

Exploring the interplay between nest vocalizations and foraging behaviour in breeding birds

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ARTICLE INFO

Article history:

Received 18 September 2020

Initial acceptance 1 March 2021

Final acceptance 7 July 2021

Available online 9 September 2021

MS. number: 20-00707R

Keywords:

bird
communication
foraging behaviour
reproductive partner
vocalization

In many bird species, reproductive partners sing together each time they meet on the nest. Because these nest ceremonies typically correspond to the return of one partner from foraging and to the subsequent departure of the other partner, we hypothesized that the foraging decisions of departing birds may be facilitated by the vocalizations accompanying their partner's return on the nest, providing these vocalizations reflect foraging conditions. We examined this hypothesis in pairs of Adélie penguins, *Pygoscelis adeliae*, by longitudinally monitoring their nest vocalizations and their spatial distribution when foraging at sea across the guard stage, when both parents regularly alternate foraging at sea and chick attendance at the nest. We found that the acoustic characteristics of the vocalizations produced during nest relief ceremonies reflected some characteristics of the foraging trips of both the returning and departing partners. However, these acoustic characteristics differed between partners and were differently related to their foraging behaviour. Accordingly, departing individuals did not adopt the same foraging behaviour as that of returning individuals. Nest vocalizations therefore do not appear to represent cues facilitating the foraging decisions of departing birds, but they may rather reflect the arousal of partners, which differently correlates with the foraging behaviour of the returning and departing individuals. Our study highlights an interplay between the vocalizations produced on the nest by reproductive partners and their foraging behaviour, thereby broadening the scope of animal vocalizations and opening a novel perspective on the regulation of foraging strategies. However, our exploratory study also highlights the complexity of examining this interplay, as the effects of nest vocalizations on foraging decisions may be complicated by other factors (e.g. intrinsic foraging capacity). This calls for the use of additional and experimental approaches (e.g. vocalization playbacks) to clarify the role of nest vocalizations as potential mediators of foraging decisions.

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In variable and unpredictable habitats, animals may benefit from altering their foraging behaviour based on the behaviour of other individuals, as such social influence may allow them to reduce the uncertainty about the consequences of their foraging decisions (Bonnie & Earley, 2007; Boyd et al., 2016; Valone & Templeton, 2002). For instance, cliff swallows, *Petrochelidon pyrrhonota*, searching for food are recruited by the squeak calls of other swallows that have already found prey (Brown et al., 1991). Conversely, animals may also indicate poor feeding conditions through their vocalizations, for instance through a change in their

production rate as observed in passerine birds (Berget et al., 2005; Lucas et al., 1999). Food calls may vary based not only on the presence or the absence of food but also on its quality, as observed in ravens, *Corvus corax*, producing more 'haa' food calls in the presence of food of high quality (Bugnyar et al. 2001). Such food calls may not necessarily act directly as referential signals for food but they may simply reflect the arousal of the individual finding food (i.e. a state of excitement possibly related to its feeding status), in response to which other individuals may adjust their behaviour (Clay et al., 2012).

Food calls may persist outside feeding grounds and may be produced in nonfeeding contexts. For instance, passerine birds returning to their nest with food may alter the quality of their song when singing on the nest (e.g. as in babblers; Smith, 2017). This

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spatial and temporal extension of food calls from the feeding ground to the breeding ground means that nesting birds about to leave the nest to feed (departing individuals, hereafter) are exposed to the food calls of individuals returning from feeding grounds before feeding themselves. This situation occurs in species providing biparental care, as in most bird species (Cockburn, 2006), where reproductive partners alternate duties on the nest. The exposure of departing individuals to the food calls of returning individuals may be beneficial, as individuals constrained to the nest because of reproductive duties (e.g. brooding) necessarily lose contact with environmental feeding conditions, which may drastically change at the same time. The most extreme example is observed in emperor penguins, *Aptenodytes forsteri*, with incubating males staying in the colony several hundreds of kilometres away from their feeding grounds for up to 4 months (Ancel et al., 2013). The vocalizations of partners returning from foraging grounds may, however, compensate for the naivety of departing birds, if these vocalizations reliably reflect the feeding conditions returning birds just encountered.

The use of vocalizations produced by reproductive partners to facilitate food consumption has already been documented in birds but exclusively on their feeding grounds. For instance, the pulse rate of calls produced by male junglefowls, *Gallus gallus*, correlates with food quality and the probability that the hen consumes this food (Cyger & Marler, 1988), but only when the latter is naïve about the presence of food (Evans & Evans, 2007). Whether such effects may occur on the nest between partners returning from feeding grounds and partners leaving the nest to find food remains unknown. In the case of species where individuals of both sexes provide parental care and produce calls (e.g. seabirds), males and females exchanging roles on the breeding grounds and being successively signaller and receiver would reciprocally benefit from such a strategy (Riebel et al., 2019; Valone, 2007). Moreover, pairs using vocalizations as facilitators of foraging decisions would have a decisive competitive advantage over other pairs. Indeed, if nest vocalizations reliably reflect the beneficial feeding conditions returning partners previously experienced, departing partners adjusting their foraging behaviour accordingly would be able to reduce the searching phase of their foraging trips (associated with a negative energetic yield) in favour of the feeding phase (associated with a positive energetic yield). In contrast, if nest vocalizations reflect poor feeding conditions, the vocalizations produced by the returning partner coming back with a low energetic yield (resulting in a low feeding rate to the offspring) may indicate to the departing partner about to leave the nest the necessity to intensify its foraging effort. In all cases, this higher coordination between partners would explain why the use of nest vocalizations to adjust foraging strategies would be functionally adaptive and selected. This scenario would also explain why so many bird partners sing on their nests (e.g. songbirds; Leonard, 2008), and provides a new perspective on the function of bird vocalizations in addition to territory maintenance, mate attraction or individual recognition (Riebel et al., 2019).

Our current lack of knowledge on nest vocalizations potentially acting as mediators of foraging decisions presumably originates from the disconnect between studies examining vocalizations and foraging behaviour independently of each other, as exemplified by the extensive research conducted in penguins. On the one hand, much research has been conducted over the last few decades on the vocalizations of penguins in their colonies, which enable inter-individual recognition, while ignoring their behaviour at sea (Aubin & Jouventin, 2002; Jouventin & Aubin, 2002; Jouventin & Dobson, 2018). On the other hand, many studies have been conducted on their foraging behaviour at sea, while ignoring their behaviour in the colony (e.g. Le Guen et al., 2018; Watanabe et al. 2020; Zimmer

et al., 2008). Interestingly, recent research has shown that penguins vocalize not only in the colony but also at sea, at the water surface (Choi et al., 2017; McInnes et al., 2020) and even underwater (Thiebault et al., 2019), thereby highlighting a potential interplay between vocalizations and foraging strategies on their feeding grounds. For instance, the calling activity of gentoo penguins, *Pygoscelis papua*, at the sea surface is related to their subsequent diving behaviour (Choi et al., 2017), while it increases in the presence of more profitable prey in African penguins, *Spheniscus demersus* (McInnes et al., 2020). At-sea calls may, therefore, influence the foraging behaviour of other penguins present on the feeding grounds by indicating the location and the quality of available prey, which may explain why penguins present on the same feeding grounds dive synchronously and forage more efficiently (McInnes et al., 2017; Takahashi et al., 2004; Tremblay & Cherel, 1999). If foraging penguins produce vocalizations with given characteristics because of the prey they encounter on their feeding grounds and retain these characteristics until they reach the nest to relieve their partner, they may also influence the foraging behaviour of their breeding partner leaving the nest. Given the short duration between the time when the returning penguin leaves the feeding grounds and the time when the departing penguin starts to feed (in chick-rearing Adélie penguins, ca. 10 h including the transit time needed by the returning partner to reach the colony, the time when both partners are present on the nest and the transit time needed by the leaving partner to reach the feeding ground; Nesti et al., 2010), feeding conditions are likely to be stable between these two time points. If the feeding conditions previously encountered by returning partners were favourable, departing penguins may benefit from adopting the same foraging behaviour as returning partners based on nest vocalizations, as this strategy would allow them to increase feeding efficiency by reducing the searching phase of their foraging trips and the overall duration of their foraging trips (resulting in higher provisioning rate to the chicks). In contrast, if the feeding conditions previously encountered by returning partners were unfavourable, departing partners may need to intensify their foraging effort to find food and compensate for the low foraging efficiency of their partner (thereby resulting in long foraging trips). These alternative scenarios may explain why penguins have been found to perform both short and long foraging trips (Ropert-Coudert et al., 2004).

If nest vocalizations facilitate the foraging decisions of birds, they should reflect some components of the foraging behaviour of both the returning and the departing partner. We therefore examined in our study (1) whether vocalization characteristics during nest relief ceremonies reflected some components of the foraging behaviour of the returning partner (production specificity hypothesis), and (2) whether the foraging characteristics of the departing partner reflected some characteristics of the vocalizations produced during the previous nest relief ceremony (perception specificity hypothesis). To examine these two hypotheses, we used a longitudinal approach across the guard stage of Adélie penguins when parents alternate foraging at sea and chick attendance at the nest.

METHODS

Penguin Monitoring

The study took place in a colony of Adélie penguins on Ile des Pétrels, near the French polar station Dumont d'Urville (66°40S, 140°00E), Terre Adélie, Antarctica during the austral summer 2019–2020. Adélie penguins are present in their colony only during the short austral summer when they breed. Their reproductive season is divided into four successive phases: (1) courtship, (2)

incubation, (3) guard stage and (4) crèche stage. During courtship, both partners are present on the nest, during incubation and the guard stage, one partner is present on the nest while the other forages at sea (both parents regularly switching duties), and during the crèche stage, both parents simultaneously forage at sea and irregularly come back to the colony to feed their offspring. In our study, at the end of the courtship period, 212 individuals belonging to 106 pairs of Adélie penguins were identified with a given number painted on their breast feathers with hair dye, and with two coloured marine tapes inserted in their neck feathers. Nests were visually monitored every 2.5 h (from 0530 to 0130) to note which individual was on the nest and which was at sea to forage, as well as their reproductive performance (number of eggs or chicks). To determine the sex of monitored penguins, we used a combination of parameters including relative size during courtship, copulatory position and incubation routine, males being larger and taking the first incubation shift.

Acoustic Monitoring

After clutch completion, Song Meters SM4 (Wildlife Acoustics Inc. Maynard, MA, U.S.A.) equipped with two microphones (omni-directional with sensitivity of -35 ± 4 dB re 1V/Pa @ 1 kHz) were deployed close to nine nests among the 106 monitored nests. Even though Adélie penguins nesting at the periphery of colonies may show a lower reproductive performance (and hence not necessarily be representative of the whole colony; Tenaza, 1971), we selected peripheral nests because their location at the edge of colonies facilitated their subsequent individual acoustic monitoring (see below). We assumed that the effects of nest position within colonies on the reproductive performance of penguins would be minimal in our study, as the shape of colonies on Ile des Pétrels is very irregular. Moreover, we selected large peripheral nests made of a large number of pebbles, suggesting that reproductive penguins were of good quality (Ainley, 2002). Song meters were attached on stakes inserted in pre-existing rock crevices located 1.25 ± 0.12 m from the nests, approximately at the same height as the head of a standing penguin. Continuous 16-bit stereo recordings with no signal amplification were conducted at 48 kHz with a high-pass 220 Hz filter to reduce environmental noise (e.g. penguin neighbours, other bird species, wind), the frequency range of Adélie penguins' vocalizations being between 800 and 5000 Hz (Jouventin, 1982). Batteries were replaced and data downloaded every 6 days until the end of the guard stage.

