

Original Article

Signals of need and quality: Atlantic puffin chicks can beg and boast

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Need and hunger models of honest begging predict that lower-quality offspring should call more, or beg, to signal their poor body condition or hunger. In contrast, quality models of begging predict that offspring of higher fitness should call more, or boast, to signal their viability to parents. We observed 2 types of calls in Atlantic puffin (*Fratercula arctica*) chicks: a shorter peep call and a longer screech call. Poorly fed chicks screeched during a higher proportion of parental visits than well-fed chicks. Food-supplemented chicks showed a decrease in the proportion of food visits with screech calls, whereas control chicks did not. Chicks in good body condition peeped more than chicks in poor body condition and these chicks showed a greater increase in the peep call rate after supplemental feeding than chicks that started off in poorer condition. Screech calls may signal need and/or hunger to parents, whereas peep calls may signal chick quality. This combination of signals should allow parents to make strategic resource-based decisions, allocating more food to hungry or lower-quality chicks when resources are abundant and preferentially feeding high-quality chicks when resources are scarce.

Key words: Atlantic puffin, chick begging, parent–offspring conflict, seabird.

INTRODUCTION

Parents use the begging behavior of their chicks to make provisioning decisions, but it is unclear whether parents allocate resources on the basis of chick need or chick quality (Royle et al. 2002; Mock et al. 2011). Mock et al. (2011) distinguish between the long-term function of begging as indicating overall need and the short-term function of begging to signal current levels of hunger. Researchers disagree about whether hunger models are distinct from need models (Johnstone and Kilner 2011; Mock et al. 2011) or whether hunger is just the proximate expression of need (Grodzinski et al. 2011) as in the “fuel-gauge hypothesis” of hunger (Grodzinski and Lotem 2007). Mock et al. (2011) revived an alternate model of honest signals: that calls signal chick quality (as in Grafen 1990). These models predict that high-quality offspring use begging to boast about their viability to their parents, similar to the way that sexually selected signals are used. Quality models are based on Zahavi's (1975) original handicap principle, further developed quantitatively by Grafen (1990). Thus, need and hunger models predict that hungrier and/or more needy offspring will beg more (Godfray 1991), whereas quality models predict that higher quality (less needy?) offspring will beg more (Grafen 1990). Both need and quality models

assume that begging signals have evolved because offspring viability is “cryptic,” suggesting that more direct information is not readily available to parents.

Many studies support the view that chick begging is an honest signal of need (Cotton et al. 1996; Leonard and Horn 2001; Noguera et al. 2010; Martín-Gálvez et al. 2011), with recent research focused on distinctions between current hunger and more long-term indicators of need (Marques et al. 2009; Kim et al. 2011; Kitamura et al. 2011). Other studies suggest that chicks must be signaling their quality to their parents (Mock et al. 2005, 2009) using specific visual (Dugas 2009; Jacob and Heeb 2013) and/or auditory signals (Boncoraglio et al. 2012). In studies relating to chick quality, chicks in better body condition (Jacob and Heeb 2013) or with less oxidative damage (Boncoraglio et al. 2012) produced stronger signals than lower-quality chicks. Similarly, parent house sparrows (*Passer domesticus*) fed chicks more often after their signal strength was experimentally enhanced (darkened mouth color, Dugas 2009). Mock et al. (2011) note that models of need assume that “whole brood survival” is always “parents’ life-history objective” (p. 913). This assumption ignores the possibility that parental strategies may change over the chick-feeding period as resources fluctuate or brood requirements increase (Royle et al. 2002). If resources decrease, for example, parents may be forced to switch from feeding the neediest offspring to feeding the highest-quality and most

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viable offspring (Royle et al. 2002). The possibility of this resource-based switch in parental tactics suggests that chicks would benefit from being able to signal both current need and overall quality.

Atlantic puffins (*Fratercula arctica*) are long-lived Alcids seabirds that nest in earth burrows and rear only 1 offspring per breeding season (Harris and Birkhead 1985; Hudson 1985; Lowther et al. 2002). Atlantic puffins have flexible parental investment patterns with chick fledging ages that vary with adult condition, as well as with the likelihood of chick survival (Williams et al. 2008; Erikstad et al. 2009). Studying chick begging and adult provisioning in the absence of sibling competition, as in species with single-chick broods, can simplify interpretation of the role of begging signals during parent–offspring conflict. Begging calls have been studied in several Procellariiformes species with single-chick broods (Granadeiro et al. 2000; Quillfeldt 2002; Quillfeldt and Masello 2004; Träger et al. 2006; Duckworth et al. 2009; Gladbach et al. 2009), but not in any Alcids species, except for 1 previous study on Atlantic puffins (Harris 1983). Harris (1983) found that puffin parents increased their chick-provisioning rates after hearing playbacks of chick calls, indicating that these calls affect parental provisioning decisions. Godfray's (1991) model for single-chick broods suggests that an evolutionary stable strategy can be achieved if offspring beg strictly according to need and parents respond directly to the those signals. Godfray notes that this model may only be appropriate through a normal range of chick conditions but may not apply when chicks are in very poor condition, a situation that can occur when resources are very limited. It is under these extreme conditions that chicks may need to signal quality to encourage their parents not to abandon the current breeding attempt. Chicks would therefore benefit from being able to signal both current need and overall quality in case resources are poor enough to make parents shift tactics.

