


RESEARCH ARTICLE

Food provisioning in Magellanic penguins as inferred from stable isotope ratios

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Rationale: Food provisioning is considered one of the main traits affecting offspring fitness. Differences in food provisioning between sexes, particularly in dimorphic species, could affect the amount and type of food provided, due to differences in the amount of food carried to the nest as a result of differential resources exploitation. Quantitative evidence for sexual differences in food provisioning by parents in penguins is scarce. The Magellanic penguin is moderately sexually dimorphic and breeds along a broad latitudinal range, with birds north and south of this range being essentially dietary specialists while those at intermediate latitudes consume a more diverse diet.

Methods: We used stable isotope analysis of carbon and nitrogen by isotope ratio mass spectrometry to examine if there was a differential parental contribution to chicks in ten Magellanic penguin colonies throughout its latitudinal breeding distribution. We used the heuristic Euclidean isotopic distance (ED) and individual isotope distances between the chicks and their parents as a proxy for diet similarity (the smaller the distance, the more similar the diet).

Results: The analysis showed that chicks tended to have a more similar diet to that of their male parent and that this pattern was more evident at colonies and in seasons where penguins had a more diverse diet, which could be explained by differences in diet between parents. Distance in $\delta^{15}\text{N}$ values, but not in $\delta^{13}\text{C}$ values, differed between both sexes and their chicks in all the pairs sampled, suggesting that $\delta^{15}\text{N}$ values drive the differences found in ED between chicks and their parents.

Conclusions: We have developed an approach that provides the first assessment of the extent of differential food provisioning between male and female Magellanic penguins. Results suggest chicks have a diet more similar to that of their male parent, probably related to the higher trophic level of male penguin prey.

1 | INTRODUCTION

Food provisioning is one of the crucial services that parents provide to their offspring and it has been positively linked with offspring survival in many altricial and semi-altricial bird species.^{1,2} Most birds have biparental care, although parents may have a differential contribution to chick provisioning.³ The overall bulk of food provided by any parent depends on the frequency with which it feeds the brood^{4,5} and the meal size.^{1,6,7} Many studies have demonstrated trophic segregation between sexes in both dimorphic and monomorphic seabirds,^{2,8,9} which may result in different patterns of food acquisition and thus a differential contribution of each parent when feeding the offspring. In sexually dimorphic species, differences in body size can also affect

the bulk and type of food provided by parents of different sex by either the amount of food carried to the nest or the differential ability to exploit resources related to body size (e.g. ¹⁰).

Differences in food provisioning between sexes have been reported in many seabird species, including albatrosses, shearwaters, auks, and terns.^{2,8,11,12} Quantitative evidence for the differential investment in food provisioning by parents in penguins is scarce, although there are a few studies that point to this. For example, in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*Eudyptes chrysocome*), females provide most of the food during the chick-rearing period.^{13,14} On the other hand, Adélie penguin (*Pygoscelis adeliae*) females perform long trips more frequently than males, resulting in a lower provisioning rate than males.¹⁵ In ecological studies,

stable isotope analysis has been widely used to track the sources of mass-energy in ecosystems and migration patterns, or for trophic studies.¹⁶ Because animals incorporate the isotopic composition of what they eat in proportion to the mass consumed corrected by a discrimination factor,^{17,18} stable isotope mixing models are good estimators of proportions consumed, integrating both the feeding rate and the amount of various types of food.

The Magellanic penguin (*Spheniscus magellanicus*) is a semialtricial and moderately sexually dimorphic species (on average males are 20% heavier than females¹⁹) that breeds in a broad latitudinal range (40–55°S) along the Atlantic and Pacific coasts of South America including the Malvinas/Falkland Islands.²⁰ During breeding, this species is a central-place forager, constrained to return to the colony to feed the chicks, which both parents do apparently equally.²¹ Some studies, however, have reported differences in the foraging behaviour between sexes,^{9,22–24} which means that there may be differential provisioning of resources to their chicks. In the present study, we used stable isotope analysis to assess the possible differences in food provisioning between sexes in the Magellanic penguin. For this, we measured stable isotopes in Magellanic penguin chicks and assessed the similarity of these values to those of their parents according to adult sex, colony, and variability of diet.

