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Functional characterization of begging calls in Thin-billed Prions *Pachyptila belcheri* chicks

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Abstract. Chicks beg to solicit food and care from their parents. Previous studies of nocturnally feeding Thin-billed Prions (*Pachyptila belcheri*) showed that chicks convey information about their condition to their parents by means of begging calls. However, those studies used tape-recorders with a limited recording duration, which precluded the recording of complete nights, so only the first begging sessions per night were analysed. Here we present data on begging call intensities and the acoustic parameters of begging elements obtained using digital voice recorders, which enabled complete nights to be recorded. Chicks used from one to five begging sessions per night. We found that the parameters of the first calling sessions did not reflect body condition, whereas the duration of begging sessions and the number of begging calls over the whole night was correlated with the chicks' body condition and the sizes of the meals delivered by the parents. The acoustic parameters of begging call elements were not correlated with body condition. Chicks did not change call frequencies according to their state of nutrition. All call parameters, including the acoustic parameters of chick begging calls, were highly chick-specific. We further tested for age effects and found strong correlations between call features and the age of chicks. The results of the present study show that some begging parameters, e.g. the duration of begging sessions and the number of begging calls over the whole night, are connected with condition, while others, such as acoustic parameters, are linked with individual chick recognition.

Key words: Parent-offspring communication, signaling, provisioning, *Pachyptila belcheri*, seabirds, begging, nestling condition

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INTRODUCTION

According to life-history theory, animals have to make a trade-off between current reproduction and reproductive effort in future seasons. This means that adult birds must find a balance between providing food for chicks and maintaining their own body condition. Maintenance of the own body condition would increase the survival prospects to chicks in the following breeding season.

There is more than one possible strategy of how the adult birds might deal with this conflict. Either the provisioning of food to chicks follows an intrinsic rhythm that mainly depends upon the body condition of feeding adults, or it could be adjusted to chick demands, or adults could compromise between these two goals.

Altricial avian chicks are entirely dependent on their parents during the growth period, and they

generally use visual, posturing or vocal signals to obtain food and/or heat from them (Kilner & Johnstone 1997, Royle et al. 2002, Sacchi et al. 2002). They communicate their own needs by begging, and parents use this information to adjust their investment. For example, change in mouth colour signalled need among the seed-regurgitating finches (Kilner & Davies 1998) and hungry chicks of House Sparrows *Passer domesticus* change their posture (Kedar et al. 2000). Nevertheless, these two kinds of signals are unlikely to be effectively received by burrow-nesting birds that provide food to their chicks in the darkness of the burrow at night and therefore may mainly use vocal communication. Indeed, the intensity of begging (generally number and the rate of begging calls within a begging call session) is known to advertise the chick's body condition for many bird species (e.g. Mondloch 1995, Cotton et al. 1996, Kilner & Johnstone 1997, Royle et al. 2002).

One means for chicks to convey this information as soon as parents arrive in the nest is using acoustic characteristics of a single call element like its duration, frequency and amplitude (Leonard & Horn 2001, Sacchi et al. 2002).

Seabirds of the order Procellariiformes are suitable for such studies because they have only one chick, meaning there is no vocal sibling competition (see also Quillfeldt 2002). Ruling out sibling competition makes evaluating the calls a lot simpler. Another advantage is that there is no size difference between male and female chicks, and hence that there is no difference in nutritional requirements between sexes. In several procellariiform species, parents were found to respond to chicks' begging signals and meet the individual demands of their offspring, if the environmental context allowed it: Manx Shearwaters *Puffinus puffinus* (Quillfeldt et al. 2004, Hamer et al. 2006), Cory's Shearwater *Calonectris diomedea* (Grandeiro et al. 2000, Quillfeldt & Masello 2004, Träger et al. 2006, Quillfeldt et al. 2007d) and Wilson's Storm-Petrel *Oceanites oceanicus* (Quillfeldt 2002, Gladbach et al. 2009). While these previous studies were mostly based on the analysis of call rates and numbers, two studies also included acoustical parameters of begging call elements. The results from these two studies were in part contradictory. While the begging calls of Cory's Shearwaters did not contain information on body condition (Träger et al. 2006), Wilson's Storm-Petrels chicks increased the acoustical frequency of their calls when they were hungrier (Gladbach et al. 2009). As the effect size in the latter study was small, this raises the possibility that there may be little causal relationship between a chick's nutritional requirements and the acoustical parameters of its begging calls.

Since both the rate and number of calls can only be assessed over time, it has been suggested that particular features of single begging elements could convey much more rapid information about the chick's body condition (Sacchi et al. 2002, Gladbach et al. 2009). This hypothesis has seldom been tested but has received experimental support for a multiparous species, the Barn Swallow *Hirundo rustica* (Sacchi et al. 2002).

Like all procellariiform seabirds, Thin-billed Prions have single-egg clutches and are socially monogamous, with both parents being involved in the care and the raising of a single large chick. Prions are nocturnal petrels, making long feeding trips during the day and returning to the nests at night during the ca. 55 days of the nestling period.