Because little work has been done on the begging signals of puffins, we first recorded begging calls under natural conditions in order to identify any call types that were displayed during parental provisioning visits to the burrow. Harris (1984) notes that “chicks often call when being fed and also give plaintive peeps when hungry” (p. 90), which suggests that puffin chicks may have more than 1 call. Next, we recorded chick begging calls under natural and food-supplemented conditions in order to analyze differences in chick calls both between and within burrows. Chick and adult behavior was first observed with no experimental treatment. Later, chicks in the experimental group were supplementally fed, allowing within-burrow comparisons of the same chicks as well as between-burrow comparisons with unsupplemented control chicks. The goals of this study were to 1) identify puffin chick begging call types and 2) examine the relationship between the chicks' use of begging calls and both their feeding rates and body condition, in order to evaluate need and quality hypotheses of chick begging.

MATERIALS AND METHODS

Species and study site

Audiovisual recording took place in 22 burrows at Gull Island, Witless Bay Ecological Reserve, Newfoundland (47°15'N, 52°46'W), during the chick-rearing stage of the 2009 ($N = 9$) and 2010 ($N = 13$) breeding seasons. Approximately 140 000 pairs of breeding Atlantic puffins return to breed on Gull Island each spring (Robertson et al. 2004) and they feed mostly on capelin (*Mallotus villosus*), the preferred prey species of chick-provisioning puffins in

the Northwest Atlantic (Brown and Nettleship 1984; Montevecchi 1993). In 2009 and 2010, capelin availability was low as indicated by adult provisioning behavior and by reports of capelin abundance and spawning distribution compiled from observations by local fishermen (Nakashima B, personal communication).

Field recordings

Four burrow scope cameras (Peep-a-Roo monochrome 1.0 diameter video probe, Sandpiper Technologies, Manteca, CA) retrofitted with omnidirectional microphones (RadioShack 33-3013) and connected to a DVR recording system (Archos AV400 Series DVR) were used to record parent–offspring interactions within active puffin burrows. Cameras were deployed in burrows and dawn-to-dusk recordings took place for 9 days, beginning at approximately 1300 hours Newfoundland daylight time (NDT) on the first day and ending at approximately 1300 hours on the 10th day resulting in 9 full days of recording per burrow. Cameras were pressed into the earth wall of the burrow and the presence of the camera did not appear to affect the adult's behavior (e.g., the parents still entered the burrows quickly the first time they visited after the camera was installed). Chicks remained undisturbed until the fourth day of videotaping when each chick being recorded was temporarily removed from the burrow at approximately 1300 hours, and tarsus, wind chord, and mass measurements were taken. Chicks were then returned to the burrow and given 1 capelin (approx. weight—20 g). A single capelin per day was given to each experimental chick for the next 6 days ($N = 17$). Video recordings also continued for the control burrows ($N = 5$) where chicks did not receive supplemental feeding. The sample size was small because this study was initially conceived as a within-subjects design (change in behavior for the same burrows before and after supplemental feeding), and a small number of control burrows were added to confirm that there was no difference in parental feedings rate over a 1-week period in the approximately 7-week chick-rearing period. There were no differences in survival in the control and experimental burrow, and for the sexed chicks, no difference in the proportion of males and females in the 2 groups. One experimental chick died before the supplemental feeding day and another had no usable data prior to supplemental feeding, problems that reduced the experimental sample to 15 for any within-chick comparisons before and after supplemental feeding. On the 10th day, each of the 4 cameras was removed from the burrow and deployed in other active burrows where the recording and the supplemental feeding procedures were repeated. We dealt with the problem of the video recording system occasionally malfunctioning, which reduced the number of usable observation hours, by converting measures such as feeding rate to a rate per hour of usable hours of recording.

