

REPRODUCTIVE VOCALISATIONS OF THE DEGU (*OCTODON DEGUS*): A COMMUNALLY NESTING CAVIOMORPH RODENT.

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1 ABSTRACT

Caviomorphs are well known for their social nature and the often wide variety of vocal sounds used in intra-species communication, making them ideal candidates for the study of vocalisations. Particular interest has previously been shown in the reproductive vocalisations of one such species, the degu (*Octodon degus*). Here I categorise and describe vocal sounds relating to reproduction in the degu, including those used by adults (post copulation; during pup care) and those used by pups (receiving care; playing; during parental separation). Of the repertoire of 15 vocal categories identified for the degu, I find that use of the four reproduction-specific categories varies significantly with season as expected in a seasonally breeding species. I identify that certain vocal categories are used uniquely by pups, and that a vocalisation used by adults relating to pup care has an alternative function than was previously hypothesised.

2 INTRODUCTION

Octodon degus are a semifossorial diurnal caviomorph rodent native to the semi-arid scrublands of central Chile. Degus are highly social species; they are known to have a complex behavioural and vocal repertoire [1, 2] and use a variety of vocalisations for intra-species communication. Despite this little research has been carried out in this area, with only a few papers outlining some of the degus reproductive vocalisations; in particular what has been referred to as the 'mothering call' [1, 2, 3, 4, 5, 6, 7, 8]. The 'mothering call' is said to be used only by the female degu during lactation/nursing [7, 8]. Poeggel and Braun [2] suggest that the 'mothering call', although highly individual between degus, does have common acoustic properties that make it easily recognisable to a pup to allow it to identify a lactating female. I recently demonstrated that the 'mothering call' is in fact a composite of two vocalisation categories used by the degu, consisting of 'trill' and 'warble' vocalisations, the former of which is specific to this call [3]. Further vocalisations relating to reproduction and pup care have been previously identified. A 'distress' call, referred to as the 'loud whistle' [3] is made by pups in the absence of their mother [1], a care-giving adult [3], or in isolation [3, 9]. Braun *et al.* [1] did not determine whether this vocalisation was specific to pups, nor provide a sonogram or detailed analysis of these calls. Male degus are also reported to use a post-copulatory call, referred to as the 'bark' [3]. This is known to be a common occurrence among hystricomorph rodents [9]. Details relating to the specific structure, causation and function of the reproductive vocalisations of the degu have yet to be comprehensively outlined. Degus are seasonal breeders both in the wild [13] and in captivity [14], so reproductive vocalisations are expected to coincide with this period.

3 METHODOLOGY

A sample of eleven adult and six juvenile degus, and a collection of pups, were used in this study. The adult group consisted of both male (n=5) and lactating and non-lactating female (n=6) degus, the juvenile group also contained males (n=2) and females (n=4). The juveniles were aged between

7-58 weeks old during the study (degus over 58 weeks old are classed as adult [10]), with adults in the age range of 59 weeks up to 7 years. Several litters of pups (n=21) were also used consisting of both males and females. During pup vocalisation it was not possible to identify pup sex without manual intervention. In this study 'pups' were defined as being aged 0 days up to 6 weeks old as weaning typically occurs when pups are 4-6 weeks old [11, 12]. Degus were divided into colonies of either sex-segregated groupings or mixed sex groupings, with a maximum colony size of 5 individuals (not including pups).

Using a Sharp® MDMS702H2 MiniDisc recorder and Vivanco® EM216 digital microphone, recordings were taken of the vocalisations from all degus in the sample (in an environment familiar to them) over a period of 36 months. After each vocalisation the time, degu ID and behaviour at the time of vocalisation were noted, except in the case of pup vocalisations where individual identification was not possible. In all cases the microphone was held within a metre from the source, and background noise was kept to a minimum. The recorded frequency capability was 20-22050 Hz with a sampling frequency of 44.1 KHz. The microphone had an optimised frequency range of 20-16000 Hz. Data was collected by the author; a person with whom the degus were all familiar so that their presence would be unlikely to affect the results. All vocalisations recorded were produced voluntarily by the degus; observations and recordings took place in each degu's captive housing.

