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ABSTRACT

Two manipulations were performed on domestic piglets to determine whether differences in calling during periods of separation from the mother can indicate differences in need. In both cases, the aim was to manipulate the piglet's need for the sow's attention. In the first manipulation a 'thriving' piglet (i.e. the piglet with the heaviest weight and most rapid weight gain) and a 'non-thriving' one (lightest and slowest weight gain) were selected from each of 15 litters. The two piglets were removed from the sow and litter and recorded for 13 min in separate isolated enclosures. For the second manipulation, two piglets of intermediate weight and weight gain were selected from each of the same 15 litters, and were removed from the sow during nursing under one of two conditions. The 'unfed' piglet was removed just before the milk ejection and the 'fed' one just after receiving milk. Both were recorded as in the first manipulation. 'Non-thriving' and 'unfed' piglets called more and used more high-frequency calls, longer calls, and calls that rose more in frequency than their 'thriving' and 'fed' litter-mates. By means of a playback experiment, the assumption that sows respond to these piglet calls was tested. Sows were more likely to vocalize and approach the loudspeaker during playback of the piglet isolation calls than during playback of white noise. It is argued that if a piglet's calls provide reliable information about its need for the sow's resources, then this calling can be used as a measure of its welfare. These results are consistent with theoretical models of honest signalling.

As the issue of animal welfare gains importance in the scientific community and among the general public, the problem of evaluating welfare also becomes more important. Research on the behaviour of animals has helped to develop a number of approaches to the assessment of animal well-being (Dawkins 1980, 1990; Fraser & Broom 1990). The idea that an animal's vocalizations can provide information about its state or condition has some intuitive appeal, but two elements are required before this assumption can be added to the repertoire of techniques for welfare assessment. At a minimum, for the animal and call being studied, some aspect of vocal behaviour must change in a consistent way with the animal's condition. To provide some generality, a theoretical framework is also needed to predict which calls in which situations provide useful information about condition. This framework will also allow us to address more general issues, such as why an animal should signal, why signals should provide reliable information about the signaller's needs, and why other animals might respond to these signals.

What types of empirical relationships might exist between animal calls and the caller's needs or condition? One possibility is that there is no relationship: callers simply use whatever signals they can to manipulate the behaviour of a receiver in a way that is beneficial to themselves (Dawkins & Krebs 1978; Krebs & Dawkins 1984). Of course, receivers should come to ignore a signal if they gain no benefit by responding. In this way, communication can be viewed as an evolutionary arms race, with signallers attempting to manipulate receivers, and receivers attempting to avoid this manipulation by responding only when a response is beneficial to themselves.

Alternatively, signals may provide reliable or 'honest' information about need or condition (Zahavi 1987). In one form of honest signalling, all signallers in need of a response call at the same minimum level required for communication (Maynard Smith 1994). This 'cost-free' reliable signalling may occur if receivers gain some benefit by responding, if senders and receivers rank the possible outcomes of the interaction in the same order, and, normally, if the frequency distribution of the condition being signalled is bimodal. For example, a young mammal might signal a discrete condition, such as being outside the nest, by such a cost-free call.

Two other forms of honest signalling are possible, both of which require a cost to signalling above the minimum needed for effective communication. In honest signalling of quality, a positive relationship exists between the signaller's condition and the extent of signalling. This relationship should occur if the costs of signalling are less for higher quality individuals, such that they can call more than a lower-quality individual for the same cost (Grafen 1990). For example, an unmated male bird might provide a reliable signal of his resistance to parasites if singing were less costly to him than to less resistant males.

In honest signals of need, a negative relationship exists between calling and condition (Godfray 1991; Maynard Smith 1991, 1994; Johnstone & Grafen 1992). Such signals might be directed towards receivers that can provide a resource to the signaller. For a receiver to benefit from providing the resource, the fitnesses of the two animals must in some way be connected, as is the case with genetic relatives. For example, as nestling birds become hungrier they might be more likely to beg, or to beg more, for food from their parents.

When suckling piglets become separated from the sow and litter-mates, they typically become very active and produce a series of vocalizations. These usually begin with relatively quiet, low-frequency sounds, but often progress to louder, higher-frequency ones (Fraser 1975). Piglets kept with the sow and litter rarely if ever use these calls, but when the sow is removed from the pen the piglets become vocal (Fraser 1975). For pigs kept in pens in which sows can leave their litters, piglets call when the sow is absent, especially as the time since the last nursing increases (E. A. Pajor, unpublished data). Sows also seem to respond to these calls by returning to nurse when piglets become vocal.

