates during dives. We assume that the clear variation in diving behavior reflects the response of the birds to the varying prey types and availability around the different colonies, but note that, despite this, some colonies fare markedly better than others in breeding.

Keywords Diving behavior · Diving effort · Foraging effort · *Spheniscus magellanicus* · Patagonia · Conservation

Zusammenfassung

Flexible Suche nach Fisch: unterschiedliche Tauchmuster von Magellan-Pinguinen *Spheniscus magellanicus* aus verschiedenen Kolonien

Seevögel müssen Umweltveränderungen bewältigen und können vermutlich ihre Nahrungssuche anpassen, um ihre Fitness zu maximieren, vor allem bei starkem Selektionsdruck für optimales Verhalten während der Jungenaufzucht, wenn der Energiebedarf besonders hoch ist. In vier verschiedenen Kolonien [Punta Norte (42°S), Bahía Bustamante (45°S), Puerto Deseado (47°S) und Puerto San Julián (49°S)] im argentinischen Teil Patagoniens wurden während der frühen Kükenaufzuchtphase 42 Brutvögel mit Tiefenmessern ausgerüstet. Obwohl Magellan-Pinguine angeblich eine geringe Flexibilität im Nahrungssuchverhalten zeigen, konnten deutliche Unterschiede im Tauchverhalten zwischen den Kolonien festgestellt werden. Wenngleich die südlichen marinen Ökosysteme im

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Allgemeinen, und das von den untersuchten Magellan-Pinguinen genutzte Gebiet im Speziellen, normalerweise durch ihre Stabilität gekennzeichnet sind, kann nicht gänzlich ausgeschlossen werden, dass Unterschiede zwischen den Jahren die Ergebnisse beeinflusst haben könnten. Die Kolonien, die in der Mitte des Brutverbreitungsgebietes liegen, Bahía Bustamante und Puerto Deseado, zeigten den größten Aufwand für Tauchen und Nahrungssuche. Die Bahía Bustamante Pinguine tauchten von allen Vögeln am tiefsten und am längsten und benötigten die längsten Erholungsphasen an der Wasseroberfläche nach ihren Tauchgängen. Puerto Deseado Pinguine zeigten die höchsten Werte im Tauchaufwand. Vögel aus beiden Kolonien hatten die höchsten Ab- und Auftauchgeschwindigkeiten während der Tauchgänge. Wir nehmen an, dass die Unterschiede im Tauchverhalten die Antwort der Vögel auf variierende Beutetypen und deren Verfügbarkeit um die verschiedenen Kolonien reflektiert. Ungeachtet dessen ist aber darauf hinzuweisen, dass das Brutgeschäft in einigen Kolonien deutlich besser läuft als in anderen.

Introduction

Seabirds are exposed to considerable heterogeneity with, for example, prey abundance and availability changing both spatially and temporally (Hunt 1990; Fauchald and Erikstad 2002; Weimerskirch 2007) so that birds have to adjust their foraging behavior (Morrison et al. 1990; Pichegru et al. 2011; Zimmer et al. 2011a; Cook et al. 2012). The challenges faced by diving seabirds are particularly onerous because they must allocate their time into periods at the surface when they acquire oxygen but cannot obtain food, and periods underwater, when they can search for food at selected depths but are constrained to regularly breathe at the surface (Wilson et al. 2010, 2011). Penguins are the most specialized avian divers and show extreme physiological specialization for foraging underwater (Kooyman 1989; Williams 1995; Butler and Jones 1997), as well as considerable plasticity in their behavior according to changing circumstances. For example, they change feeding strategy with ambient light levels (Wilson et al. 1993; Pichegru et al. 2011), the extent of sea ice (Watanuki et al. 1997), the availability and type of prey (Watanuki et al. 1993; Sala et al. 2012a), and the stage of the breeding season, with the associated energy demands (Charrassin et al. 1998, 1999; Ropert-Coudert et al. 2004; Hennicke and Culik 2005; Raya Rey et al. 2012). Changing behavior, with associated effort, is considered to modulate the breeding success of the colonies, manifest by, e.g., chick growth rate and mortality

(Petersen et al. 2006; Ballance et al. 2009; Boersma and Rebstock 2009; Sala et al. 2012b) and ultimately impact population trends (Sala et al. 2012b).

The Magellanic penguin (*Spheniscus magellanicus*) breeds in colonies located on both Argentinean and Chilean Patagonian coasts, nesting on the Atlantic coast between Isote Redondo (41°26'S) in Río Negro and Isla Martillo (54°54'S) in Tierra del Fuego (Schiavini et al. 2005), extending up to the Pacific to Isote Pájaro Niño (33°27'S) (Simeone et al. 2003). Over the Patagonian Shelf, Magellanic penguins feed mainly on small pelagic fish such as Anchovy (*Engraulis anchoita*), Fuegian Sprat (*Sprattus fuegensis*), and, to a lesser extent, Hake (*Merluccius hubbsi*) and Squid (*Illex* sp., *Loligo* sp.) (Williams 1995; Frere et al. 1996; Wilson et al. 2005), all prey species that are commonly associated with oceanographic frontal systems (Hansen et al. 2001; Acha et al. 2004). As with many other penguin species (e.g. Hennicke and Culik 2005; Bost et al. 2009), Magellanic penguins depend on exploiting areas of high productivity, which may be located at some distance from the colonies. This explains why, during the breeding season, birds may swim tens or even hundreds of kilometers to feed their chicks, being able to travel up to 120 km in 24 h (Sala et al. 2012b). Since the distribution and abundance of the prey preferred by Magellanic penguins are not constant throughout the breeding range (Frere et al. 1996; Wilson et al. 2005), birds must modulate their diving and/or foraging behavior over their range to satisfy their energy demands (Wilson et al. 2005; Sala et al. 2012a, b).

Previous studies have suggested that, where the reproductive success and/or rate of population change of individual colonies is low, Magellanic penguin foraging effort is particularly high (Boersma and Rebstock 2009; Sala et al. 2012b). These studies have focused on the horizontal component of foraging trips (i.e. distances covered, trip duration, etc.), paying little attention to foraging effort in the vertical (depth) dimension and its possible connections with colony-specific demographic processes on land. Although some studies have examined the diving behavior of Magellanic penguins in Patagonia (e.g., Peters et al. 1998; Walker and Boersma 2003; Wilson et al. 2005; Raya Rey et al. 2010, 2012), none of them have emphasized the extent to which foraging patterns underwater might affect colony breeding success (but see Radl and Culik 1999).

We used animal-attached tags to investigate the foraging effort of Magellanic penguins at different breeding colonies. Our objectives were (1) to study the diving effort of breeding Magellanic penguins from four colonies along the Patagonian coast during the early chick-rearing period to elucidate whether there are differences between colonies, (2) to determine how foraging effort is related to the specifics of diving behavior, and (3) to determine whether the

Table 1 Details of deployments on Magellanic penguins *Spheniscus magellanicus* during the early chick-rearing period (November–December 2005–2008) at four Patagonian colonies

Site	Study year	Type of device	No. of birds equipped	No. of birds with data	No. of birds with complete trips	No. of dives
Punta Norte	2008	GPS-TDlog	10	9	9	6,447
		Daily diary	5	5	1	2,508
Bahía Bustamante	2005	Daily diary	6	3	3	1,483
	2006	GPS-TDlog	6	1	1	641
		Daily diary	6	5	1	1,962
	2007	Daily diary	1	1	1	512
Puerto Deseado	2006	Daily diary	8	6	4	5,245
Puerto San Julián	2007	GPS-TDlog	7	6	6	6,126
		Daily diary	8	6	5	6,254
Total			57	42	31	31,178

diving (and/or foraging) effort of breeding penguins can be used as a short-term indicator of environmental well-being that may affect the health of populations over time. Behind these objectives underlies the hypothesis that foraging effort, expressed through diving behavior, is principally determined by certain attributes of target prey species (i.e. abundance, availability, and spatial distribution in the water column, wet mass, and energy content) and this, in turn, shall be a good proxy, to some extent, of the productivity (i.e. population growth rate) registered in the studied colonies. The predictions derived argues that: (1) those colonies that consume preys with a lesser revenue, in terms of wet mass and/or energy content, will display a greater foraging effort that will be expressed in the diving metrics (see Sala et al. 2012a); and (2) the locations that have the highest values in population growth rates will be those that present a lower relative foraging effort (see Sala et al. 2012b).

Methods

Study sites and period

We conducted fieldwork during early chick-rearing, between November and December during 2005, 2006, 2007, and 2008, at four colonies along the Patagonian coast, Argentina: Punta Norte (42°04'S, 63°49'W), Bahía Bustamante (45°10'S, 66°29'W), Puerto Deseado (47°45'S, 65°52'W), and Puerto San Julián (49°16'S, 67°42'W). All necessary permits for the described field studies were obtained from the Subsecretaría de Turismo y Áreas Protegidas and Dirección de Fauna y Flora Silvestre (Chubut Province, Argentina), and the Dirección de Fauna Provincial, Consejo Agrario Provincial (Santa Cruz Province, Argentina).