Because adults can make long foraging trips, up to 8 days away from the nest (Quillfeldt et al. 2007c), chicks are not attended every night (Quillfeldt et al. 2007a). When adults arrive, Thin-billed Prion chicks use two different call types, "rhythmic calls" and "long begging calls" (Quillfeldt 2002, Quillfeldt et al. 2006). Young beg only in the presence of adults, and the present analysis only included "long begging calls". Adults spend variable time in the nest, short visits are used when food is scarce, while under good condition they may spend the whole night in the burrow and feed the chick several times. We have no indication that adults recognize individual chicks. Chick-switching experiments suggest that rather parents recognize the nest and any chick present in the nest will be fed (Quillfeldt et al. 2006).

A previous study of Thin-billed Prions demonstrated a strong positive correlation of chicks' begging with chicks' body condition and meal size delivered by parents using parameters obtained from call counts (call number and mean and maximum call rate), but without analysis of acoustic structure of begging call elements (Quillfeldt et al. 2006). Furthermore, the use of tape-recorders with limited recording duration had made it impossible so far to record complete nights. Instead, first begging sessions per night were analyzed during previous studies. We here present data on begging call intensities and acoustic parameters of begging elements, using digital voice recorders, which enabled recording of complete nights.

The purpose of this study on Thin-billed Prions was to examine: (1) how information on the body condition of individual nestlings is encoded in the acoustic structure of begging call elements, (2) how begging efforts are distributed across the night and (3) age effects on chick begging behaviour.

METHODS

Study site

The study was carried out at the New Island Nature Reserve, Falkland Islands (51°43'S, 61°17'W). Thin-billed Prions show the typical procellariiform pattern of a single-egg clutch and slow chick development, with an average fledging period of 50 days (Strange 1980). They are small nocturnal petrels, and the absence of adults from the nest burrow during the day provides the opportunity to collect data on chick provisioning with relatively low disturbance to the birds.

Thin-billed Prions breed on the Falkland, Crozet and Kerguelen Islands. New Island, in the Falkland Islands, is the most important known breeding site for Thin-billed Prions. Up to 2 million pairs were estimated to breed on this island in 2001/2002 (Catry et al. 2003). The life cycle and basic biology of Thin-billed Prions have been described by Strange (1980). More recently, studies of the biology of Thin-billed Prions were carried out on Kerguelen, including studies of sexual dimorphism in voice and morphology (Genevois & Bretagnolle 1995), feeding ecology (Chastel & Bried 1996, Cherel et al. 2002) and parental investment (Weimerskirch et al. 1995, Duriez et al. 2000). At New Island, recent studies explored variability in provisioning and parent-chick interactions (Quillfeldt et al. 2003, 2006, 2007 a, b, c, 2008 a, b, c 2009 a, b, Catry et al. 2007).

Chick measurements

We randomly selected 39 nests in 2007. From 1st January to 1st March 2007 we followed these nests, measuring and weighing chicks during the day and recording their calls at night (e.g. Quillfeldt et al. 2003, 2006). If chicks had already hatched on our first visit, we estimated the hatching date (to the nearest day) by calibrating wing length against wing growth in chicks of known age (e.g. Quillfeldt et al. 2003, 2006). We weighed chicks daily in the morning to the nearest g using a digital balance.

We calculated the index of chick body condition (BC index) at the beginning of each night for each bird. Previously, BC index was calculated using the body mass (m), relative to the multi-year mean mass for chicks of each age (m_{mean}), using the formula: $\text{BC index} = m/m_{\text{mean}} * 100$ (e.g. Quillfeldt et al. 2006). Since food was scarce in the previous years and 2007 was a rich year, the mean body mass of 2007 differed from that of previous years. Therefore, only the mean chick mass of 2007 was used to calculate the BC index to increase accuracy. In species with a pattern of peak mass and mass recession, like Procellariiformes and Psittaciformes, body condition indices relative to age are more adequate than mass controlled for measures of body size. In these chicks, growth of structural size and body mass does not occur in a parallel fashion (e.g. approx. quadratic growth of mass, but logistic tarsus growth, with maximum tarsus often reached well before the end of the nestling stage (see also Masello & Quillfeldt 2002). Thus, mass vs. structural size in chicks of these groups is not independent of chick

age. Meal size being large compared to body mass, BC index largely reflects recent provisioning efforts. This BC index varied between 55 and 161 (mean = 105 because the breeding season had relatively favourable feeding conditions).

We calculated meal sizes and feeding frequencies from changes in chick body mass recorded overnight, using equations to correct for mass lost through digestion, respiration and excretion between weightings. Briefly, we calculated weight change before and after feeding events, in relation to the weight of the chick at the beginning of the night. We first determined if chicks had been fed, using a regression equation from intervals before feeding. For nights with feedings, we calculated the daily mass loss using the regression equation for the mass loss after feeding, starting with the evening weight. Meal sizes were calculated as the sum of the observed mass change overnight and the estimated metabolic mass loss. More details are described in Quillfeldt et al. (2003).

Recordings and begging data from call counts (begging session parameters)

The vocal behaviour of nestlings at each of the study nests was recorded overnight, by placing a microphone connected to a digital recording device in the nest burrow, immediately above the nest chamber. Begging call recordings were carried out as described in Quillfeldt et al. (2006), with the difference that digital recording devices (dnt MemoPen digital voice recorders in Standard-Play Modus with a frequency range of 500 Hz to 3500 Hz) were used instead of tape recorders. Audio recordings were made all through the night, beginning at dusk (around 10 pm at the latest). Some recordings were too quiet, and these had to be excluded from further analysis. The original .tss files from the digital voice recorders were transformed to .wav files using Power Voice software.