Our study had two aims. The first was to determine whether these separation calls of piglets vary in relation to the piglet's need or condition. As described above, at least four possible outcomes could be predicted: (1) there is no relationship between calling and need or condition, (2) all animals in need call at the same minimum level, (3) animals in better condition (i.e. with less need) call more, and (4) animals in worse condition (i.e. with more need) call more. In the last three cases, calling provides a reliable indicator of need/condition and can potentially provide both the sow and ourselves with information about piglet well-being.

A second aim was to determine if and how sows respond to these isolation calls. For piglets to gain some advantage from calling, these calls must affect the behaviour of potential receivers. Our observations of natural interactions suggested that sows respond to calling piglets by approaching them and by vocalizing

themselves. By means of a playback experiment, we determined whether this response is to the calls themselves or to some other aspect of the situation.

METHODS

Our approach was to monitor the vocal behaviour of piglets that differed in their need to elicit a response to their calls. The experiment included two manipulations, performed on 60 piglets from 15 litters. Litters were subjected to both manipulations on the same day (at 10 days of age) and in a randomized order. Both manipulations were performed within a 3-h period, beginning at approximately 1530 Eastern Standard Time.

Manipulation 1: Long-term Condition

We weighed piglets and calculated the linear regression of these weights on birth weight. The residual weight gain of each piglet (i.e. gain relative to that predicted on the basis of birth weight) was measured by calculating residuals from this regression line. Two piglets were selected from each litter: a 'thriving' piglet (i.e. with the highest body weight and largest positive residual weight gain), and a 'non-thriving' piglet (with the lowest weight and largest negative residual weight gain). Thriving piglets averaged ($\pm _{SE}$) 3730 ± 190 g body weight and 186 ± 15 g/day weight gain, versus 2350 130 g and 78 ± 15 g/day for the non-thriving piglets. In litters where these two measures (weight at 10 days and residual weight gain) did not correspond, we randomly selected a piglet from the bottom third and a piglet from the top third of both distributions. The two piglets were simultaneously removed from the sow while they were sleeping.

Manipulation 2: Short-term Condition

In the first manipulation, any differences in the vocal behaviour of the two piglets could reflect fixed differences between individuals: large piglets might call differently from small piglets not because they are in less need, but just because they are large. To determine whether differences in vocal behaviour vary with need in a flexible way, we must impose shorter-term effects on animals that are otherwise similar. With this idea in mind, two piglets of intermediate body weight and residual weight gain (from the middle third of both distributions described above) were selected from each litter and removed from the sow during a single nursing episode. Sows nurse their litters approximately once an hour, and although each nursing bout can last several minutes, the milk is available to piglets for only about 10-20 s. The onset of a nursing bout and the timing of the actual milk ejection can be determined from the sow's vocalizations and the piglets' mouth movements (Whittemore & Fraser 1974). We used these cues to remove one 'unfed' piglet from the udder just before the milk ejection and a second 'fed' piglet immediately after the milk ejection.

For both manipulations, piglets were brought to visually and acoustically isolated enclosures immediately after their removal from the sow. The two piglets were allocated to the two enclosures at random. Each enclosure consisted of a wooden pen measuring 0·5 × 0·5 × 0·5 m, lined in soft foam rubber. A Beyerdynamic MCE 86 N(C) microphone was placed 10 cm above the top of each of pen, such that the distance between the piglet's mouth and microphone was approximately 0·5 m. The signals from these microphones were fed to the left and right channels of a Sony WM-D6C tape-recorder via a Symetrix SX202 preamplifier. After the piglets were placed in the enclosures, the tape-recorder was started and the two piglets were recorded simultaneously for 13 min.

Spectral and Statistical Analyses

When piglets are separated from the sow they call in a distinctive manner (Fig. 1). It is difficult to predict which characteristics of these calls will be most useful, except that features more expensive to produce

may be more likely to vary with need. The energetic costs of calling probably increase with call rate and duration (Ryan 1988), and particularly high- or low-frequency calls may be more expensive to produce. Some of these features may also make the calls easier to detect or localize by predators, again increasing their cost.

