

Are acoustical parameters of begging call elements of thin-billed prions related to chick condition?

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Abstract Chicks of burrowing petrels use begging calls to advertise their hunger levels when parents arrived at the nest. In a previous study, adult thin-billed prions *Pachyptila belcheri* responded to higher begging call rates of their single chick by regurgitating larger meals. We tested whether acoustic parameters of begging call elements may also be involved in signalling. To describe variation in begging, we determined begging session parameters, namely the duration, number of calls and the mean and maximum rate of calling. We then digitised calls and carried out a semi-automatic extraction of six acoustic parameters of call elements, including mean and maximum acoustic frequency, the length of call elements and the location of the maximum frequency and amplitude within calls. Chicks showed strong individual differences in all parameters. While the session parameters were correlated with body condition and with the meal size the chick received, none of the acoustic parameters were related to body condition and provisioning. A cross-fostering experiment showed the same pattern, as only session parameters changed related to an experimentally altered body condition, while acoustical cues appear to play no role in signalling hunger levels. We suggest that this may be

explained by the absence of sibling competition in these birds. As parents do not need to decide which chick to feed, immediate information on condition at the time of adult arrival may not be required.

Keywords Parent–offspring communication · Signalling · Provisioning · *Pachyptila belcheri* · Seabirds

Introduction

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 and Johnstone 1997; Sacchi et al. 2002; Royle 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 seed-regurgitating finches (Kilner and Davies 1998), and hungry chicks of house sparrow *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, 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 and Johnstone 1997; Royle et al. 2002). However, both the begging duration and the number of calls are only available at the end of each begging call session. One means for chicks to convey this information as soon as parents arrive in the nest is to modify the acoustic characteristics of a single call element

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such as duration, frequency and amplitude (Leonard and Horn 2001; Sacchi et al. 2002).

Many smaller procellariiform seabirds (petrels, shearwaters, storm-petrels, etc.) nest in burrows where chick feeding takes place exclusively at night and are a particularly relevant model for the study of vocal begging behaviour (see also Quillfeldt 2002). It is the only avian order in which all species have an obligate clutch size of one, thus excluding sibling competition as a factor in the evolution of begging call structure. Previous studies indicated that chick begging calls convey information about their nutritional status and that parents act upon this by adjusting their feeding effort in Manx shearwaters *Puffinus puffinus* (Hamer et al. 1999), Cory's shearwater *Calonectris diomedea* (Granadeiro et al. 2000; Quillfeldt and Masello 2004; Träger et al. 2006) and Wilson's storm-petrel *Oceanites oceanicus* (Quillfeldt 2002). These previous studies were based on the analysis of call rates and numbers. Because 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 several multiparous species (e.g. barn swallow *Hirundo rustica* in Sacchi et al. 2002, yellow-headed blackbirds *Xanthocephalus xanthocephalus* in Price et al. 1996, tree swallows *Tachycineta bicolor* in Leonard and Horn 2001). Current evidence for uniparous species is, however, purely correlational (Wilson's storm-petrels in Gladbach et al. 2009) and one recent study found no supporting evidence (Cory's shearwater in Träger et al. 2006), which raises the possibility that there may be little causal relationship between a chick's nutritional requirements and the acoustical parameters of its begging calls in the absence of within-brood competition.

A previous study of thin-billed prions *Pachyptila belcheri* demonstrated a strong positive correlation of chicks' begging with chicks' body condition and the immediate response in terms of 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).

The purpose of this study was to examine (1) how information on the body condition of individual nestlings is encoded in the acoustic structure of begging call elements of thin-billed prions and (2) if the acoustic structures influence the meal size delivered by parents. We also conducted a cross-fostering experiment, changing heavy against light chicks in order to expose chicks to different feeding conditions and to test for its effect on acoustic structures of begging calls.

Materials and methods

Birds and study site

The study was carried out at the New Island Nature Reserve, Falkland Islands (51°43' S, 61°17' W). Thin-billed prions breed in 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 two 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 has been described by Strange (1980). More recently, studies of the biology of thin-billed prions were carried out in Kerguelen, including studies of sexual dimorphism of voice and morphology (Genevois and Bretagnolle 1995), feeding ecology (Chastel and 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 (Catry et al. 2007; Quillfeldt et al. 2003, 2006, 2007a, b, c, 2008a, b, c, d, 2009a, b).