As in the previous studies (Quillfeldt et al. 2006), we counted the number of calls during the first call session and calculated parameters of begging sessions from call counts: total number of calls in a begging session, duration of the begging session, mean call rate (calls/min) and maximum call rate in a begging session. Begging after a pause of 10 minutes or more was regarded as a new session (as used previously, e.g. Quillfeldt et al. 2006).

We further counted all begging sessions (between one and five sessions per night) of chicks of the age class 10–20 days ($N = 118$ nights).

Table 1. Abbreviations used for the acoustic parameters of begging calls of Thin-billed Prion chicks.

Abbreviation	Parameter explanation	Unit
CallDur	Call duration	ms
Fmax	Maximal frequency	Hz
Fmean	Mean frequency	Hz
PeakFTot	Frequency with largest amplitude in power spectrum	Hz
LocFMax	Location of the maximal frequency of a begging call	-
LMaxAmp	Location of the maximal amplitude of a begging call	-

We only included chicks of 10–20 days of age in this to exclude age effects, and because counting all sessions for all chick ages would have been too time consuming. In the latter analysis, the daily variation in begging behaviour reflected not only the chick's need at the time of the first adult arrival, but also the chick's behaviour during the rest of the night.

Acoustical analysis

Short samples of five to seven calls from the beginning, middle and end of the begging sessions, respectively, were extracted using Cool Edit 96. These parts were selected randomly, but taking recording quality into account (good signal quality and absence of interfering calls from attending adults or neighbours).

We then produced spectrograms using Avisoft SASLab Pro 4.2 (FFT-length: 512, time resolution: 1 ms and frequency range: 0–4 kHz) and saved them as .txt files. We finally used the software ConAn 0.93 (described in Mundry & Sommer 2004) to realize a semi-automatic analysis of acoustic parameters of the fundamental frequency. We included six acoustic parameters in the present analysis (Table 1): the duration of elements (call duration), their maximum and mean frequency (Fmax and Fmean), the frequency with the largest amplitude (PeakFTot) and the location of maximum frequency and maximum amplitude, normalized to element duration (LocFMax and LMaxAmp). We averaged these data for each part of the begging call session (a total of 238 chick nights with acoustical and session parameters).

The begging calls from the different stages in the begging sessions, beginning, middle and end, were different in two of the six parameters (Table 2). Both parameters, Fmean and PeakFTot, were frequency parameters. When compared to the other stages in a post-hoc analysis, the calls at the beginning had a lower frequency than calls later in the session. We then calculated mean values of the whole begging session, which were used for further statistics.

Statistical analysis

Statistical tests were performed with SPSS 11.0.0. Kolmogorov-Smirnov tests were used to test for normality in all call parameters (all $p > 0.2$). Principal Component Analysis (PCA) was used to summarize the six acoustical parameters. Three principal components were extracted, using varimax rotation (Table 3). This procedure was justified as indicated by the Kaiser-Meyer-Olkin Measure of Sampling Adequacy equalling 0.584 and thus reaching the required level (0.5) and Bartlett's test of sphericity revealing significance ($\chi^2 = 656.9$, $df = 15$, $p < 0.001$) and used as dependent variables in General Linear Models (GLM) with body condition as the covariate. The PCA extracted three new factors that summarized the six previously mentioned acoustical call parameters (Table 3). PC1 was most strongly influenced by the three frequency parameters (Fmax, Fmean and PeakFTot). PC2 stands for CallDur and PC3 summarised mainly LocFMax and LmaxAmp. The cumulative percentage explained by 3 components was 84% (Table 3).

Table 2. Comparison between the mean parameters of different stages of a begging session (beginning, middle and end), using One Way Repeated Measures ANOVA. ^{a, b} denote homogenous subsets defined by Tukey post-hoc analyses.

Parameter	Beginning	Middle	End	Test
CallDur	246.4 ± 9.0	233.2 ± 8.3	227.9 ± 11.5	$F_{19,2} = 1.630$, $p = 0.209$
Fmax	3121.5 ± 96.2	3256.1 ± 91.4	3253.4 ± 64.0	$F_{19,2} = 2.085$, $p = 0.138$
Fmean	2428.6 ± 97.5 ^a	2609.5 ± 81.1 ^b	2620.3 ± 52.2 ^b	$F_{19,2} = 4.270$, $p = 0.021$
PeakFTot	2308.0 ± 102.2 ^a	2631.8 ± 82.8 ^b	2621.3 ± 54.8 ^b	$F_{19,2} = 7.046$, $p = 0.002$
LocFMax	0.51 ± 0.03	0.48 ± 0.03	0.52 ± 0.03	$F_{19,2} = 0.614$, $p = 0.546$
LMaxAmp	0.53 ± 0.03	0.51 ± 0.04	0.50 ± 0.04	$F_{19,2} = 0.297$, $p = 0.745$

Table 3. Rotated Components Matrix of a Principal Component Analysis (PCA) carried out on six acoustical parameters of begging calls of Thin-billed Prion chicks. The parameters with a high influence on components are underlined.