Figure 1. Sonagram of a 1-s section from one of the five 30-s sequences of isolation calls used as stimuli in the playback experiment.
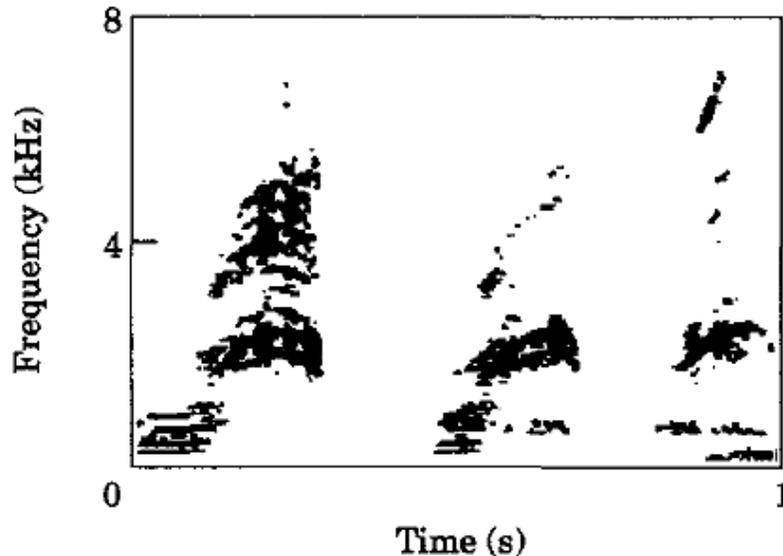
To describe the time course of the piglet's vocal response to isolation, we measured the number of calls produced in the first, second, fourth, eighth and twelfth minutes of recording. We then sampled the first 16 s from each of these 1-min periods, and made detailed spectrographic measures of every call within this sample ($N = 3957$ calls). Using Signal software (Engineering Design 1991) and a personal computer, we measured call duration (s), and the frequency (kHz) of maximum amplitude (i.e. frequency of the loudest band in the call). We also measured the frequency of the two next loudest bands within 20 dB of the loudest, and used these measures to calculate a 'weighted' frequency (kHz). Each of the softer frequencies was weighted by the factor $1 - ((dB_1 - dB_2)/20)$, where dB_1 is the amplitude of the louder frequency and dB_2 the amplitude of the softer. Each call was also divided into three equal parts, and the weighted frequency of the last third was subtracted from that of the first, giving an indication of any rise or fall in frequency (kHz). For each of these variables, we calculated a mean using all of the calls in the 16-s sample and then used these mean values in the statistical analysis. Quantitative measures of vocalizations tend to be correlated, so these analyses should not be considered as independent. They were tested separately so as to identify call attributes that best reflect the animal's condition.

The analysis of variance model included, as between-subject effects, the manipulation (long-term versus short-term condition), the piglet's condition classified as good ('fed' or 'thriving') or poor ('unfed' or 'non-thriving'), and the interaction of manipulation by condition. The effect of time (i.e. differences between minutes 1, 2, 4, 8 and 12) was included as a within-subject effect. To perform more sensitive tests of the effects of interest, we also included the between-subject effects of litter ($N = 15$), enclosure ($N = 2$), and the interaction of litter by enclosure. Using 60 piglets, this analysis resulted in 27 degrees of freedom for the error term. One subject did not call during one of the 1-min periods and was removed from all analyses involving spectrographic measurement, resulting in 26 error degrees of freedom for these analyses.

Although we treated the variation between calls as continuous, it is possible that the calls can be classified into distinct types (see Jensen & Algers 1984). If these distinct types are meaningful to the animals, then analysing the calls by type might better reveal the differences between the experimental conditions. Discontinuities and multimodality in the distribution of call variables are possible indications of the presence of distinct call types. To scan for any multi-modality, we plotted the univariate distributions of each of the four spectrographic measures (duration, frequency of the loudest band, weighted frequency, and change in weighted frequency), and the six possible bivariate plots, for a subsample of 1069 calls from 12 piglets.

Playback Experiment

To determine whether at least one function of these piglet calls is to attract the sow's attention, we performed a playback experiment. We used as subjects 10 lactating sows, temporarily removed from their litters that ranged in age from 1 to 3 weeks. Sows were tested individually in a visually and acoustically isolated room measuring 2 × 2 m, with a loudspeaker (Fostex 6301B) placed in one corner and a 1 × 1-m area adjacent to the loudspeaker marked on the floor. At the beginning of each trial, a sow was led from its pen and litter approximately 20 m to the experimental room. Once in the room, a 3-min period began in which no stimuli were presented. Playback was then presented for 30 s from a DAT player (Sony TCD-D3). This was followed by another 3-min period of silence, another 30 s of playback and another 2 min of silence. Sows were video- and audio-taped during the entire 9-min trial. Each sow was presented with two sounds (one during each playback period): white noise and a sequence of calls from an isolated piglet. We alternated the order of the sounds to which sows were exposed (calls followed by noise, or noise followed by calls) in each trial, so that five sows received each of the orders. Also, we used five different sequences of piglet separation calls, each recorded from a different individual. These too were alternated so that each sequence was played to two different sows. All sequences were long, loud, high-frequency calls played at a high rate. A section from one of these five sequences of isolation calls is shown in Fig. 1. We scored two measures of sow response: number of calls and time with head in the 1 × 1-m area adjacent to the speaker. These responses were scored during the 30 s of playback and the 30 s following playback.