Briefly, 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. Both males and females feed the chick, and radiotracking at New Island has shown that both sexes undertook trips of 1–8 days' duration (median 3 days: Quillfeldt et al. 2007c). In consequence, the chicks are not fed every night, but in some nights, they receive a large double meal by both parents. Therefore, the body condition of chicks can fluctuate considerably on a day-to-day basis. The mean interval between successive feedings ranged from 1.4 days in good conditions to 1.8 days in poor conditions (Quillfeldt et al. 2007b).

As described in Quillfeldt et al. (2006), thin-billed prions used two types of calls. In response to the arrival of an adult, chicks first used rhythmic call series, which lasted for a few seconds up to 45 min, followed by long begging calls, which are uttered during feedings, and many times after the adult ceases feeding. Adults stay in the nest for either only a short period and leave straight after provisioning or remain there throughout the night, probably depending on the environmental conditions, especially food availability. Video observations have shown that feeding bouts can be terminated either by the adult ceasing to feed or the chick ceasing to beg (unpubl. data). Chicks rarely beg in the absence of a parent.

Similar provisioning behaviour, including the use two different call types: “rhythmic calls” and “long begging

calls” has been described for other procellariiforms (Wilson’s storm-petrels: Quillfeldt 2002, Manx shearwaters: Quillfeldt et al. 2004).

Chick measurements

We randomly selected 27 nests in 2003 and 37 nests in 2004. From 8 January 2003 to 4 February 2003 and from 14 January 2004 to 10 February 2004, 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 determined the hatching date (to the nearest day) by calibrating wing length against wing growth in chicks of known age. We weighed chicks daily at 07:30 and 19:30 hours 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 using a multi-year mean chick body mass as reference. We calculated BC index using the body mass at 19:30 hours each evening (m), relative to the multi-year mean mass for chicks of each age (m_{mean}), using the formula: $\text{BC index} = m/m_{\text{mean}} \times 100$ (e.g. Quillfeldt et al. 2006). 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 and 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 57 and 151 (mean=96 because the study period included periods of relatively low body weights).

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).

Molecular sexing was carried out from blood samples as described in Quillfeldt et al. (2007c).

Recordings and analysis of begging calls

The vocal behaviour of nestlings at each of the study nests was recorded overnight, by placing a small microphone in the nest burrow, immediately above the nest chamber. This microphone was connected to a portable tape recorder placed outside the nest entrance. The recorders were switched on at 23:00 hours each night (before the first adults returned) and recorded at low speed until the end of the tape (about 95 min). Because not all recordings contained begging call sessions, sample sizes ranged between 1 and 8 successfully recorded begging call sessions per nest and period.

Chicks between 10 and 30 days of age were included in the analyses, as begging intensity is independent of age during this period (Quillfeldt unpubl. data). In the GLM, we included only those 10 chicks from 2003 and 15 chicks from 2004 that had successfully been recorded for three or more nights.

Because our recordings terminated before the adults left the burrows at the end of the night, we may have missed some late feedings. In order to compare all chick nights, we, therefore, included only first begging call sessions of each chick and night in the analyses of begging behaviour. This way, daily variation in begging behaviour reflected the chick’s need at the time of the first adult arrival.

We counted the number of calls during the call session and calculated parameters of begging sessions (i.e. a series of long begging calls, followed by at least 10 min silence) from call counts, as previously described in Quillfeldt et al. (2006): 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. We only included data for nights when we could record the entire begging session, followed by at least 10 min without begging calls.

For the acoustical analyses, we digitised calls from audiotapes, using the software CoolEdit 96, with a sample rate of 16 kHz and 16-bit resolution. For further analysis, we selected six consecutive individual calls from the beginning, the middle and the end of the first begging call session, respectively. 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 4.2 (FFT-length—512, time resolution—1 ms and frequency range—0–8 kHz) and saved them as .txt-files. We finally used the software ConAn 0.93 (described in Mundry and Sommer 2004) to realise a semi-automatic analysis of acoustic parameters of the fundamental frequency. We included six acoustic parameters in the present analysis: 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, normalised to element duration (LocFMax and LMaxAmp). We averaged these data for each part of the begging call session. A proportion (six of 44 recordings in 2003 and 10 of 45 recordings in 2004) could be counted but were too poor quality for semiautomatic acoustical analysis, such that the final sample size for the control period was 89 sessions for count parameters and 73 sessions for acoustical parameters.

