PUPS OF THE DEGU (OCTODON DEGUS) INCLUDE ULTRASONIC FREQUENCIES IN CARE-ELICITING CALLS

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1 ABSTRACT

Previous research into the juvenile vocalisations of the degu (*Octodon degus*), a semi-fossorial caviomorph rodent from central Chile, revealed interesting features of the calls used to elicit care from an adult, suggesting features present in the ultrasonic region. Here, it is determined that such vocalisations can include frequencies from 2.8 – 61.6 kHz, demonstrating ultrasonic harmonics well above the range that was previously recorded, although most energy is contained within the 10 kHz region. This provides the first reported case of ultrasound production by the species. These 'loud whistle' calls were found to have properties that varied significantly between behavioural contexts and between litters, suggesting the potential for individual litter and context recognition by adult degus. Features of the vocalisation such as duration were found to vary significantly with pup age, indicating changes to the qualities with pup growth and development. Finally, the recommended recording range for this species is given as 20 Hz – 65 kHz.

2 INTRODUCTION

Degus (*Octodon degus*) are a social and highly vocal species of herbivorous, semi-fossorial caviomorph rodent, originating from the semi-arid scrublands of central Chile. Degus have a complex social structure and in the wild live in small, female-biased groups. Female degus are seasonal breeders, nesting and nursing their pups communally in underground burrows [1;2;3;4;5]. After a comparatively lengthy gestation period of 90 days, females give birth to an average of 6 pups [6;7;8]. Degu pups, like those of most caviomorphs, have a high degree of precocity and mobility at birth, being born fully furred and with eyes and ears open [9], a unique feature amongst rodents. Pups largely remain in the burrows during the weaning process until Chilean spring [10] when they begin to take part in longer foraging bouts on the surface.

Degus are known to have a broad vocal range comprising 15 unique vocalisations [11] and have middle ear morphology very similar to that of other caviomorph species [12]. Although the exact hearing range of the species has yet to be behaviourally determined, microelectrode mapping has indicated that the auditory cortex of the degu responds to frequencies between 100 Hz – 35 kHz [13]. Previous investigation into the vocalisations of the degu raised interesting questions regarding the highest frequencies produced by pups, as harmonics were identified up to the recording limit of 22 kHz [11]. Further work was therefore required to investigate the possibility that pups produce ultrasonic harmonics in their vocalisations. Here, I focus on the 'loud whistle' vocalisations unique to pups of age 0 days - 6 weeks, used to elicit care from an adult [11], in order to look for high frequency harmonics and investigate changes in the properties of the call with age and behavioural context. The 'loud whistle' is one of two calls exclusively produced by degu pups, the other being the 'low whistle' [11]. Pups produce only these two vocalisations until they are around one week old after which time more adult vocalisations begin to be used.

3 METHODOLOGY

A sample of four litters of degu pups, kept and bred in a private collection, were used for recording over two breeding seasons (November-April annually); pups were born March-April on site. In this study, 'pups' were classed as being between 0 days to 6 weeks old, as this is the typical age at which degus are fully weaned [14;15]. Adult degus had all been bred for at least two generations in captivity in the UK (the exact genetic origin prior to being obtained by the collection was unknown). Litters were housed in separate, steel mesh colony cages of dimensions 70 x 45 x 100 cm (length, width, height). The two colonies were positioned 1.5 m apart in the same room of approximate dimensions 3 x 3 x 3 m and were not acoustically isolated from one another at any time. Generations were designated the terms ‘F1’, ‘F2’, etc; the term ‘F1’ refers to the first filial generation of two separate breeding lines. The term ‘F2’ refers to the second filial generation produced by crossing two unrelated F1 animals. Litter 1 contained a total of six F2 generation pups (n_{male} = 4; n_{female} = 2) housed with three adult female degus (one lactating mother and two directly related non-lactating females). Litter 2 contained a total of seven F1 generation pups (n_{male} = 2; n_{female} = 5) housed with four adult female degus (one lactating mother and three directly related non-lactating females). Litters 3 and 4 the following season consisted of a total of ten F2 generation pups (n_{male} = 2; n_{female} = 8) housed with one lactating mother and two directly related non-lactating females (the three litter 4 pups were cross-fostered within 48 hours post partum due to maternal complications). All litters were distantly related through the dam/sire line of litter 2, except for litters 1 and 3, which were directly related (i.e. had the same mother and father).