RESULTS

Piglets from both conditions and in both manipulations called at a high rate, as is typical for piglets isolated from the sow and litter-mates (Fig. 2). The rate of calling increased during the first 2 min of isolation, but then declined gradually to near the initial level. This change was reflected by a significant within-subject effect of time in the analysis of call rate ($F_{4,108} = 34 \cdot 74$, $P < 0 \cdot 001$).

Piglets called more if they were relatively light and slow-gaining ('non-thriving') compared to litter-mates that were heavy and gaining well ('thriving'; Fig. 2a). Also, they called more if they had just missed a milk ejection ('unfed') than if they had received milk ('fed'; Fig. 2b). The effect of piglet condition (i.e. 'thriving' or 'fed' versus 'non-thriving' or 'unfed') was highly significant ($F_{1,27} = 14 \cdot 36$, $P < 0 \cdot 001$). There was no significant difference in this rate of calling between the two manipulations (long-term versus short-term; $F_{1,27} = 0 \cdot 09$, $P > 0 \cdot 1$), no interaction between manipulation type and piglet condition ($F_{1,27} = 2 \cdot 18$, $P > 0 \cdot 1$), and no interaction between manipulation or condition and the within-subject effect of time ($P > 0 \cdot 1$).

The spectrographic measures from the calls also revealed differences (Fig. 3). For each of the four variables, the mean for piglets in the poor conditions (i.e. 'non-thriving' or 'unfed') was higher than that of their litter-mates in the good conditions (i.e. 'thriving' or 'fed'). This effect of condition was significant for two of the variables: duration ($F_{1,26} = 4 \cdot 34$, $P < 0 \cdot 05$), and change in frequency ($F_{1,26} = 7 \cdot 43$, $P < 0 \cdot 05$). There was no significant difference between the two manipulations for any of these variables, and the

interaction between condition and manipulation was significant only for the change in frequency ($F_{1,26}$ = 7·65, $P < 0·05$).

Figure 2. The mean (± SE) number of calls uttered by piglets during the first, second, fourth, eighth and twelfth minutes of separation from the sow. (a) Results from manipulation 1 (long-term condition), comparing calls of piglets that were of high body weight and rapid weight gain ('thriving') with calls from litter-mates that were of relatively low body weight and slow weight gain ('non-thriving'). (b) Results from manipulation 2 (short-term condition), comparing calls of piglets that had just received milk ('fed') with calls from those that had just missed a milk ejection ('unfed').
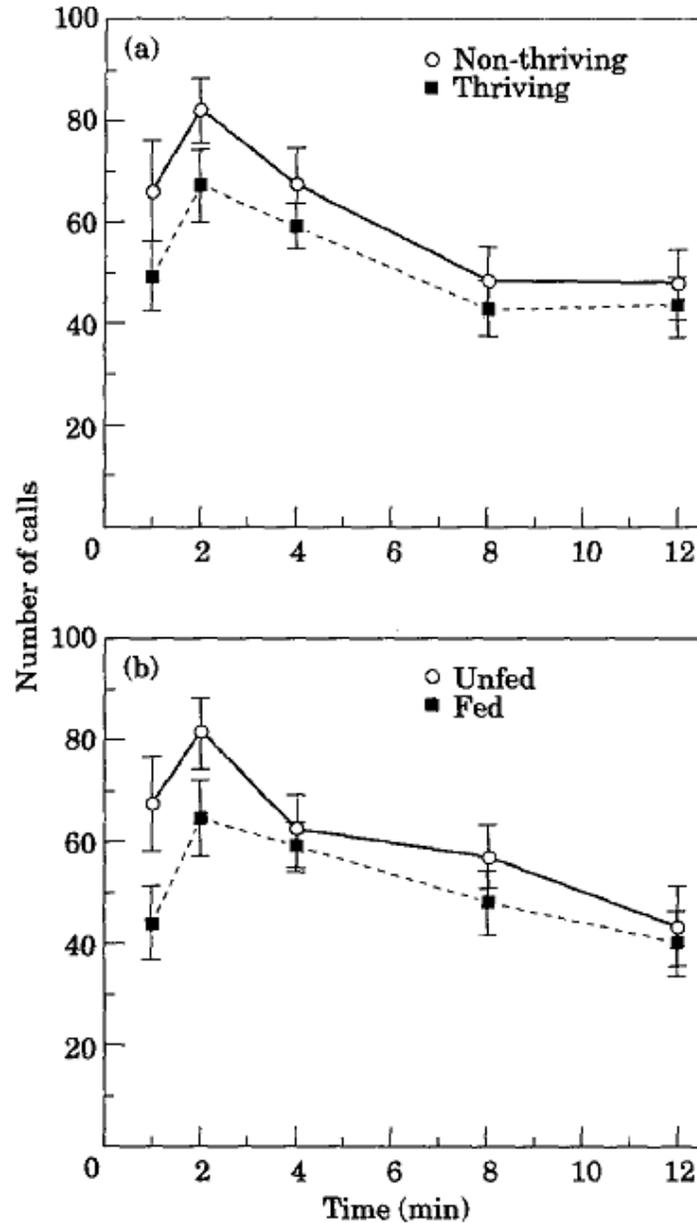
To determine whether calls can be divided into discrete types, we plotted the univariate and bivariate distributions by individual. A visual scanning of these plots showed them to be consistently multi-modal for only one variable, the frequency of the loudest band (Fig. 4). The distribution for each of the 12 piglets