Experimental manipulation

After a control period of 16 days during which each chick was within its own nest, a cross-fostering experiment was conducted in 2003 and 2004 as described in Quillfeldt et al. (2006). We exchanged heavy (BC index over the control period over 110) with light (BC index below 90) chicks in order to expose chicks to different feeding conditions and thus alter chick body condition experimentally (see Quillfeldt et al. 2006). Within pairs ($N=5$ in 2003, $N=6$ in 2004), chicks were matched for age (16–22 days). After pair-wise exchange of the chicks between their nests on 24 January in 2003 and on 30 January in 2004, they were weighed twice daily as in the control period. They remained in their foster nests after the end of the study. In 2003, all 10 chicks could be followed successfully until the end of the field season. In 2004, in contrast, five chicks disappeared into inaccessible parts of the tunnels of the nests, and three chicks were older than 30 days, such that we were only able to include four chicks with successful recordings in the dataset.

Statistical analysis

Statistical tests were performed in SPSS 15.0. We tested for differences between the three begging call session parts of six calls (beginning, middle and end) for each acoustic parameter with univariate analyses of variance with the call session part as fixed factor and the bird as random factor. In order to avoid pseudo-replication, we only used the first recorded night of each bird for this analysis. Because we found no difference between these three parts for all acoustic parameters (all $P>0.6$), we averaged the data of the three parts of the begging call session to calculate means per begging call session for each acoustic parameter, which therefore consisted of 24 individual calls, distributed across the begging call session.

We tested normality using Kolmogorov–Smirnov tests and by checking plots of the data. Only one out of the total of 11 analysed parameters differed from normality ($p>0.2$ for all parameters except session duration). Since visual inspection of the session duration distribution indicated it to be more or less symmetric, we decided to include this variable without any transformation.

None of the count or acoustical parameters differed between the begging calls of male and female chicks, when years were tested independently or together (t tests of chick means, male vs. female chicks, all $p>0.120$). Likewise, the begging intensity was similar between the years; thus, all chicks were combined in one dataset. We used Pearson correlations of the first begging session recorded to test if the acoustical parameters correlated with the total number of calls in a begging session.

We used GLM (i.e. ANCOVA) based on Type III sum of squares to test for the influence of body condition on different begging features. We carried out a separate GLM 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. In order to control for individual differences between chicks and to avoid pseudo-replication (e.g. Quillfeldt 2002), we included chick as a categorical independent variable (“random factor”) into all GLM. 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). 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_effectsize.htm). When several tests of a single null hypothesis were carried out, we corrected p values for the number of tests, applying the following equation $P_{\text{corr}} = 1 - (1 - \alpha')^k$ derived from conversion of the Dunn–Šidák method (Sokal and Rohlf 1994). In this equation, P_{corr} denotes the corrected p value, α' equals the originally derived p value, and k equals the number of tests. We used Pearson correlations to test for changes of begging parameters in relation to changes in body condition during the cross-fostering experiment. We correlated the difference in begging parameters between the last recorded session during the control period and the first recorded session during the experimental period and the corresponding difference in body condition.

Results

Acoustic parameters, body condition and meal size

The total number of calls in a begging session was correlated with the other count parameters (Pearson correlations, session duration: $R_{24}=0.660$, $P<0.001$, maximum call rate: $R_{24}=0.701$, $P<0.001$, mean call rate: $R_{24}=0.523$, $P=0.009$). In contrast, none of the acoustical parameters correlated with the total number of calls in a

begging session (call duration: $R_{24}=0.015$, $P=0.945$, F_{\max} : $R_{24}=-0.049$, $P=0.822$, F_{mean} : $R_{24}=-0.086$, $P=0.691$, PeakFTot : $R_{24}=0.020$, $P=0.926$, LocFMax : $R_{24}=0.353$, $P=0.090$, LmaxAmp : $R_{24}=0.071$, $P=0.742$).

There was a significant negative relationship between chick body condition and three of the four count parameters (Table 1, 2). Specifically, we observed a strong effect of body condition on the total number of calls in a session. Chicks with lower body condition uttered more calls than chicks with higher body condition. The acoustical parameters, in contrast, were not significantly impacted, either when analysed independently or controlling for the total number of calls in the session (Table 1, 2).