Recordings were taken at random intervals by the author from a distance of approximately 1 m. Colony degus were all familiar with the author, a person who was well tolerated by the mothers around the pups. Pups were accustomed to the presence of the author as they were checked and weighed daily as part of the routine health monitoring of the litters. Pups did not show indicators of distress such as fleeing, hiding or freezing during recordings. Due to the large size of data files and high sample rate, only short segments (around 30 seconds per recorded unit) could be captured at a time, so recordings were made only while pups were vocalising. Recording equipment consisted of an M-Audio (Avid Technology, Inc.) MicroTrack 24/96 professional 2-channel mobile digital recorder connected via a ¼” TRS port to a Vivanco EM216 microphone. The microphone was optimised for 14 kHz, but was tested with the digital recorder, using a tone generator, to be capable of detecting frequencies between 500 Hz - 48 kHz with an accuracy of ±251 Hz. All recordings were saved to the digital recorder directly in 24-bit mode, at a sample rate of 96 kHz, in uncompressed (.wav) format so as to eliminate any possible data compression effects. The recorded frequency range capability was 20 Hz – 48 kHz. In addition, a calibrated, flat response GRAS Sound and Vibration 40BF ¼” free field microphone, connected to a National Instruments USB6251 DAQ card, was also used for recording purposes. Audio data were saved, uncompressed, directly to a PC in .wav format using MatLab at a sample rate of 200 kS s^{-1}. The recorded frequency range capability was 4 Hz – 100 kHz.

During data collection, the litter number, age range and behavioural context at the time of vocalisation were noted. Microphones were positioned 0.3 – 1 m from the source, and only vocalisations produced from pups of the litter proximal to the microphone were included in analysis. In season 1, pups were divided into five age categories; <1 week, 1-2 weeks, 2-3 weeks, 3-4 weeks and 5-6 weeks. Due to technical complications, data for pups 4-5 weeks old were unable to be included. Due to availability of equipment, data in season 2 were only collected from pups in the 2-3 week old age range and used to compare to recorded data from other pups in this age range. The behavioural context was similarly divided into five broad categories, including ‘receiving care/grooming’, ‘approach of lactating female’, ‘separation/isolation’, ‘in nest (other)’ and ‘out of nest (other)’. All behavioural contexts arose naturally in the colony environment (i.e. the animals were not experimentally manipulated).

Stored audio .wav files were reviewed for presence of pup vocalisations and each ‘loud whistle’ call (as classified by Long (2007) [11]) was analysed using Adobe Audition 1.0 in order to obtain values for maximum frequency (F_{max}), minimum frequency (F_{min}), duration of call, number of harmonics and overall frequency modulation. Frequency modulation was determined by assessing the start, middle and end frequencies of the call. For example, if the start frequency was notably higher than the middle or end frequencies, the call had negative modulation (the reverse is true for positive modulation). Frequencies containing the most energy were investigated by performing a Fast Fourier Transform on vocalisations. Frequency values were subject to a small software error of ±39 Hz for 96 kHz files, and ±82 Hz for 200 kHz files. Data were analysed by one-way ANOVA using the GLM module of Statistica 5.1 (Statsoft, Inc.). Dependent variables (F_{max}, F_{min}, duration, number of harmonics, modulation) were examined for significant variation with pup age, behavioural context and litter sample (independent variables).

4 RESULTS

A total of 1053 ‘loud whistle’ events were analysed. Pups produced ultrasonic harmonics in their ‘loud whistle’ vocalisations up to 61.6 kHz. Typical parameters were between 3 – 40 kHz, containing 12 unmodulated harmonics, with duration 0.15 s. Most energy was contained in the 10 kHz region (± 4.9 kHz). An example sonogram is provided in Figure 1.