	PC1	PC2	PC3
Fmax	<u>0.801</u>	0.466	0.044
Fmean	<u>0.967</u>	0.062	-0.013
PeakFTot	<u>0.923</u>	-0.121	-0.086
CallDur	0.074	<u>0.905</u>	0.006
LocFMax	< 0.001	0.407	<u>-0.778</u>
LMaxAmp	-0.054	0.318	<u>0.826</u>
% variance explained	41%	22%	22%

General Linear Models (GLM) were used to control for individual differences in call parameters and to avoid pseudo-replication (nests as independent variable, parameters as covariates). Homogeneity of error variances was checked by plotting residuals against predicted values. Initially, we included the interaction between the factor chick and the covariates into the model, but removed it if it did not reveal significance (e.g. Engqvist 2005). Separate GLM were carried out for each acoustic and call count parameter. We tested whether adults responded to chick calls by regurgitating more or less food using a GLM with meal size as dependent variable and begging parameters as covariates. As a measure of effect sizes we used partial Eta-Square values (η^2 , i.e. the proportion of the effect + error variance that is attributable to the effect) in case of variables and covariates tested with a GLM. The sums of the partial Eta-Square values are not additive (e.g. http://web.uccs.edu/lbecker/SPSS/glm_effect-size.htm). The t values indicate the direction (positive or negative) of the correlation to the variable.

To test whether the number of begging sessions changed with chick age, we correlated (using Spearman's rho), for each chick with $N > 9$ recorded nights separately, the number of sessions per night with the chicks age and then summarised all these tests using a one-sample t-tests of the null-hypothesis that the average correlation equals zero.

Multiple testing of essentially the same H_0 and/or the same data set required some error-level correction. We did this using Fisher's omnibus test. This procedure combines a number of p-values into a single chi-square-distributed variable with its degrees of freedom equalling twice the number of p-values (Haccou & Meelis 1994, Quinn & Keough 2002).

RESULTS

Differences between chicks

All acoustical parameters differed strongly between chicks (Table 4, Fig. 1). Two of four parameters of begging sessions (maximum call rate and mean call rate) differed between chicks (Table 5).

Variation of begging parameters with age

There was a strong age effect on call parameters. Within the acoustical parameters (Table 4), age influenced the Principal Components 2 and 3 which are most connected with call durations and the relative location of the maximum amplitude and frequency. In contrast, frequencies did not change with age (PC1 in Table 4). The strongest influence was recorded for the duration of call elements (CallDur, Table 4, Fig. 2).

All four parameters of begging sessions (duration, total call count, maximum call rate and mean call rate) increased with age (Table 5).

Chicks uttered between one and five begging sessions in a night. Younger chicks used more second and third sessions during the night than

Table 4. Results of General Linear Models explaining the influence of body condition and chick age on acoustical parameters (PC1–3), call duration. The nest is included as factor.

Source	df	F	p	η^2	t
PC1					
Body condition	1	2.8	0.095	0.013	-1.68
Age	1	1.7	0.197	0.008	-1.30
Nest	19	3.8	< 0.001	0.250	
Error	216				
Total	238				
PC2					
Body condition	1	4.2	0.042	0.019	2.04
Age	1	110.7	< 0.001	0.339	10.52
Nest	19	12.3	< 0.001	0.520	
Error	216				
Total	238				
PC3					
Body condition	1	0.03	0.868	0.000	-0.17
Age	1	28.3	< 0.001	0.116	5.31
Nest	19	5.9	< 0.001	0.340	
Error	216				
Total	238				
CallDur					
Body condition	1	1.2	0.278	0.005	1.09
Age	1	130.8	< 0.001	0.377	11.44
Nest	19	14.6	< 0.001	0.563	
Error	216				
Total	238				

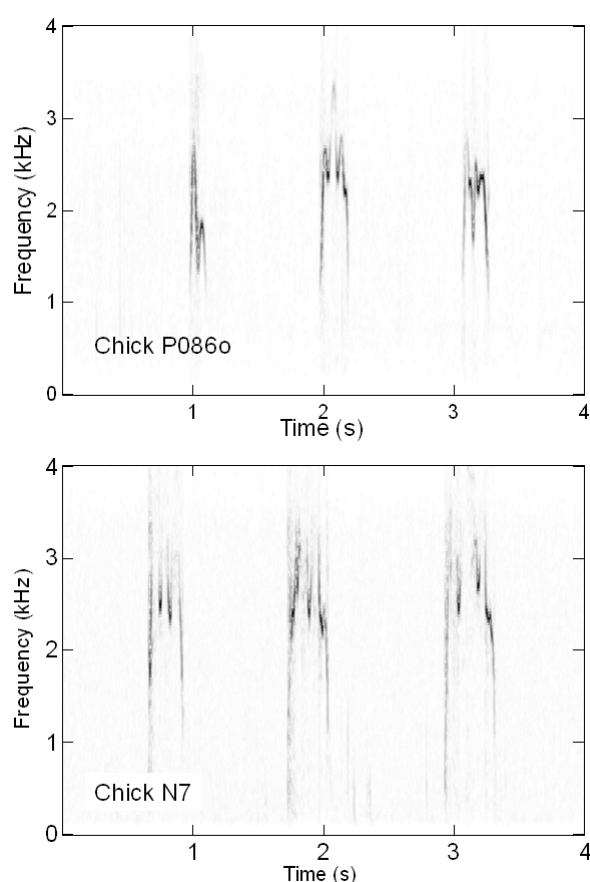


Fig. 1. Examples of long begging calls of two nestling Thin-billed Prions, showing individual differences (e.g. shorter, lower-pitched calls in P0860). Spectrogram pictures were produced using Sound Ruler version 0.9.6.0 (available at <http://soundruler.sf.net>).