2 | EXPERIMENTAL

2.1 | Stable isotope analysis

Birds were sampled in January and early February (no intra-seasonal differences in adult blood stable isotope ratios were found in previous studies^{25,26}) during the 2012 and 2013 breeding seasons (Magellanic penguins breed between September and March, so our study encompasses two different years; for this reason we refer to seasons using the starting year as a reference point) at ten locations in a 41–52° latitudinal range along the Argentinean continental range of the species (Table 1, Figure 1). Penguins were captured from the leg with a hook on nests. Whole blood samples (cell + plasma) of 0.5 mL

were obtained from the metatarsal veins of 378 individual Magellanic penguins, of which 121 were adult females, 122 were adult males, and 135 were chicks. All samples were taken under permits provided by the Administración de Parques Nacionales, and Government of the Chubut and Santa Cruz provinces. All chicks were more than 3 weeks old, as determined by sampling date and/or their weight.²¹ The weight of the sampled chicks ranged between 0.9 and 3.5 kg, so we assumed that the maternal effect on stable isotope signatures was mostly diluted, as the mean half-life of stable isotope bird blood is 11.4 days²⁷ and chicks have increased their weight by a factor of between about 10 and 40 times. Magellanic penguins feed mainly on schooling fish, with anchovy (*Engraulis anchoita*) being the dominant prey in the north, and sprats (*Sprattus fuegensis*) in the south of the distribution.^{28,29} Penguins from colonies in the centre of the distribution have a more diverse diet but can rely on schooling fish in years of large recruitments of these species.^{25,28,29} In the present study, we sampled colonies where penguins are essentially diet specialists (>65% contribution is composed by one prey, e.g. Punta Norte and Cabo Vírgenes, where the diet is based mainly on anchovy and sprat, respectively) as well as colonies with more diverse diet where, depending on abundance and distribution of schooling fish in a particular breeding season, birds can feed on their preferred prey, or on less profitable prey (mixed diet colonies, e.g. Isla Quiroga, where birds consume schooling fish and squid²⁵) (see Table 1 for details). Magellanic penguins lay two eggs and their breeding success is highly variable depending on the breeding season.¹⁹ In nests containing chicks, blood was taken from the chick and its associated parent. At the time that the samples were obtained, Magellanic penguin parents take turns to feed at sea and brood the chicks; thus, normally there was only one adult in the nest and for this reason samples were not taken from family groups. However, in the few cases where we found the two parents in the nest during the change-over period, both adults were sampled. For the cases where two chicks were present in the nest, one was randomly chosen to take the blood sample. Bill morphometry (length and depth) is considered one of the most dimorphic sexual traits in Magellanic penguins³⁰ and this was

TABLE 1 Colonies sampled and their location

Colony	Lat.	Long.	Diet	Adults	Chicks	ED Females	N	ED Males	N
Islote Lobos (IL)	41.90S	65.00 W	Mixed (a)	10	8	0.65(0.64)	4	0.16(0.15)	4
Punta Norte (PN)*	42.08S	63.85 W	Specialist (b,c)	10	10	0.12(0.07)	5	0.17(0.13)	5
Punta Tombo (PT)	44.03S	65.18 W	Specialist (d)	10	9	0.08(0.05)	5	0.02(0.01)	4
Isla Leones (ILE)	45.10S	65.60 W	Specialist (e)	10	10	0.15(0.12)	4	0.12(0.12)	6
Isla Tova (IT)	45.11S	66.01 W	Specialist (e)	13	8	0.19(0.13)	3	0.18(0.07)	5
Isla Vernacci Norte (VN)	45.18S	66.50 W	Specialist (e)	70	16	0.16(0.17)	5	0.13(0.11)	11
Isla Quiroga (IQ)	47.75S	65.93 W	Mixed (f,g)	30	19	0.51(0.64)	10	0.02(0.02)	9
San Julián (SJ)	49.27S	67.70 W	Mixed (f)	30	18	0.41(0.50)	9	0.14(0.14)	9
Monte Entrance (ME)	50.13S	68.37 W	Mixed (f)	30	21	0.16(0.22)	11	0.11(0.11)	10
Cabo Vírgenes (CV)	52.37S	68.40 W	Specialist (b,f,g)	30	15	0.20(0.10)	10	0.15(0.14)	5
TOTAL				243	134	0.28(0.4)	66	0.12(0.11)	68