Deployment of devices

Thirty-four Magellanic penguins were equipped with multichannel archival tags [daily diaries (DD); see Wilson et al. 2008 for details] and another 23 birds were instrumented with GPS-TDR loggers (GPS-TDlog; Earth and Ocean Technologies, Kiel, Germany). For a complete description of logger deployment, see Sala et al. (2012a). The details of deployments per colony (i.e. numbers of devices, birds with data, dates, etc.) are given in Table 1. Since previous studies on the species did not establish any differences between sexes for the variables studied during the early chick-rearing period (Raya Rey et al. 2010, 2012), data for the sexes were pooled. The database employed was the same used in Sala et al. (2012a).

Data analysis of diving behavior

Penguin diving behavior was analyzed using bespoke software (SNOOP; Gareth Thomas, Freeware, Swansea, Wales, UK), specially designed to detect automatically (and/or be manually adjusted) the three characteristic phases of a dive (descent, bottom, and ascent phases; see below), and to collate the times and depths of these for all dives. We defined a 'dive' as having occurred for all submersions that exceeded 1.5 m depth (see Sala et al. 2012a). We defined the bottom phase of each dive, during which the penguins are most likely to hunt (Wilson et al. 1995), according to three conditions: it could only occur (1) at depths >85 % of the maximum depth of the dive, (2) was limited by two points of inflection in the rate of change of depth (indicating the start and end of a period of a well-defined bottom phase), and (3) when the overall rate of change of depth for the whole period did not exceed 0.25 m s⁻¹ (Sala et al. 2012a). Using this procedure, we analyzed a total of 31,178 dives made by 42 birds (see Table 1).

In order to assign dive efficiencies correctly, we distinguished between diving and resting phases of birds at sea using bout-ending criteria as exemplified by Takahashi et al. (2003). Within diving behavior bouts, we distinguished between foraging and non-foraging dives by constructing a frequency distribution of maximum dive depths for each colony as well as a further frequency distribution of the bottom durations of the dives. The former were all bimodal, and we assumed that the shallowest of these modes in each case could be putatively assigned to traveling rather than foraging behavior (Wilson and Wilson 1995). These were further refined to concur with traveling rather than foraging behavior by only using those dives within the shallowest bracket with bottom durations of <4 s as traveling dives because Magellanic penguins forage virtually exclusively during an extended bottom phase of dives (Simeone and Wilson 2003; Wilson et al. 2010). All other dives that did not concur with the traveling dive criteria were considered to be foraging dives.

Basic diving variables Using the definitions above, we calculated the total number of dives per foraging trip (both traveling and foraging types). For just those dives classified as foraging, we obtained the time invested in each of the three sub-surface phases of a dive (descent, bottom, and ascent phases), the post-dive interval (recovery time at the surface following dives), dive depths (mean and maximum values), and vertical velocities (up and down; calculated as the rate of depth change).

Diving effort variables To quantify diving effort during foraging immersions, we calculated:

1. the diving efficiency (DE; defined as the bottom time divided by the dive cycle time; Ydenberg and Clark 1989),
2. the proportion of the dive duration spent in the bottom phase (PDDBP; defined as the bottom duration divided by the dive duration), and
3. the dive to pause ratio (defined as dive duration divided by post-dive interval; Walton et al. 1998).

We also used an index to represent dive effort (DEff), consisting of the dive duration divided by the dive cycle duration (Zimmer et al. 2011b).

Foraging effort variables We defined variables related with distance travelled underwater as indicators of the effort made during foraging underwater:

1. the distance travelled per dive (defined as the dive duration multiplied by 2.1 m s^{-1} , assuming a constant mean swimming speed underwater recorded for free-ranging Magellanic penguins; see Wilson et al. 2011 and references therein),
2. the total distance swum per trip (the sum of all distances covered in all dives),

3. the total way vertical at bottom per dive (the vertical distance swum during the bottom phase of the dive), and
4. the mean wiggle (i.e. elements of the dive profile during which at three points the vertical speed passes below 0 m s^{-1} ; see Bost et al. 2007; Halsey et al. 2007; Sala et al. 2012a) amplitude (defined as the total vertical distance covered during the bottom phase divided by the number wiggles of a dive).

Finally, we defined an index of capture efficiency (CEI) as the dive efficiency (DE) multiplied by the number of wiggles made per minute at the bottom (WPMBT) following Zimmer et al. (2010).

Statistical analysis

To account for repeated measures on dive analysis, and to avoid pseudo-replication, general linear mixed-effects models (GLMMs) were applied with restricted maximum likelihood estimations (REML) for comparisons of behavioral variables between colonies. As the maximum depth influences other dive metrics (e.g., Wilson et al. 1997), we included maximum dive depth as a covariate into the model [except for those variables considered as foraging effort (see above), not strictly related to the maximum depth; see Cook et al. 2012]. Where significant differences were detected, a Tukey's post hoc multiple comparisons test was used to compare between colonies. In our models, colony identity was defined as a fixed factor, while bird identity was categorized as a random factor (Crawley 2007; Zuur et al. 2009). To deal with non-Gaussian distributions, we used GLMMs with poisson errors and log-link function corrected for overdispersion (Crawley 2007; Zuur et al. 2009). To evaluate, and thus validate, the classification methodology as 'foraging' and 'non-foraging' dives (see above), we compared the number of wiggles per dive using GLMMs where the identity of the bird was considered as a random factor and the 'dive type' as a fixed factor. To analyze possible differences in the variables studied between years, we compared the basic diving parameters (i.e. maximum dive depth, dive duration, bottom duration, post-dive interval, etc.) using GLMMs where the bird identity was considered as a random factor and the 'year' as a fixed factor. Since there were no differences between basic diving parameters (for the breeding site with more than 1 year of records; see Table 1), data from all breeding seasons were pooled (GLMMs $L_{\text{ratio}} = 1.8\text{--}4.1$, all $P > 0.1$).

For the foraging trip-based parameters (i.e. total number of dives, number of foraging and non-foraging dives, percentage of foraging dives, and total distance swum per trip), we obtained a unique value per individual and then a grand

mean per colony, only considering those individuals with a completed record of the foraging trip (see Table 1). We then performed a non-parametric Kruskal–Wallis statistical test to compare between colonies; and the differences among means were tested by Dunn’s post hoc contrasts (Zar 1999). Following the approach proposed by Zimmer et al. (2011a), and in order to select those most relevant variables to reach our objectives, and also because many of these dive-based parameters are highly correlated, we performed a principal component analysis (PCA) (Elliott et al. 2008). By doing so, we describe the complex interaction of factors involved in the foraging activity of a penguin species by interpreting primary output from PCA. Proportion data were arcsine-transformed and variables that were not normally distributed were \log_{10} -transformed prior to analyses. The identity of the colony was used as a classification criterion. We have reduced the number of dimensions selected for analysis to three nonredundant axes according to the Kaiser criteria (i.e. only considering axes with an eigenvalue >1 ; Zimmer et al. 2011a). We selected the first three dimensions with the highest loadings (axes 1, 2, and 3) for presentation and interpretation of data as these axes together explained 100 % of the total variability. The first two dimensions of PCA results are presented by a biplot (Fig. 6a). Also, to assist the interpretation of the data, Table 5 includes the first three PCA component loadings of dive-based parameters for the performed PCA. In addition, we also performed a hierarchical clustering method (i.e. unweighted pair-group method using an arithmetic average; UPGMA) with the principle of hypothesis testing (MDGC) proposed by Valdano and Di Rienzo (2008) to show overall differences in foraging and diving effort variables between colonies (Fig. 6b). This method is based on a hybrid technique that joins a hierarchical cluster analysis, based on Mahalanobis distance (Mahalanobis 1948), with the principle of hypothesis testing for multivariate statistics. While other algorithms do not take into account the fact that each treatment is represented by a set of replicated observations, Valdano and Di Rienzo (2008) recommend using MDGC to decide the number of clusters in these cases. This technique is successful in answering, on the basis of inferential statistics, the problems of determining the number of groups in hierarchical cluster analysis (see Márquez et al. 2010). The graphical output of the MDGC test (Fig. 6b) is a very useful tool, since it shows a clear distinction between statistically different diving (and foraging) behavior parameters from each locality as well as their relationships. Clustering of multivariate objects is here used as an exploratory data method in order to obtain more knowledge about the structure of the observations and/or variables under study (see Härdle and Simar 2007).

For all statistical tests, the threshold was taken to be 5 %. Statistical analyses were performed using the open

source statistical package R version 2.13.0 (R Development Core Team 2011). Data are given as mean \pm SD unless otherwise noted.