Chick body condition

Chicks were measured on day 4 (after 3 days of baseline recording) of the experiment and body condition was calculated by dividing chick mass by tarsus length. Although tarsus length increases with chick age, it is not affected by nutritional status (Cook and Hamer 1997), whereas body mass varies with feeding conditions (Baillie and Jones 2004). Therefore, dividing chick mass by tarsus length gives an index of chick condition, adjusted for chick age.

Video and audio analysis

Presupplemental feeding video footage taken from day 1 at 1300 hours to day 4 at 1300 hours and supplemental feeding video

footage taken from day 7 at 1300 hours to day 10 at 1300 hours in each burrow were viewed in QuickTime Player v.6.6 (©Apple Inc.) and coded for a series of chick and adult behaviors using logger.app (©A. Earle, Memorial University). Only events occurring in the presence of an adult were coded and included: time of adult visit, type of feeding visit, type of fish, presence/absence of chick begging call types, occurrence of screech calls at a visit, and number of peep calls 60 s before and after the adult is visible in the nest. Peep calls were counted for the earliest morning visit during the pre- or postsupplemental feeding period in which parents brought food to the chicks. Food visits were chosen for the peep analysis because these visits rarely had any of the longer screech calls that would have resulted in a reduced count of the peep calls.

Returning adults did not always bring food to chicks so we recorded whether parents brought food at each visit to the burrow. The type of fish was recorded at the species level when possible but was later classified as either high quality (capelin or sandlance, *Ammodytes* spp.) or low quality (larval fish and invertebrates). In cases where the visit or fish type was unclear due to obstruction of the camera lens, these parameters were coded as unknown. Subsequent 24-h recordings confirm that puffin chicks are not fed at night so the dawn-to-dusk recordings capture all feeding visits.

The mean number of food, no-food, and unknown visits per chick is shown in Table 1. Parental visits were classified according to whether or not adults brought food for their chicks in the experimental (baseline, supplemental feeding) and control (early, late, Table 1) conditions. Approximately a third of visits were classified as feeding status “unknown,” which happened if the parent’s body came between the camera (lodged in the burrow wall) and the chick in the end of the burrow. Chick calls were then analyzed by type and in terms of whether they occurred more often during food or no-food visits.

Statistical analysis

The proportion of each type of adult visit (food, no-food, unknown, high-quality food, low-quality food) in which chicks used each type of begging call was calculated for every individual burrow before and after supplemental feeding. Wilcoxon signed-rank tests were used to compare the proportion of visits: 1) with each type of begging call during known food visits and during no-food visits, 2) use of screech begging calls during high- vs. low-quality food visits, and 3) change in the proportion of visits with screech calls after supplemental feeding. The Mann–Whitney *U* test was used to compare the change in the proportion of visits with screech calls between the experimental and control groups. Bayes’ theorem was used to calculate estimated feeding rates for each chick, such that the proportion of screech calls for known food and no-food visits could be

used to estimate the probability that chicks were fed on an unknown visit where the chick could be heard but not seen. For example, the probability that a chick was fed on parental visits when it did not screech or $p(F/NSc)$ is calculated as follows:

$$p(F/NSc) = \frac{p(NSc/F) \cdot p(F \text{ visits})}{p(NSc/F) \cdot p(F \text{ visits}) + p(NSc/NF)}$$

In this equation, $p(NSc/F)$ is the proportion of known feeding visits with no screeches, $p(F \text{ visits})$ is the proportion of known visits that the chick was fed, and $p(NSc/NF)$ is the proportion of visits in which the chick did not screech when its parents visited without bringing food. The resulting probability was multiplied by the number of visits of that type (i.e., unknown visits with or without screech calls) for each chick to get an estimate of the number of unobserved feeds. The estimated number of unobserved feeds was added to the number of known feeds for each chick and divided by the number of hours of video to get an estimated feeding rate per chick. A 2-way Anova with repeated measures was used to compare the estimated feeding rate before and after supplemental feeding and to check for differences in feeding rates between years. Relationships between chick body condition, estimated adult provisioning rate, and use of particular begging calls were analyzed using linear regressions. Means are given with confidence intervals (proportions) or standard errors (non-proportional data). Statistical tests were performed using SPSS Statistics 20.0.

RESULTS

Call types and usage

We identified 2 types of begging calls, both of which occurred in the presence of adults: peep calls and screech calls (Figure 1). Peep calls consisted of regular narrow-band call elements in the shape of an inverted U. These “peeping” calls were repeated at regular intervals (Figure 1, top).

Screech calls were flat in shape with a gradual rise and some frequency modulation early in the call. These “long” calls had multiple harmonics and were repeated at irregular intervals (Figure 1, bottom). Unlike peep calls, screech calls did not occur at all parental visits. Overall, chicks gave screech calls on 46% of visits, with chicks making between 1 and 20 calls (average of approximately 5 screech calls) on the visits in which screech calls occurred.