sampled showed two or three different peaks, with few intermediate values, suggesting that piglets may be using more than one call type. Moreover, the distributions were separated at similar locations: approximately 250 and 500 Hz.

Using these results we classified calls into three different types depending on whether the frequency of the loudest band was (1) less than 250 Hz, (2) between 250 and 500 Hz, or (3) greater than 500 Hz (Fig. 5). For the first two classes of vocalizations, the difference in the number of calls between the experimental conditions was not significant (Fig. 5a, b; $P > 0.1$). The difference was significant for number of calls greater than 500Hz, however, with piglets in poor condition (i.e. 'non-thriving' and 'unfed') giving more calls (Fig. 5c; $F_{1,26} = 8.27$, $P < 0.01$).

Playback Results

The results of the playback experiment indicated that sows do respond to the calls of isolated piglets. Compared to the playback of white noise, playback of the piglet separation calls led to more calls from the sow during the 30-s playback period ($\bar{X} \pm$ SE, 8.9 ± 3.4 versus 2.3 ± 1.6; paired $t = 3.15$, $P < 0.01$), more time with the sow's head near the loudspeaker during the playback period (22.6 ± 1.7 s versus 8.7 ± 2.6 s; paired $t = 3.05$, $P < 0.01$), and more calls from the sow during the 30·s period immediately after the playback (6.3 ± 1.3 versus 1.8 ± 0.8; paired $t = 3.68$, $P < 0.005$).

DISCUSSION

In summary, piglets of low body weight and slow weight gain, and piglets that had missed a milk ejection, called more, used more high-frequency calls, used longer calls and used calls with a greater increase in frequency, than piglets that were of relatively high body weight and rapid weight gain, or that had just received milk. These results confirm that piglets in greater need of the sow's resources call more and use different calls compared to those in lesser need. The fact that all piglets called (even those that were 'fed' and 'thriving'), indicates that the calls do not only advertise need for milk, as might be expected in a begging call. Rather, they also seem to advertise a more general need to be reunited with the sow, perhaps because of the multiple costs of separation including missed feeding opportunities, poor thermal environment, and risk from predators.

The results of the playback experiment showed that sows do respond to the piglet calls. Sows responded by vocalizing and approaching the playback speaker. Sows produced some vocalizations that were very long (> 1 s in duration), which we have also heard sows produce after their litters were abruptly removed for weaning. These vocalizations may signal the sow's location to the piglets. It may not always benefit the sow to respond maximally to all calls, especially when young are in conflict with parents over the extent of the parent's investment in their care (Trivers 1974). Given the relationship between the extent of calling and need, we might expect sows to show stronger responses to the calls of the more needy piglets. Results from an on-going experiment indicate that sows do show a much stronger response to extreme calls from needy piglets than to lower-frequency, shorter-duration and lower-call-rate sequences from less needy litter-mates (unpublished data). The results of the present experiment showed that sows responded strongly to the isolation calls even though these calls were not from their own piglets. Preliminary results from our on-going experiment suggest that sows respond similarly to isolation calls from their own and other litters. A sow has little opportunity to learn to recognize the calls from her own piglets because the litter is very rarely separated from her. In the wild, sows return to a kin group once their litter is approximately 10 days of age (Newberry & Wood-Gush 1985; Jensen & Redbo 1987). Thus any calling piglet is likely to be related to the sow, perhaps favouring a less discriminating response.