Video Observation of Nest Relief Ceremonies

As it was impossible to disentangle the respective vocalizing behaviour of both partners during the nest relief ceremonies recorded with microphones, some nest relief ceremonies occurring among the 106 monitored nests during the period of acoustic monitoring were opportunistically recorded with a digital video camera (Hero 8 Black, GoPro Inc., San Mateo, CA, U.S.A.) placed close to the nest before the returning partner reached the nest and until partners exchanged duties (i.e. the returning partner started brooding chicks). These videos were used to examine the overall organization of nest relief ceremonies until the completion of nest exchange. Among the 65 nest relief ceremonies filmed during the guard stage, nine were simultaneously recorded by microphones.

Foraging Monitoring

We examined the foraging behaviour of the penguins from the nine nests that were monitored with song recorders. Their foraging behaviour was monitored during the guard stage when Adélie

penguins regularly need to come back to their nest to feed their offspring. During this stage, foraging penguins therefore need to maximize food intake and minimize the time they spend exploring their environment (as shown by shorter foraging trips throughout this breeding stage than in other breeding stages; Clarke et al., 2006; Widmann et al., 2015).

In detail, before the fifth foraging trip after clutch completion, penguins were equipped with GPS devices (CatLog, $5.0 \times 2.2 \times 0.8$ cm, measurement frequency: once every 5 min; Catnip Technologies Ltd, Anderson, SC, U.S.A.), which were thermosealed with heat shrink tubing before deployment to make them waterproof (after thermosealing, devices measured $8.0 \times 2.5 \times 1.4$ cm and weighed 25 g). When considering the potential effects of instrumentation in diving animals, three parameters must be considered: (1) the shape of instruments (2) their attachment position and (3) their cross-sectional area relative to that of animals (Bannasch et al., 1994). In our study, devices were streamlined during the thermosealing process and attached to the lower back of penguins to reduce drag (Bannasch et al., 1994). Moreover, devices were attached to feathers with mastic, cyanoacrylate glue and black Tesa tape to reduce the potential irritation of penguins by the devices (Wilson et al., 2008). Finally, the cross-sectional area of our devices (1.7% of the cross-sectional area of penguins; Widmann et al., 2015) was close to the optimal size theoretically recommended for diving animals (ca. 1%; Bannasch et al., 1994; Culik & Wilson, 1991) even though the effects of GPS deployment may greatly vary irrespective of its size presumably because of variation in the environmental conditions encountered by instrumented penguins (Clarke et al., 2006). As environmental conditions cannot be anticipated before deployment, potential related effects need to be systematically checked.

In our study, penguins were equipped with GPS devices for one ($N = 1$ individual), two ($N = 10$ individuals) or three ($N = 6$ individuals) consecutive foraging trips resulting in a total of 39 trips between the fifth and the seventh foraging trip after clutch completion (one device was lost, as one female did not come back from her second foraging trip after being equipped). Because Adélie penguins breed relatively synchronously, we could equip all penguins with GPS devices over a short period of 13 days (between 23 December and 4 January; see Appendix Fig. A1). Before, during and after GPS deployment, nests were visually monitored every 2.5 h (from 0530 to 0130) to note the identity of the individual on the nest (and hence the identity of its partner foraging at sea). This longitudinal visual monitoring before, during and after deployment enabled us to use equipped penguins as their own controls to examine the potential effects of deployment on the duration of their foraging trips.

Beak morphology may provide a link between vocalizations and feeding behaviour in birds including penguins, as larger beaks are usually related to longer vocal sequences with lower frequencies and to the capture of larger prey (Chávez-Hoffmeister, 2020; Favaro et al., 2017; Giraudeau et al., 2014; Palacios & Tubaro, 2000; Podos, 2001; Volkman et al., 1980). In Terre Adélie, breeding Adélie penguins mostly feed on two types of prey: small krill (mainly *Euphausia superba*) occupying more oceanic areas and larger fish (mainly *Pleuragramma antarcticum*) occupying more coastal areas (Cherel, 2008). If the relationships between beak morphology and feeding behaviour described above apply to Adélie penguins, individuals with larger beaks would be more likely to feed on coastal fish, and hence perform shorter foraging trips than individuals with smaller beaks (irrespective of the vocalizations they were exposed to before leaving the nest). To correct for these potential morphological effects, we measured beak height (maximal distance between the lower part of the lower beak and the upper part of the upper beak at the base of the beak), width (maximal distance

between the right and left part of the beak at the base of the beak) and length (maximal distance between the tip and the base of the upper beak) with a digital calliper (± 0.01 mm) when GPS devices were recovered. We did not consider birds' body mass, as it depends on their stomach content (which may weigh up to 25% of Adélie penguins' body mass during the guard stage; [Emison, 1968](#)) and how much food was already given to the chicks.

Data Analyses

Acoustic data

Based on observations of the nine nests monitored with song recorders, we knew roughly when partners exchanged duties between foraging trips. We could therefore easily retrieve vocalizations produced during nest relief ceremonies a posteriori in sound recordings. These nest relief ceremonies were isolated and analysed with Raven Pro 1.6.1 (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). A bandpass filter (300–22 000 Hz) was first applied to reduce the amount of noise contained in acoustic signals. Then vocal sequences were isolated based on the visual inspection of spectrograms ([Fig. A2](#)). A sequence was defined as a series of phrases starting after a silent phase, showing an increase and a subsequent decrease in vocal frequency and intensity, and finishing with a silent phase irrespective of its duration ([Jouventin & Dobson, 2018](#)). All the vocal parameters extracted for each sequence were averaged between the recordings made by the right and the left microphones of each song recorder. These parameters are summarized and defined in [Table 1](#).

Video data

We manually analysed the 65 nest relief ceremonies that we filmed during the guard stage with VLC Media Player (VideoLAN, Paris, France), and noted the status (returning or departing) of the individual initiating vocalizations (except for five nest relief ceremonies, for which it was impossible to clearly determine this parameter), the duration between the arrival of the returning partner and the time when partners exchanged duties on the nest (i.e. exchange latency), the number of vocal sequences preceding task exchange, and the number of loud mutual displays ([Sladen, 1958](#); see below) before birds switched to other vocalizations (quiet mutual displays or individual vocalizations). Vocal sequences were defined as any audible vocalizations starting and ending with silence, while loud mutual displays corresponded to the simultaneous vocalizations of both partners standing, facing each other and waving their necks back and forth while uttering a loud cackling call with open bills ([Sladen, 1958](#)). We also noted whether neighbours visible on the video observed vocalizing partners and/or sang at the same time.

Foraging data

The coordinates associated with each foraging trip could be retrieved and isolated based on our observations of the nests. Because 85% of sampling intervals during foraging trips corresponded to our sampling setting (one measure every 5 min), data were not redistributed to get fixed time intervals. First, the distance between successive data points was calculated with the Vincenty's formulae using a macro in Excel (<https://www.contextures.com/>

Table 1
Summary of the vocal and foraging parameters measured in this study

Parameters	Grouping	Definition
Vocalizations	Centre frequency (Hz)	Vocalization PC1 (0.82)
	Frequency 95% (Hz)	Vocalization PC1 (0.97)
	Bandwidth 90% (Hz)	Vocalization PC1 (0.97)
	Aggregate entropy	Vocalization PC1 (0.97)
	Frequency 5% (Hz)	Vocalization PC2 (0.72)
	Sequence duration 90% (s)	Vocalization PC2 (0.64)
Foraging	Silent intervals (s)	Vocalization PC2 (−0.56)
	Foraging trip duration (s)	Foraging PC1 (0.84)
	Cumulative distance (km)	Foraging PC1 (0.79)
	Maximal distance (km)	Foraging PC1 (0.79)
	Forth-transit duration (s)	Foraging PC1 (0.90)
	Cumulative distance at first inflection point (km)	Foraging PC1 (0.89)
	Back-transit duration (s)	Foraging PC1 (0.76)
	Cumulative distance at second inflection point (km)	Foraging PC1 (0.78)
	Kernel 95% (ha)	Foraging PC1 (0.71)
	Forth-transit sinuosity	Foraging PC2 (−0.73)
	Central sinuosity	Foraging PC2 (−0.76)
Back-transit sinuosity	Foraging PC2 (−0.63)	

The intensity of vocalizations was not analysed, as it depended on the distance between the penguins and the song recorders (which differed slightly between nests), the orientation of vocalizing penguins relative to the song recorders (which we could not control) and the direction of the wind. For statistical analyses, some parameters were grouped together with principal component analyses (PCA loadings are given in parentheses).

[excellatitudelongitude.html#code](#)), which allowed us to measure the overall cumulative distance for each foraging trip. Using the same formulae, we were also able to find the maximal distance from the colony during each foraging trip. Then, for each foraging trip, we expressed foraging time as a percentage of the total foraging time (time between the departure from the colony to the return to the colony) and foraging distance as a percentage of the maximal distance from the colony. This approach allowed us to define three foraging phases: forth transit, central phase, back transit (Fig. A2). Foraging phases were separated by inflection points, which locations were found with the R package MCP which uses regressions with multiple change points (here two inflection points) between generalized and hierarchical linear segments using Bayesian inference (Lindeløv, 2020). We then calculated the sinuosity within each foraging phase using the R package trajr with the TrajSinuosity2 function which does not require a constant step length (McLean & Skowron Volponi, 2018). Finally, we estimated the foraging range of penguins for each foraging trip by calculating 95% kernel density estimates with the R package adehabitatHR (Calenge, 2015). All foraging parameters are summarized and defined in Table 1. All R analyses were conducted in R Studio version 1.2 (R version 3.6.3; R Core Team, 2020).

Statistical Analyses

General considerations

The acoustic and GPS data for each individual that we monitored with a song recorder and a GPS device and that we considered for statistical analyses are summarized in Table 2.

Nest relief ceremonies occurring under windy conditions were excluded from statistical analyses, resulting in a sample size of 66 nest relief ceremonies recorded with microphones between the fourth and the eighth foraging trip following clutch completion (Table 2). We only considered the first five sequences of each nest relief ceremony, as they were louder and clearly stood out in sound recordings. These vocalizations also corresponded to vocalizations produced before partners exchanged tasks on the nest (see below). To simplify statistical analyses and because of the high correlation

between sequences, vocal parameters were averaged over these five sequences.

All statistical tests included the interactions between sex and potential covariates. Covariates were included in the same models when the variance inflation factor, $VIF < 3$ (Dormann et al., 2013). The normality of residuals was assessed with Shapiro - Wilk tests and data were log transformed when necessary for residuals to reach normality. Effects sizes (η^2) and their 90% confidence intervals (Steiger, 2004) were estimated for each fixed factor. Results are expressed as means \pm SE and the significance level was set at $\alpha < 0.05$. All statistics were conducted in SPSS 22.00.