We analyzed the proportion of visits with screech calls in relation to the known feeding status of the visit. There was considerable individual variation in the use of screech calls in food and no-food visits. Chicks used screech calls in 0–29% of visits when parents brought food and between 50% and 100% of visits when

Table 1

Mean number of visits per nest \pm SE (mean percentage per nest of the total visits) divided into visit type for supplementally fed ($N = 16$) and control chicks ($N = 5$)

Visits	No food	Food	Unknown
Supplementally fed			
Presupplemental	2.18 \pm 0.47 (27%)	3.87 \pm 0.83 (39%)	2.56 \pm 0.64 (33%)
Supplemental	2.00 \pm 0.74 (21%)	4.06 \pm 0.94 (48%)	1.93 \pm 0.63 (31%)
Control			
Early	4.20 \pm 1.15 (34%)	3.40 \pm 0.93 (30%)	4.00 \pm 1.30 (36%)
Late	0.60 \pm 0.93 (16%)	4.60 \pm 0.93 (48%)	3.40 \pm 1.02 (36%)

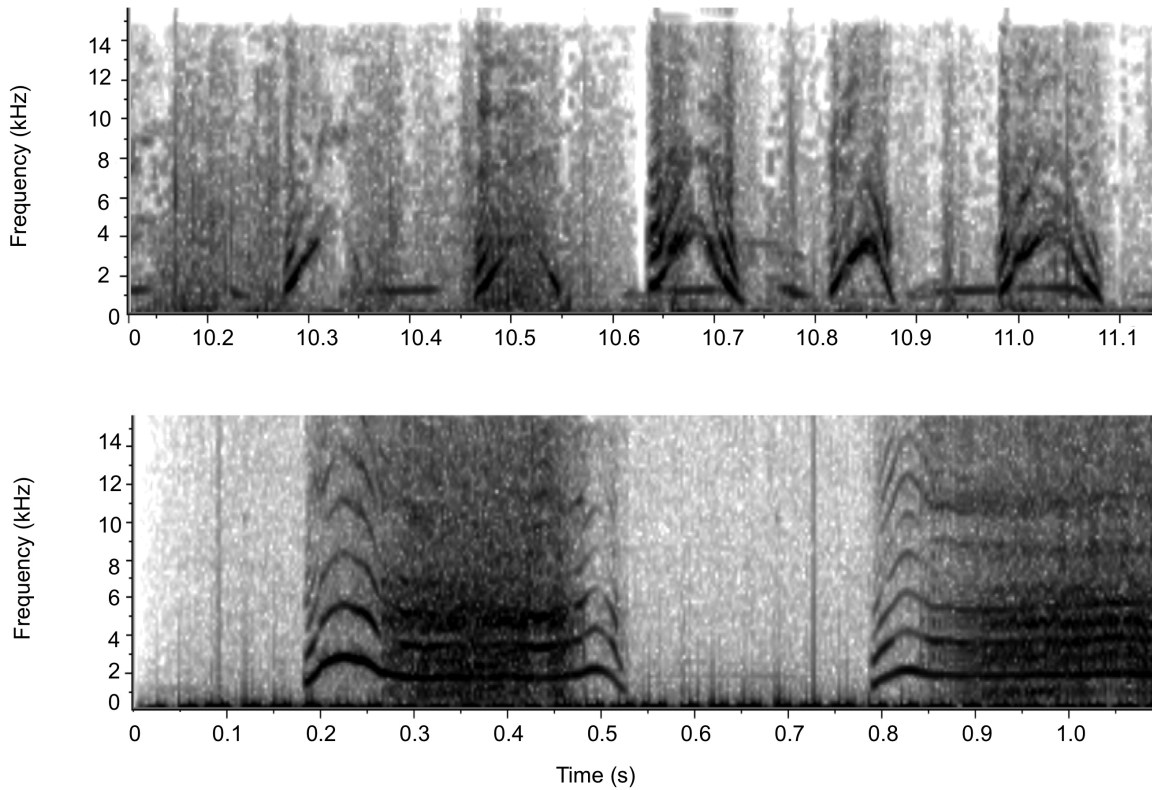


Figure 1 Top, peep (rhythmic) chick begging call and bottom, screech (long) chick begging call frequencies measured in kHz (*y* axis) over time in seconds (*x* axis).