Results

A total of 31,178 dives was analyzed with 17,795 classified as foraging and 13,383 as traveling. The large number of undulations associated with the bottom phase of dives taken to be foraging confirmed their function (GLMMs; Punta Norte: $N_{(\text{dives})} = 8,955$, $N_{(\text{Ind.})} = 14$, $X^2 = 2,206$, $P < 0.0001$; Bahía Bustamante: $N_{(\text{dives})} = 4,598$, $N_{(\text{Ind.})} = 10$, $X^2 = 480$, $P < 0.0001$; Puerto Deseado: $N_{(\text{dives})} = 5,245$, $N_{(\text{Ind.})} = 6$, $X^2 = 2,065$, $P < 0.0001$; Puerto San Julián: $N_{(\text{dives})} = 12,380$, $N_{(\text{Ind.})} = 12$, $X^2 = 1,480$, $P < 0.0001$; see “Methods”).

Basic diving variables

Penguins from Bahía Bustamante had both the fewest overall dives and fewest foraging dives (519 and 182, respectively) during their foraging excursions, while penguins from Puerto San Julián had the most dives overall (1,099) and the highest number of traveling dives (665), with birds from Punta Norte having the most foraging dives per trip (593) (Table 2).

The overall mean of dive depth was 25.2 ± 17.0 m, with the deepest dive being recorded from a bird at Puerto Deseado at 88.7 m. Penguins spent an overall mean of 80.4 ± 29.5 s submerged during foraging dives, and the longest dive recorded was 188 s (by a penguin from Punta Norte). There was strong correlation between the duration and maximum depth reached during dives ($y = -0.016x^2 + 2.60x + 28.30$; $r^2 = 0.64$, $F_{1,31,175} = 2,424$, $P < 0.0001$).

Penguins from different colonies used the water column differently during foraging dives (Fig. 1). Birds from Punta Norte, Puerto San Julián, and Bahía Bustamante had monomodal distributions in the frequency of dive depths and durations (Fig. 1a, b, d), albeit with differences between colonies (Table 2), while those from Puerto Deseado showed a bimodal distribution of the maximum depths reached (Fig. 1c). During foraging dives, Bahía Bustamante penguins dived significantly deeper and longer than birds from the other colonies (with mean maximum depths and durations of 52 m and 118 s, respectively) (Table 2). These penguins also needed most time at the surface to recover from their dives ($X^2_{(3)} = 16.6$, $P = 0.0009$; Table 2). For all the colonies, the surface recovery period increased linearly with the duration of the dives (Punta Norte: $r^2 = 0.83$, $F_{1,16} = 80.6$, $P < 0.0001$;

Table 2 Summary statistics of basic diving variables (see text) for Magellanic penguins, during the early chick-rearing period, according to colony

Colony	Punta Norte	Bahía Bustamante	Puerto Deseado	Puerto San Julián	Statistic _(df)	<i>P</i>
Total number of dives (<i>n</i>)	720.7 (236.1) [453–1,228]	519.3 (121.5) [324–657] ^a	817.8 (357.5) [519–1,323]	1,099.7 (337.9) [694–1,946] ^a	$H_{KW(3)} = 14.6$	0.002
No. of foraging dives (<i>n</i>)	593.3 (208.1) [369–1,036] ^b	182.2 (77.7) [100–312] ^{b,c}	534.3 (159.8) [395–756] ^c	444.1 (135.2) [234–656]	$H_{KW(3)} = 15.5$	0.002
No. of non-foraging dives (<i>n</i>)	127.4 (47.0) [79–207] ^d	337.2 (81.3) [224–449]	283.5 (198.0) [124–567]	665.6 (322.8) [390–1,563] ^d	$H_{KW(3)} = 23.6$	<0.0001
Percentage of foraging dives (%)	82.0 (4.9) [72.8–90.7] ^{b,c}	34.5 (9.5) [22.7–48.7] ^b	68.0 (8.1) [57.1–76.1]	41.7 (11.1) [19.7–57.8] ^d	$H_{KW(3)} = 24.1$	<0.0001
Dive depth (m)	22.2 (4.8) [12.2–31.6] ^b	51.8 (6.4) [39.1–65.4] ^{a,b,c}	23.9 (7.0) [11.4–33.8] ^c	21.0 (4.4) [16.4–35.9] ^a	$X^2_{(3)} = 50.1$	<0.0001
Dive duration (s)	79.4 (22.8) [50.4–164.7] ^d	117.7 (16.9) [66.9–157.6] [*]	76.7 (26.1) [39.4–154.6]	71.0 (11.9) [48.1–121.2] ^{d,*}	$L_{ratio(3)} = 7.9$	0.049
Descent duration (s)	21.3 (9.9) [12.5–71.8] ^e	37.5 (9.3) [15.3–72.7] ^c	17.0 (8.8) [7.5–55.7] ^{c,e}	17.4 (3.7) [10.3–37.8]	$X^2_{(3)} = 16.3$	0.001
Bottom duration (s)	37.7 (6.0) [28.6–68.3]	46.8 (8.0) [28.9–68.1]	41.9 (8.8) [27.8–69.6]	36.8 (6.7) [28.7–52.1]	$X^2_{(3)} = 2.4$	0.4993
Ascent duration (s)	20.3 (8.8) [9.6–67.1]	33.4 (7.6) [14.5–57.9]	17.8 (8.1) [8.1–51.6]	16.8 (4.2) [10.6–35.9]	$X^2_{(3)} = 7.7$	0.0533
Post-dive interval (s)	22.0 (9.7) [12.6–71.2] ^d	38.6 (12.4) [14.7–94.3] [*]	19.9 (9.0) [8.7–56.0] ^{f,*}	26.1 (5.9) [16.5–54.8] ^{d,f}	$X^2_{(3)} = 16.6$	0.0009
Descent rate (m s ⁻¹)	0.84 (0.26) [0.40–1.65] ^{d,e}	1.29 (0.24) [0.65–1.80] ^{a,c}	1.27 (0.23) [0.59–2.19] ^{c,e}	1.08 (0.15) [0.61–1.64] ^{a,d}	$L_{ratio(3)} = 38.6$	<0.0001
Ascent rate (m s ⁻¹)	0.90 (0.26) [0.50–2.15] ^{d,e}	1.43 (0.28) [0.77–2.33] ^a	1.07 (0.25) [0.64–2.59] ^e	1.14 (0.17) [0.80–1.83] ^{a,d}	$X^2_{(3)} = 29.0$	<0.0001

Results are based on 31 birds (penguins with completed foraging trips) for the first four variables and on 42 individuals with a total of 17,795 dives for the remaining variables. Mean values, standard deviation (SD), and range [min–max] are given. Mean values and significant statistical values are shown in bold. Kruskal–Wallis test with a Dunn’s multiple comparison contrast or Generalised Linear Mixed-effects Models (GLMM) with a Tukey’s multiple comparison test to compare between colonies were used

The significant differences ($P < 0.05$) in the results of post hoc Dunn’s or Tukey’s contrast are shown by the superscript letters as follows: * nearly significant contrast ($0.1 > P > 0.05$). ^a Bahía Bustamante vs. Puerto San Julián; ^b Punta Norte vs. Bahía Bustamante; ^c Bahía Bustamante vs. Puerto Deseado; ^d Punta Norte vs. Puerto San Julián; ^e Punta Norte vs. Puerto Deseado; ^f Puerto Deseado vs. Puerto San Julián

Bahía Bustamante: $r^2 = 0.69$, $F_{1,14} = 31.3$, $P < 0.0001$;
 Puerto Deseado: $r^2 = 0.76$, $F_{1,15} = 47.8$, $P < 0.0001$;
 Puerto San Julián: $r^2 = 0.83$, $F_{1,12} = 60.6$, $P < 0.0001$).

In addition, pause duration increased as a function of the maximum dive depth (Fig. 2). Differences in dive duration (and depth) were also reflected in the descent phase of the dives, being highest in Bahía Bustamante penguins ($X^2_{(3)} = 16.3$, $P < 0.001$; Table 2). Vertical velocities (descent and ascent rates) were also different between colonies (Table 2). Penguins from Bahía Bustamante and Puerto Deseado descended the water column significantly faster than birds from the other two colonies ($L_{ratio(3)} = 38.6$, $P < 0.0001$; Table 2) and Bahía Bustamante penguins ascended the water column markedly faster than their conspecifics at other colonies ($X^2_{(3)} = 29.0$, $P < 0.0001$; Table 2).

Diving effort

Dive efficiency decreased with increasing dive depth (Fig. 3). Penguins from Bahía Bustamante had a lower DE than other birds, primarily because the post-dive recovery periods at the surface were longer ($L_{ratio(3)} = 20.8$, $P = 0.0001$; Table 3), but also because birds only spent 40 % of their dive duration in the bottom phase of their dives (PDDBP; Table 3). The greatest dive effort (DEff; see “Materials and methods”) occurred in Puerto Deseado birds ($X^2_{(3)} = 16.0$, $P = 0.001$; Table 3).