Data reduction

We reduced the number of vocal and foraging parameters by conducting principal component analyses (PCA) after standardizing data. We were able to extract two vocalization components that explained 51% and 18% of the variance, respectively, resulting in a combined variance explained of 69%. We were also able to extract two foraging components that explained 60% and 13% of the variance, resulting in a combined variance explained of 73%. The first vocalization component was positively related to aggregate entropy and vocalization frequencies (except frequency 5%) while the second vocalization component was positively related to frequency 5% and sequence duration 90% and negatively related to silent intervals (Table 1). The first foraging component was positively related to foraging extent (i.e. foraging trip duration, cumulative distance, maximal distance, forth-transit duration, cumulative distance at first inflection point, back-transit duration, cumulative distance at second inflection point), while the second foraging component was negatively related to sinuosity in each foraging phase (Table 1).

Data representativeness

To assess the representativeness of our data during the period of foraging monitoring, we first examined how foraging trip duration (as measured through visual nest monitoring) and vocal parameters varied temporally for penguins monitored with song recorders and GPS devices. To this end, we considered all foraging trips (and

Table 2

Summary of the GPS and acoustic data used in our statistical analyses for each individual monitored with a GPS device at sea and a microphone close to its nests

Nest	Sex	Trip 4		Trip 5		Trip 6		Trip 7		Trip 8	
		GPS	Acoustic								
A	Female		✓	✓		✓	✓		✓		✓
	Male		✓	✓	✓	✓	✓		✓		✓
B	Female		✓	✓	✓	✓	✓		✓		✓
	Male		✓	✓	✓	✓	✓		✓		✓
C	Female			✓		✓	✓		✓		✓
	Male			✓	✓	✓	✓		✓		✓
D	Female		✓	✓	✓	✓		✓	✓		✓
	Male		✓	✓	✓	✓		✓	✓		✓
E	Female		✓	✓	✓	✓		✓	✓		✓
	Male		✓	✓	✓	✓	✓		✓		✓
F	Female		✓	✓	✓	✓	✓	✓	✓		✓
	Male		✓	✓	✓	✓	✓	✓	✓		✓
G	Female		✓	✓	✓	✓	✓	✓	✓		✓
	Male		✓	✓	✓	✓	✓	✓	✓		✓
H	Female		✓	✓	✓	✓	✓	✓	✓		✓
	Male		✓	✓	✓	✓	✓		✓		✓
I	Female		✓	✓	✓	✓					
	Male		✓	✓	✓	✓					
Total	Females	0	8	8	7	8	6	3	7	0	6
	Males	0	8	9	7	8	6	3	6	0	5

These nine nests were selected among 106 nests that had been visually monitored since the beginning of the reproductive season. For these nine nests, penguins were equipped with a GPS between the fifth and up to the seventh foraging trip after egg laying. Microphones were present close to the nest before and after this period. Some acoustic data are missing because of the occurrence of windy conditions masking vocalizations, while some GPS data are missing because one partner did not come back (Female I).

the nest relief ceremonies following those trips) when penguins were equipped with GPS devices (fifth, sixth and seventh trips after clutch completion), as well as the preceding trip (fourth trip) and the following trip (eighth trip; Table 2). This period encompasses the guard stage from its early to its late stage (the foraging behaviour of Adélie penguins remaining stable across the guard stage; Widmann et al., 2015). We conducted a general linear mixed model analysis (GLMM; identity link-function) with foraging trip duration and vocalization PC scores as dependent variables, foraging trip as a repeated fixed factor, sex of the returning individual as a fixed factor and 'individual ID nested in nest ID' as a random factor. We also examined potential monitoring effects on the reproductive performance of penguins by comparing the number of offspring (eggs and chicks) produced by the nine pairs monitored with song recorders and GPS devices and nesting at the edge of colonies with that of the other 97 pairs only visually monitored. To this end, we fitted a GLMM (Poisson distribution; log link-function) with number of offspring (between zero and two eggs or chicks) as the dependent variable, reproductive stage (egg laying, hatching, end of the guard stage) as a repeated fixed factor, treatment (song recorder/GPS versus visual monitoring) as a fixed factor and 'Nest ID' as a random factor.

Data repeatability

To investigate the temporal repeatability of foraging and vocalization parameters, we examined whether foraging and vocalization PC scores measured for a given foraging trip or nest relief ceremony (N) correlated with the same parameters measured for the following foraging trip or nest relief ceremony of the same individual ($N + 2$) or of its partner ($N + 1$). To this end, we conducted a GLMM analysis (identity link-function) with PC scores as dependent variables, sex of the returning individual as a fixed factor, corresponding PC scores for the preceding trip as covariates and 'individual ID nested in nest ID' as a random factor (to create a repeated measure structure with foraging trips being repeated). Foraging PC1 scores, foraging PC2 scores, vocalization PC1 scores and vocalization PC2 scores were examined in separate models.

Video data

Among the 65 nest relief ceremonies filmed during the guard stage, only a few corresponded to the returns of the same individuals across this period. We, therefore, did not examine video data longitudinally but only examined the differences between nest relief ceremonies following the return of males and females. To this end, we first examined whether returning individuals initiated vocalizations (no: 0; yes: 1) using a mixed model (binary distribution; logit link-function) with sex of the returning individual as a fixed factor and 'individual ID nested within nest ID' and 'foraging trip number' as random factors. We examined differences between sexes for other parameters using similar mixed models with the same binary distribution (observation by neighbours, vocalizations by neighbours) or with a normal distribution (identity link-function; exchange latency, number of vocal sequences before exchange, last mutual display before other vocalizations). Finally, we examined whether the average duration of the first five sequences analysed from videos reflected the average duration of the first five sequences analysed from microphones by using a Student paired t test and a Pearson correlation. Note that video and acoustic data were independently analysed by different observers.

Testing the production and perception specificity hypotheses

To test the production specificity hypothesis, we examined how the characteristics of foraging trips were related to the vocal parameters of the following nest relief ceremonies, by conducting GLMM analyses (identity link-function) with vocalization PC scores

as dependent variables, sex of the returning individual as a fixed factor, foraging PC scores as covariates and 'individual ID nested in nest ID' as a random factor (foraging PC1 and PC2 scores were used as covariates in the same models, since VIF was below 3; Dormann et al., 2013).

To test the perception specificity hypothesis, we examined how the vocal characteristics of nest relief ceremonies were related to the foraging characteristics of the following foraging trip. To this end, we conducted GLMM analyses (identity link-function) with foraging PC scores of the next foraging trip as dependent variables, sex as a fixed factor, vocalization PC scores as covariates and 'individual ID nested in nest ID' as a random factor. Vocalization PC1 and PC2 scores were analysed in the same models (VIF < 3).

We repeated the two models testing the production and perception hypotheses by including beak dimensions as covariates to control for their potential effects on vocalizations and foraging parameters (beak dimensions of the returning individual in models testing the production specificity hypothesis, beak dimensions of the departing individual in models testing the perception specificity hypothesis). We tried to reduce the number of parameters to characterize the beak morphology of penguins using a PCA. However, the first and only axis of this PCA only explained a low percentage of the variance (54%). Moreover, as opposed to beak height and width, beak length did not load on this axis. We therefore considered each beak dimension (height, length, width) in our analyses. As beak length and height only tended to differ between males and females (GLMM: length: $F_{1, 8} = 4.96$, $P = 0.057$; height: $F_{1, 8} = 5.19$, $P = 0.053$; width: $F_{1, 6} = 0.05$, $P = 0.83$), we included all beak covariates (VIF < 3) in our models.

Ethical Note

Authorization for bird manipulation and access to Restricted Areas were obtained from the Terres Australes et Antarctiques Françaises (TAAF). The experiments listed here have been authorized by the Ethic Regional Committee 84 (project number 10343-2017062316008722_v3_notification_de_decision) and the Conseil National de la Protection de la Nature (n°2019-09-20x-01059). Penguins were treated carefully throughout the monitoring period; their head was covered with a hood to minimize stress during GPS deployment and recovery (Cockrem et al., 2008). During the manipulation of adults, chicks were collected (to avoid depredation by Antarctic skuas, *Stercorarius maccormicki*) and kept under warm conditions in a shelter, while the nest was protected with a grid to prevent nest pebbles from being stolen by neighbours. The overall manipulation lasted less than 10 min (from capture to release). We also assessed that the behaviour and reproductive performance of penguins monitored with song recorders and GPS devices were not affected by the monitoring itself (see Results).

RESULTS

Data Representativeness

Between the fourth and the eighth foraging trips following clutch completion, foraging trip duration (1.47 ± 0.07 days) did not differ significantly between males and females (GLMM: $F_{1, 17} = 2.25$, $P = 0.15$, $\eta^2 = 0.12$ [0.00, 0.34]) and remained stable across foraging trips (GLMM: $F_{4, 54} = 0.96$, $P = 0.44$, $\eta^2 = 0.07$ [0.00, 0.13]) irrespective of the sex of foraging penguins (GLMM: $F_{4, 54} = 0.25$, $P = 0.91$, $\eta^2 = 0.02$ [0.00, 0.02]; Fig. A3). Similarly, vocal parameters did not differ following the return of males and females (GLMM(vocalization PC1): $F_{1, 16} = 0.07$, $P = 0.79$, $\eta^2 = 0.01$ [0.00, 0.14]; GLMM(vocalization PC2): $F_{1, 17} = 0.01$, $P = 0.91$, $\eta^2 = 0.01$ [0.00, 0.02]) and remained stable across the guard stage

(GLMM(vocalization PC1): $F_{4, 42} = 1.49, P = 0.22, \eta^2 = 0.12$ [0.00, 0.22]; GLMM(vocalization PC2): $F_{4, 45} = 1.21, P = 0.32, \eta^2 = 0.10$ [0.00, 0.18]) irrespective of the sex of the returning partner (GLMM(vocalization PC1): $F_{4, 42} = 0.27, P = 0.89, \eta^2 = 0.03$ [0.00, 0.04]; GLMM(vocalization PC2): $F_{4, 45} = 0.90, P = 0.38, \eta^2 = 0.07$ [0.00, 0.15]; Fig. A3). Overall, these results show that the foraging and vocalizing behaviours of penguins were stable across the guard stage and suggest that penguins behaved similarly during, before and after the deployment period.

Even though the number of offspring per nest decreased significantly over time (1.96 ± 0.02 eggs/nest, 1.68 ± 0.05 hatchlings/nest, 1.46 ± 0.07 chicks/nest at the end of the guard stage; GLMM(reproductive stage): $F_{2, 312} = 11.94, P < 0.001, \eta^2 = 0.07$ [0.03, 0.12]), this temporal decrease was similar in penguins monitored with song recorders and GPS devices and nesting at the edge of colonies and in penguins only monitored visually (GLMM(monitored type): $F_{1, 312} = 0.04, P = 0.85, \eta^2 = 0.01$ [0.00, 0.01]; GLMM(reproductive stage*monitored type): GLMM: $F_{2, 312} = 1.41, P = 0.25, \eta^2 = 0.01$ [0.00, 0.03]; Fig. A4).

Temporal Correlations During the Guard Stage

The behaviour of penguins during a given foraging trip was significantly related to their behaviour during their next foraging trip (Table 3) with more extensive foraging trips (higher foraging PC1 scores) being followed by more extensive trips performed by the same individuals (Fig. 1a). In contrast, penguins performing more tortuous foraging trips (higher foraging PC2 scores) foraged less tortuously in their next foraging trip (Fig. 1b). The characteristics of the vocalizations (vocalizations PC1 and PC2 scores) produced during a nest relief ceremony following the return of a given individual were positively correlated with the vocalization characteristics of the next nest relief ceremony following the return of the same individual (Fig. 1c and d).