The recorded sound files were transferred onto PC via a datalink cable and saved in .wav format. Each sound file was converted into a FFT spectrograph with Hann windowing using Alien Connections® Pristine Sounds 2000 software, and then cleaned to reduce background noise. Cleaning was performed using the Image Noise Suppression feature of Pristine Sounds, whereby a section of the sound clip, containing white noise only (i.e. no vocal sounds), was selected and scanned by the software. The noise was then processed at a strength of 15% (maximum 200%) for each of the four set frequency bands (>5 kHz; 1-5 kHz; <1 kHz; 0-50 kHz) with overwork protection. Each file was cleaned only once before analysis. Recorded vocalisations were grouped into general categories based on spectrographic appearance and behaviour at time of use. Each category was given a name chosen to represent the sound's profile, rather than basing the name on a behavioural association. This scheme is therefore extensible if any other behaviours are found to be associated with the sound at a later date. Categories were identified as being specific to reproduction if they occurred either during, or shortly before or after reproductive behaviours, such as after copulation, giving pup care, or pup-specific sounds. The parameters for each vocalisation were then analysed to establish minimum frequency, maximum frequency, harmonic quality and frequency modulation. The duration of each call and number of units used in succession were also determined.

4 RESULTS

In total, 1648 reproduction-specific vocalisations were recorded and analysed. Of the 15 vocal categories used by the degu [3], four were found to be directly related to reproduction. All reproductive vocalisations were recorded from November to April (recordings were taken throughout the 36 month duration), which corresponds to the breeding season of captive degus in the UK. A detailed description of these four vocal categories, using their profile and expression, is provided. The likely function of each vocalisation is deduced based on their behavioural context and effect on other degus in hearing range. Example sonograms are provided in Figure 1, the four vocalisations have been divided according to 'pup' or 'adult' usage with a common timescale to facilitate comparison. Table 1 provides a summary of recorded samples according to vocal category and behavioural context.

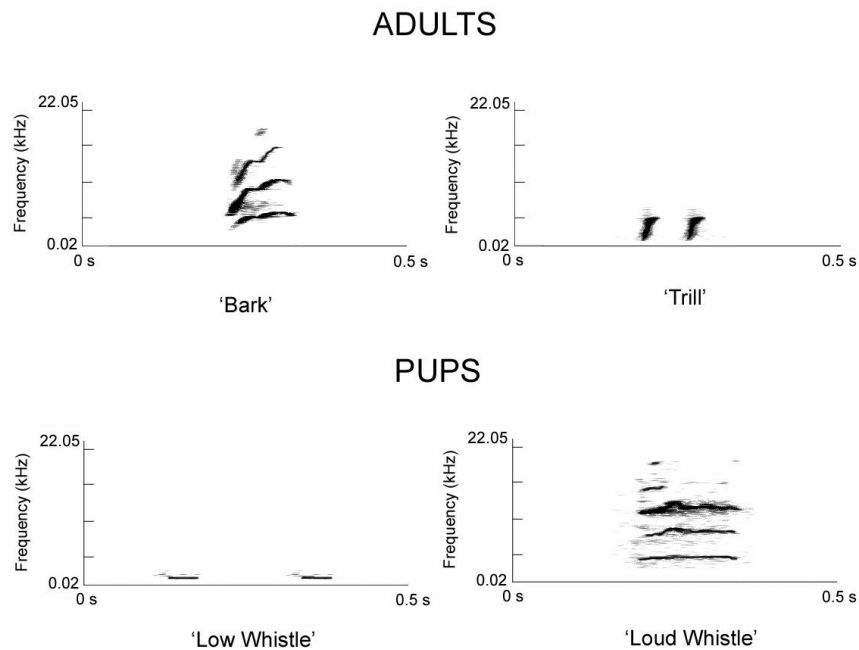


Figure 1. Example sonograms of the four reproductive vocalisation types identified. Frequency range of all sonograms 0.02-22.05 kHz; lines represent 5 kHz increments. Vocalisations inserted into a sonogram of fixed duration to produce a standardised total duration of 0.5 seconds. Note that the 'trill' is displayed as one part of the composite 'mothering call' (i.e. does not include the 'warble' portion [3] which is not specifically related to reproduction).