Foraging effort

The distances travelled per dive (defined as the dive duration multiplied by 2.1 m s^{-1} ; see “Methods”) were

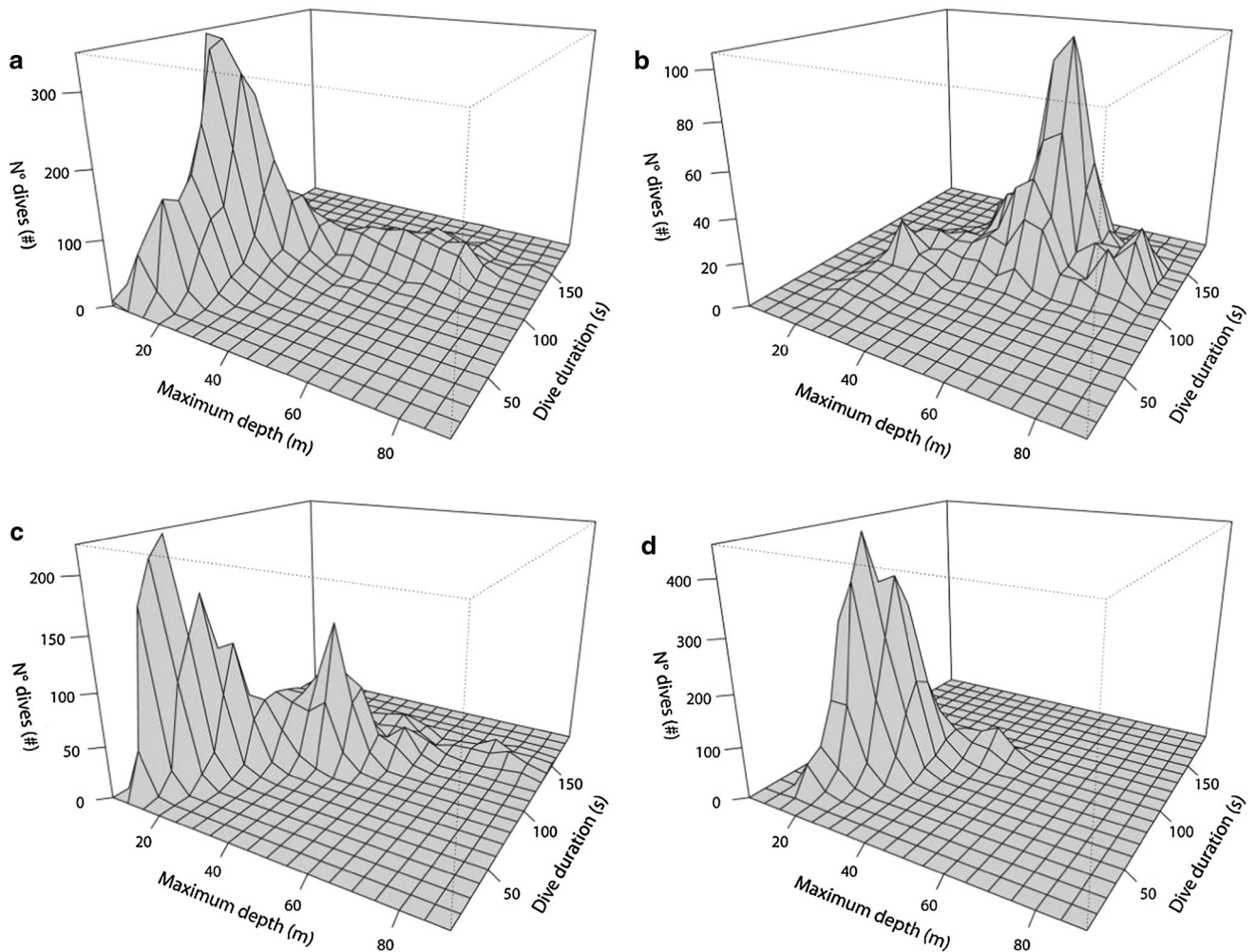


Fig. 1 Frequency distribution by depth and duration for the foraging dives made by Magellanic penguins *Spheniscus magellanicus* from **a** Punta Norte, **b** Bahía Bustamante, **c** Puerto Deseado, and **d** Puerto San Julián; during foraging trips at-sea

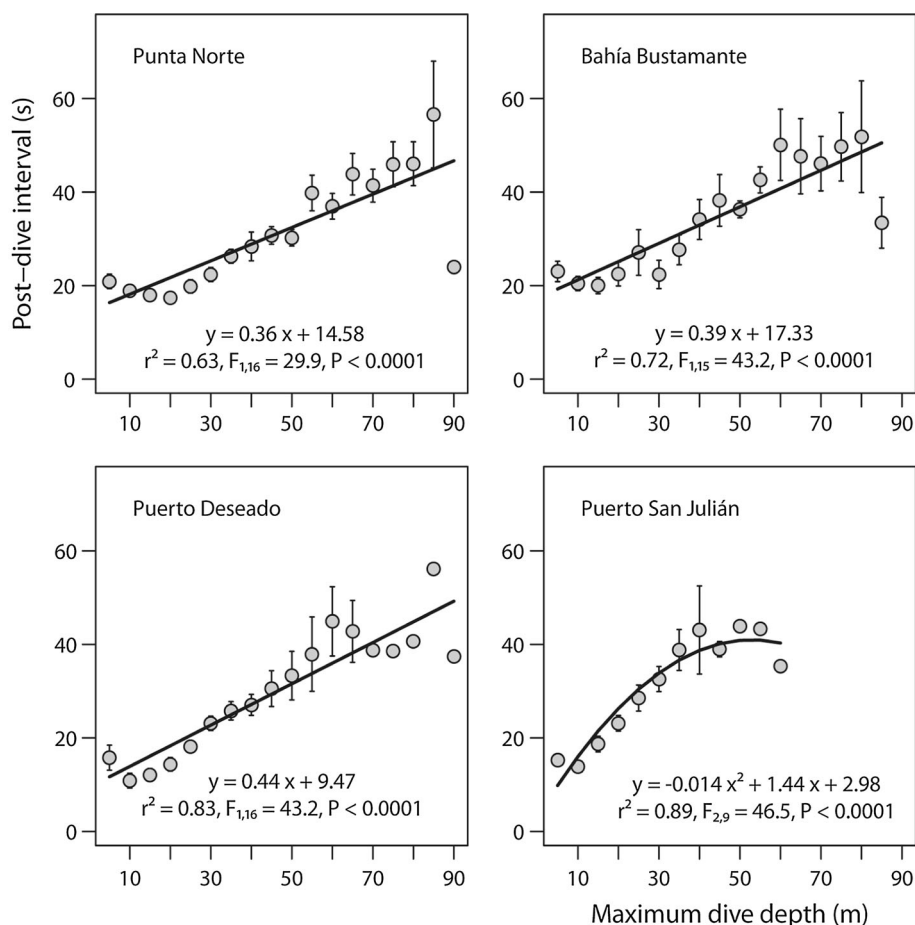
highest for penguins from Bahía Bustamante, swimming up to 66 % more than individuals from the other colonies ($L_{\text{ratio}(3)} = 43.9$, $P < 0.0001$; Table 4). However, foraging penguins from Puerto San Julián swam the greatest total distances underwater (i.e. the sum of all distances covered in all dives), these being approximately twice those travelled by Bahía Bustamante birds (127 vs. 77 km, respectively; $H_{\text{KW}(3)} = 9.4$, $P = 0.0244$; Table 4). The greatest traveling effort in terms of the total vertical distances covered during the bottom phase was made by birds from Puerto Deseado and Bahía Bustamante, being about double the rest (~ 23 vs. ~ 12 m, respectively; $X^2_{(3)} = 37.7$, $P < 0.0001$; Table 4). The mean wiggle amplitude was 37–57 % higher in Bahía Bustamante than in the other colonies ($X^2_{(3)} = 38.4$, $P < 0.0001$; Table 4). Finally, the number of wiggles per minute of bottom phase (WPMBT; cf. Raya Rey et al. 2012) and the capture efficiency index (CEI, see “Methods”; cf. Zimmer et al. 2010) were

highest for penguins from Puerto Deseado, being almost three times greater than in Bahía Bustamante and twice that of Punta Norte and Puerto San Julián ($X^2_{(3)} = 19.7$, $P = 0.0002$; $X^2_{(3)} = 42.4$, $P < 0.0001$; respectively; Table 4). The WPMBT generally decreased as dive depth increased, down to values of ca. 1.5 wiggles min^{-1} (Fig. 4). The CEI also decreased with increasing dive depth, showing maxima that concurred at the same depth as those in the WPMBT (Figs. 4, 5). Of particular note was that Puerto Deseado penguins had CEI-values at 45–50 m depth that were more than double those for the other colonies (Fig. 5).