The behaviour of penguins during a given foraging trip was not followed by a similar foraging behaviour by their partner both in terms of foraging extent (foraging PC1 scores) and sinuosity (foraging PC2 scores; Table 3, Fig. 1e and f). In contrast, vocalization PC1 scores during a nest relief ceremony following the return of a given individual were positively correlated with the same scores during the next nest relief ceremony following the return of its partner (Table 3, Fig. 1g). This pattern was not observed for vocalization PC2 scores (Table 3, Fig. 1h).

Observation of Nest Relief Ceremonies

The probability of returning individuals initiating vocalizations at the beginning of nest relief ceremonies did not deviate significantly from 50% ($57 \pm 8\%$; one-sample binomial test: $P = 0.37$) and did not differ between returning males and females (mixed model: $F_{1, 17} = 20.07, P = 0.79, \eta^2 = 0.54$ [0.23, 0.69]). Partners exchanged nest tasks on average 221 ± 28 s after the arrival of the returning partner, and produced 11 ± 1 vocal sequences, among which 7 ± 1 loud mutual displays, before exchanging tasks, irrespective of the sex of the returning individual (mixed model(exchange latency): $F_{1, 63} = 2.20, P = 0.14$, mixed model(number of vocalizations): $F_{1, 63} = 0.77, P = 0.39, \eta^2 = 0.01$ [0.00, 0.08], mixed model(number of loud mutual displays): $F_{1, 63} = 0.36, P = 0.55, \eta^2 = 0.01$ [0.00, 0.07]). Partners also produced 7 ± 1 loud mutual displays before switching to other vocalizations, irrespective of the sex of the returning individual (mixed model: $F_{1, 63} = 0.08, P = 0.78, \eta^2 = 0.01$ [0.00, 0.05]). A high percentage of nest relief ceremonies (89%) were observed by neighbours during the first five vocalizations of nest relief ceremonies, irrespective of the sex of the returning individual (mixed model: $F_{1, 63} = 0.01, P = 0.99, \eta^2 = 0.01$ [0.00, 0.01]). In contrast, few nest relief ceremonies (7.5%) were accompanied by vocalizations produced by neighbours. This percentage tended, however, to be higher following the return of males than the return of females (15% and 0%, respectively; mixed model: $F_{1, 63} = 3.86, P = 0.054, \eta^2 = 0.06$ [0.00, 0.17]). Finally, even though sequences recorded by video cameras were longer than sequences simultaneously recorded by microphones (6.7 ± 0.4 and 4.8 ± 0.4 s, respectively; paired t test: $t_8 = 7.97, P < 0.001$) presumably because visual observations included behaviours preceding and following actual vocalizations (e.g. waving movements of the neck) that were difficult to distinguish from the vocalizations, both sequence durations were strongly and positively correlated (Pearson correlation: $r = 0.85, P = 0.004$). Overall, these results suggest that the first five sequences that we considered for acoustic analyses reflected the vocalizing behaviour of both partners, mostly producing loud mutual displays before exchanging tasks on the nest, and that neighbours were unlikely to interfere with audio recordings.

Production Specificity Hypothesis

Vocalization PC1 scores did not reflect any foraging parameters during the previous foraging trip with or without considering beak

Table 3
Results of GLMMs examining the temporal correlation of foraging and vocalization parameters between a given foraging trip or nest relief ceremony (N) and the next

Correlation	Factors	Foraging PC1	Foraging PC2	Vocalization PC1	Vocalization PC2
Intra-individual	Sex	$F_{1, 11} = 0.48, P = 0.50$ $\eta^2 = 0.04$ [0.00, 0.29]	$F_{1, 12} = 11.97, P = 0.51$ $\eta^2 = 0.50$ [0.12, 0.67]	$F_{1, 8} = 0.01, P = 0.91$ $\eta^2 = 0.01$ [0.00, 0.04]	$F_{1, 14} = 0.15, P = 0.70$ $\eta^2 = 0.01$ [0.00, 0.19]
	PC scores	$F_{1, 12} = 6.17, P = 0.029$ $\eta^2 = 0.34$ [0.02, 0.56]	$F_{1, 3} = 36.30, P = 0.007$ $\eta^2 = 0.92$ [0.20, 0.95]	$F_{1, 27} = 14.10, P = 0.001$ $\eta^2 = 0.34$ [0.11, 0.52]	$F_{1, 37} = 4.53, P = 0.04$ $\eta^2 = 0.11$ [0.00, 0.27]
	Sex*PC scores	$F_{1, 12} = 0.08, P = 0.79$ $\eta^2 = 0.01$ [0.00, 0.19]	$F_{1, 3} = 7.08, P = 0.07$ $\eta^2 = 0.70$ [0.00, 0.82]	$F_{1, 27} = 0.03, P = 0.87$ $\eta^2 = 0.01$ [0.00, 0.04]	$F_{1, 37} = 0.10, P = 0.75$ $\eta^2 = 0.01$ [0.00, 0.08]
Between partners	Sex	$F_{1, 15} = 4.02, P = 0.06$ $\eta^2 = 0.21$ [0.00, 0.44]	$F_{1, 17} = 1.28, P = 0.28$ $\eta^2 = 0.07$ [0.00, 0.28]	$F_{1, 13} = 0.84, P = 0.38$ $\eta^2 = 0.06$ [0.00, 0.31]	$F_{1, 14} = 0.09, P = 0.76$ $\eta^2 = 0.01$ [0.00, 0.17]
	PC scores	$F_{1, 25} = 3.24, P = 0.08$ $\eta^2 = 0.11$ [0.00, 0.31]	$F_{1, 25} = 1.30, P = 0.26$ $\eta^2 = 0.05$ [0.00, 0.22]	$F_{1, 42} = 21.46, P < 0.001$ $\eta^2 = 0.34$ [0.15, 0.49]	$F_{1, 46} = 2.14, P = 0.15$ $\eta^2 = 0.04$ [0.00, 0.16]
	Sex*PC scores	$F_{1, 25} = 1.05, P = 0.32$ $\eta^2 = 0.04$ [0.00, 0.20]	$F_{1, 25} = 0.10, P = 0.76$ $\eta^2 = 0.01$ [0.00, 0.11]	$F_{1, 42} = 1.40, P = 0.24$ $\eta^2 = 0.03$ [0.00, 0.15]	$F_{1, 46} = 1.11, P = 0.30$ $\eta^2 = 0.02$ [0.00, 0.13]

For intraindividual correlations, the next foraging trips or nest relief ceremonies considered were those following the return of the same individuals (N + 2). For correlations between reproductive partners, the next foraging trips or nest relief ceremonies considered were those following the return of the partner (N + 1). In the column 'Factors', 'sex' corresponds to the sex of returning individuals and 'PC scores' correspond to the same PC scores as those being tested. Statistically significant results are highlighted in bold. The results of these analyses are illustrated in Fig. 1.

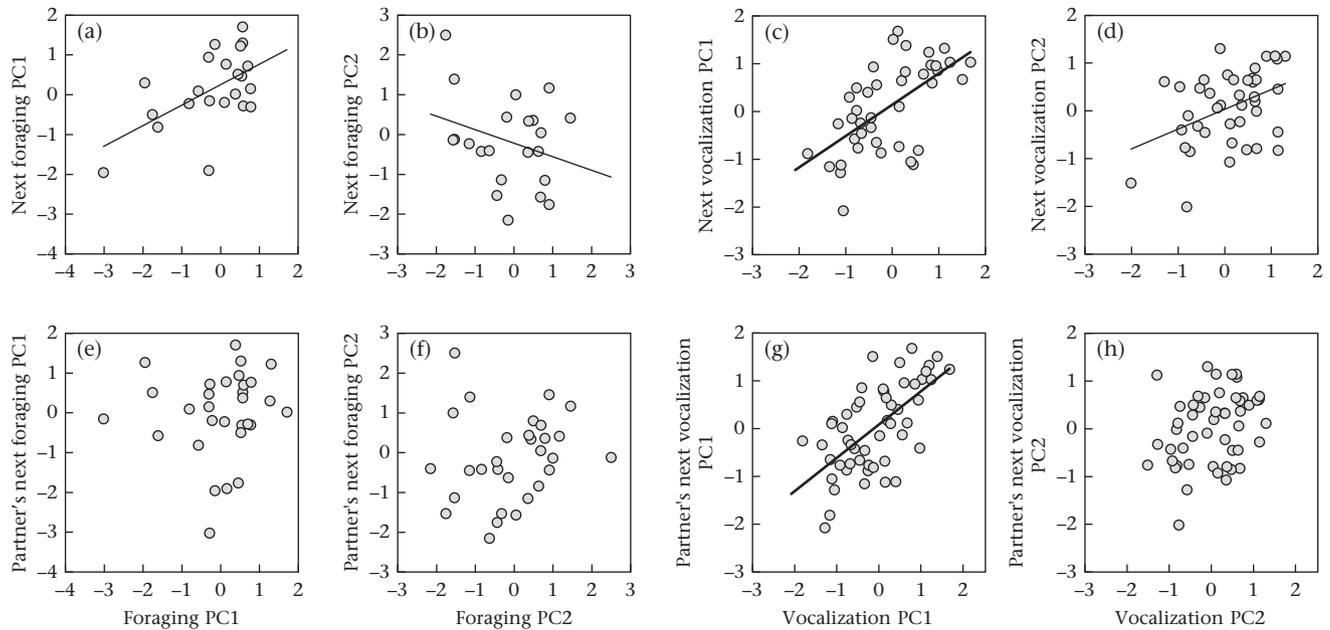


Figure 1. Temporal correlations of foraging and vocalization parameters during the guard stage of nine pairs of Adélie penguins. (a, e) Foraging PC1 score, (b, f) foraging PC2 score, (c, g) vocalization PC1 score and (d, h) vocalization PC2 score. The next foraging trips or nest relief ceremonies considered were those following the return of (a–d) the same individual ($N + 2$) or (e–h) its partner ($N + 1$). Regression lines represent significant relationships. The parameters that PC scores reflect are defined in Table 1 and sample sizes are given in Table 2.

dimensions in the models (Table 4, Fig. 2). Vocalization PC2 scores did not reflect either foraging PC2 scores but tended to reflect (without considering beak dimensions) or significantly reflected (with beak dimensions as covariates) foraging PC1 scores differently, however, depending on the sex of the returning individual (Table 4). By repeating our models for each sex separately, we found that vocalization PC2 scores reflected foraging PC1 scores following the return of males (GLMM(without beak covariates): $F_{1, 5} = 7.96$, $P = 0.040$, $\eta^2 = 0.61$ [0.03, 0.77]; GLMM(with beak covariates): $F_{1, 5} = 8.92$, $P = 0.032$, $\eta^2 = 0.64$ [0.04, 0.79]) with higher vocalization PC2 scores being associated with higher foraging PC1 scores during the previous foraging trip (Fig. 2d). This relationship was not observed following the return of females (GLMM(without beak covariates): $F_{1, 12} = 0.63$, $P = 0.44$, $\eta^2 = 0.05$ [0.00, 0.30]; GLMM(with beak covariates): $F_{1, 7} = 1.70$, $P = 0.23$, $\eta^2 = 0.20$ [0.00, 0.49]). Finally, vocalization PC2 scores tended to be related to the beak dimensions of the returning individual (Table 4). Overall, these results suggest that more extensive foraging trips performed by males were followed by nest relief ceremonies with higher minimal frequencies, longer vocal sequences and shorter silent intervals.