We observed a very strong difference between chicks for all the begging parameters (Table 1, 2), except for the location parameters LocFMax and LcMAXamp after α correction. Even where there was a within-chick effect of body condition (in the case of total call number, call session duration, maximum call rate), the effect sizes indicated that the differences between chicks had a stronger influence than body condition on acoustical parameters and explained most variance (Table 1, 2). To assess among-chick effects of body condition on acoustic parameters, we compared the mean body condition of each chick with each of the means of their acoustic parameters during the same nights. Mean

Table 1 Within-chick effects of chick body condition and chick age on parameters of begging call sessions of thin-billed prion chicks (age 10 to 30 days)

Dependent	Independents	F	t	P value	P_{corr}	Effect size
Number of calls in session	BC index	13.1	-3.6	0.001	0.002	0.175
	Chick	4.7		<0.001	<0.001	0.646
	Age	<0.1	<0.1	0.962		<0.001
Session duration (min)	BC index	8.1	-2.8	0.006	0.022	0.116
	Chick	2.2		0.006	0.022	0.464
	Age	0.1	-0.1	0.896		<0.001
Maximum call rate	BC index	7.2	-2.7	0.010	0.039	0.103
	Chick	4.2		<0.001	<0.001	0.619
	Age	0.6	0.7	0.459		0.009
Mean call rate (calls/min)	BC index	3.7	-1.9	0.058	0.213	0.057
	Chick	3.8		<0.001	<0.001	0.588
	Age	0.1	0.7	0.786		<0.001

The relation between begging parameters (dependent variables) and body condition (covariate) was tested using GLM, including chick as a random factor (this table for count parameters; see Table 2 for acoustical parameters). Significant p values are marked bold; t values are included to indicate the direction of the relationship. As a measure of effect sizes, we report partial Eta-Square values (η^2). None of the interactions were significant (all $P>0.05$). df were 24 (based on 25 nests) and 88 (based on 89 recorded nights)

P_{corr} p values corrected for the number of tests (four for count parameters)

Table 2 Within-chick effects of chick body condition and chick age on acoustical parameters of begging call elements of thin-billed prion chicks (age 10 to 30 days)

Dependent	Independents	F	t	P value	P_{corr}	Effect size
Duration of begging call (ms)	BC index	1.7	-1.3	0.199		0.036
	Chick	4.2		<0.001	<0.001	0.686
	Age	2.6	1.6	0.113		0.054
F_{\max} (Hz)	BC index	2.3	-1.5	0.134		0.048
	Chick	8.6		<0.001	<0.001	0.818
	Age	5.4	2.3	0.024	0.136	0.106
F_{mean} (Hz)	BC index	0.6	-0.8	0.455		0.012
	Chick	5.6		<0.001	<0.001	0.745
	Age	2.6	1.6	0.114		0.053
PeakFTot (Hz)	BC index	1.1	-1.0	0.298		0.024
	Chick	2.3		0.007	0.041	0.547
	Age	2.6	1.6	0.114		0.053
LocFMax	BC index	0.5	0.7	0.470		0.011
	Chick	2.4		0.006	0.034	0.551
	Age	6.8	-2.6	0.012	0.070	0.129
LocMaxAmp	BC index	5.8	2.4	0.020	0.114	0.111
	Chick	1.8		0.042	0.320	0.485
	Age	0.5	0.7	0.478		0.011

The relation between begging parameters (dependent variables) and body condition (covariate) was tested using GLM, including chick as a random factor (this table acoustical parameters, see Table 1 for count parameters). For the acoustical parameters, the tests were additionally carried out using total call number as a co-variate (Table 3). Significant p values are marked bold; t values are included to indicate the direction of the relationship. As a measure of effect sizes, we report partial Eta-Square values (η^2). None of the interactions were significant (all $P>0.05$). df were 24 (based on 25 nests) and 88 (based on 89 recorded nights)

P_{corr} p values corrected for the number of tests (six for acoustic parameters)

body conditions were not correlated with any call count or the acoustic parameters (Pearson correlation: all $P>0.2$).

The meal size a chick received was correlated to the call count parameters, but not the acoustical parameters of begging (Table 3). In the analysis of provisioning, we did not find important differences between chicks, as chick as factor did not contribute significantly to explain the variability in the GLM (Table 3).