older chicks ($t = -4.0$, $df = 14$, $p = 0.001$, Fig. 3). The proportion of chicks that used only one call session increased with age, from 28% in the youngest age class (0–10 days) to 69% in the oldest age class (older than 40 days).

The first begging session was not the most important, at least for the younger age classes (e.g. Fig. 4). The analysis of begging calls in the first begging session in relation to the total number of calls during the whole night indicates that in many nights, only a rather small percentage of the begging calls was contained in the first session (Fig. 4) and suggests that the first session did not necessarily contain all information.

We compared the distribution of mean begging parameters (total call counts, session duration, maximal call counts per minute and call rates) in first, second, third, fourth and fifth sessions (Table 6). The mean total number of calls decreased slightly from session to session as did

Table 5. Results of General Linear Models explaining the influence of body condition and chick age on call count parameters (duration of the first begging session, duration of all begging session during the night, maximal call count per minute and call rate per minute).

Source	df	F	p	η^2	t
Duration (1 st session)					
Body condition	1	0.02	0.878	< 0.001	-0.15
Age	1	15.8	< 0.001	0.068	3.98
Nest	19	0.9	0.523	0.077	
Error	216				
Total	238				
Total # calls (1 st session)					
Body condition	1	1.0	0.330	0.004	-0.98
Age	1	36.3	< 0.001	0.144	6.03
Nest	19	1.4	0.140	0.108	
Error	216				
Total	238				
Max (1 st session)					
Body condition	1	0.4	0.513	0.002	-0.66
Age	1	38.5	< 0.001	0.151	6.20
Nest	19	3.9	< 0.001	0.258	
Error	216				
Total	238				
Rate (1 st session)					
Body condition	1	2.1	0.151	0.010	-1.44
Age	1	14.5	< 0.001	0.063	3.80
Nest	19	2.6	0.001	0.184	
Error	216				
Total	238				

the session duration. The mean and maximum rate, in contrast, showed slight increases. It should be noted that the sample size is much smaller in later sessions, which increases the standard error.

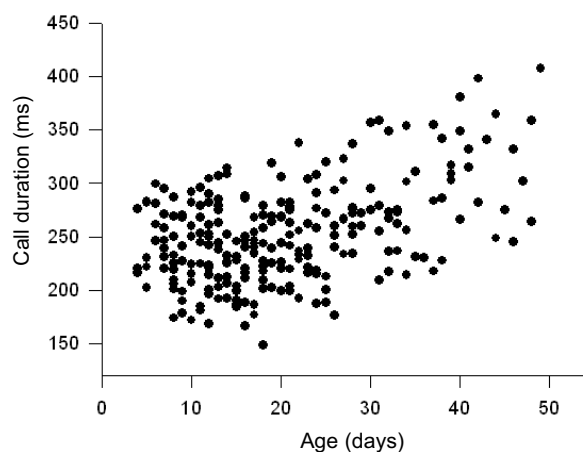


Fig. 2. The duration of individual begging calls of nestling Thin-billed Prions increased with age.

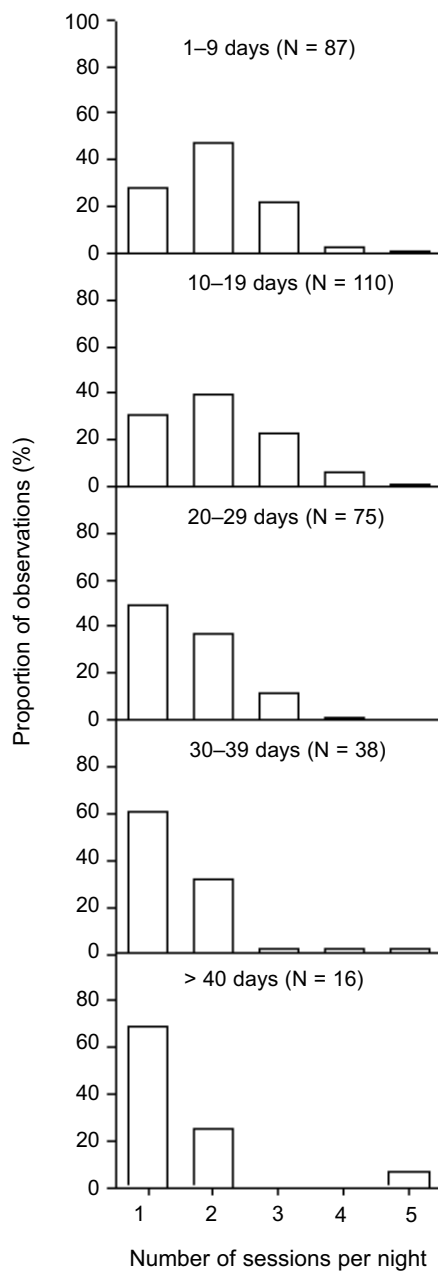


Fig. 3. Distribution of the number of begging sessions of individual Thin-billed Prion chicks during the nights of recording in relation to their age.