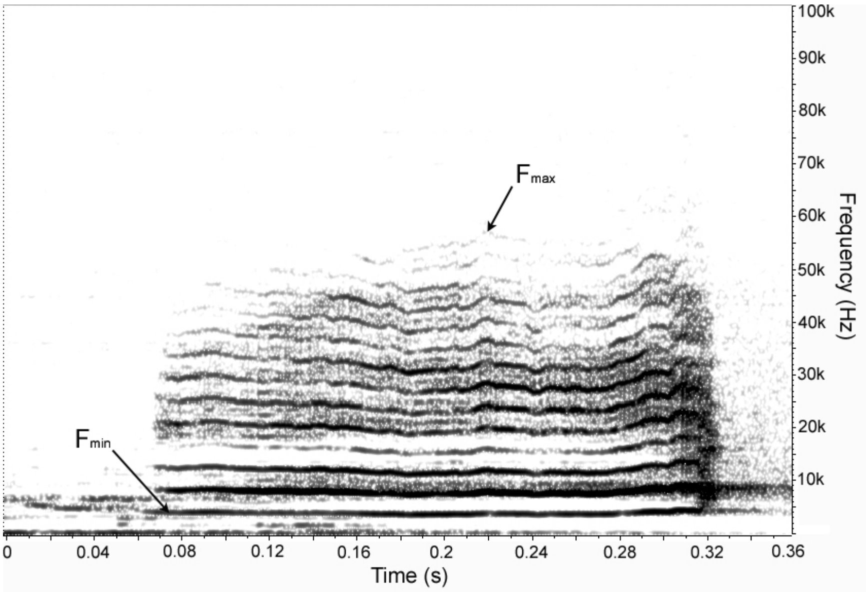

Figure 1: Example sonogram of a ‘loud whistle’ vocalisation produced by a pup of age 3-4 weeks. This sample was recorded with the GRAS microphone and DAQ card combination (range 4 Hz – 100 kHz). Arrows indicate F_{max} and F_{min}. Windowing: Blackmann-Harris, 512 band resolution.

4.1 EFFECT OF PUP AGE ON ‘LOUD WHISTLE’ PROPERTIES

Data for pups of the same age range were collated and compared to the same sample of pups at other age ranges. Pup age had a significant effect on F_{max} ($p<0.0005$; $F_{[4,995]} = 22.18$), F_{min} ($p<0.0005$; $F_{[4,995]} = 130.38$), call duration ($p<0.0005$; $F_{[4,995]} = 69.69$), number of harmonics ($p<0.0005$; $F_{[4,995]} = 150.83$) and frequency modulation ($p<0.0005$; $F_{[4,995]} = 10.09$). Pups aged 3-4 weeks had a significantly higher F_{max} than pups aged <1 week to 2-3 weeks ($p<0.05$; $F_{[1,484]} = 5.96$), while pups aged <1 week had a significantly lower F_{min} than pups aged 1-2 weeks to 5-6 weeks ($p<0.0005$; $F_{[1,486]} = 99.43$). Significantly longer call durations were observed in pups of ages 2-3 weeks ($p<0.0005$; $F_{[1,306]} = 45.68$) and 5-6 weeks ($p<0.0005$; $F_{[1,304]} = 34.87$) than other ages. Pups aged <1 week produced calls with significantly more harmonics than pups of other ages ($p<0.0005$; $F_{[1,486]} = 37.01$). The overall most common modulation type was ‘flat’ (unmodulated) for all age ranges.

4.2 EFFECT OF BEHAVIOURAL CONTEXT ON ‘LOUD WHISTLE’ PROPERTIES

Behavioural context had a significant effect on F_{max} ($p<0.0005$; $F_{[4,995]} = 6.38$), F_{min} ($p<0.0005$; $F_{[4,995]} = 62.02$), call duration ($p<0.0005$; $F_{[4,995]} = 30.42$), number of harmonics ($p<0.0005$; $F_{[4,995]} = 82.22$) and frequency modulation ($p<0.0005$; $F_{[4,995]} = 10.23$). Calls produced during entry of a lactating female into the nest had a significantly lower F_{max} than calls produced during separation ($p<0.05$;

$F_{[1,389]} = 7.42$), while calls produced during grooming had a significantly lower F_{min} than those produced during approach of a lactating female ($p<0.0005$; $F_{[1,345]} = 72.85$). Calls produced during separation and out of the nest (other) had a significantly longer duration than those produced in the other contexts recorded ($p<0.005$; $F_{[1,300]} = 10.86$). Calls produced during grooming and approach of a lactating female had significantly more harmonics than those produced in the other contexts recorded ($p<0.0005$; $F_{[1,329]} = 13.97$). Figure 2 shows the variation in the behavioural contexts in which 'loud whistles' were used with pup age.