Type of diet, 'mixed' refers to colonies where there is no dominant prey species in the diet (but could be specialist in certain breeding season where high densities of schooling fish occur close by), 'specialist' refers to colonies where a single prey item dominates the diet (>65% proportion by biomass in diet). ED refers to Euclidean distance (standard deviation). References for diet composition are: (a) J. Ciancio, unpublished data, (b) ⁵⁵, (c) ²³, (d) ⁵⁶, (e) ²⁶, (f) ²⁵, (g) ²⁹.

Note that Islote Lobos showed a mixed diet, in spite of its location in the extreme of the northern distribution.

*Also known as Estancia San Lorenzo

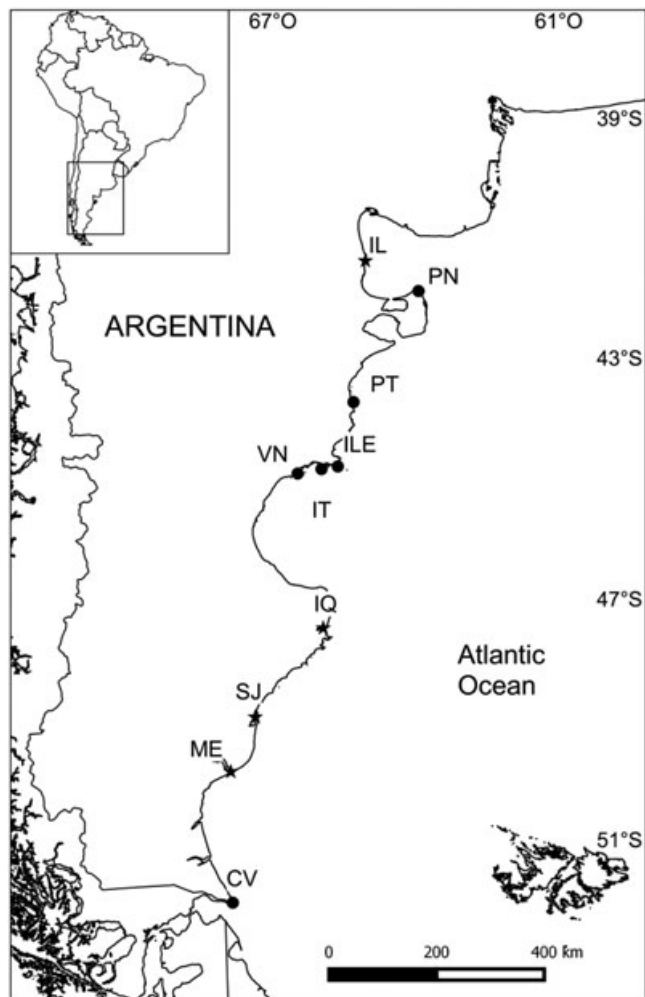


FIGURE 1 Location of Magellanic penguin colonies along the Patagonian coast of Argentina where birds were sampled. Circles and stars indicate colonies where penguins show specialist and mixed diets, respectively

measured in all adult individuals sampled. Adult birds were initially sexed by visual inspection of their morphometry in the field followed by a discriminant function on the bill dimensions (97% accurate) to confirm the assignment to sex.^{30,31} One adult individual with ambiguous sex classification and its chick was removed from the data set (value of the discriminant function close to 0).

Blood samples were preserved in 70% ethanol prior to C and N stable isotope analysis. Subsequently, the samples were dried at 60°C for 48 h and ground to a fine powder before stable isotope analysis was carried out at the Stable Isotope Facility, University of California, Davis (Davis, CA, USA) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd, Crewe, UK). The stable isotope ratios are measured against the reference standards Vienna PeeDee Belemnite for $\delta^{13}\text{C}$ values and atmospheric air for $\delta^{15}\text{N}$ values, expressed as $X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where X is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value and R is the corresponding $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio. Secondary isotopic reference materials used were Nylon (SDs were 0.056 and 0.05 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively), Bovine Liver (SD 0.007 and 0.07 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values), USGS-41 Glutamic Acid (SD 0.17 and 0.16 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values), and Glutamic Acid (SD 0.06 and 0.26 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values).