Figure 3. The mean (± SE) (a) duration, (b) frequency of loudest band, (c) weighted frequency, and (d) change in frequency, for calls uttered by piglets in 'poor' and 'good' conditions during the first 16 s of each of the five 1-min periods sampled. Results are combined from the two manipulations. Piglets that were 'unfed' and 'non-thriving' are included in the 'poor' condition, and piglets that were 'fed' and 'thriving' form the 'good' condition.
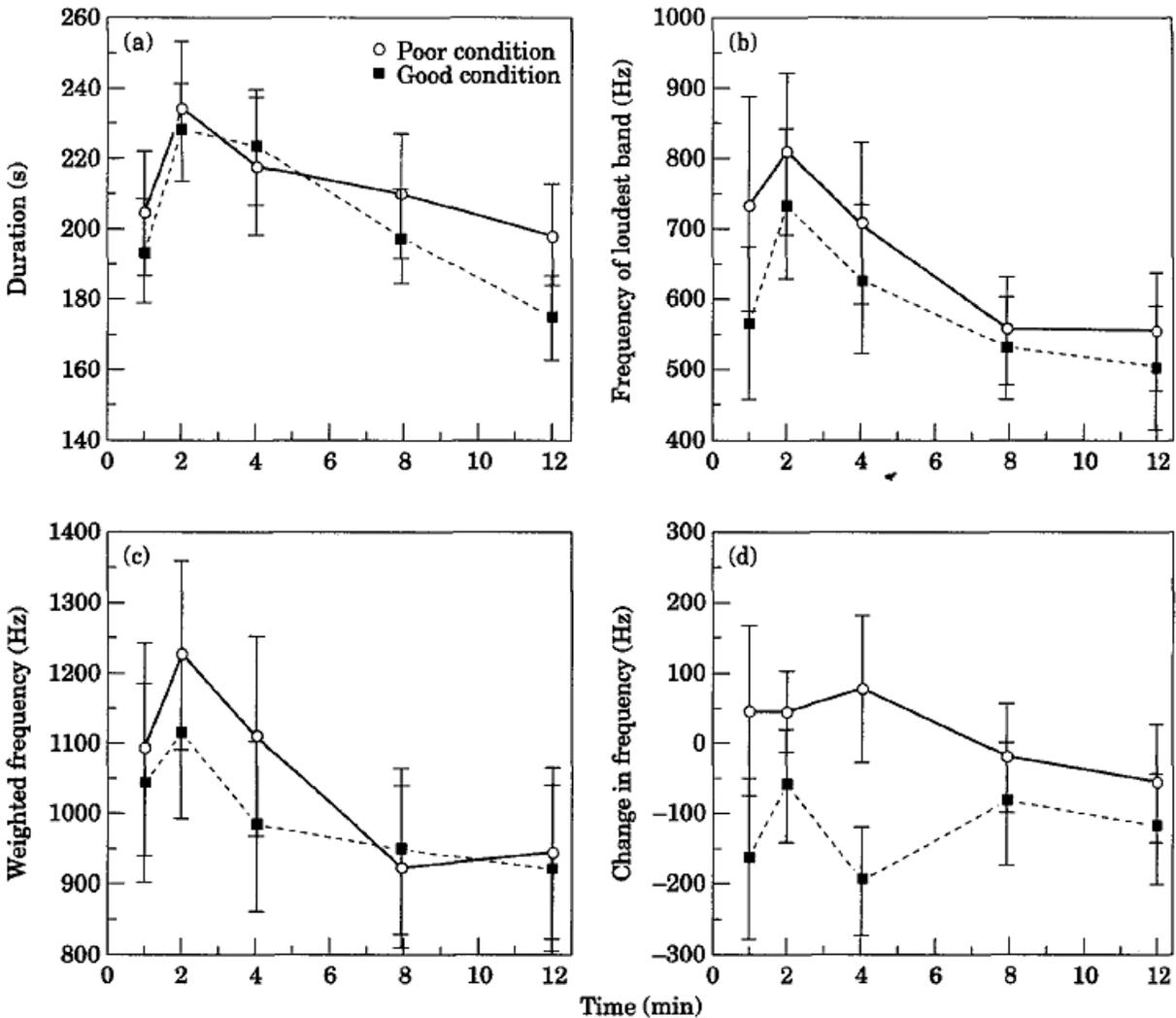

To a certain extent, the isolation calls of piglets may correspond to the 'cost-free' signalling envisaged by Maynard Smith (1994): all animals in need signal this need in a similar, minimal way, regardless of the extent of need. When piglets are with the sow and litter-mates they do not produce these calls, but when isolated they do (Fraser 1975). At least initially (during the first few seconds of isolation), the calls produced by almost all piglets are fairly quiet, low frequency, and produced at a low rate. Thus the presence or absence of these calls seems to serve as a reliable signal of a simple change in state (isolated or not).