Perception Specificity Hypothesis

Without considering beak dimensions, foraging PC1 scores reflected vocalization PC1 scores (but not vocalization PC2 scores) during the previous nest relief ceremony, irrespective of the sex of the returning individual (Table 5, Fig. A5). These results suggest that nest relief ceremonies with higher frequencies were followed by more extensive foraging trips. However, when adding beak dimensions in the model, this relationship disappeared (Table 5, Fig. 3). In contrast, foraging PC2 scores did not reflect any vocalization parameters during the previous nest relief ceremony when not considering beak dimensions. Adding beak dimensions as covariates in the model made the relationship between foraging PC2 scores and vocalization PC1 scores emerge differently,

however, depending on the sex of the returning partner (Table 5). By repeating our model for each sex separately, we found that foraging PC2 scores reflected vocalization PC1 scores following the return of females ($F_{1, 10} = 11.09$, $P = 0.008$, $\eta^2 = 0.53$ [0.11, 0.70]), with higher foraging PC2 scores being associated with lower vocalization PC1 scores during the previous nest relief ceremony (Fig. 3c). This relationship was not observed following the return of males ($F_{1, 8} = 0.34$, $P = 0.58$, $\eta^2 = 0.04$ [0.00, 0.33]). Finally, foraging PC2 scores tended to be related to the beak dimensions of departing individuals (Table 5). Overall, these results suggest that vocal sequences with higher entropy and higher frequencies during nest relief ceremonies following the return of females were associated with more tortuous subsequent foraging trips performed by males, but only when beak dimensions were taken into account in the models.

DISCUSSION

Using a longitudinal approach across the guard stage of Adélie penguins, we found that the acoustic characteristics of the vocalization sequences produced by reproductive partners during nest relief ceremonies reflected some characteristics of the foraging trips of both the returning and the departing individuals. However, these vocalization characteristics differed between both trip categories. By testing the production hypothesis, we found no significant association between any foraging parameters and the vocalization PC1 scores (reflecting frequency-related parameters and the entropy of vocalization sequences) in the subsequent nest ceremony. However, we found a significant association between foraging PC1 scores (reflecting foraging extent) and the subsequent vocalization PC2 scores (reflecting the low frequency and duration of vocalization sequences). This relationship was only significant for males, even though females showed the same direction of effect. By testing the perception hypothesis, we found that vocal PC1 scores reflected the extent of the next foraging trip of males and females. This second relationship disappeared, however, when

Table 4

Results of GLMM examining the effects of foraging characteristics on the vocal parameters during the subsequent nest relief ceremony (production hypothesis) without or with the beak dimensions of returning individuals as covariates

	Vocalization PC1 scores		Vocalization PC2 scores	
Sex of returning individual	$F_{1, 16} = 0.09, P = 0.77$ $\eta^2 = 0.01 [0.00, 0.15]$	$F_{1, 9} = 0.01, P = 0.94$ $\eta^2 = 0.01 [0.00, 0.04]$	$F_{1, 14} = 0.11, P = 0.74$ $\eta^2 = 0.01 [0.00, 0.18]$	$F_{1, 7} = 1.21, P = 0.31$ $\eta^2 = 0.15 [0.00, 0.46]$
Foraging PC1 scores	$F_{1, 23} = 1.56, P = 0.22$ $\eta^2 = 0.06 [0.00, 0.25]$	$F_{1, 15} = 1.22, P = 0.29$ $\eta^2 = 0.08 [0.00, 0.30]$	$F_{1, 18} = 0.05, P = 0.83$ $\eta^2 = 0.01 [0.00, 0.10]$	$F_{1, 12} = 0.42, P = 0.53$ $\eta^2 = 0.03 [0.00, 0.27]$
Foraging PC2 scores	$F_{1, 17} = 0.03, P = 0.87$ $\eta^2 = 0.01 [0.00, 0.06]$	$F_{1, 14} = 0.01, P = 0.97$ $\eta^2 = 0.01 [0.00, 0.03]$	$F_{1, 12} = 0.33, P = 0.58$ $\eta^2 = 0.03 [0.00, 0.25]$	$F_{1, 11} = 0.61, P = 0.45$ $\eta^2 = 0.05 [0.00, 0.31]$
Beak height		$F_{1, 11} = 2.47, P = 0.14$ $\eta^2 = 0.18 [0.00, 0.45]$		$F_{1, 9} = 3.63, P = 0.09$ $\eta^2 = 0.29 [0.00, 0.54]$
Beak length		$F_{1, 11} = 0.13, P = 0.72$ $\eta^2 = 0.01 [0.00, 0.21]$		$F_{1, 9} = 1.45, P = 0.26$ $\eta^2 = 0.14 [0.00, 0.42]$
Beak width		$F_{1, 12} = 0.91, P = 0.36$ $\eta^2 = 0.07 [0.00, 0.33]$		$F_{1, 10} = 4.44, P = 0.06$ $\eta^2 = 0.31 [0.00, 0.55]$
Sex*foraging PC1 scores	$F_{1, 23} = 0.03, P = 0.87$ $\eta^2 = 0.01 [0.00, 0.05]$	$F_{1, 15} = 0.20, P = 0.66$ $\eta^2 = 0.01 [0.00, 0.19]$	$F_{1, 18} = 3.97, P = 0.06$ $\eta^2 = 0.18 [0.00, 0.40]$	$F_{1, 12} = 6.00, P = 0.030$ $\eta^2 = 0.33 [0.02, 0.56]$
Sex*foraging PC2 scores	$F_{1, 17} = 0.01, P = 0.99$ $\eta^2 = 0.01 [0.00, 0.02]$	$F_{1, 14} = 0.24, P = 0.64$ $\eta^2 = 0.02 [0.00, 0.20]$	$F_{1, 12} = 0.86, P = 0.37$ $\eta^2 = 0.07 [0.00, 0.32]$	$F_{1, 11} = 1.37, P = 0.27$ $\eta^2 = 0.11 [0.00, 0.37]$
Sex*beak height		$F_{1, 11} = 0.41, P = 0.53$ $\eta^2 = 0.04 [0.00, 0.28]$		$F_{1, 9} = 0.11, P = 0.75$ $\eta^2 = 0.01 [0.00, 0.24]$
Sex*beak length		$F_{1, 11} = 1.41, P = 0.26$ $\eta^2 = 0.11 [0.00, 0.38]$		$F_{1, 9} = 3.93, P = 0.08$ $\eta^2 = 0.30 [0.00, 0.56]$
Sex*beak width		$F_{1, 12} = 2.16, P = 0.17$ $\eta^2 = 0.15 [0.00, 0.41]$		$F_{1, 10} = 0.01, P = 0.93$ $\eta^2 = 0.01 [0.00, 0.03]$

Statistically significant results are highlighted in bold.

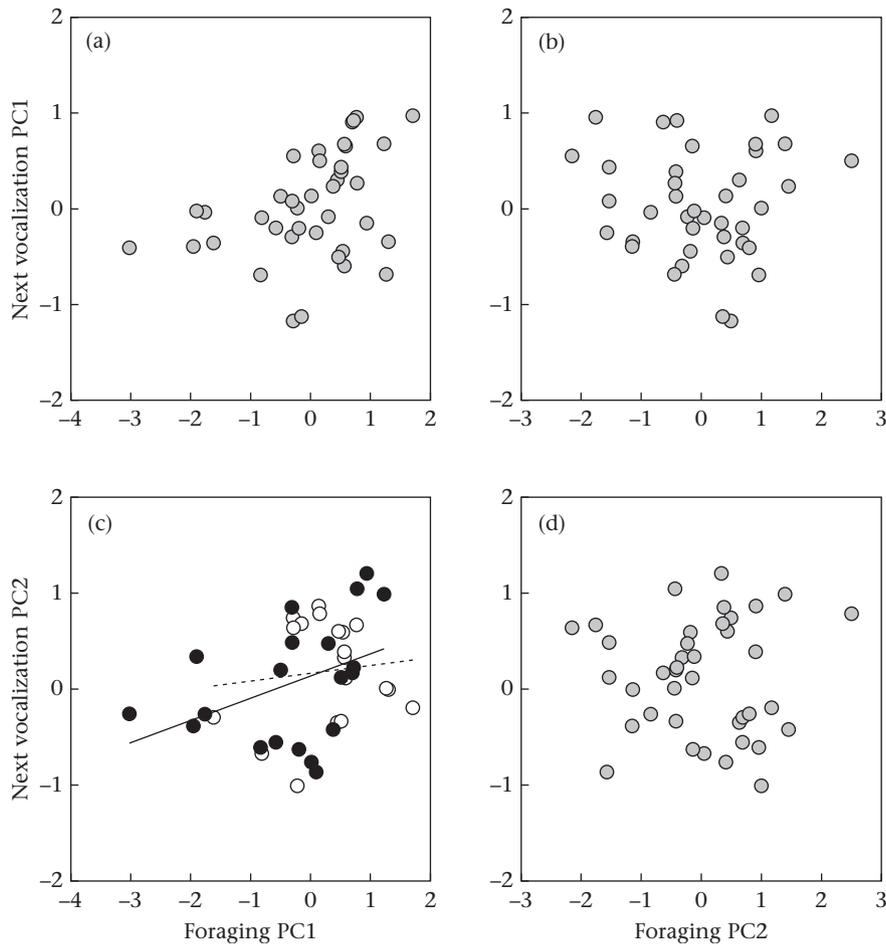


Figure 2. Relationships between foraging characteristics and the characteristics of the vocalization sequences produced by Adélie penguins from nine different pairs during the subsequent nest relief ceremonies (production hypothesis). (a) Relationship between foraging PC1 scores and the subsequent vocalization PC1 scores following the return of males and females. (b) Relationship between foraging PC2 scores and the subsequent vocalization PC1 scores following the return of males and females. (c) Relationship between foraging PC1 scores and the subsequent vocalization PC2 scores following the return of females (white symbols, dashed regression line) or the return of males (black symbols, solid regression line reflecting a significant relationship). (d) Relationship between foraging PC2 scores and the subsequent vocalization PC2 scores following the return of males and females. The parameters that PC scores reflect are defined in Table 1 and sample sizes are given in Table 2. Presented values are values predicted by statistical models with beak dimensions as covariates (Table 4).