Diving patterns

PCA made on 18 variables of foraging dives reduced these metrics to three principal components, which were mainly related to diving mode (PC1; i.e. basic diving variables closely related to depth and duration), foraging effort (PC2;

Fig. 2 Post-dive interval as a function of maximum dive depth for Magellanic penguins from each colony. The number of penguins and dives with respect to site are given in Table 1. Values are grand means \pm 1SE. The *black line* corresponds to the curve that best fitted the data



i.e. mainly those variables most strictly related to the wiggle performance) and diving frequency (PC3) (Table 5). In general, PCA was in concordance with results gathered by general linear mixed-effects models. Thus, PC1 indicated that penguins from Bahía Bustamante dived deeper and for longer periods, travelled greater distances underwater per dive, and spent longer recovery time at the surface (Fig. 6a). This, led to lower values of DE and proportion of time diving in the bottom phase (i.e. PDDBP), which clearly differed from the other colonies (Fig. 6a). Conversely, PC2 showed that birds from Puerto Deseado experienced exceptionally high foraging activity during dives, characterized by the highest number of wiggles, and wiggles per time in the bottom. They also showed the highest value of capture efficiency index and the greatest vertical distances travelled in the bottom phase, which clearly differed to the foraging penguins from Punta Norte and Puerto San Julián (Fig. 6a). Finally, PC3 described that the highest diving frequency values (i.e. dive effort and dive to pause ratio) corresponded to Punta Norte birds, followed by Puerto Deseado and Bahía Bustamante, and the lowest were represented by penguins from Puerto San Julián (Table 5).

Overall, the dendrograms calculated by the Mahalanobis distance matrix (UPGMA) showed that the greatest distances occurred between Bahía Bustamante and the rest of the studied colonies (Fig. 6b). The shortest distance happened between Punta Norte and Puerto San Julián. However, according to the principle of hypothesis testing (MDGC) proposed by Valdano and Di Rienzo (2008), each penguin colony presented a differentiated diving behavior with significant statistical differences [the horizontal black line (in bold) in Fig. 6b, corresponds to the cut-off criterion ($P = 0.05$) obtained with the MDGC test].

Discussion

There is increasing evidence that penguins show considerable plasticity in their diving behavior (e.g., Wilson et al. 1996; Ropert-Coudert et al. 2004; Hennicke and Culik 2005; Petersen et al. 2006; Chiaradia et al. 2007; Pichegru et al. 2011). In particular, Magellanic penguins appear to adjust their foraging behavior to prey abundance and other variables (Radl and Culik 1999; Wilson et al. 2011; Raya Rey et al. 2012; but see Walker and Boersma 2003).

Fig. 3 Dive efficiency (DE; see text) as a function of maximum dive depth for Magellanic penguins from each colony. Number of penguins and dives with respect to each site are given in Table 1. Values are grand means \pm 1SE. The black line corresponds to the curve that best fitted the data

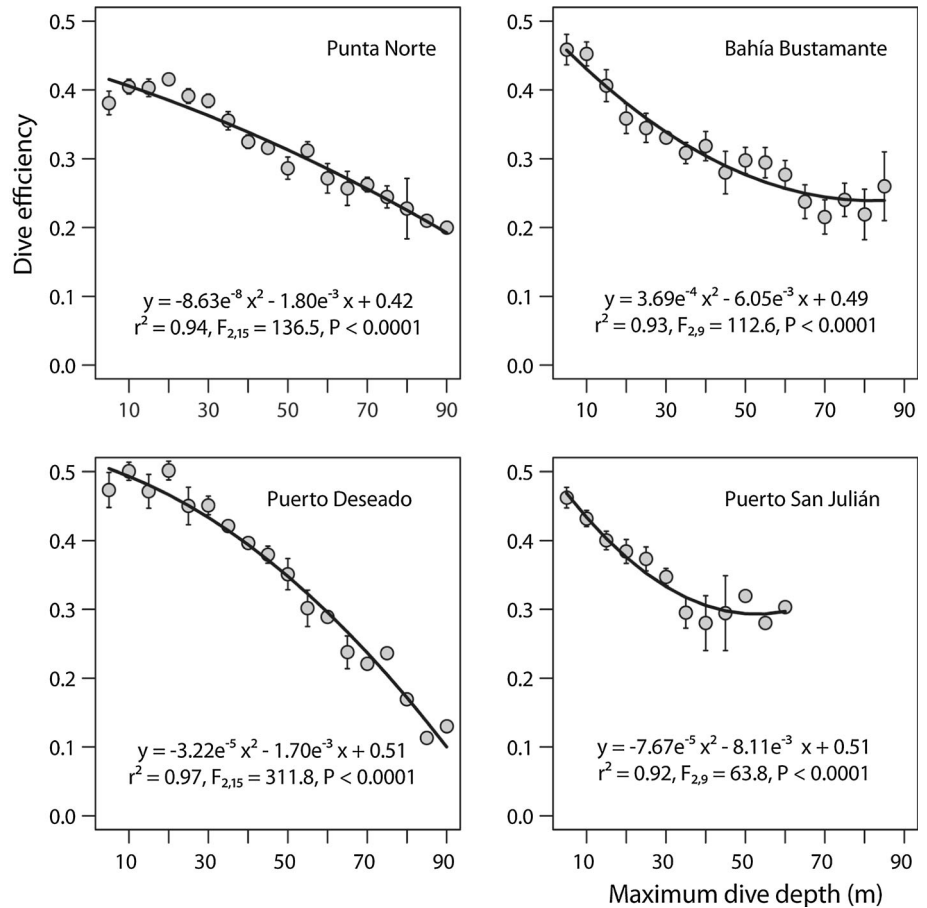


Table 3 Summary statistics of diving effort variables (see text) for Magellanic penguins ($n = 42$), during the early chick-rearing period, according to colony

Colony	Punta Norte	Bahía Bustamante	Puerto Deseado	Puerto San Julián	<i>N</i>	Statistic _(df)	<i>P</i>
Dive efficiency (DE)	0.38 (0.05) [0.19–0.47] ^a	0.30 (0.05) [0.23–0.34] ^b	0.45 (0.05) [0.30–0.53] ^{a,b,c}	0.38 (0.05) [0.26–0.50] ^c	17,532	$L_{ratio(3)} = 20.8$	0.0001
Proportion of dive duration in bottom phase (PDDBP)	0.48 (0.06) [0.26–0.59] ^a	0.40 (0.06) [0.24–0.58] ^b	0.56 (0.06) [0.37–0.65] ^{a,b,c}	0.52 (0.06) [0.37–0.66] ^c	17,795	$L_{ratio(3)} = 16.4$	0.001
Dive to pause ratio	7.7 (3.0) [2.9–27.1] ^{d,e}	5.0 (2.8) [1.5–14.5] ^d	5.0 (1.2) [2.7–10.5]	4.3 (1.5) [2.2–9.2] ^e	17,795	$\chi^2_{(3)} = 24.6$	<0.0001
Dive effort (DEff)*	0.75 (0.003) [0.73–0.79] ^a	0.72 (0.003) [0.71–0.74] ^b	0.78 (0.002) [0.71–0.79] ^{a,b,c}	0.72 (0.003) [0.71–0.73] ^c	17,795	$\chi^2_{(3)} = 16.0$	0.001

Mean values, standard deviation (SD), and range [min–max] are given. Mean values and significant statistical values are shown in bold. Generalised Linear Mixed-effects Models (GLMM) with a Tukey’s multiple comparison test to compare between colonies were used

The significant differences ($P < 0.05$) in the results of post hoc Tukey’s contrast are shown by the letters in superscript as follows: * data were \log_{10} -transformed for the statistical analysis. ^a Punta Norte vs. Puerto Deseado; ^b Bahía Bustamante vs. Puerto Deseado; ^c Puerto San Julián vs. Puerto Deseado; ^d Punta Norte vs. Bahía Bustamante; ^e Punta Norte vs. Puerto San Julián

Our results show that birds from the various colonies use the water column differentially (Fig. 1). Bathymetry data (Parker et al. 1997) of the foraging areas around the colonies (Sala et al. 2012b) make it clear that bottom topography plays no appreciable role in this. Dive depth selection impacts virtually all other dive parameters

because deeper dives have longer transit phases between the surface and the foraging (bottom phase) depth (Tremblay and Cherel 2000; Charrassin et al. 2002; Cook et al. 2012). In addition, longer dives require longer recovery periods (Parkes et al. 2002; Wilson 2003; Zimmer et al. 2010), so it is clear that a first examination of

Table 4 Summary statistics of foraging effort variables (see text) for Magellanic penguins, during the early chick-rearing period, according to colony