Correlation of call parameters with body condition

When only first begging call sessions were included, a marginally significant correlation was detected between the PC2 of acoustical begging parameters and body condition, while all other acoustical parameters did not correlate with chick body condition (Table 4). Fisher's omnibus test detected no overall effect of body condition on acoustical parameters ($\chi^2 = 11.3$, $df = 6$, $p = 0.079$). Further, the parameter most closely related with PC2 (CallDur) did not correlate with condition on its own (Table 4).

None of the begging session parameters correlated with body condition (Table 5). When only chicks of the age class 10–20 days were included, this was confirmed for first begging call sessions (Table 7, Fisher's omnibus test: $\chi^2 = 5.0$, $df = 8$, $p = 0.756$). However, the analysis of all begging call sessions of the night revealed significant correlations between chick body condition and the total call number and the duration of all sessions (Table 7, Fisher's omnibus test: $\chi^2 = 33.1$, $df = 8$, $p < 0.001$). The total number of calls and the duration of begging sessions during the night negatively correlated with body condition, indicating that chicks with lower body condition increased the duration of begging and total number of calls during the night.

Thus, body condition correlated with begging parameters measured over the whole night, but not with those measured only during the first begging session.

Effect of call parameters on meal size

We measured the influence of begging parameters measured over the whole night and during the first session on meal sizes delivered by parents. No significant correlation between begging session parameters and meal size was found if only first sessions are included (Table 8, Fisher's omnibus test: $\chi^2 = 5.2$, $df = 8$, $p = 0.738$). However, three begging parameters of all sessions (total number of calls, duration of sessions and

Table 6. Mean (\pm s.e.) begging session parameters of first to fifth begging sessions during the night.

	Begging session				
	1 (N = 118)	2 (N = 78)	3 (N = 34)	4 (N = 9)	5 (N = 1)
Total # calls	370.2 \pm 18.9	317.3 \pm 16.1	307.4 \pm 30.4	278.0 \pm 38.7	185.0
Duration (min)	12.8 \pm 0.7	9.6 \pm 0.5	9.7 \pm 0.8	8.6 \pm 1.9	8.0
Maximum (calls / min)	43.8 \pm 0.9	46.2 \pm 0.9	46.2 \pm 2.0	47.9 \pm 2.4	34.0
Rate (calls / min)	29.2 \pm 0.8	33.5 \pm 0.9	31.7 \pm 1.6	35.2 \pm 3.2	23.1

Table 7. Influence of body condition on begging parameters measured over the whole night and during the first begging session. General Linear Models with the begging parameters as dependent variables (the total number of begging calls, total duration of begging sessions, the maximal begging call rate and the mean call rate), body condition as covariate and chick as categorical variable (factor) was used. Only chicks of age 10 to 20 days were included in this analysis.

Dependent variable	df	F	p	η^2	t
All sessions					
Total # calls	1	12.09	< 0.001	0.114	-3.48
Duration	1	14.60	< 0.001	0.134	-3.82
Maximum	1	3.05	0.084	0.031	-1.75
Rate	1	0.09	0.771	< 0.001	0.29
1st session					
Total # calls	1	1.19	0.278	0.012	-1.09
Duration	1	0.75	0.388	0.008	-0.87
Maximum	1	0.01	0.910	< 0.001	0.11
Rate	1	0.05	0.832	< 0.001	-0.21

maximum of the whole night) still showed a stronger correlation with meal size than the same parameters calculated for only the first begging session (Table 8, Fisher's omnibus test: $\chi^2 = 20.8$, $df = 8$, $p = 0.008$).

DISCUSSION

Begging calls, through their number and rate, constitute an honest signal of need in Thin-billed Prions (Quillfeldt et al. 2006). In a previous study of this species, begging increased with decreasing body condition and parents responded to more intense begging by delivering increased meal sizes (Quillfeldt et al. 2006).

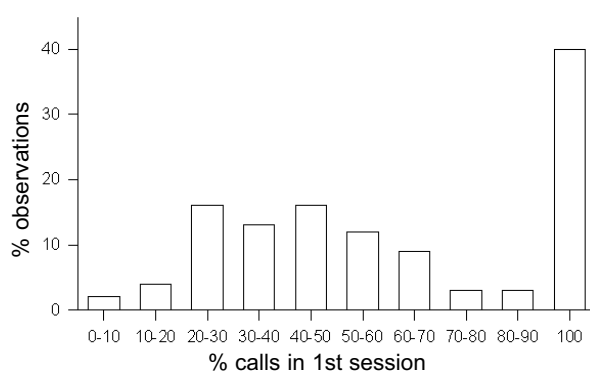


Fig. 4. Percentage of begging calls in the first begging session relative to the total number of calls during the whole night for chicks of the age class 10–20 days. If chicks used only one begging session, then 100% of the calls were contained in this session.