Table 5
Results of GLMM examining the effects of vocal parameters during the previous nest-relief ceremony on foraging characteristics (perception hypothesis) without or with the beak dimensions of departing individuals as covariates

	Foraging PC1 scores		Foraging PC2 scores	
Sex of returning individual	$F_{1, 11} = 2.87, P = 0.12$ $\eta^2 = 0.21 [0.00, 0.47]$	$F_{1, 10} = 0.16, P = 0.70$ $\eta^2 = 0.02 [0.00, 0.24]$	$F_{1, 10} = 0.12, P = 0.73$ $\eta^2 = 0.01 [0.00, 0.22]$	$F_{1, 9} = 3.22, P = 0.11$ $\eta^2 = 0.26 [0.00, 0.53]$
Vocalization PC1 scores	$F_{1, 15} = 4.75, P = 0.046$ $\eta^2 = 0.24 [0.00, 0.47]$	$F_{1, 14} = 0.77, P = 0.40$ $\eta^2 = 0.05 [0.00, 0.28]$	$F_{1, 23} = 2.16, P = 0.16$ $\eta^2 = 0.09 [0.00, 0.28]$	$F_{1, 18} = 1.34, P = 0.26$ $\eta^2 = 0.07 [0.00, 0.28]$
Vocalization PC2 scores	$F_{1, 14} = 0.05, P = 0.83$ $\eta^2 = 0.01 [0.00, 0.12]$	$F_{1, 16} = 0.16, P = 0.70$ $\eta^2 = 0.01 [0.00, 0.17]$	$F_{1, 23} = 0.64, P = 0.43$ $\eta^2 = 0.03 [0.00, 0.18]$	$F_{1, 18} = 2.67, P = 0.12$ $\eta^2 = 0.13 [0.00, 0.35]$
Beak height		$F_{1, 10} = 0.01, P = 0.97$ $\eta^2 = 0.01 [0.00, 0.03]$		$F_{1, 10} = 2.93, P = 0.12$ $\eta^2 = 0.23 [0.00, 0.49]$
Beak length		$F_{1, 11} = 0.27, P = 0.62$ $\eta^2 = 0.02 [0.00, 0.26]$		$F_{1, 9} = 4.00, P = 0.08$ $\eta^2 = 0.31 [0.00, 0.56]$
Beak width		$F_{1, 10} = 0.98, P = 0.35$ $\eta^2 = 0.09 [0.00, 0.37]$		$F_{1, 10} = 4.54, P = 0.06$ $\eta^2 = 0.31 [0.00, 0.56]$
Sex*vocalization PC1 scores	$F_{1, 15} = 0.84, P = 0.38$ $\eta^2 = 0.01 [0.00, 0.28]$	$F_{1, 14} = 0.19, P = 0.67$ $\eta^2 = 0.01 [0.00, 0.19]$	$F_{1, 23} = 1.37, P = 0.25$ $\eta^2 = 0.06 [0.00, 0.23]$	$F_{1, 18} = 4.88, P = 0.040$ $\eta^2 = 0.21 [0.01, 0.43]$
Sex*vocalization PC2 scores	$F_{1, 14} = 2.30, P = 0.15$ $\eta^2 = 0.14 [0.00, 0.38]$	$F_{1, 16} = 0.33, P = 0.57$ $\eta^2 = 0.02 [0.00, 0.21]$	$F_{1, 23} = 0.42, P = 0.52$ $\eta^2 = 0.02 [0.00, 0.16]$	$F_{1, 18} = 0.40, P = 0.53$ $\eta^2 = 0.02 [0.00, 0.20]$
Sex*beak height		$F_{1, 10} = 0.29, P = 0.60$ $\eta^2 = 0.03 [0.00, 0.28]$		$F_{1, 10} = 0.04, P = 0.84$ $\eta^2 = 0.01 [0.00, 0.13]$
Sex*beak length		$F_{1, 11} = 1.56, P = 0.24$ $\eta^2 = 0.12 [0.00, 0.39]$		$F_{1, 9} = 3.36, P = 0.10$ $\eta^2 = 0.27 [0.00, 0.53]$
Sex*beak width		$F_{1, 10} = 0.03, P = 0.88$ $\eta^2 = 0.01 [0.00, 0.10]$		$F_{1, 10} = 0.03, P = 0.87$ $\eta^2 = 0.01 [0.00, 0.10]$

Statistically significant results are highlighted in bold.

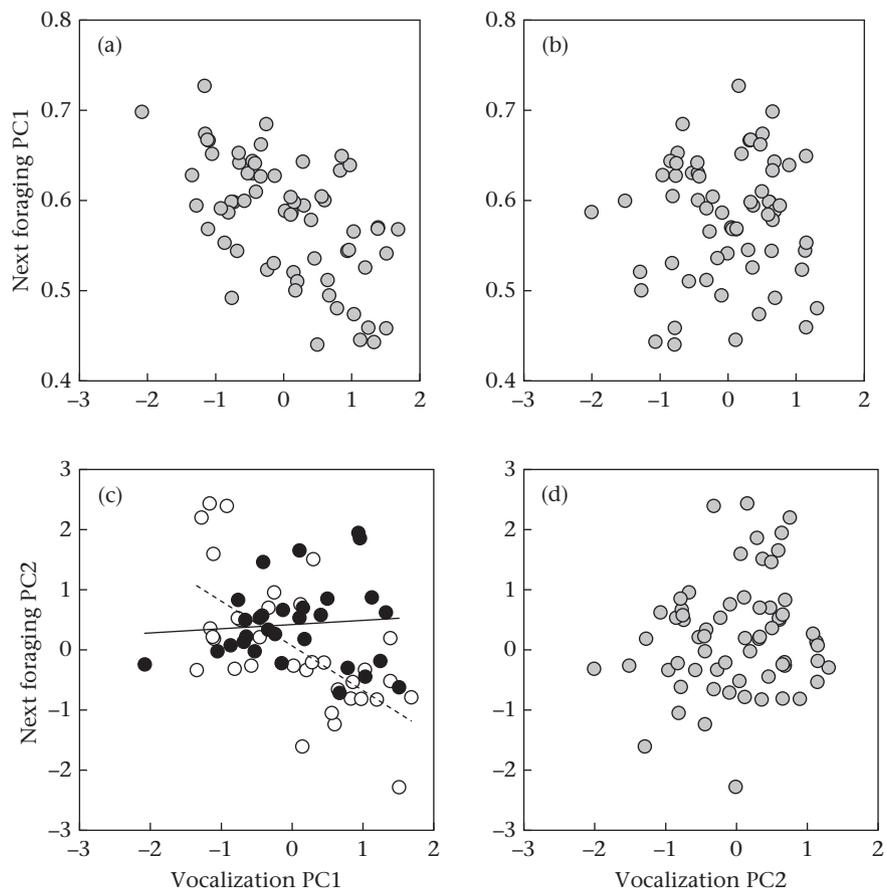


Figure 3. Relationships between vocalization characteristics and the characteristics of the foraging trips subsequently performed by Adélie penguins from nine different pairs (perception hypothesis). (a) Relationship between vocalization PC1 scores and the subsequent foraging PC1 scores following the return of males and females. (b) Relationship between vocalization PC2 scores and the subsequent foraging PC1 scores following the return of males and females. (c) Relationship between vocalization PC1 scores and the subsequent foraging PC2 scores following the return of females (white symbols, dashed regression line reflecting a significant relationship) or the return of males (black symbols, solid regression line). (d) Relationship between vocalization PC2 scores and the subsequent foraging PC2 scores following the return of males and females. The parameters that PC scores reflect are defined in Table 1 and sample sizes are given in Table 2. Presented values are values predicted by statistical models with beak dimensions as covariates (Table 4).

correcting for interindividual differences in beak morphology and may therefore rather reflect the intrinsic capacity of penguins using higher frequencies and entropies to forage further, as beak morphological characteristics may affect both vocalization and foraging capacities in birds (Chávez-Hoffmeister, 2020; Favaro et al., 2014; Giraudeau et al., 2014; Palacios & Tubaro, 2000; Podos, 2001; Volkman et al., 1980). In contrast, correcting for interindividual differences in beak morphology made the relationship between vocalization PC1 scores (reflecting frequency-related parameters or the entropy of vocalization sequences) and foraging PC2 scores in males (reflecting the sinuosity of their subsequent foraging trips) emerge. This relationship may therefore reflect the actual effects of the vocalizations produced during nest relief ceremonies on the foraging behaviour of departing males, irrespective of their vocalization and foraging capacity. These results show that the consideration of morphological traits possibly linking nest displays and foraging behaviour is essential when examining the interplay between these parameters.

To conclude that nest vocalizations facilitate the foraging decisions of birds, they must be related to the foraging behaviour of the returning and the departing partners. We therefore investigated here both the relationships (1) between the foraging behaviour of the returning partner and the subsequent vocalizations produced on the nest, and (2) between the vocalizations produced on the nest and the subsequent foraging behaviour of the departing partner. The fact that the vocalization characteristics associated with foraging characteristics differed between the trips of the returning and the departing partners suggests that vocalization parameters in Adélie penguins reflect different foraging characteristics for both individuals (Table 6). Thus, the exposure of departing birds to nest vocalizations reflecting the foraging behaviour of their partner did not lead them to adopt the same behaviour. This result emphasizes that the relationship between nest displays and the foraging behaviour of the departing partner should not be taken for granted even when these nest displays reflect the foraging behaviour of the returning partner (Table 6). For

instance, a recent study conducted in Cape gannets, *Morus capensis*, found significant correlations between the length of nest displays (i.e. dance ceremonies) and the foraging behaviour of the partner returning to the nest (Courbin et al., 2020). However, while this study implied that nest displays may facilitate foraging decisions, it did not explicitly test this hypothesis, as (1) morphological traits were not considered (e.g. larger gannets may perform shorter foraging trips and dance longer; Mullers et al., 2009) and (2) the foraging behaviour of the departing partner was not monitored. In our study, the foraging behaviour of penguins appears to be mostly intrinsically determined, as it was autocorrelated across foraging trips. Instead of being cues directly facilitating the foraging decisions of the departing partner, the vocalizations produced by penguins on the nest may, therefore, rather reflect their arousal after or before foraging, which correlates differently with the foraging behaviour of the returning and departing partners (Table 6; Clay et al., 2012). In vocalizing animals, a heightened state of arousal is typically associated with higher frequency-related parameters and shorter intervals between vocal bouts (Filippi et al., 2017). For instance, alarm calls are typically short and of high amplitude in situations of high urgency (Clay et al., 2012; Suzuki, 2016). If this pattern applies to breeding Adélie penguins, our results suggest that the short vocal sequences (lower vocalizations PC2 scores) produced during nest relief ceremonies following short trips (lower foraging PC1 scores) performed by males (Fig. 2c) reflect a high level of excitement, possibly because such trips enable parents to provision chicks at a higher rate (Ropert-Coudert et al., 2004).