Our results show that for isolated piglets that vary in their need to be reunited with the sow, the extent of calling is positively related to the extent of need. In this way the calling is like the begging of chicks (e.g.

Redondo & Castro 1992; Smith & Montgomerie 1992). This positive relationship between calling and need corresponds to the costly signalling of need that can occur among relatives (Godfray 1991; Maynard Smith 1991, 1994; Johnstone & Grafen 1992). In the case of isolation calls, the intended receiver seems to be the sow (as suggested by our observations of natural interactions and by the results of the playback experiment) or the litter-mates, and thus would normally be a relative. The signals also seem to be more costly than the minimum required for communication. Compared to the initial calling, the isolation calls are louder, longer, higher and at a faster rate, especially when produced by the more needy animals. Our observations of natural interactions show that isolated piglets will call in this extreme fashion even when the sow is only a few metres away and is in visual contact. Little is known about the costs of signalling, but under natural conditions signals might attract predators, and may be physiologically expensive to produce (Ryan 1988; Eberhardt 1994; but see also Hornet al., in press).

Figure 4. The frequency distribution of data from a representative piglet for one call variable, frequency of the loudest band.
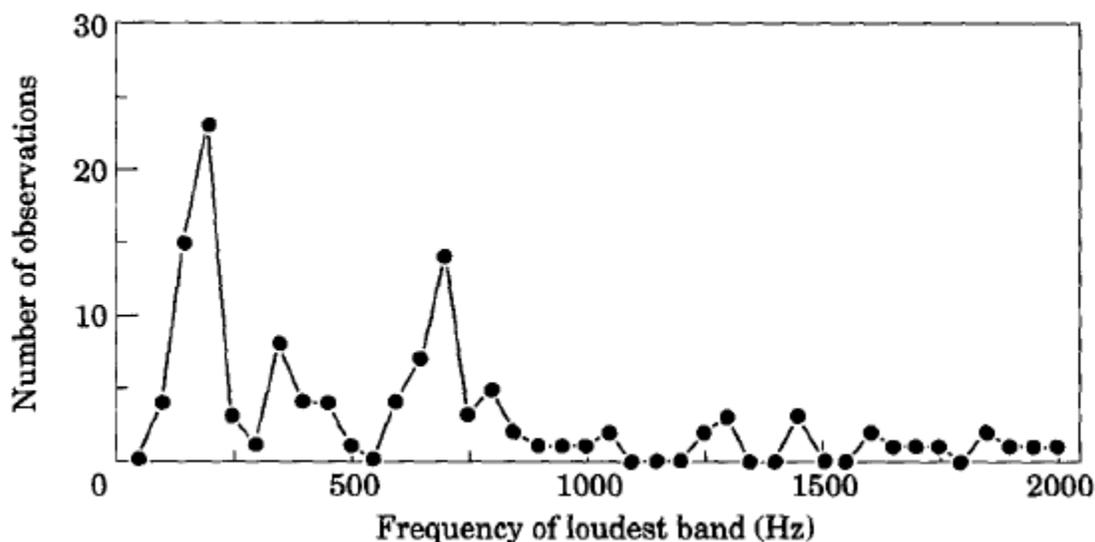
We found no evidence for a positive relationship between condition and signalling, as might be expected in intra-sexual contests or mate attraction where listeners require reliable indicators about the high quality of their rival or potential mate. The requirement for this type of signalling is that individuals in better condition can produce the same signal at a lower cost (Grafen 1990). Interestingly, this discrepancy in the price of signalling can lead to a certain level of individual cheating in otherwise honest systems of communicating need between relatives (Johnstone & Grafen 1993). For example, if certain piglets could produce extreme isolation calls more easily than others, we might expect these individuals to exaggerate their calls to reflect a higher than actual level of need.

Several studies have shown positive relationships between vocal signalling and need. For example, a recent study by Evans (1994) showed that the calling of young American white pelicans, *Pelecanus erythrorhynchos,* started as the animal became chilled, increased as body temperature fell, and then ceased when the animal was re-warmed. Parents will also respond to these calls by brooding their chicks (Evans 1992). Similarly, the ultrasonic calls of isolated rat pups tend to increase if their body temperature is lowered (e.g. Olivier et al. 1994) and the mother responds to these calls by retrieving the young and returning them to the nest (but see Blumberg & Alberts 1990). Preliminary tests with piglets indicate that they also call more when isolated in a cold enclosure (unpublished data).