Vocalisation Category	Bark	Trill	Loud Whistle	Low Whistle
Context				
Playing with familiar conspecific (pup)	-	-	45	35
Suckling (pup)	-	-	7	192
Parental separation/isolation (pup)	-	-	21	89
Pup care (adult)	-	412	-	-
After mating attempt (adult)	847	-	-	-

Table 1. Number of recordings made in each reproduction-related vocal category during specific behavioural events.

Bark

Profile- A loud, repetitive sound of average duration 0.125 ± 0.03 s. This vocalisation has a mean highest frequency of 15.8 ± 2.0 kHz and a mean lowest frequency of 2.8 ± 1.1 kHz, consisting typically of 3 harmonics with positive-negative modulation (24.1%). Most commonly used 11+ times in succession (but use ranged from 6 to 20+ times in succession in this study), it can be used exclusively for periods of up to 60 minutes.

Expression- Usually vocalised with an open mouth and pinning back of the ears. With regard to reproduction, it is used by adult males after mating, but may have other uses relating to environmental concern^[3]. Not turned toward conspecific during vocalisation.

Effect- Increased vigilance and silence of conspecifics within auditory range.

Likely function- In the case of males post copulation this is likely to serve as a territorial warning directed toward other males.

Trill

Profile- A soft, repetitive sound of average duration 0.027 ± 0.008 s. This vocalisation has a mean highest frequency of 4.1 ± 0.8 kHz and a mean lowest frequency of 1.3 ± 1.1 kHz, consisting of a positively modulated fundamental frequency (100%). Most commonly used 5 times in succession (but use ranged from singular to 20 times in succession in this study), it is usually followed by 'warble' and 'whine' vocalisations [3].

Expression- No obvious outward physical characteristics. Turned toward pups during vocalisation. The 'trill' is used exclusively by both lactating and non-lactating adult females during pup nursing and care.

Effect- No obvious effects are visible.

Likely function- Not currently known; may have a neurological effect on the pups.

Loud Whistle

Profile- A loud sound of average duration 0.225 ± 0.11 s. This vocalisation has a mean highest frequency of 15.1 ± 3.4 kHz and a mean lowest frequency of 1.8 ± 0.8 kHz, consisting typically of 4 unmodulated harmonics (23.3%). Most commonly used 2 times in succession (but use ranged from singular to 5 times in succession in this study), it is often interspersed with 'low whistle' vocalisations.

Expression- Usually vocalised with an open mouth, not turned toward conspecific during vocalisation. Used exclusively by male and female pups whilst playing away from the nest with a littermate or during parental separation/isolation. Its use decreases until pups are roughly two weeks old.

Effect- May stimulate retrieval and return to nest of the subject by parental conspecific.

Likely function- Used to promote care and protection of the subject from potential danger.

Low Whistle

Profile- A soft sound of average duration 0.094 ± 0.06 s. This vocalisation has a mean highest frequency of 3.4 ± 2.0 kHz and a mean lowest frequency of 1.1 ± 0.4 kHz, consisting typically of an unmodulated fundamental frequency (37.3%). Most commonly used 3 times in succession (but use ranged from singular to 15 times in succession in this study), may be interspersed with 'whine' vocalisations.

Expression- No obvious outward physical characteristics. Usually directed toward conspecific during vocalisation. Used exclusively by male and female pups more or less continuously from birth, most commonly during pup care and during isolation. Its use decreases until pups are roughly two weeks old.