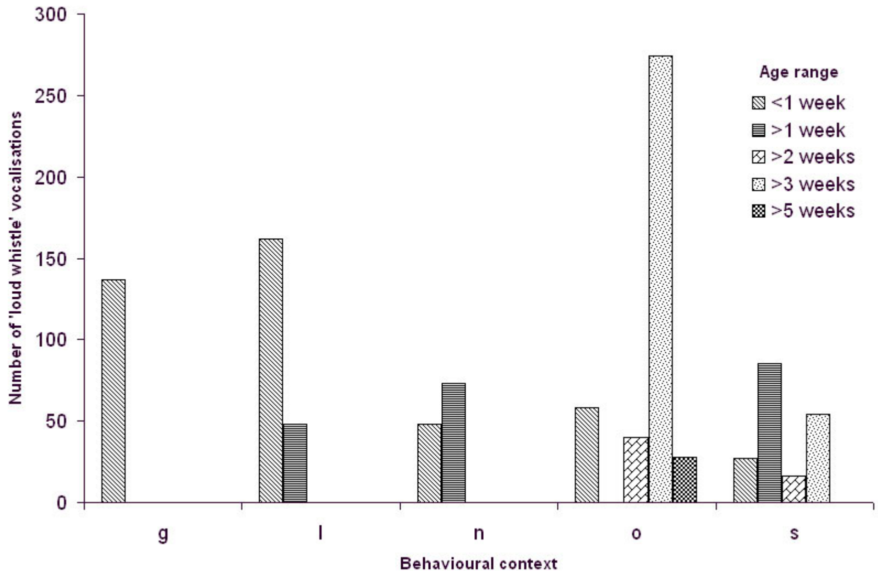

Figure 2: Variation in the behavioural context of 'loud whistle' vocalisations with pup age range. Contexts include receiving grooming from an adult (g), entry of a lactating female into the nest (l), in nest (other) (n), out of nest (other) (o) and separation/isolation (s).

4.3 EFFECT OF LITTER SAMPLE CONTEXT ON 'LOUD WHISTLE' PROPERTIES

Data for pups from different litters were collated and matched for age. Litter sample was found to have a significant effect on F_{min} ($p<0.0005$; $F_{[1,998]} = 233.25$), call duration ($p<0.0005$; $F_{[1,998]} = 16.32$), number of harmonics ($p<0.0005$; $F_{[1,998]} = 371.14$) and frequency modulation ($p<0.0005$; $F_{[1,998]} = 35.08$). Pups in litter 1 produced significantly lower F_{min} than litter 2 and produced significantly longer calls. Litter 1 also produced calls with significantly more harmonics than litter 2. At 3-4 weeks old and with behavioural context 'out of nest (other)', significant variation was also found in both the F_{max} ($p<0.05$; $F_{[1,35]} = 4.35$), F_{min} ($p<0.005$; $F_{[1,35]} = 14.05$), number of harmonics ($p<0.0005$; $F_{[1,35]} = 15.01$) and duration ($p<0.05$; $F_{[1,35]} = 8.99$) of directly related litters 3 and 1. Pups in litter 3 produced significantly higher F_{max}, lower F_{min}, significantly more harmonics and shorter calls than litter 1.

5 DISCUSSION

While it is clear that degu pups do include ultrasonic harmonics (above 22 kHz) in their 'loud whistle' vocalisations, it is not currently obvious whether the inclusion of ultrasound is intentional (i.e. for a specific behavioural reason), or simply as a function of the small size of the pups' larynx and underdevelopment of the vocal cords (particularly since most of the energy is contained around the 10 kHz region). It is apparent that many features of this vocalisation are linked to pup age (and therefore size), in particular, the effect of age on call duration may be explained by the increasing lung size and capacity (as pups aged 5-6 weeks had significantly longer 'loud whistle' calls than at other ages). This, however, does not explain the finding that pups of age 2-3 weeks also had significantly longer call durations than pups of age 3-4 weeks. This may be explained by the variation in behavioural context with age (Figure 2). At over 2 weeks old, pups typically begin exploring out of the nest and away from their mother which, of the context terms used in this study, frequently gives rise to an increase in isolation/separation and out of nest (other) contexts (both of which have significantly longer durations than other contexts) than earlier ages. At over 3 weeks, pups appear to be increasingly able to find their way around the enclosure and back to the nest, which can lead to a reduction in the frequency of isolation/separation context-related 'loud whistles'. Data confirm that while 'loud whistle' calls associated with grooming, approach of a lactating female and in the nest (other) contexts were most frequently observed in pups aged <1 week and 1-2 weeks, those calls associated with isolation/separation were more common in pups of age 1-2 weeks. 'Loud whistle' calls associated with context out of the nest (other) were far more prevalent in pups of age 3-4 weeks, and at age 5-6 weeks this was the only context associated with 'loud whistle' samples. It can be hypothesised that the longer duration of care-eliciting calls in isolation/separation contexts and in situations unfamiliar to the pups in the first few weeks of life reflect the degree of need the pups have for adult attention. It may also be speculated that, since the pups may be at a greater distance than normal from a care-giving adult at the time of vocalisation in these contexts, it increases the chance that a nearby adult will be able to detect and locate the pup from its call, and according to the motivation-structure rules of Morton (1977) [16], the inclusion of higher frequencies are more likely to attract adult attention. This may therefore explain why calls produced during separation/isolation have a significantly higher F_{max} than other contexts requiring care from an adult. However, it must also be considered that higher frequencies are more readily attenuated (particularly inside a burrow environment [17]), which is just such an environment where pups of this age are likely to spend the majority of time [10].