Based on these previous results, the purpose of the present study was to examine (1) how information on the body condition of individual nestlings is encoded in the acoustic structure of begging call elements on Thin-billed Prions, (2) how begging efforts are distributed across the night and (3) age effects on chick begging behaviour.

Does acoustic structure of begging call elements encode information on body condition?

There was little difference in acoustic parameters between the beginning, middle and end of the begging session. If chicks convey information about their body condition to the parents via call features such as specific frequencies, we would have expected the acoustical parameters to change progressively as the chicks become satiated.

While some previous studies have found acoustical parameters of begging call elements to be important in parent-chick interactions (Barn Swallows: Sacchi et al. 2002), or to contain at least additional information (Wilson's Storm-Petrels: Gladbach et al. 2009), another study did not find evidence that acoustic features of call elements are involved in the information exchange (Cory's Shearwaters: Träger et al. 2006). In the latter study, no acoustic features of call elements correlated with body condition. In the Barn Swallows, hungrier chicks enhanced the duration of individual syllables in the begging call and both Barn Swallow and Wilson's Storm-Petrel nestlings increased the peak frequency of begging calls when they were in poorer condition. However, Wilson's Storm-Petrel parents did not respond to

Table 8. Influence of begging session parameters measured over the whole night and during the first session on meal sizes delivered by parents. General Linear Models with meal size as dependent variable, the begging parameters as covariates (the total number of begging calls, total duration of begging sessions, the maximal begging call rate and the mean call rate) and chick as categorical variable (factor) was used. Only chicks of age 10 to 20 days were included in this analysis.

Begging variable	df	F	p	η^2	t
All sessions					
Total # calls	1	4.033	0.048	0.042	2.01
Duration	1	4.247	0.042	0.044	2.06
Maximum	1	5.264	0.024	0.054	2.29
Rate	1	0.249	0.619	0.003	0.50
1st session					
Total	1	0.029	0.865	< 0.001	-0.17
Duration	1	0.079	0.779	< 0.001	-0.28
Maximum	1	1.123	0.292	0.012	1.06
Rate	1	0.774	0.381	0.008	0.88

changes in acoustic begging call parameters (Gladbach et al. 2009), suggesting a minor importance of this component of the begging signal.

Our results are in line with the findings for Cory's Shearwaters (Träger et al. 2006), as acoustical parameters did not seem to play a role in signalling body condition in Thin-billed Prions.

We found that all acoustical parameters differed between individuals, but did not serve to manipulate parents to feed more. The "voice" (i.e. acoustical parameters) of a chick might thus be genetically determined and vary with age rather than influenced by current body condition. This supports the notion that immediate assessment of chick condition through acoustical characteristics of single call elements might be important mainly for allocating food resources between chicks in multi-chick broods.

It is surprising that adults apparently do not discriminate between chicks, given their individual vocal differences (e.g. Quillfeldt et al. 2006). However, as chicks usually remain in their burrows throughout the chick-rearing period, adults might simply have no necessity to learn the chick identity from the begging calls.

Distribution of begging efforts across the night and influence on begging session parameters

In previous studies, the use of tape-recorders with limited recording duration had made it impossible to record complete nights. Instead, first begging sessions per night were analyzed during previous studies of begging in burrowing petrels (e.g. Quillfeldt 2002, Hamer et al. 2006, Quillfeldt et al. 2006, Träger et al. 2006). We here used digital voice recorders, which enabled recording of complete nights. We found that chicks used one to five begging sessions per night (e.g. Table 6). Especially younger chicks used a high number of begging sessions per night (Fig. 3), and the first session often only contained a small percentage of the total begging effort (Fig. 4).

We found that the parameters of first call sessions did not reflect body condition (Table 5), while the duration of begging sessions and the number of begging calls over the whole night correlated with the body condition of chicks (Table 7) and the meal sizes delivered by the parents (Table 8). The amount adults fed was correlated to three parameters of begging measured over the whole night: the total number of begging calls, the total duration of all begging sessions and maximum call rate (Table 8).

During the study period, the chicks experienced good conditions and high feeding rates (Quillfeldt et al. unpubl. data), exceeding those reported during a previous study period of three years (Quillfeldt et al. 2007a). During good conditions, chicks begged less urgently (Quillfeldt et al. 2007a), and thus may be less likely to put all their begging effort into the first begging session. This may explain why the parameters of first call sessions did not reflect body condition.

When comparing between first to fifth sessions, the mean total number of calls and the session duration decreased only slightly from session to session (Table 6). Since the mean and maximum rate did not change towards the later begging sessions, it seems chicks solicited more food by continuing their begging behaviour over time rather than altering the call behaviour itself. Thin-billed Prion chicks with lower body condition begged for longer and increased the number of calls during the night.

In summary, the present results show that chicks succeed in soliciting more food by increasing the time spent begging and the number of calls uttered rather than altering the call features. The fact that Thin-billed Prions have an obligate clutch size of one might play an important role in this, as parents do not have to immediately be able to assess the condition of chicks in order to allocate portions of food to chicks in poorer condition.