2.2 | Data treatment

Considering the uncontrolled sources of uncertainty (e.g. variability in basal stable isotopes in food webs across the sampled colonies), we chose the heuristic Euclidean distances (ED)³² between offspring and parent as a proxy of diet similarity. This is given by:

$$\text{ED} = \sqrt{(\delta^{13}\text{C}_{\text{chick}} - \delta^{13}\text{C}_{\text{adult}})^2 + (\delta^{15}\text{N}_{\text{chick}} - \delta^{15}\text{N}_{\text{adult}})^2}$$

where ED is the isotopic Euclidean distance and the other terms are the isotopic ratios for chick and adults, respectively. In short, if we assume that parents have different stable isotope signatures due to differential diets, the chick would be expected to be more similar to the parent that provides most food. Hence, the ED to this parent should be the smaller. In addition, we used the isotopic niche concept³³ as a proxy of diet diversity to explore how the diversity in adult diet relates to the ED between the chick and its parent. For this, we estimated the isotopic standard ellipse area corrected for small sample size (SEAc)³⁴ of adult birds for all combinations of colony and season. We used generalized linear mixed effect models (GLMMs)³⁵ and generalized linear models (GLMs) with a gamma distribution and log link function to evaluate the effects of adult sex, SEAc (both fixed terms), colony, and breeding season (both random effects, colony nested by breeding season) on chick-parent ED and the differences between chicks and their parent's sex by individual isotopic distance. The GLMMs were fitted using the function 'lmer' from the package 'lme4' and the GLM with 'glm'; both functions were in R³⁶ (version 3.1.3). For model selection we used a backwards selection procedure.³⁷

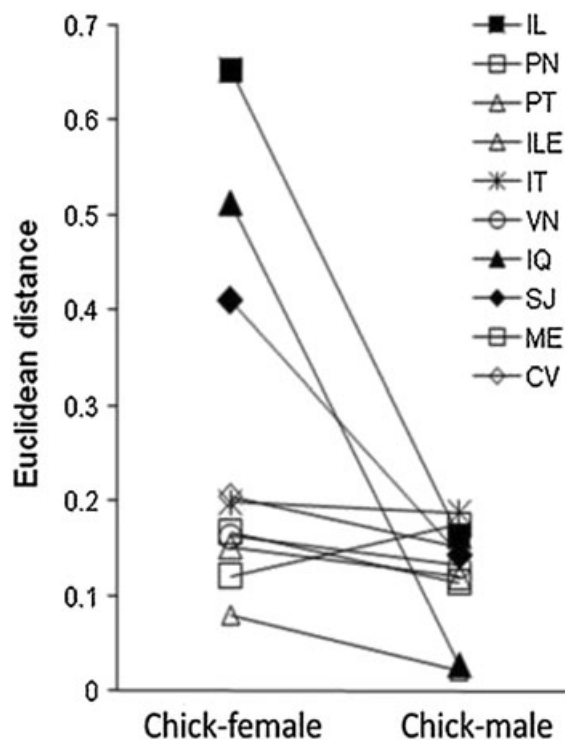


FIGURE 2 Profile plot of mean values for chick-parent Euclidean distances by colony and sex. Note that significant differences for the Euclidean distance were found between the chick-male and chick-female pairs in three colonies where penguins show a mixed diet (IL, IQ, SJ, solid symbols). For colony names, see Table 1

TABLE 2 Summary of stable isotope analysis results

	Mean $\delta^{13}\text{C}$ value (‰)	Mean $\delta^{15}\text{N}$ value (‰)	Range $\delta^{13}\text{C}$ C value (‰)	Range $\delta^{15}\text{N}$ value (‰)
Chicks	-17.17	17.10	-20.15 to -16.26	15.45-17.71
Males	-17.78	17.57	-19.53 to -16.74	14.99-17.72
Females	-17.87	17.50	-19.97 to -15.98	14.61-17.82

Removing the terms one by one following a decreasing level of complexity. We composed complete models including all predictors and tested for alternative structures for random factors using Akaike's information criterion. We then eliminated non-significant predictors ($P > 0.05$) one at a time and checked if the elimination of each of the variables significantly modified the model fitting by comparing residual deviances using a χ^2 test with the function 'anova' using the goodness-of-fit chi-squared test (χ^2 parameter).

