

Bioacoustics

The International Journal of Animal Sound and its Recording, 2007, Vol. 16, pp. 223–244

0952-4622/07 \$10

© 2007 AB Academic Publishers

VOCALISATIONS OF THE DEGU *OCTODON DEGUS*, A SOCIAL CAVIOMORPH RODENT

C.V. LONG*

Dept. Electronic and Electrical Engineering, Loughborough University, Loughborough LE11 3TU, UK

ABSTRACT

Caviomorph species are well known for their social nature and variety of vocal sounds used in intra-species communication, making them ideal candidates for the study of vocalisations. Here, I provide a much needed categorisation for one such species, the Degu *Octodon degus*. By analysing 3535 vocal sounds, I demonstrate that there are 15 distinct categories for degu vocalisations, showing that degus have a wider and more complex vocal repertoire than was previously assumed. I find that the use of vocal sounds varies widely with season and behavioural context, consistent with interaction in a complex social hierarchy. I identify that certain categories are not used by pups and that others may be gender-specific. In addition, I find that vocalisations used by lactating females may have an alternative function to that previously assumed. By examining the frequency range of the vocalisations identified, I predict that the hearing range of the degu lies between 71 Hz to 21.7 kHz. Finally, I describe the structure, causation and likely function of each vocal type.

Keywords: *Octodon degus*, vocalisation, communication, caviomorph species, vocal behaviour.

INTRODUCTION

Octodon degus is a semifossorial diurnal caviomorph rodent native to the semi-arid scrublands of central Chile. In the wild, degus live in structured social groups of 1-2 males and 2-5 females (Fulk 1976). Degus are known to have a complex behavioural and vocal repertoire (Braun *et al.* 2003; Poeggel & Braun 1996) and use a variety of vocalisations for intra-species communication. Some of the more common vocalisations observed include an 'alarm call' (Shelley & Blumstein 2004; Fulk 1976; Yáñez 1976; Eisenberg 1974), a 'protest squeak' and 'protest growl' (Eisenberg 1974), a 'squeal' (Eisenberg 1974), a 'post-copulatory call' (Eisenberg 1974), a 'mothering call' (Braun & Scheich 1996) and a 'distress whistle' (Braun *et al.* 2003; Eisenberg 1974). The variety of behavioural contexts in which

*E-mail: degutopia@btinternet.com

these vocalisations occur are known to include warning others of unpredictable events, aggression between conspecifics, contact between adults, isolation of pups, playing in pups/juveniles (Poeggel & Braun 1996), 'aroused but not frightened' and post copulation (Eisenberg 1974). Further details are unclear and specific vocalisation categories are largely undefined.

Although vocal communication is frequent in this social caviomorph, little research has been carried out to formally characterise the acoustic properties, with the exception of the most "distinctive and specific" vocalisation of the degu, the 'mothering call' (Braun *et al.* 2003; Ziabreva *et al.* 2003a; Ziabreva *et al.* 2003b; Braun & Poeggel 2001; Braun & Scheich 1996; Poeggel & Braun 1996; Braun & Scheich 1991). The 'mothering call' is said to be used only by the female degu during lactation/nursing (Braun & Scheich 1991; Braun & Scheich 1996). Poeggel & Braun (1996) 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, and may have a soothing effect. This vocalisation, however, was not analysed in detail by Poeggel & Braun. A 'distress whistle' is made by pups in the absence of their mother (Braun *et al.* 2003). Braun *et al.* (2003) suggest that such 'distress calls' are frequency modulated whistle sounds, between 2-8 kHz, with an average duration of 0.2-0.4 seconds per call. Braun *et al.* (2003) did not determine whether this vocalisation was specific to pups, nor provide a sonogram or detailed analysis of these calls. It has been suggested that "young degus" exposed to a novel environment decrease the use of the 'distress whistle' after the fourth or fifth day of exposure (Reynolds & Wright 1979), but the circumstances of 'distress whistle' use, or the age of the degu studied was not tested. Eisenberg (1974) identified pup 'isolation calls' as being of duration 0.085-0.165 seconds, with "emphasised frequencies" of 1.2 and 2.8 kHz. While Eisenberg only used a small sample size of recordings, some parameters of other vocalisation types were given, including 'warning squeak' (0.07 seconds; 12-24 kHz), 'protest squeak' (0.23-0.48 seconds; 2-4 kHz), 'protest growl' (0.69 seconds; <4 kHz), 'cluck' (0.017-0.046 seconds; 2 and 4 kHz), 'post-copulatory cry' (0.143 seconds; <5 kHz) and 'pup gurgles' (0.042-0.086 seconds; 0.9-3.4 and 3.5 kHz). Similar studies on other caviomorphs show that the guinea pig *Cavia porcellus* also has pups that emit a 'distress whistle' (Monticelli *et al.* 2004). Monticelli *et al.* determined that these whistles were used uniquely by guinea pig pups when isolated from their mother and/or siblings. The guinea pig 'distress whistle' was characterised by short, high-pitched pulses, with a broadband frequency spectrum given in fast, repetitive sequences. Whistles were of (sequence) duration 17 to 22 seconds, had distinct harmonic quality (up to five harmonics in each segment of the call), a dominant frequency of around 6 kHz and a