Effect- No visible outward effect.

Likely function- Possibly aids location of pups and the nest by parents and conspecifics, since degus nest communally [15].

5 DISCUSSION

The results of this study can be tied in with the previous results of other studies to give some interesting findings.

The 'mothering call' initially outlined in Braun and Scheich [7] could be evaluated based on the sonogram and behavioural context provided in their paper. It can be seen that this 'mothering call' is actually composed of two vocalisation types given in close succession; the 'trill' and the 'warble' [3], the former of which is unique to this call. Braun and Scheich suggest that this sound (sequence) is made exclusively by lactating females, to allow pups to identify them. Here it was determined that the 'mothering call' (a combination of 'trill' and 'warble' vocalisations) is used by both lactating and non-lactating female degus when nursing, grooming or cleaning pups. This indicates that the

composite 'maternal call' may not be used for identification by pups, but could have some other function derived from its "soothing effect" (for example that outlined by Ziabreva *et al.* [4]).

The use of the 'bark' after mating attempts or successful copulation made it possible to assume it analogous to the 'post copulatory cry' outlined by Eisenberg [9]. While the duration of the 'bark' was found to be similar (0.125 s and 0.143 s respectively), Eisenberg's dominant frequency figure of below 5 kHz fell slightly beneath this study's findings of dominant frequencies around 5-6 kHz. Since Eisenberg used only a few recorded samples, this could reflect slight individual variations unique to each degu, which would be a useful feature if the hypothesis that this is a territorial call is correct. This may also be suggested by the appearance of two lowest frequency distribution peaks in the data, which could be further investigated in future studies. It is also interesting to note that the 'bark' is not specific to reproductive behaviours [3], or even male degus [3], but by far the most common usage is post copulation.

The 'loud whistle' was found to be analogous to the 'distress whistle' [1] or 'isolation call' [9] in the sense that it is used exclusively by pups in several behavioural contexts, including in response to parental separation/isolation. This study's 'loud whistle' frequency range and duration correlated with the findings of Braun *et al.* [1]; however the data given by Eisenberg [9] appeared to correlate more closely with the data for the 'low whistle' vocalisation identified in this study, which is used by pups even when suckling from their mother in the nest. The 'low whistle' is the vocalisation used most frequently by pups in a variety of behavioural contexts, meaning it was recorded more frequently by this study, while the 'loud whistle' was identified as being some form of distress call intended for parental/care giving conspecifics. Interestingly, the 'loud whistle' was found to be used more frequently by pups during play with a conspecific than during isolation, but this may be due to the fact that play behaviour is far more commonly observed than parental separation or isolation in the captive environment. Why pups use the 'loud whistle' during play, a normally pleasurable experience, is not clear; a possible explanation may be that some (particularly very young) pups find rough play with littermates stressful, or that they become cold quickly during play outside the nest away from a care giving adult.

It is worth noting that the relatively high maximum frequency of the 'loud whistle' and the interesting sonographical properties may indicate an ultrasonic component to this vocalisation in the degu. This was briefly tested with an ultrasound detector with positive initial results. The possible use of ultrasound by pups has interesting implications regarding the hearing range of the adult degu, which has yet to be investigated.

6 CONCLUSIONS

In this study I identified and described in detail the four vocalisations of the degu related to reproduction, providing a much needed reference point for future studies in this area. Of the four, two were found to be used exclusively by pups, and two by adults. The use of reproductive vocalisations varied with season, as expected in a seasonally breeding species. The vocalisations used by lactating mothers were found to have a less clearly defined role than was hypothesised in a previous study. Detailed analysis has shown that vocalisations such as the 'loud whistle' could contain ultrasonic elements. Thus, the role of ultrasonics needs to be addressed in future research, as well as a detailed test of the degu's exact hearing range. Aspects of individuality to vocal categories such as the 'bark' could also be explored in future studies.

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