Even though the foraging behaviour of departing partners was not found to reflect the foraging behaviour of the returning partner in the present study, male and female partners from pairs of Adélie penguins were previously found to share the same spatial foraging range between coastal and oceanic areas based on plasma isotopic measurements (Beaulieu, Ropert-Coudert et al., 2010). Moreover, when penguins were temporarily handicapped and hence foraged in more coastal areas (based on plasma isotopic measurements),

Table 6

Summary of the different possible and nonexclusive relationships between the characteristics of nest vocalizations (a or b) and the foraging characteristics (A or B) of the returning and departing partners

Scenario	Foraging characteristic (returning individual)	Nest vocalization characteristic	Foraging characteristic (departing individual)	Interpretation
1	A	→ a →	A	1a. Vocalizations are cues facilitating the foraging decisions of departing individuals (under favourable feeding conditions encountered by the returning partner) 1b. The same vocalization characteristics reflect the arousal of returning and departing partners, and similarly correlate with their respective foraging behaviour
2	A	→ a →	B	2a. Vocalization characteristics are cues unrelated to arousal) affecting the foraging decisions of departing partners (under unfavourable feeding conditions encountered by the returning partner) 2b. The same vocalization characteristics reflect the arousal of returning and departing partners, which differently correlates with their foraging behaviour
3	A B	→ a × × b →	A B	3a. Different vocalization characteristics reflect the arousal of returning and departing partners, which correlates with different foraging characteristics in returning and departing individuals
4	A	→ a ×	B	4a. Vocalization characteristics reflect the arousal of returning partners, which correlates with their previous foraging behaviour
5	A	× b →	B	5a. Vocalization characteristics reflect the arousal of departing partners, which correlates with their subsequent foraging behaviour
6	A, B	× a, b ×	A, B	6a. Vocalizations are not involved in the regulation of foraging decisions

Arrows indicate significant relationships between vocalization and foraging characteristics (assumed to be independent of the intrinsic vocalizing and foraging capacity of partners), while the crosses indicate no relationships. For each scenario, one or two interpretations (a and b) are provided. The results of the present study support the third scenario.

their nonhandicapped partners followed the same foraging strategy (Beaulieu, Spée, et al., 2010). As coastal and oceanic areas differ in their availability in fish and krill (Cherel, 2008), penguin vocalizations may still facilitate foraging decisions regarding prey location and quality but at a coarser scale (coastal versus oceanic) than the scale we considered here (precise surface coordinates), and may also integrate a rough indication of the depth where penguins feed (which was not considered here). This coarse scale may be related to the low degree of production and perception specificity associated with graded signal variation (Suzuki, 2016), such as the variation in vocalization characteristics we measured in our study.

In the current work, video analyses indicated that the roles of reproductive partners were balanced during nest relief ceremonies. This may be related to the fact that the benefits of nest relief ceremonies should be equivalent for partners both alternating between the roles of signaller and receiver. However, even though nest relief ceremonies were always performed by the same males and females across the guard stage, the characteristics of their accompanying vocalizations were specific to the return of a given partner (as all of these characteristics were repeatable following the return of a given individual but not following the return of its partner). Moreover, the relationships between the vocalizations produced during nest relief ceremonies and the foraging behaviour of penguins at sea were more marked in males. Indeed, the vocalizations produced on the nest only significantly reflected some components of the behaviour of males during both their previous and next foraging trips (Fig. 3). This difference between males and females may be due to a higher sensitivity of males to acoustic changes in the vocalizations produced during nest relief ceremonies (as found in zebra finches, *Taeniopygia guttata*, with only males responding to changes in call frequencies; Vicario et al., 2001). Ultimately, this difference suggests that the vocalizations produced during nest relief ceremonies may contribute to the sexual conflict between partners in Adélie penguins, with only females being able to affect the foraging behaviour of their partner. Females may also use the foraging response of departing males to nest vocalizations as a marker of individual quality. This may explain why females breeding with a male that has been temporarily handicapped (and hence unable to show much foraging plasticity) show a higher divorce rate during the subsequent breeding season (while a higher divorce rate is not observed when females have been temporarily handicapped; Beaulieu, Raclot, et al., 2009). Disentangling the precise contribution of each partner in the vocalizations produced at the nest following the return of females, as well as examining the respective costs and benefits of the behavioural response of foraging males to these vocalizations would be necessary to examine this point.

Because of the intensity of Adélie penguins' vocalizations, their active space (i.e. the area around the signal source over which the signal remains detectable and recognizable) inevitably extends much further than the nest where they are produced. The vocalizations of Adélie penguins can be heard by conspecifics up to 16 m away from their nest (Aubin & Jouventin, 2002), and may thus be theoretically perceived by birds from more than 500 surrounding nests (assuming an even distribution of nests across the colony and a nest density of 1.5 nests/m² density; Beaulieu, Thierry et al., 2009). This suggests that the vocalizations produced by partners during nest relief ceremonies may affect not only the foraging behaviour of the departing partners participating in these nest relief ceremonies but also the foraging behaviour of departing neighbours. Eavesdropping on vocalizations from other nests to facilitate foraging decisions may contribute to the hypothesized function of 'information centres' attributed to animal colonies (Evans et al., 2016; Ward & Zahavi, 1973) and may explain why within-colony spatial segregation may reflect variation in foraging

behaviour (Sánchez et al., 2018). In our study, these presumed facilitating effects between nests may explain why most nest relief ceremonies were observed by neighbours that themselves mostly remained silent (especially following the return of females). The stability of neighbour exposure within a given reproductive season but also across reproductive seasons in colonies of Adélie penguins (because of their high nest site fidelity; Beaulieu, Raclot, et al., 2009) may underlie why all individuals in a colony would reciprocally benefit from being heard by their neighbours and from listening to their neighbours (Clay et al., 2012). Importantly, these effects would necessarily be less important for peripheral nests with fewer neighbours (as in our study). Peripheral individuals may compensate for this lack of social interactions with neighbours by relying more strongly on the vocalizations produced by their partner. The relationships between nest vocalizations and the foraging behaviour of departing penguins may therefore be stronger in peripheral nests than in more central nests. This point should be the focus of future studies.

Our exploratory study suggests that the function of bird vocalizations extends beyond the classical framework of individual recognition and territory defence and opens a novel perspective on the regulation of foraging strategies through the vocalizations produced by partners on their nest remotely from their foraging grounds. However, our study was based on a relatively small number of pairs, which may limit the robustness of our results. Moreover, to reduce the number of analyses presented in our study, we conducted PCAs, and the amalgamation of parameters might have hidden subtle relationships between individual vocalization and foraging parameters. Finally, because our results are correlational, the underlying factors and potential confounding factors responsible for the relationships that we found remain unclear. For instance, irrespective of the vocalizations penguins heard on their nest before leaving the colony, those foraging extensively consistently showed this behaviour across foraging trips, while penguins using a more tortuous foraging behaviour during a given foraging trip showed the opposite behaviour during their next foraging trip (thereby suggesting that penguins alternate exploratory and nonexploratory foraging trips). Hence, the effects of nest vocalizations on foraging decisions are intermingled with the intrinsic foraging capacity of birds. To control for one confounding factor potentially affecting both the vocalizing and foraging behaviours of penguins, we considered their beak morphology (which indeed tended to affect the vocalizations and the foraging behaviour of penguins in our study). However, other potential factors such as the pre-exposure of the studied individuals to the nest relief ceremonies of their neighbours or encountering other foraging individuals on the feeding grounds may also blur the relationship between vocalizations and foraging behaviour. By highlighting these limitations and the complexity of studying nest vocalizations as mediators of foraging decisions, we hope that our study will lay the foundation for future studies using additional approaches to examine this interplay. Among all the possible perspectives, further studies may (1) examine whether the syntax of the vocalizations produced by birds on their nest is related to components of their foraging behaviour, (2) monitor the acoustic environment of departing birds at a broader scale than just the nest (by simultaneously examining the acoustic environment and the foraging behaviour of direct neighbours), (3) use loggers indicating where foraging individuals exactly find which food and with whom (e.g. time-depth recorders, accelerometers, proximity loggers, cameras) or (4) examine the relationship between nest vocalization and foraging behaviour after experimentally manipulating the intrinsic foraging capacity of animals through temporary handicap approaches. However, the most conclusive approach would be to expose departing birds to

the playback of their partners' vocalizations, the acoustic properties of which have been experimentally modified (as already conducted in studies examining mate choice in relation to song quality in songbirds; e.g. Caro et al., 2010; Lyons et al., 2014). Only such approaches, complementary to the approach used in our exploratory study, will allow us to uncover the causal effects underlying the relationships between the vocalizations produced by birds on their nest and their foraging behaviour.

Author Contributions

M.B. conceived the study, collected and analysed data and wrote the first draft of the manuscript. T.R. and C.M. collected data in the field, A.K. organized and prepared GPS loggers before fieldwork and J.K. analysed videos. M.D. and Y.R.C., respectively, led the programmes 'Hearing in penguins' and l'AMMER, which enabled data collection in the field. All authors actively contributed to the final version of the manuscript and gave final approval for publication.

Data Availability

The data set supporting this study is available in Mendeley (<https://doi.org/10.17632/vt34k2njzx.1>) and in the Supplementary Material.

Declaration of Interest

None.

Acknowledgments

This research arose from a collaboration between the project "Hearing in Penguins" led by the German Oceanographic Museum and the program l'AMMER of the French Polar Institute (Adélie penguins as Monitor of the Marine Environment; Prog. 1091). MB was funded through the project 'Hearing in penguins' by the German Environmental Agency through the Federal Ministry for the Environment Nature Conservation and Nuclear Safety (grant no. FKZ3777182440). We would like to thank the French Polar Institute (IPEV) and its staff in Dumont d'Urville Station for logistical support. We are also grateful to the Antarctic Science Bursary, the Zone Atelier Antarctique (ZATA) and the WWF-UK for funding part of this research.

Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2021.08.015>.

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Appendix

Table A1
Structure of the statistical models used in this study

Analysis	Model structure	Distribution
Data representativeness	Foraging trip duration ~ Foraging trip number * Sex + (1 nest_ID/Individual_ID)	Normal
	Vocal PC1 scores ~ Foraging trip number * Sex + (1 nest_ID/Individual_ID)	Normal
	Vocal PC2 scores ~ Foraging trip number * Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC1 scores ~ Foraging trip number * Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC2 scores ~ Foraging trip number * Sex + (1 nest_ID/Individual_ID)	Normal
Repeatability	N offspring ~ Reproductive stage * Treatment + (1 nest_ID)	Poisson
	Vocal PC1 scores ~ Vocal PC1 scores * Sex + (1 nest_ID/Individual_ID)	Normal
	Vocal PC2 scores ~ Vocal PC2 scores * Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC1 scores ~ Foraging PC1 scores* Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC2 scores ~ Foraging PC2 scores* Sex + (1 nest_ID/Individual_ID)	Normal
Video data	Vocalization initiation ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Binary
	Neighbour observation ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Binary
	Neighbour vocalization ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Binary
	Exchange latency ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Normal
	N vocalizations ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Normal
	Last mutual display ~ Sex + (1 nest_ID/Individual_ID) + (1 Foraging trip number)	Normal
Production hypothesis	Video sequence duration ~ Recorder sequence duration + (1 Nest ID)	Normal
	Vocal PC1 scores ~ Foraging PC1 scores* Sex + Foraging PC2 scores* Sex + (1 nest_ID/Individual_ID)	Normal
Perception hypothesis	Vocal PC2 scores ~ Foraging PC1 scores* Sex + Foraging PC2 scores* Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC1 scores ~ Vocal PC1 scores* Sex + Vocal PC2 scores* Sex + (1 nest_ID/Individual_ID)	Normal
	Foraging PC2 scores ~ Vocal PC1 scores* Sex + Vocal PC2 scores* Sex + (1 nest_ID/Individual_ID)	Normal

All models are mixed models (GLMM; except for video sequence duration for which a paired *t* test was used). The GLMM used for the production and perception hypotheses could also include beak parameters in addition to the parameters represented here.