Figure 5. The mean (± SE) number of calls with the frequency of the loudest band (a) less than 250Hz, (b) between 250 and 500Hz, (c) and greater than 500Hz, uttered during the first 16 s of each of five 1-min periods sampled. Results are combined from manipulations 1 and 2. Piglets that were 'unfed' and 'non-thriving' are included in the 'poor' condition, and piglets that were 'fed' and 'thriving' form the 'good' condition.'
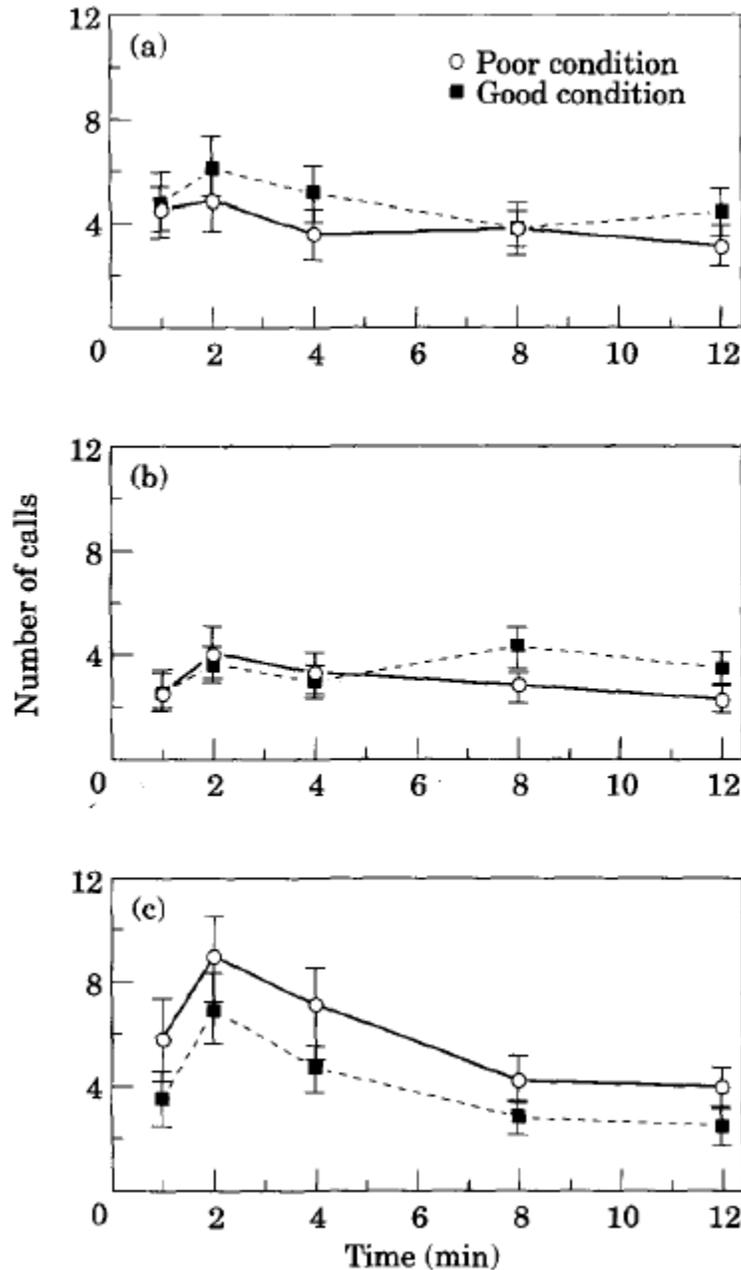
The scientific assessment of animal well-being has been approached with numerous behavioural measures including environmental preference testing, behavioural indicators of distress and frustration, studies of stereotyped and other abnormal behaviour, and studies of the strength of an animal's motivation to perform thwarted activities (e.g. Dawkins 1980, 1990; Fraser & Broom 1990). Despite considerable discussion over the interpretation of individual measures, there is little in the way of unifying theory. The concept of investment in costly behaviour patterns may help to unify various approaches. If

animals are adapted to be reasonably efficient in their use of time and energy, then perhaps we can evaluate the biological importance of a resource to an animal on the basis of the effort the animal is willing to expend in order to obtain it. The use of motivational testing in animal welfare assessment is, implicitly at least, based on this premise (Dawkins 1990). If access to a resource involves a cost (e.g. requiring the animal to perform a number of key pecks), we can determine the price animals are willing to pay for it. From a signalling perspective, the operant apparatus can be considered analogous to a model receiver that, according to our programming, responds only after receiving a certain level of signalling.

Our study provides an example of how signals may be useful in assessing the well-being of animals. The vocal response of piglets to isolation is much the same at 2-4 weeks (when they are typically weaned) as it is at 10 days (Fraser 1975). Thus variation in vocal behaviour of piglets during weaning might be used to evaluate how well different environments, diets and management practices correspond to the animals' needs.

ACKNOWLEDGMENTS

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