The cross-fostering experiment

When comparing the experimental period with the control period, the change in the body condition of chicks was negatively correlated to the change in three of four call count parameters (Fig. 1, number of calls: $R_{13}=-0.756$, $P=0.002$, session duration: $R_{13}=-0.494$, $P=0.072$, maximum call rate: $R_{13}=-0.571$, $P=0.033$, mean call rate: $R_{13}=-0.667$, $P=$

Table 3 Within-chick effects of parameters of begging call sessions and acoustical parameters of begging call elements on chick provisioning

Parameter (covariate)	<i>F</i>	<i>t</i>	<i>P</i> value	<i>P</i> _{corr}	Effect size
Total number of calls in session	15.0	3.9	<0.001	0.001	0.192
Session duration (min)	5.0	2.2	0.029	0.110	0.074
Maximum call rate (calls/min)	4.8	2.2	0.032	0.121	0.071
Mean call rate (calls/min)	6.6	2.6	0.013	0.049	0.095
Duration of begging call element (ms)	3.5	1.9	0.067	0.340	0.070
Maximum frequency (Fmax in Hz)	1.1	1.1	0.292	0.874	0.024
Mean frequency (Fmean in Hz)	0.2	0.5	0.643	0.998	0.005
PeakFTot (Hz)	0.4	-0.7	0.515	0.987	0.009
LocFMax	0.1	-0.3	0.762	1.000	0.002
LocMaxAmp	2.4	-1.5	0.129	0.564	0.048

The relation between begging parameters (covariates) and meal size received by the chick (dependent) was tested using GLM, including chick as a random factor (Table 1 for count parameters, Table 2 for acoustical parameters). Significant *p* values are marked bold; *t* values are included to indicate the direction of the relationship. As a measure of effect sizes we report partial Eta-Square values (η^2). The effect of chicks (factor in the GLM) was not significant for any of the GLM (all $P > 0.7$)

*P*_{corr} *p* values corrected for the number of tests (four for count parameters and six for acoustic parameters)

0.009). In contrast, the change in acoustical parameters did not correlate with the change in body condition during the experiment (call duration: $R_{13} = -0.131$, $P = 0.655$, Fmax: $R_{13} = -0.233$, $P = 0.423$, Fmean: $R_{13} = -0.162$, $P = 0.580$, PeakFTot: $R_{13} = -0.381$, $P = 0.179$, LocFMax: $R_{13} = 0.101$, $P = 0.731$, LmaxAmp: $R_{13} = 0.125$, $P = 0.670$).

Discussion

Acoustic parameters of begging calls as a signal

The purpose of this study was to examine how information on the body condition of individual nestlings is encoded in the acoustic structure of begging call elements of thin-billed prions and if the acoustic structures influence the meal size delivered by parents. We found that only the count parameters were correlated with body condition and with the meal size the chick received, while none of the acoustic parameters were related to body condition and provisioning. The same pattern was observed during a cross-fostering experiment, suggesting that acoustical parameters play no role in the signalling system.

This is in line with a previous study of a Procellariiform seabird (Träger et al. 2006) but in contrast to studies

showing the importance of call frequency in other species. For example, light-weight chicks begged at a relatively high frequency (Sacchi et al. 2002) in barn swallow as well as in Wilson's storm-petrels (Gladbach et al. 2009). Leonard and Horn (2001) also underlined the potential role of the amplitude, with larger nestlings tree swallows *T. bicolor* increasing the amplitude of their calls when they were deprived of food but did not denote an importance of its position within the call's elements.

In thin-billed prions, the number and rate of begging increased at low body condition, and parents responded to more intense begging by delivering increased meal sizes (Quillfeldt et al. 2006). Our results do not suggest that acoustic parameters provide parents with additional information of a chick's state. In the context of the temporal and spatial unpredictability of food resources in the marine environment and of parent-offspring conflict (Trivers 1974), signalling theory (Bergstrom and Lachmann 1997, 1998) predicts that parents may use honest signals of the chick's state to adjust their feeding behaviour. We found that parents regulated meal size according to variation in the call rate, but not the acoustic parameters. Because adults could not be followed individually, we could not test the influence of begging on adult behaviour during subsequent feedings, for example on the length of the next feeding trip. Thus, the present findings suggest that the acoustical parameters of begging call elements of thin-billed prions convey no information on chick condition. We conclude that the acoustical features we measured did not play a role in the signalling system. This is supported by the results of the