3 | RESULTS

In total, we studied the stable isotope ratios in whole blood from 242 adult individuals and 134 chicks (Table 1). The EDs ranged from 0 to 0.46 ‰ (mean = 0.12) and from 0.001 to 1.48 ‰ (mean = 0.28) for chick-male and chick-female pairs, respectively (Figure 2), while the $\delta^{15}\text{N}$ values ranged between 14.61 ‰ and 17.82 ‰ and the $\delta^{13}\text{C}$ values ranged between -20.15 ‰ and -16.4 ‰ for all sampled penguins (Table 2). The model selection procedure identified sex and SEAc as the best explanatory variables for ED and for the differences between chicks and their parent's sex by individual isotopic distance (model 'c' in Table 3). The male parent ED was shown to be smaller than that of the female parent (coef = -0.62, $t_{132} = -3.5$, $P < 0.001$) and ED increased with SEAc (coef = 1.43, $t_{132} = 3.8$, $P < 0.001$). The model selection procedure by individual isotopic distance showed $\delta^{15}\text{N}$ values (coef for sex in $\delta^{15}\text{N}$ model = -0.46, $t_{132} = -3.2$, $P < 0.001$) and not $\delta^{13}\text{C}$ values (coef for sex in $\delta^{13}\text{C}$ values selected model = -0.18, $t_{132} = -1.23$, $P = 0.21$) as the driver of the difference between distance to different parent sex. Both distances by individual isotope ratios increased with SEAc ($\delta^{15}\text{N}$ values: coef = 0.67, $t_{132} = 2.13$, $P = 0.034$; $\delta^{13}\text{C}$ value: = 0.81, $t_{132} = 2.61$, $P = 0.009$). For all cases where both parents of a chick were sampled ($n = 4$ chicks, from Monte Entrance and Isla Quiroga colonies), the chick-male ED was smaller than the chick-female ED (0.11 ± 0.1 mean difference between parents). The mean ED values observed were 0.12 for chick-male and

0.23 for chick-female pairs, similar to the mean of the overall sample (0.12 and 0.28, respectively).

While in females the ED increased with diet diversity in the colony (measured as SEAc), it did not seem to change in males from all colonies studied (Figure 3). Furthermore, while during the 2013 season males and females showed similar EDs to their chicks, during the 2012 season females displayed larger EDs to chick (all colonies but Islote Lobos, Figure 3).

4 | DISCUSSION

The quantity of food provided by parents is crucial in modulating seabird reproductive success and is usually estimated via indirect measurements or proxies, such as the provisioning rate and/or meal size.^{3,38} Estimating rate and/or meal size is, in general, time consuming and may result in disturbance of sampled individuals. To our knowledge, this study is the first to use a simple variable or proxy (the ED) that integrates all food provided by parents (provisioning rate + amount of food on each feeding event) to assess sexual roles in chick provisioning in birds with different parental diets.

In order to use stable isotopes to estimate the contribution of sources in a mixture, the sources have to be isotopically different.³⁹ If both sexes consume mainly schooling fish such as anchovy and sprat,²⁸ which, in addition, form aggregations according to body size,^{40,41} these prey would be expected to have less variation in stable isotope ratios. This would explain the lower differences in ED to the chick between sexes found in two types of colony: (a) colonies where penguins are essentially specialists or (b) colonies with mixed diet during seasons of high availability of this prey, when the SEAc appears to be smaller (Figure 3, e.g. anchovy stock can vary between 100,000 and 3 million t^{42}). Intersexual trophic segregation has been observed in many penguin species, probably due to intersex competition for food during periods of low abundance of prey (see review in Xavier et al;⁴³ also see Raya Rey et al⁹ for an example on Magellanic penguins). Unfortunately, there were no acoustic surveys for schooling fish stocks during the study period. However, the 2012 season seemed to be a period of low abundance of these stocks, as inferred by other schooling fish predator's diet⁴⁴ and the poor Magellanic penguin breeding success during this breeding season.⁴⁵