The variations in F_{min} and number of harmonics between behavioural contexts are interesting to note. Although the upper limit of adult degu hearing is currently unknown, it is hypothesised that adult degus are able to detect these variations in minimum frequency (at around 3 kHz) as they lie within the adult vocal communication range (71 Hz – 22 kHz [11]). In addition, the similarity of the degu middle ear to other caviomorph species [12] suggest it may have a similar hearing range; the guinea pig (*Cavia porcellus*) has a hearing range of 86 Hz – 46.5 kHz (at 50 dB SPL) [18], while the chinchilla's range (at 60 dB SPL) extends from 50 Hz – 33 kHz [19]. This might indicate that adult degus are able to distinguish between the care needs of pups using 'loud whistles' in various contexts based on the length, minimum frequency and the number of harmonics in the call. Since significant differences in call qualities were also observed between litter samples, it is further possible to speculate that adult degus may be able to discriminate between the 'loud whistles' of their own pups, and the 'loud whistles' from pups of other litters. Since degus are well known for their communal nesting habits, the benefit of adults being able to distinguish one litter from another is clear (note that mother degus have previously been found to distinguish odours of their own pups and those of another female [20], but do not discriminate between pups during retrieval [21]). This would prove an interesting area for further research, particularly since pups of a closely related caviomorph, the guinea pig (*Cavia aperea* f. *porcellus*), produce somewhat similar care-eliciting 'whistles' which have been found to be individually distinguishable by the mother [22], although the exact properties of the call that might allow this have not been closely examined. These guinea pig isolation calls are often referred to as a 'wheet' call and have an average duration of 0.32 s with most energy contained in the 500 Hz – 3.5 kHz region [23]. These calls have multiple harmonics but do not include anything above 10 kHz [22].

Genetic relationship did not appear to influence the structure of the 'loud whistle' calls, with pups in litter 1 (season 1) and directly related litter 3 (season 2) having significantly different qualities at 3-4 weeks old under the same behavioural context. In the case of call duration, this could be explained by a difference in pup mass; Litter 1 was found to weigh significantly more than Litter 3 at both two weeks (unpaired t-test; $t = 12.5$; $p<0.0005$) and three weeks old ($t = 14.5$; $p<0.0005$), with Litter 3 having shorter calls. This may have been due to the larger litter size for Litter 3, or to differences in the pup sex ratio. What was not tested is the similarity of 'loud whistle' qualities between pups from the same litter, which would allow assessment of the potential for individual pup recognition. It is suggested that future studies individually mark pups to aid visual identification during recording/vocalisation.

No frequencies were found to be produced by the degu pups (or the adults present during recording) between 61.6 – 100 kHz. The author therefore recommends an optimum frequency range of 20 Hz – 65 kHz be utilised for future studies recording the vocalisations of this species (particularly where pup calls are included).

6 CONCLUSIONS

The typical frequency range of the ‘loud whistle’ vocalisation, used uniquely by degu pups (aged 0 days – 6 weeks) to elicit care from an adult, was identified as 2.8 – 41 kHz, containing 12 unmodulated harmonics, with duration 0.15 s. The maximum frequency recorded was 61.6 kHz, although most energy was contained in the 10 kHz region. This provides the first documented evidence that degu pups include ultrasonic harmonics above the 22 kHz originally identified. These ‘loud whistle’ vocalisations were found to contain qualities that varied significantly between litters and with behavioural context at the time of use, suggesting that there may be potential for individual litter and context recognition by adult degus. While it appeared that some features of these calls, such as duration and minimum/maximum frequency, varied significantly with age, suggesting unintentional changes associated with pup growth and development, this could also be explained by the variation in behavioural context over time. The ideal recording range recommended for this species (particularly where pups are present) is 20 Hz – 65 kHz.

ACKNOWLEDGEMENTS

I would like to thank Drs. James Flint and Paul Lepper of Loughborough University for technical support and helpful discussion, Dr. Matthew Mason of Cambridge University and referees for useful feedback in improving the manuscript.

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