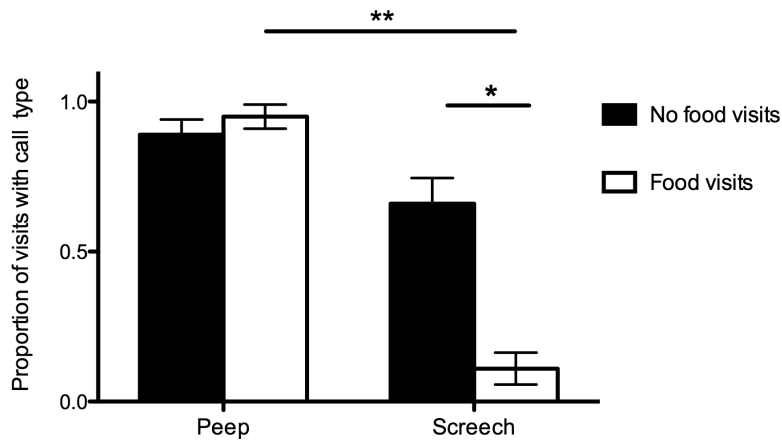


Figure 2 Mean proportion \pm SE of visits with peep and screech calls when adults brought food or did not bring food. $**P < 0.001$; $*P = 0.014$.

parents brought no food. Screech calls occurred in a significantly higher proportion of known no-food visits (0.74) than known food visits (0.15, Wilcoxon signed-rank test, $n = 16$, $P = 0.001$, Figure 2). There was no difference in the proportion of parental visits with screech calls during low-quality (larval fish and invertebrates, 0.18 ± 0.10) and high-quality (capelin and sandlance, 0.08 ± 0.06) food visits (Wilcoxon signed-rank test for chicks with both types of feeds, $n = 10$, $P = 0.29$).

In contrast to the irregular occurrence of screech calls, chicks emitted peep calls at almost all parental visits ($>96\%$ parental visits). Counts of peep calls were totaled for the minute before and the minute after the parent was first observed on the video (mean,

259.7 ± 18.5 calls per visit). Overall, use of screech calls appeared to vary more than use of peep calls between food and no-food visits.

Effects of supplemental feeding on chick begging

After supplemental feeding, chicks emitted screech calls in a lower proportion of no-food visits (Wilcoxon signed-ranks test, $n = 16$, $P = 0.04$) and overall visits ($P = 0.001$), whereas control chicks ($n = 5$) showed no change (Table 2). The proportion of screech calls at feeding visits did not decrease after supplemental feeding (Wilcoxon signed-ranks test, $n = 16$, $P = 0.17$), but experimental chicks showed a greater decrease in the proportion of screech calls

at food visits than did control chicks over a similar time period (Mann–Whitney U test, $n = 21$, $P = 0.03$, Table 2).

In addition, chicks in better body condition increased their peep call rate more after supplemental feeding than chicks in poorer condition (calls in minute before the parent was visible on camera, Pearson's $r = 0.82$, $n = 15$, $P = 0.003$ and overall calls, $r = 0.69$, $P = 0.028$).

Estimating overall feeding rates

Bayes' theorem was used to estimate adult provisioning rate before and after supplemental feeding. There was no change in estimated feeding rate from before to after supplemental feeding (2-way Anova, $F_{1,18} = 1.07$, $P = 0.32$), no difference between years ($F_{1,18} = 1.33$, $P = 0.26$), and no significant interaction ($F_{1,18} = 3.51$, $P = 0.08$).

Begging calls in relation to estimated chick-feeding rates and body condition

Chick body condition and estimated feeding rate were not significantly correlated (Pearson's $r = 0.23$, $n = 15$, $P = 0.33$), probably because the former reflects hatching mass and feeding rate in the weeks since hatching and the latter reflects current feeding rate. Thus, it was reasonable to test which of these variables best predicted the observed pattern of peep and screech calls.

We used a linear regression to determine whether peep call rate (dependent variable) was best predicted by body condition or by estimated feeding rate (independent variables). The overall regression for peep call rate was significant (adjusted $R^2 = 0.412$, degrees of freedom [df] = 2,10) with chick body condition as the only significant predictor (Table 3). There was a significant positive

relationship between peep call rate and body condition such that chicks in better body condition gave more peep calls than chicks in poorer condition (Figure 3). There was also a significant positive correlation between the 6-day growth rate of chicks (g/day) between the 2 measurement days and number of peeps chicks emitted in the 30 s before their parent was visible on camera (Pearson's $r = 0.754$, $P = 0.031$), indicating that faster-growing chicks peeped more than slower-growing ones.