Colony	Punta Norte	Bahía Bustamante	Puerto Deseado	Puerto San Julián	Statistic _(df)	<i>P</i>
Distance travelled per dive (m)	166.7 (16.6) [142.3–195.5] ^a	247.3 (13.6) [225.1–270.0] ^{a,b,c}	161.1 (39.6) [96.9–246.1] ^c	149.1 (20.0) [119.0–196.0] ^b	$L_{\text{ratio}(3)} = 43.9$	<0.0001
Total distance swum per trip (km)*	106.5 (24.28) [77.7–159.0]	76.60 (22.0) [44.2–107.7] ^b	112.3 (52.1) [49.9–177.5]	126.8 (42.0) [76.04–239] ^b	$H_{\text{KW}(3)} = 9.4$	0.0244
Total way vertical at bottom per dive (m)	12.2 (1.9) [8.3–15.4] ^{a,d}	20.8 (5.6) [14.9–39.0] ^{a,b,c}	25.3 (6.1) [11.2–37.5] ^{c,d,e}	11.1 (2.4) [8.2–16.0] ^{b,e}	$X^2_{(3)} = 37.7$	<0.0001
Mean wiggle amplitud (m wiggle ⁻¹)	15.9 (1.4) [13.7–18.8] ^a	23.6 (5.7) [17.4–35.3] ^{a,b,c}	17.2 (1.8) [15.5–21] ^c	15.0 (1.0) [13.1–18.0] ^b	$X^2_{(3)} = 38.4$	<0.0001
Wiggles per minute at bottom time (WPMBT)	1.48 (0.20) [1.17–1.84] ^d	1.50 (0.32) [1.00–2.21] ^c	2.61 (0.54) [1.83–3.26] ^{c,d,e}	1.52 (0.42) [0.98–2.22] ^c	$X^2_{(3)} = 19.7$	0.0002
Capture efficiency index (WPMBT × DE)	0.52 (0.07) [0.39–0.63] ^{a,d}	0.40 (0.04) [0.32–0.44] ^{a,b,c}	1.15 (0.28) [0.72–0.1.56] ^{c,d,e}	0.55 (0.15) [0.35–0.87] ^{b,e}	$X^2_{(3)} = 42.4$	<0.0001

Results are based on 31 birds (penguins with completed foraging trips) for the Total distance swum and on 42 individuals with a total of 17,795 dives for the rest of variables. Mean values, standard deviation (SD), and range [min–max] are given. Mean values and significant statistical test are shown in bold. Kruskal–Wallis test with a Dunn’s multiple comparison contrast or Generalised Linear Mixed-effects Models (GLMM) with a Tukey’s multiple comparison test to compare between colonies were used

The significant differences ($P < 0.05$) in the results of post hoc Dunn’s or Tukey’s contrast are shown by the superscript letters as follow: * total distance travelled underwater throughout the foraging trip, including foraging and non-foraging dives. ^a Punta Norte vs. Bahía Bustamante; ^b Bahía Bustamante vs. Puerto San Julián; ^c Bahía Bustamante vs. Puerto Deseado; ^d Punta Norte vs. Puerto Deseado; ^e Puerto Deseado vs. Puerto San Julián

intercolony variation should consider dive depth selection. Here, our data from Punta Norte, Puerto Deseado, and Puerto San Julián correspond roughly to those recorded by other authors (e.g., Peters et al. 1998; Radl and Culik 1999; Walker and Boersma 2003; Raya Rey et al. 2010, 2012), with mean dive depth being of the order of 20 m. However, the mean depth of foraging dives of Bahía Bustamante Magellanic penguins exceeded these by a factor of two (Table 2). Unsurprisingly, therefore, these birds also executed the longest, and consequently the fewest, foraging dives during their trips at sea (Table 2). Furthermore, Bahía Bustamante was the only colony for which we have studied more than one season and found no interannual differences in the basic diving parameters (see “Methods”). However, this concerns only one site and we cannot exclude entirely that interannual differences may have also affected our results and that interannual variability in the oceanographic environment where Magellanic penguins forage differs between sites. Southern marine ecosystems, in general, and the area exploited by Magellanic penguins from the studied colonies in particular, are usually characterized by their stability (Acha et al. 2004; Rivas et al. 2006). This presumably accounts for the remarkable interannual consistency in the foraging routes taken by Magellanic penguins from Punta Tombo, as documented by Boersma et al. (2009) (cf. Sala et al. 2012b), and other Patagonian seabirds (Quintana et al. 2010, 2011; Harris

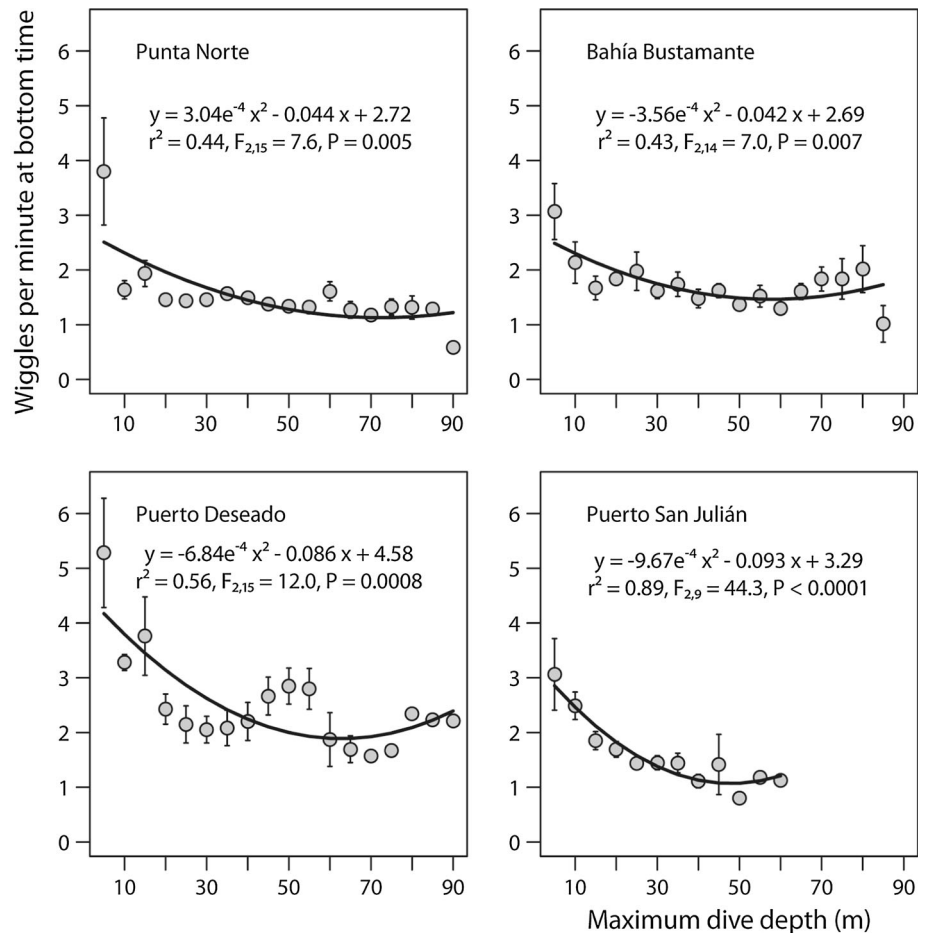
et al. 2012). Evidence of individual consistency in foraging behavior within and amongst seasons reinforces the notion that the environment surrounding the studied colonies (Acha et al. 2004) and, presumably, targeted prey are stable enough in a similar way over time, even years.

Colony-specific diving patterns and plasticity in diving behavior

We propose that there are three primary types of diving patterns exhibited by Magellanic penguins from the four colonies studied, grouped according to: (1) the birds of Punta Norte and Puerto San Julián, (2) those from Puerto Deseado; and (3) those from Bahía Bustamante (see Fig. 6b).

Punta Norte and Puerto San Julián Penguins from these sites mainly executed foraging dives to intermediate maximum depths (between 15 and 30 m; Fig. 1a, d) and had similar values for DE, proportion of bottom time (PDDBP), and dive effort (DEff) (Table 3). However, the dive to pause ratio differed between the two colonies, being higher for Punta Norte than for Puerto San Julián (Fig. 6a; Tables 3, 5). If penguins attempt to maximize foraging efficiency by minimizing the time at the surface compared to that underwater (cf. Shepard et al. 2009), this would imply that Puerto San Julián birds expend more energy than Punta Norte birds during diving. The explanation for

Fig. 4 Number of wiggles per minute at bottom time (WPMBT) as a function of maximum dive depth for Magellanic penguins from each colony. Number of penguins and dives with respect to each site are given in Table 1. Values are grand means \pm 1SE. The black line corresponds to the curve that best fitted the data