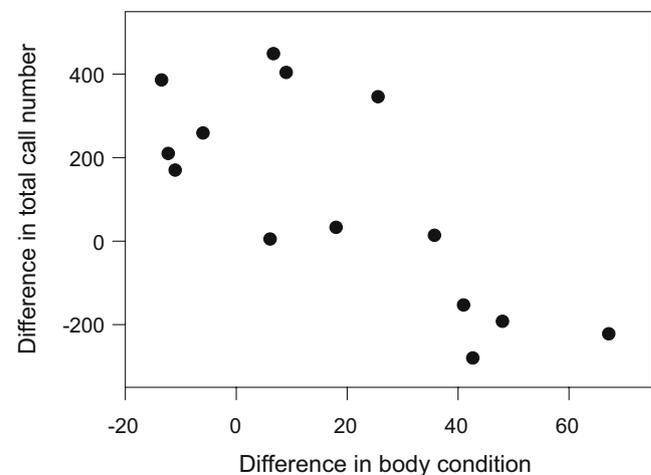


Fig. 1 Change in body condition and begging after exchanging heavy (BC index over the control period over 110) with light (BC index below 90) chicks in a cross-fostering experiment. Chicks exposed to better feeding conditions reduced their begging call number. The difference in begging parameters was calculated between the last recorded session during the control period and the first recorded session during the experimental period. The corresponding difference in body condition was calculated from the same days

cross-fostering experiment, where we were able to detect effects with the “traditional” counted parameters of begging intensity even with a relatively low sample size (Quillfeldt et al. 2006), but not with the acoustical parameters presented here. In summary, acoustical parameters of calls were not related to natural variation in chick body condition, experimental manipulation did not alter acoustical parameters and parents did not adjust their food delivery in relation to these characteristics of begging calls. These results suggest that although the acoustical properties of calls can provide instantaneous cues to the chick’s begging behaviour in other species, these cues may not be necessary components of the signal of need in chicks of uniparous species. It is thus possible that immediate assessment of chick condition through characteristics of single call elements is important mainly in the context of allocating food resources between siblings in multi-chick broods.

Individual differences in acoustic parameters

We observed a very strong difference between chicks for all the acoustic and count parameters. Because this species has an obligate clutch size of one, these inter-individual acoustic differences are not required for parents to discriminate between different chicks or fledglings in a brood. Further, in a clutch size of one, there is no need to allocate food between siblings of a single brood in relation to offspring sex or quality (Kölliker et al. 1998; Draganoiu et al. 2006). Nevertheless, as thin-billed prions are nocturnal on their breeding colonies and nest in burrows, they must have to localise their nest and feed their chicks in complete darkness, using very few visual cues (except maybe during moonlit nights). Bonadonna and Bretagnolle (2002) showed that thin-billed prions, as other petrel species nesting in burrows and returning home in darkness, use olfaction to recognise their burrow. They demonstrated that anosmic prions show an impaired homing performance. Nevertheless, in their study, thin-billed prions seem to be more capable of compensating for anosmia than other species. They proposed two possible explanations for this result: some methodological bias or that thin-billed prions are able to shift to an alternative mechanism to find their burrow entrance. They proposed that birds could shift to vision when olfactory cues were not available. The olfactory experiments on thin-billed prions were performed during incubation and the tested adults, deprived of their smell, needed to find an empty burrow. The birds in the experiment thus could not use chick calls to orient to the nest.

Procellariiform calls are species specific and much more variable between than within species (Bretagnolle 1996; Mougeot and Bretagnolle 2000). It is not known whether acoustic signals of chicks could be an efficient alternative way to find burrows. For example, vocal signature is

known as a cue to identify kin in dense colonies and crèches in penguin species (Lengagne et al. 2000; Jouventin and Aubin 2002; Miyazaki and Waas 2003; Mathevon et al. 2003; Searby et al. 2004; Searby and Jouventin 2005). However, prions will readily attend and feed chicks in cross-fostering experiments, as in the present study, suggesting that parents do not distinguish between their own and foster offspring. Moreover, according to our observations, thin-billed prion chicks do not often call before the parents arrive, maybe because calling may give away the location of the chick to potential predators (Briskie et al. 1999; Mougeot and Bretagnolle 2000). Therefore, individual differences in call structures are unlikely used in the homing behaviour of parents.

Another possibility is that individual differences in vocalisations are genetically fixed and that some of this variation between chicks in begging calls reflects the variability of calls found between individual adults. This possibility could be explored in the future, for example by looking at relationships between acoustical features of begging calls and juvenile calls of nestlings.

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