A linear regression was also used to determine whether the proportion of visits with screech calls was best predicted by chick body condition or estimated feed rate. The overall regression for the proportion of visits with screech calls was significant (adjusted $R^2 = 0.290$, $df = 2,17$) with estimated feeding rate as the only significant predictor (Table 3). There was a negative relationship between the proportion of visits with screech calls and feeding rate, such that the proportion of visits with screech calls was higher for poorly fed chicks (Figure 3). Similarly, chicks that gave no screech calls on the last day before the start of supplemental feeding were fed at a significantly higher rate ($0.25 + 0.03$ feeds per daylight hour) in the previous 3 days than chicks that gave screech calls (0.13 ± 0.01 , $t_{12} = 4.02$, $P = 0.002$, includes only burrows with 3 full days with visible video). Although body condition was not significantly correlated with the overall proportion of visits with screech calls (Pearson's $r = -0.38$, $n = 16$, $P = 0.15$), it was negatively correlated with the proportion of food visits with screech calls (Pearson's $r = -0.59$, $n = 16$, $P = 0.020$), indicating that chicks in poor body condition were more likely to use screech calls at food visits than chicks in better condition.

DISCUSSION

We documented the occurrence of 2 different call types in Atlantic puffins, which we named the “peep” and “screech” calls. These 2 calls are similar in form to the “repeat” and “whine” described for scrubwrens (*Sericornis frontalis*, Maurer et al. 2003) and the “rhythmic” and “long” calls described for Wilson's petrels (*Oceanites oceanicus*, Quillfeldt 2002). Magrath and colleagues note that scrubwren nestlings use the “repeat” calls when parents are absent and both calls when parents are present, a pattern we also see in the puffins. Maurer et al. (2003) and Magrath et al. (2010) suggest that characteristics of the “repeat” call make it more difficult for predators to localize and thus it is the better call for nestlings to use when no parents are present to warn them about predators. The functions of different call types may differ between passerines and burrow-nesting seabirds such as Wilson's petrel and Atlantic puffins. In these seabirds, the burrows protect nestlings from most predators and the burrow walls greatly attenuate the loudness of any chick calls.

The use of screech calls by puffin chicks was more variable than the use of peep calls in relation to parental feeding visits. Chicks screeched in a higher proportion of no-food visits than during visits in which parents fed their chicks. Poorly fed chicks used screech calls more often than well-fed chicks during the presupplemental feeding period. The proportion of visits with screech calls decreased after chicks received supplemental feeding, whereas there was no change in the control burrows over the same time period. Further, after supplemental feeding, the screech rate at feeding visits dropped to nearly zero, a significantly larger change than was seen in the control group. Taken together, these results suggest a strong relationship between use of screech begging calls and low levels of adult provisioning in the short term (current visit) and long term

Table 2

Mean proportion of screech calls (\pm SE) for food visits, no-food visits, and all visits before (BSF) and after supplemental feeding (ASF) for supplemented chicks ($N = 15$) and early and late for control chicks ($N = 5$)

	BSF/early	ASF/late	Change
Food visits			
Experimental chicks	0.15 (0.07)	0.01 (0.01)	-0.13 (0.07) ^a
Control chicks	0.06 (0.06)	0.12 (0.07)	0.06 (0.03) ^a
No-food visits			
Experimental chicks	0.62 (0.10) ^b	0.27 (0.09) ^b	-0.35 (0.13)
Control chicks	0.74 (0.10)	0.40 (0.24)	-0.34 (0.24)
All visits			
Experimental chicks	0.47 (0.08) ^c	0.22 (0.01) ^c	-0.29 (0.07)
Control chicks	0.41 (0.06)	0.33 (0.13)	-0.09 (0.09)

^aSignificant difference, Mann–Whitney U test, $P = 0.03$; ^{b,c}significant differences, Wilcoxon signed-rank test, $P = 0.040$ and 0.001 , respectively.

Table 3

Linear regression of the relationship of the number of peep calls and proportion of visits with screech calls (dependent variables) to body condition and estimated feeding rate (independent variables), indicated by F or t value (probability) and beta values

	Peeps	Beta	Screech	Beta
Overall (F)	5.56 (0.021)		4.80 (0.028)	
Constant	3.41 (0.006)		3.68 (0.003)	
Body condition (t)	2.53 (0.028)	0.551	-1.27 (0.227)	-0.272
Feeding rate (t)	1.60 (0.137)	0.349	-3.14 (0.013)	-0.540