Age effects on chick begging behaviour

Age had a strong effect on some acoustical parameters, such as call duration and the location of the maximum frequency and maximum amplitude within calls (Table 4). Furthermore, all four count parameters increased with age (Table 5). Older chicks spent more time in total begging, whereas younger chicks used a higher number of shorter sessions to solicit food. Begging sessions being shorter but more frequent may be related to the smaller stomach size of youngsters that favour several small meals distributed over the night. The change in acoustic parameters might furthermore be related to changes of the respiratory system and vocal organs anatomy during growth, but we lack information to support this.

While there is some change in the use and the acoustics of the long begging calls with age, these do not resemble the adult calls (described in Bretagnolle et al. 1990). In fact, chicks start using adult-like calls in the last part of the nestling period, but this is a different call type, as observed in other Procellariiformes (e.g. Cory's Shearwater:

Bretagnolle & Thibault 1995). Thus, the changes with age in the begging call characteristics here described should not be considered as ontogenesis of adult calls. Fledglings use both begging calls and adult-like calls, but the latter does not develop out of the former.

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STRESZCZENIE

[Funkcjonalna charakterystyka głosów żebrzących piskląt petrelka cienkodziobego]

W oparciu o teorię historii życiowych można rozpatrywać przyczyny zróżnicowania strategii karmienia piskląt u ptaków. Intensywność karmienia potomstwa jest, według tego podejścia, efektem kompromisu między bieżącą a przyszłą reprodukcją rodziców. Z jednej strony, zwiększenie intensywności karmienia piskląt zwiększa ich szansę na przeżycie, a więc przyczynia się do maksymalizacji bieżących efektów rozrodu ptaków dorosłych. Z drugiej zaś strony, pokarm zainwestowany w potomstwo w danym sezonie, obniża szansę skutecznego rozrodu rodziców w przyszłych sezonach, ponieważ nie został przeznaczony na utrzymanie ich kondycji. Szczególnie dobrym modelem interakcji między pisklętami a rodzicami są gniazdowniki, ponieważ młode są całkowicie uzależnione od pokarmu dostarczanego przez rodziców.

Peterek cienkodzioby, ptak charakterystyczny dla kilku archipelagów południowej półkuli (m.in. dla Falklandów), gnieźdzący się w norach i wracający do gniazd nocą, stanowi przykład

gatunku, u którego karmienie piskląt odbywa się wyłącznie w oparciu o sygnalizację dźwiękową, tj. głosy żebrzące wydawane przez pisklęta. Para wychowuje pojedyncze pisklę, dzięki czemu aspekt konkurencji głosowej pomiędzy pisklętami może być pominięty w analizach. Wcześniejsze badania na tym gatunku wykazały, że pisklęta przekazują rodzicom informację o swojej kondycji głosami żebrzącymi. W badaniach tych zastosowano jednak rejestratory, które miały ograniczony czas działania. Uniemożliwiło to nagrywanie głosów wydawanych przez całą noc i ograniczyło analizy jedynie do pierwszej sesji żebrzenia piskląt w ciągu nocy. Pisklęta petrelka żebrają dwoma rodzajami głosów, w niniejszej pracy analizowano tylko tzw. długie głosy żebrzące (Fig. 1), przedstawiono dane dotyczące intensywności żebrzenia i akustycznych parametrów głosów (Tab. 1) żebrzących zarejestrowanych za pomocą cyfrowych rejestratorów umożliwiających całonocne nagrania.

Stwierdzono, że w ciągu nocy pisklęta odzywają się intensywnie w czasie 1–5 sesji oddzielonych okresami ciszy. Głosy wydawane w trakcie jednej sesji jak i pomiędzy poszczególnymi sesjami różniły się niektórymi parametrami akustycznymi (Tab. 2, 6). Dlatego brano pod uwagę uśrednione wartości dla danej sesji i wykorzystano analizę składowych głównych (Tab. 3). Młodsze pisklęta najwięcej głosów wydawały w drugiej i trzeciej sesji (Fig. 3), a często pierwsza sesja zawierała tylko niewielką część głosów żebrzących piskląt (Fig. 4). Stwierdzono, że parametry głosów z pierwszej sesji w ciągu nocy nie odzwierciedlały kondycji piskląt. Jednocześnie, czas trwania sesji żebrzenia, maksymalne tempo wydawania głosów oraz sumaryczna liczba głosów żebrzących wydanych w ciągu całej nocy były skorelowane z kondycją ciała piskląt (Tab. 4, 5, 7) oraz rozmiarem posiłków dostarczanego przez rodziców (Tab. 8). Innymi słowy, komunikaty głosowe piskląt dobrze sygnalizowały ich potrzeby, zaś rodzice dostosowywali do nich intensywność karmienia swojego potomstwa. Analiza parametrów akustycznych sylab budujących głosy żebrzące wykazała, że nie były one skorelowane w żaden sposób z kondycją piskląt (Tab. 5). W szczególności, pisklęta nie zmieniały częstotliwości głosów w zależności od stopnia odżywienia. Jednocześnie, wszystkie parametry głosów, włączając parametry akustyczne były specyficzne osobniczo, a specyficzność ta była silnie związana z wiekiem piskląt (Fig. 2, Tab. 4, 5).