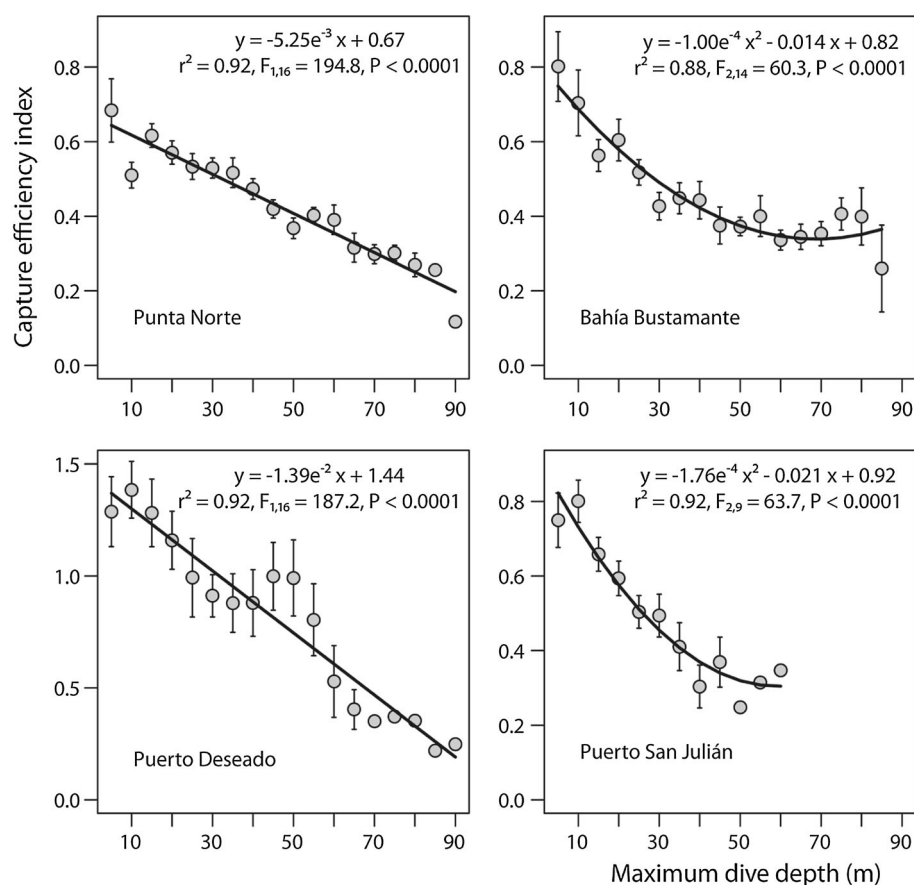


this lies in the fact that, although the minimum recovery time at the surface is generally determined by the dive duration (see above), it is actually most likely to be modulated by the oxygen used during the dive, itself a direct function of the energy expenditure of the bird. The reason that dive duration per se is most often used as a proxy, although it is rarely explicitly stated, is that diving animals generally expend more energy during longer dives because they have continuous minimum power requirements (i.e. energy expenditure; see Shepard et al. 2009). However, increases in speed, for example, increase power requirements exponentially above this so that choice of speed underwater can hugely change the oxygen debt incurred by birds during dives of standardized duration. We thus propose that the Puerto San Julián penguins have higher power requirements during the bottom phase than do birds from Punta Norte, even though, in other respects, the dives are very similar. This would be mainly modulated by the availability and type of prey captured by penguins from Puerto San Julián, obtaining significantly lower revenues on each dive, in terms of energy and wet mass, compared to those of Punta Norte (for details of prey characteristics, see Sala et al. 2012a). Assuming we are correct in this, we can

only further speculate that the reasons for these higher power requirements relate to speed, since the amount of vertical movement during the bottom phases of the dives, which incurs higher energy costs (Wilson et al. 2010, 2011) as well as the wiggles per minute at bottom time, were both very similar for the two colonies.

Puerto Deseado Only penguins from Puerto Deseado had an obviously bimodal frequency distribution of depth use during foraging dives (Fig. 1c), possibly due to them exploiting prey species with different depth distributions. In this colony, the diet is far more diverse than the rest, being composed mainly, and in order of importance, of coastal fish (e.g., *Syngnathus* sp., *Austroatherina* sp., etc.), Squid of the genus *Loligo*, Fuegian Sprat, and, to a lesser extent, Hake (Frere et al. 1996). The distribution of depths and times employed by penguins from Puerto Deseado, depicted in Fig. 1c, may correspond to the near-surface depths used by Fuegian Sprat and shore fishes with the second modal value corresponding to the deeper depths used by Hake and Squid from this area (Sánchez et al. 1995; Sabatini 2004; for discussion, see Wilson et al. 2005). Dives had high DE values, with a large proportion of time spent in the bottom phase (Tables 3, 5). The results

Fig. 5 Capture efficiency index (CEI; see text) as a function of maximum dive depth for Magellanic penguins from each colony. Number of penguins and dives with respect to each site are given in Table 1. Note the difference in the y-axis for the colony of Puerto Deseado. Values are grand means \pm 1SE. The black line corresponds to the curve that best fitted the data



are consistent with those of Sala et al. (2012a), who reported the exceptionally high diving rate values (i.e. 41.4 dives h^{-1}), as well as a high percentage time diving (in relation to resting on the surface) for this colony.

Bahía Bustamante The deeper, and therefore longer, dives conducted by the penguins from Bahía Bustamante resulted in low DE values stemming from the disproportionately long recovery times at the surface, together with the low proportion of time spent in the bottom phase (Tables 2, 5). The optimum time that diving animals should spend at the foraging depth to maximize net rate of energy gain is complex (Shepard et al. 2009 and references therein), relating particularly to total oxygen stores and recovery durations at the surface (e.g., Butler and Jones 1997). However, for a given amount of oxygen, as animals spends longer in transit between the surface and the foraging depth, they simply have less oxygen available to exploit prey at depth, which explains why bottom durations tend to decrease with depth once a certain depth has been surpassed (Wilson et al. 2005; Zimmer et al. 2010). Deep dives with reduced bottom durations are tenable as long as prey capture rates make it worthwhile. In this respect, we note that Bahía Bustamante penguins appear to have, in general, a decreasing wiggle rate with depth (Figs. 4, 5) so perhaps prey items caught at greater depths are larger or

have higher calorific value (see Sala et al. 2012a). A consequence of the long dives with long recovery periods at the surface is that Bahía Bustamante birds had a disproportionately low number of total foraging dives during foraging trips (Table 2) and fewer hours actually underwater than birds from the other colonies (see Sala et al. 2012a). This does not mean, however, that they were working less hard (cf. Chiaradia et al. 2007). Despite all this, it should be noted that the DE, WPMBT, and CEI experience an increase in their average values around 80 m deep (Figs. 3, 4, 5), which could be related to the increasing of capture success on deeper waters when targeting benthic prey such as Hake (see Sala et al. 2012a for a more detailed discussion).

Plasticity in diving behavior Walker and Boersma (2003) studied the diving behavior of Magellanic penguins from Punta Tombo and analyzed the variation between years and within breeding seasons, reporting no differences in terms of the maximum depth and duration of dives and percentage of time spent diving, although trip duration varied (Walker and Boersma 2003). While recognizing variable brood demands over time and prey availability fluctuation within and between seasons, they suggest that penguins would find it impossible to change the type of prey consumed regularly (i.e. almost exclusively Anchovy;

Table 5 Component loadings of 18 variables derived from diving behavior of Magellanic penguins breeding at four colonies from Patagonia, Argentina

Variable	PC1 61.2 %	PC2 28.4 %	PC3 10.4 %
Maximum depth (m)	0.29	0.10	0.02
Dive duration (s)	0.29	0.05	0.18
Descent duration (s)	0.29	-0.06	0.18
Bottom duration (s)	0.25	0.25	0.08
Ascent duration (s)	0.29	0.01	0.20
Pause (s)	0.29	-0.04	-0.14
Diving efficiency	- 0.27	0.18	-0.07
PDDBP ^a	- 0.27	0.14	-0.21
Vertical velocity down (m s ⁻¹)	0.14	0.34	-0.33
Vertical velocity up (m s ⁻¹)	0.23	0.19	- 0.34
Total way vertical at bottom (m)	0.09	0.42	0.05
Distance travelled per dive (m)	0.29	0.05	0.18
Dive to pause ratio	-0.18	0.15	0.54
Dive effort	-0.19	0.16	0.51
Wiggles	-0.04	0.44	0.02
Wiggles per minute at bottom time	-0.13	0.41	-0.03
Capture efficiency index	-0.21	0.31	-0.07
Mean wiggle amplitude (m wiggles ⁻¹)	0.26	0.22	0.08

Please note that, collectively, the first three principal components explained 100 % of total variance in the data. The identity of each colony was selected as classification criterion (see text). Parameters accounting for most of the variation in each principal component are shown in bold

^a Corresponds to the proportion of dive duration in bottom phase (see “Methods”)

Scolaro et al. 1999), which would explain their observations of lack of variation in diving behavior. They went further though, concluding that Magellanic penguins can only adjust the duration of their foraging trips, suggesting the absence of behavioral plasticity in relation to the diving capabilities.