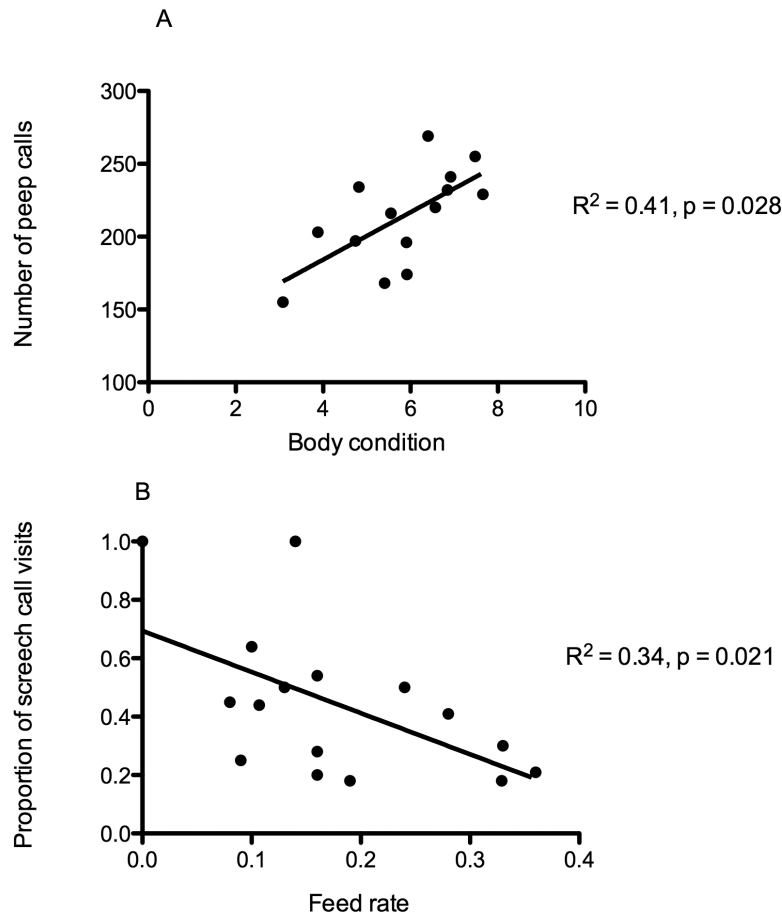


Figure 3

Significant results from the linear regressions: (A) relationship between chick peep rate and body condition (mass over tarsus) and (B) between the proportion of screech calls and the estimated feeding rate per hour.

(>24 h). Thus, we found evidence in support of both the short-term signal of hunger and a longer-term signal of need, as suggested by Mock et al. (2011), but our data do not allow us to fit the screech call into only 1 of these 2 models of begging. Consistent with this difficulty, Johnstone and Kilner (2011) argue that it is not feasible to attempt to distinguish between short- and long-term need in begging models.

In contrast to screech calls, peep calls occurred at almost every parental visit, and chicks in good body condition and with higher growth rates emitted more peep calls than chicks in poor body condition with lower growth rates. Further, chicks in good body condition increased their peep rate more after supplemental feeding than chicks in poor body condition. The findings that screech calls are negatively related to feeding status and peep call rates are positively related to chick body condition suggest that puffin chicks can both beg, to signal need or hunger, and boast, to signal quality. These 2 calls may therefore allow chicks to communicate about different fitness-related characteristics on different timescales.

Why have puffin chick calls evolved to convey both need and quality information? Adult puffins lose body mass during chick rearing even under good conditions, and at some point if foraging conditions deteriorate, they should opt to decrease investment in their chicks in favor of self-maintenance, as do other long-lived seabirds. Variation in the seasonal and yearly availability of forage fish has probably shaped parental feeding decisions, which in turn has shaped the calling strategies of the chicks. Screech calls may

stimulate parents to bring more food, as in signal of need or hunger, whereas a high frequency of peep calls may encourage parents to keep investing in the current breeding attempt. Having 2 calls may protect high-quality chicks if resources deteriorate: parents may not be able to satisfy the nutritional needs of an often-screeching chick, and they may have to abandon it. In contrast, parents may decide to work harder under poor foraging conditions for an often-peeping chick of higher quality. In previous years on our study colony, body condition of adult puffins and growth rate of chicks were positively correlated across years (Rector et al. 2012), suggesting that parental investment reflects current adult condition and foraging constraints. Similarly, puffin parents whose chicks were cross-fostered were more likely to desert if their own chick or the foster chick was relatively small (Erikstad et al. 1997). It is possible that variation in peep rate of chicks in the Erikstad et al. (1997) study contributed to the parental decision to continue investing or to desert. European starling (*Sturnus vulgaris*) chicks use separate visual and auditory displays to signal different fitness components (Jacob et al. 2011). The results of these recent studies and Kilner's (2002) discussion of the significance of multiple signals suggest that it would be highly worthwhile to examine the possible use of multiple signals in other systems.