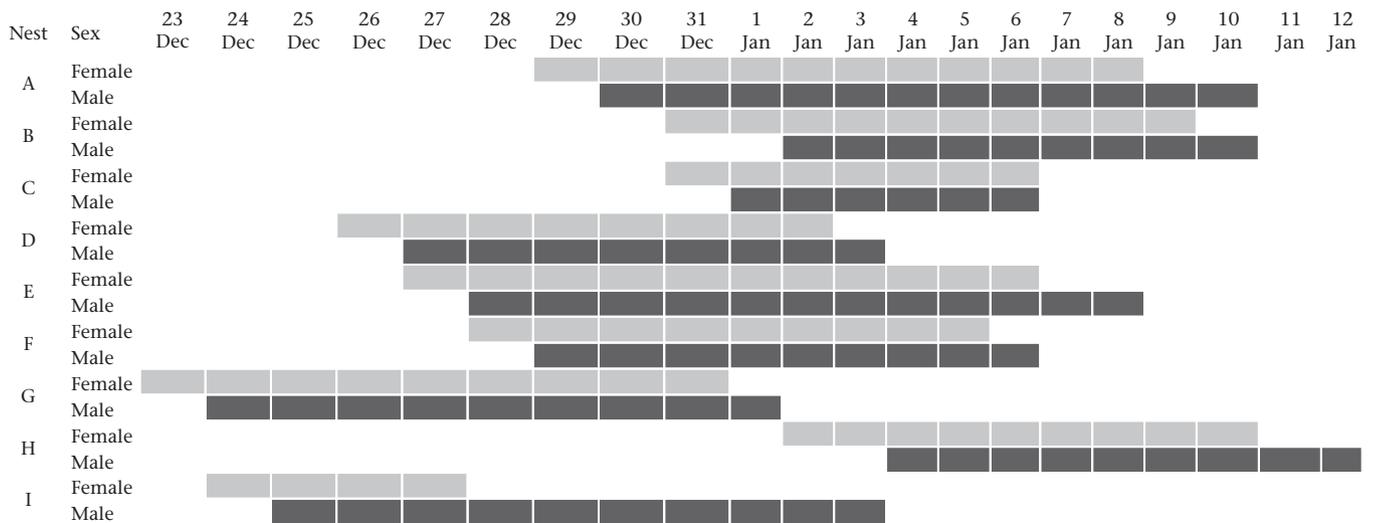


Figure A1. Period when female (light grey) and male (dark grey) Adélie penguins were equipped with GPS devices in our study. This period includes time on the nest and at sea.

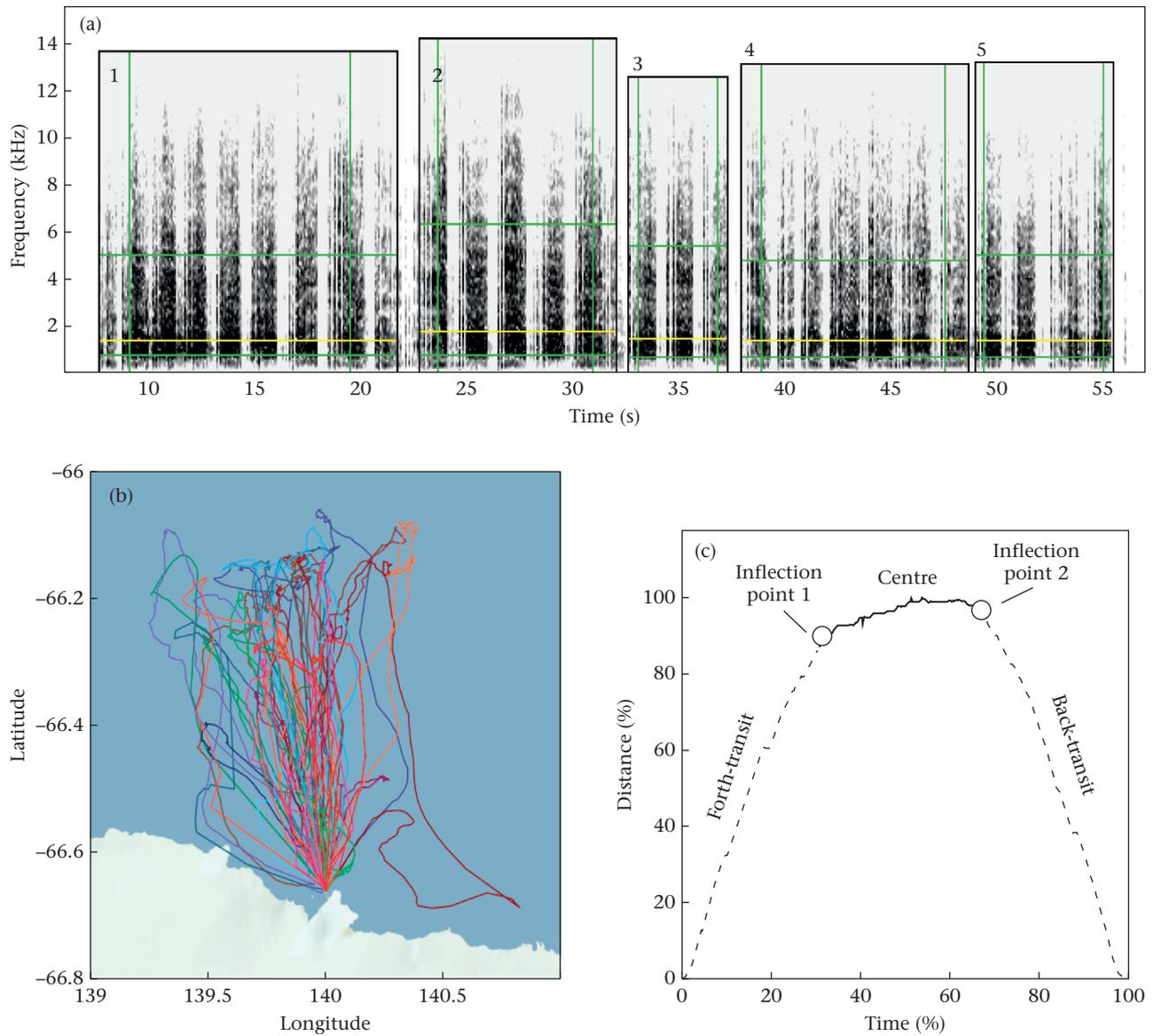


Figure A2. Representation of the raw parameters measured in this study. (a) Spectrogram showing the five first sequences of a nest relief ceremony (vertical green lines: time 5% and time 95% of each sequence; horizontal green lines: frequency 5% and frequency 95%; horizontal yellow line: centre frequency). (b) GPS tracks of Adélie penguins during the guard stage (each colour corresponds to one individual). (c) Representation of a foraging trip with foraging time (expressed in %) as a function of foraging distance (expressed in % of the maximal distance from the colony).

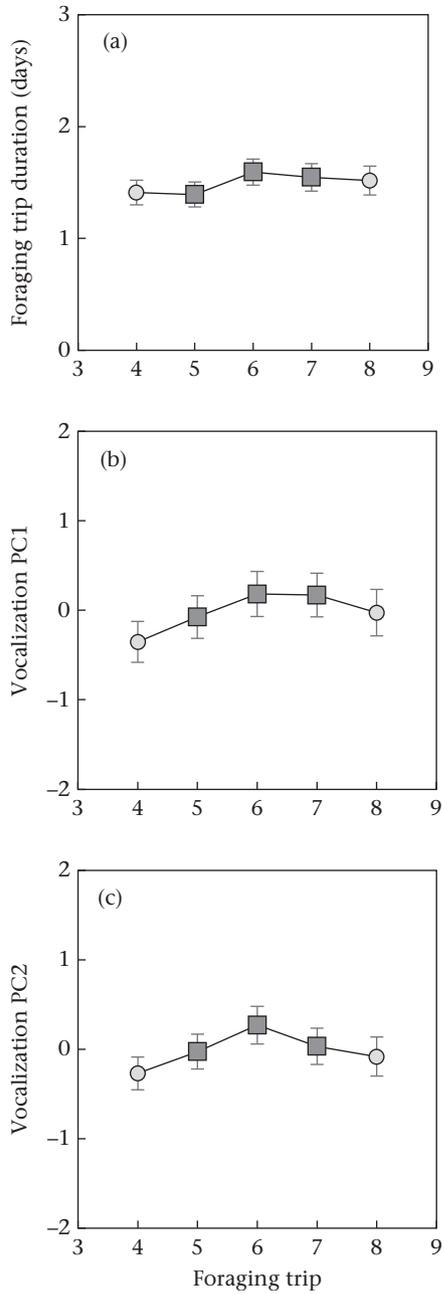


Figure A3. Temporal variation (mean \pm SE) of (a) foraging trip duration, (b) vocalization PC1 score and (c) vocalization PC2 score between the fourth and the eighth foraging trip following egg laying. Penguins were equipped with GPS between the fifth and up to the seventh foraging trip after egg laying (dark grey squares).

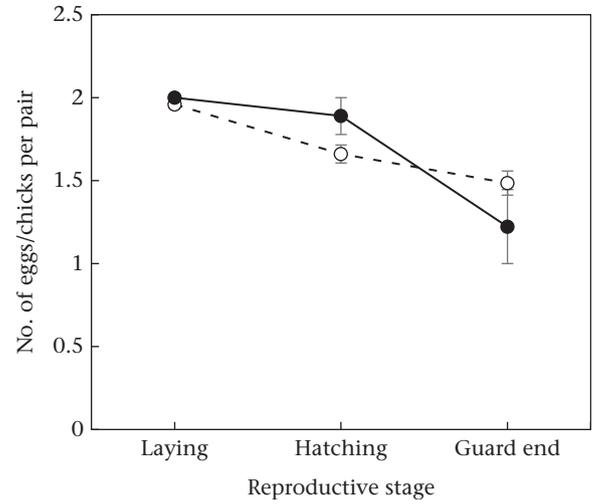


Figure A4. Reproductive performance (mean \pm SE number of eggs/chicks per pair) of penguins monitored with microphones and GPS devices (black symbols, solid line) and of penguins only visually monitored (white symbols, dashed line) across the reproductive season.

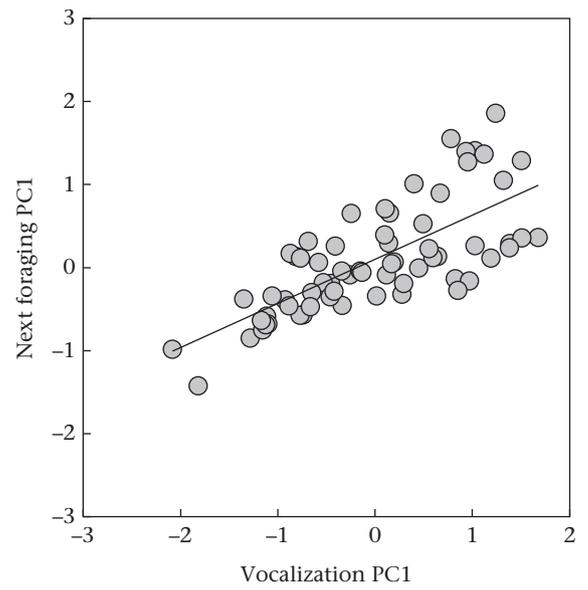


Figure A5. Relationship between vocalization PC1 scores and the subsequent foraging PC1 scores following the return of females and males. The regression line is shown. The parameters that PC scores reflect are defined in Table 1 and sample sizes are given in Table 2. Presented values are estimated by statistical models without beak dimensions as covariates (Table 4).