In contrast to this research, our results demonstrate behavioral plasticity at the level of the foraging trip, the dive, and indeed within the different phases of the dive (cf. also Raya Rey et al. 2012). Wilson et al. (2011) present the concept of the performance envelope, which describes how penguin power requirements will necessarily vary according to performance, being modulated by ‘*N*’ variables, most notable of which will be speed, depth, and swim angle with respect to the surface. These latter two parameters modulate power requirements because depth relates to hydrostatic pressure which affects penguin body air-volume, and therefore buoyancy (Wilson et al. 1992), and swim angle with respect to the surface determines the work

done by the bird in its swimming trajectory (Wilson et al. 2010). Wilson et al. (2011) argue that physical and physiological constraints mean that power use by penguins cannot vary under certain performance conditions. However, this is very different from invariance in behavioral plasticity, which has already been noted in the diving behavior of the Magellanic penguin. For example, Wilson et al. (2010) report how Magellanic penguins change the descent angle of the dive according to whether prey were caught in the previous dive or not, and how this species even loads body oxygen at the surface according to the amount of prey caught in the previous dive (Wilson 2003). Such reaction to prey abundance and spatial distribution is typical of optimal foraging in animals and has been demonstrated repeatedly (e.g., Watanuki et al. 1993; Ropert-Coudert et al. 2001, 2006; Takahashi et al. 2003; Zimmer et al. 2010), and it would be extraordinary if the Magellanic penguin did not conform to some degree.

Foraging effort

In analyzing the relationship of some of the variables used as indicators of foraging effort (i.e. distances underwater, see “Methods”) with the number of dives made by penguins from each colony, we observed: (1) an inverse relationship between the total distance travelled underwater during foraging trips and that covered during mean dives, and (2) a direct relationship between the distance travelled underwater per foraging trip and the total number of dives performed (Fig. 7).

The first relationship is derived from the fact that short dives have correspondingly relatively shorter recovery durations than long dives, so that birds executing many short dives will actually spend a greater percentage of their time underwater which, assuming constant swim speed (see “Methods”), will necessarily equate to greater distances travelled.

Sala et al. (2012b) show how measures of the foraging effort derived from the extent of horizontal movement during foraging trips correlates with population growth rates. Specifically, they found that penguins from colonies that spend more time away from their nests, traveling greater distances to and within foraging areas (i.e. Bahía Bustamante, Puerto Deseado, and Punta Tombo), are those with the lowest rates of population change. This accords with intra-colony data reported by Boersma and Rebstock (2009), who showed how increased distances between the Punta Tombo penguin colony and the foraging areas were negatively correlated with reproductive success. Inspection of diving behavior and effort can potentially enhance this picture. We note, for example, that the Magellanic penguin colonies at Bahía Bustamante and Puerto Deseado (located in the center of the breeding

Fig. 6 a Component loadings of 18 variables (black dots) derived from Magellanic Penguin foraging dives on the first two principal components (PC1 and PC2; see Table 5). The positions of the colonies arising from the PCA are shown by gray dots. **b** Hierarchical clustering analysis (UPGMA) showing overall differences among diving penguins from the four studied colonies (see “Methods”). The cut-off criterion obtained with the MDGC test is indicated with a horizontal black line and corresponds to a 95 % significance (see “Methods”)

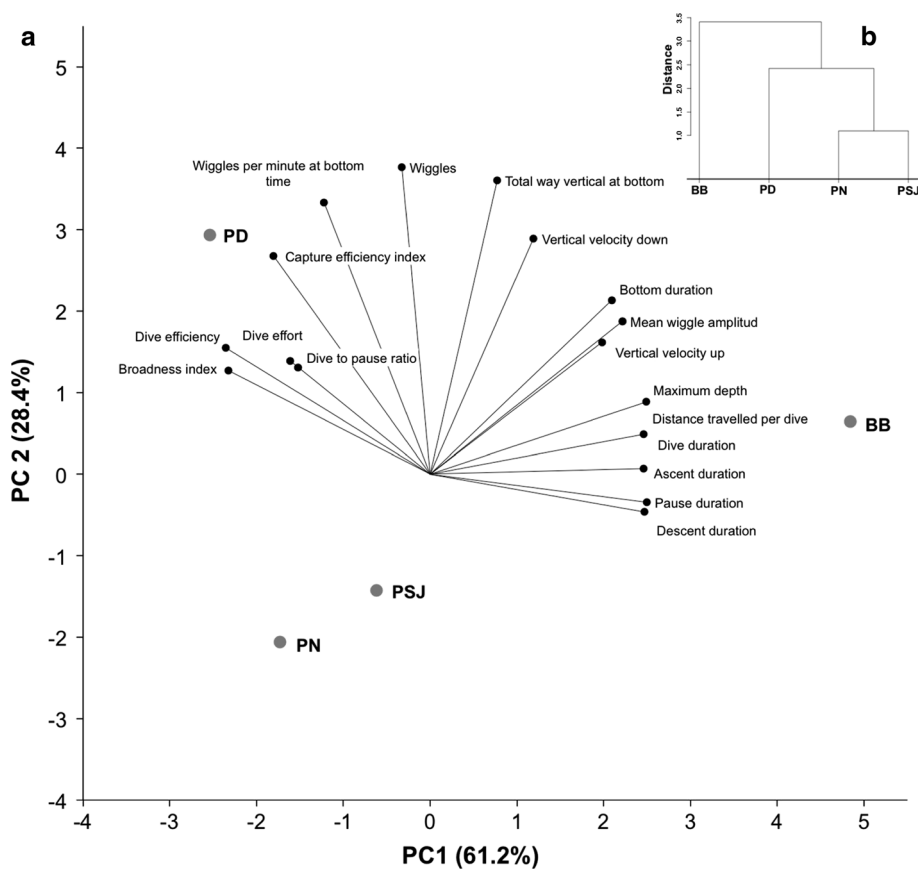
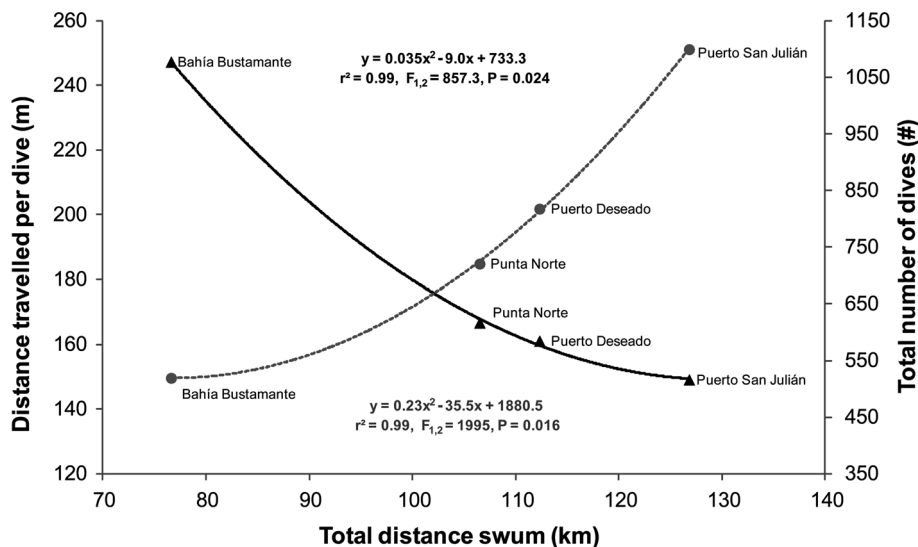


Fig. 7 Relationship between the average total distance swum per trip (km) by colony and: (1) mean total number of dives per trip (hash) (grey dots); (2) distance travelled per dive (m) (black triangles). Note that the grey dashed and black lines correspond to the curve that best fitted each dataset



range of the Patagonian coast) have lower levels of population growth rate (see Sala et al. 2012b) while taking a relatively large number of different species (see Sala et al. 2012a and references therein), and incurring some of the highest indicators of diving and/or foraging effort (see above; Tables 2, 3, 4, 5; Fig. 6a). Conversely,

the penguins of Punta Norte and Puerto San Julián are primarily monophagic (see Wilson et al. 2005 and references therein) and use well-defined, relatively shallow, depths (Fig. 1a, d), exploiting these with lower rates of descent and ascent (Table 2) which are less costly in terms of energy (see Wilson et al. 2010).

Conclusions

Our results are roughly consistent with previous studies on the diving behavior of breeding Magellanic penguins at other breeding colonies (e.g., Radl and Culik 1999; Walker and Boersma 2003; Raya Rey et al. 2010, 2012), but our particularly detailed examination of the diving behavior reveals some interesting inter-colony differences that have not been previously highlighted. Comparison of the diving (and effort) parameters calculated in our study with those obtained from Magellanic penguins at other breeding sites revealed major differences according to locality (Peters et al. 1998; Radl and Culik 1999; Walker and Boersma 2003; Raya Rey et al. 2012). We conclude that Magellanic penguins show marked plasticity in their diving behavior that is presumed to be related to the exploitation of the different prey types and that this contributes to their ability to breed while provisioning themselves along the ca. 5,000 km stretch of Argentinean and Chilean coastline encompassing a number of distinct marine ecosystems.

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