Royle et al. (2002) point out that honest signaling is more likely to evolve when parents control resources and in single-chick broods (so no sib competition). In other words, honest signals work best when chances of conflict are low, as would particularly be the case

when food was abundant. Our results suggest that environmental context is important when interpreting the behavioral responses of parents and offspring to changes in food availability. Honest signaling models, predicting that adults provision offspring in response to begging intensity, assume that adults have complete control over provisioning; however, this is rarely a true assumption. Seabird chick diet and provisioning rates are highly dependent on prey availability (Barrett 2002; Baillie and Jones 2003, 2004; Burke and Montevecchi 2008; Wilhelm et al. 2008). Because adults are selected to reduce parental care when foraging conditions are poor and offspring would generally benefit from more care than adults are selected to give under these conditions, poor prey availability may increase parent–offspring conflict and reduce the honesty of chick signals.

Associations between chick body condition and begging under natural conditions have been found in Procellariiformes seabirds with single-chick broods including Wilson's storm-petrels (*O. oceanicus*, Quillfeldt 2002; Gladbach et al. 2009), Cory's shearwaters (*Calonectris diomedea*, Träger et al. 2006), Manx shearwaters (*Puffinus puffinus*, Quillfeldt et al. 2004), and thin-billed prions (*Pachyptila belcheri*, Duckworth et al. 2009). Wilson's storm-petrel chicks have 2 distinct chick calls, a rhythmic and a long call (Quillfeldt 2002). The structures of these calls are similar to the puffin chicks' peep and screech calls, respectively. Quillfeldt (2002) found that high rates of both calls were associated with storm-petrel chicks being in poor body condition. The finding that both storm petrel calls were associated with chick need is different than the current results where we suggest that one puffin chick call signals need and the other signals quality. The relationship between begging and feeding rate for Atlantic puffin chicks in this study indicates that begging may exist as an honest signal of chick need in burrow-nesting seabirds other than Procellariiformes. Researchers have referred to begging calls as providing "cryptic" information about fitness that is not available to parents through visual signals. Visual information may be particularly difficult to use in the case of seabirds species with single chicks (no other chicks for comparison) housed in dark burrows; hence, begging calls may be the least ambiguous way for chicks to signal their condition or quality to their parents.

Parental investment theory is based on the idea that parents' current investment decreases the potential for investment in future offspring (Trivers 1974). Long-lived species should be selected to invest conservatively (Ricklefs 1987), and particularly when resources are severely limited, single chicks may be thought of as competing with their future, as yet unhatched, siblings. The cost of current investment on future reproduction has been measured in Atlantic puffins: Wernham and Bryant (1998) found that parents with food-supplemented chicks in 1 year had higher reproductive success in the next year. The reason for this carryover effect is that Atlantic puffin parents generally reduce their provisioning rates when their chicks receive supplemental food (Cook and Hamer 1997; Wernham and Bryant 1998; Dahl et al. 2005). Adult body condition generally decreases during chick rearing in Alcids (e.g., Harris and Wanless 1988; Croll et al. 1991; Jones 1994; Williams et al. 2008), so decreased workload for parents of supplementally fed chicks apparently results in parents being in better condition, which can carry over into the next breeding season.

If puffin parents reduced their provisioning rate in this study, chicks should not have reduced their use of screech calls after supplemental feeding as their food intake would have been unchanged. However, parental feeding rates before and after supplemental feeding were examined here and more extensively in a companion

study that was carried out on the same population in the same years (2009 and 2010, Rector 2011). Rector (2011) found that parental feeding rates did not change after supplemental feeding and that chick survival rate (not just growth rate) was higher in the supplementally-fed chicks than in the controls. It is likely that parents did not reduce their provisioning rates because of the low capelin abundance and short spawning duration in 2009 and 2010 (Nakashima B, personal communication). The natural provisioning rate on Gull Island in 2009 and 2010 was only 2.3 visits per day compared with 4.5 feedings per day in this same population in 1985 (Creelman and Storey 1991). Rector (2011) concluded that parents could not reduce their provisioning rate as chicks were on the verge of starvation, even though supplemented chicks were getting enough additional food to be able to reduce their use of screech calls. Two studies on Cory's shearwaters support this conclusion: parents reduced provisioning during supplemental feeding in a good breeding season (Quillfeldt and Masello 2004), but not in a poor one (Granadeiro et al. 2000).

The proportion of visits with screech calls was higher for poorly fed chicks and the proportion of visits with this call decreased after supplemental feeding. In contrast, peep calls were positively related to chick body condition, suggesting that puffin chicks can both communicate 2 different messages to their parents to both "beg" and "boast." Variation in chick begging in relation to feeding rate and body condition provides evidence that begging is an honest signal in puffin chicks.

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