The differences in ED to parents, and hence in food provisioning, would depend on the rate of provisioning, specifically how often each adult returns with food to feed the brood, and the amount of food

TABLE 3 Model structures, Akaike's information criteria, and χ^2 values of residual deviances paired comparisons of the backwards selection procedure proposed for the GLMM and GLM models

Model structures	Response variable									
	Euclidean distance				Distance in $\delta^{15}\text{N}$ value			Distance in $\delta^{13}\text{C}$ value		
	DF	AIC	χ^2	P-value	AIC	χ^2	P-value	AIC	χ^2	P-value
a) Sex + SEAc + (Season/Colony)	6	-181.5			-72.2			7.6		
b) Sex + SEAc + (Season)	5	-183.5			-73.8			5.6		
c) Sex + SEAc	4	-187.5			-77.8			1.6		
d) Sex	3	-177.9	-13.6	<0.001(c-d)	-75.5	-3.38	0.026	3.4	-3.95	0.014(c-d)
e) SEAc	3	-179.4	-11.7	<0.001(c-e)	-71.0	-7.08	0.001	-0.2	-0.15	0.626(c-e)

The random effect structure is shown in parentheses

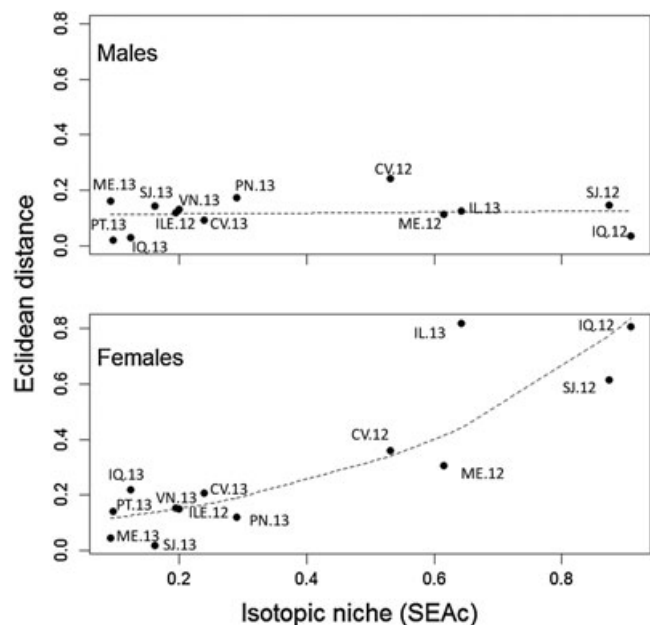


FIGURE 3 Relationship between the isotopic niche (estimated by the standard ellipse area corrected for small sample size, a proxy for the isotopic niche of a colony-season combination) and the euclidean distance to its parents. Upper panel distance to male, lower panel distance to female. For colony names, see Table 1

transferred in each feeding event. The latter could be affected by the larger size of males. Larger birds can take larger prey⁴⁶⁻⁴⁹ and have potentially higher $\delta^{15}\text{N}$ values due to their higher trophic level.⁵⁰ In this study, the larger differences in isotopic distance between chick-male and chick-female were found in $\delta^{15}\text{N}$ values.

Some studies based on indirect estimators of diet such as stable isotopes have suggested that penguins may feed on lower quality prey for themselves and provide more profitable prey to their chicks,^{23,51} although a recent study found no differences in diet between Magellanic penguin adults and their chicks.²⁶ Different self-feeding vs chick provisioning diet may affect the method proposed here, which assumes similar diet for both adults and chicks. Further analysis, in particular based on our model species, would be necessary to clarify this point. In addition, although age-related differences in diet tissue discrimination factors⁵² may affect qualitative estimations and comparisons of diet between a chick and its parents, it should not affect the method proposed here as it would equally affect the ED for both parents.

5 | CONCLUSIONS

Our results suggest chicks have a diet more similar to that of their male parent, probably related to the higher trophic level of male penguin prey. In addition, we have here developed an approach that has provided the first assessment of the extent of differential food provisioning between male and female Magellanic penguins. The application of this method to other species where feeding strategies may differ between sexes^{9,53,54} would provide a quick and easy way to quantify sex-related differences in parental provisioning.

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