mean frequency of 3 kHz. Monticelli *et al.* concluded that the 'distress whistle' in guinea pig pups was similar in structure to distress or isolation calls of other species, and may be interpreted as indicating to conspecifics that the individual is fearful and not hostile. Whether the function of the guinea pig 'distress whistle' is analogous to the function of the 'distress whistle' used by degu pups is currently unknown, but it appears to be within the frequency range described by Braun *et al.* (2003). With respect to the complete range and classification of vocalisations used by guinea pigs, a comprehensive study was completed by Berryman (1976). Berryman used a sample of 150 adult and juvenile guinea pigs to investigate the structure, causation and function of vocal sounds and corresponding behaviours. Sonograms of the vocalisations were produced and the physical form of the sounds analysed. It was possible to distinguish 11 call types, grouped by behaviour into 5 categories. Other studies have referred to specific "typical" guinea pig vocalisation types as 'purr', 'chutter', 'chirp' and 'whistle' (Suta *et al.* 2003).

With regard to speculated frequency ranges of degu vocalisations, it is expected to correlate with, and be within, the hearing range of the degu. Degus have a well-developed auditory bulla (Woods & Boraker 1975) and so are expected to have a broad hearing range. Again, little research has been carried out into the degu hearing range, so an initial prediction must be based on other species. The guinea pig is said to hear in the range 54 Hz to 50 kHz, whilst another caviomorph, the chinchilla *Chinchilla lanigera* has a hearing range of 90 Hz to 22.8 kHz (West 1985).

The full extent and character of degu vocalisations is currently unknown. The purpose of this study is to produce a similar categorisation to that carried out on guinea pigs by Berryman (1976), but specific to degu vocalisations. Such a classification would provide a valuable and much needed information resource for future studies in this area. In establishing a method for grouping/classifying vocalisations, it is necessary to determine common values such as minimum frequency, maximum frequency, duration, repetition and harmonic quality. The behaviour exhibited at the time of vocalisation is also an important factor in such classifications. In this paper I aim to establish such values and will categorise the degu's standard vocabulary.

METHODS

Animals

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, with adults in the age range of 59 weeks up to 7 years. The adult-juvenile age limit was chosen as 58 weeks for several reasons: firstly that other studies have classed degus of a similar age as adult (e.g. 53-57 weeks (Ebensperger 2001; Ebensperger & Caiozzi 2002); secondly, that degus around 52 weeks old may still be undergoing neurological development (Lee *et al.* 2004); and thirdly, that juvenile degus do not reach full body mass until they are between 40-76 weeks old (Degutopia (2004-2007) unpublished data). 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 (Novak 1999; Woods & Boraker 1975). All animals were bred in captivity for at least two traceable generations from eight original degus obtained from private individuals around the UK. Degus were divided into four colonies with a maximum colony size of 5 individuals (not including pups). Colony 1 consisted of 2 original female littermates and 1 F₁ daughter; colony 2 consisted of 3 original female littermates and 2 F₁ daughters; colony 3 consisted of 2 original male littermates and colony 4 consisted of 1 original male individual and 2 F₁ sons. All colonies were sex-segregated except for colonies 1 and 3 during breeding season each year (November-April), when one original male from colony 4 joined colony 1, and one original female from colony 2 joined colony 3.

Location

Degus were kept in a private collection, with each colony housed in the same room of approximate dimensions 4.0 × 4.0 × 3.0 metres (length, width, height). Each colony was housed in a wire mesh cage of dimensions 45 cm wide × 75 cm long × 100 cm high. For the duration of the study, colony cages were positioned at each end of the room in pairs, such that colonies 1 and 4 were placed together adjacently at one end, colonies 2 and 3 placed together adjacently at the other end, with roughly 1.0 metre between pairings. The reason for pairing colonies in this way was to allow breeding males and females to interact without direct contact, as female degus are induced ovulators (Weir 1974).

Data collection

Using a Sharp MDMS702H2 MiniDisc player and Vivanco EM216 microphone, recordings were taken over a period of 36 months of the vocalisations from all degus in the sample in an environment familiar to them. This was done at random intervals so as to avoid bias that may be caused by time of day or season. 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. 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 and were considered to represent a typical range of daily vocal communication from the sample. Observations and recordings took place in each degu's captive housing. Since the animals were kept in a private collection where breeding took place, some behavioural contexts need further clarification as follows:

- (a) Physical separation of observable conspecific – a cage mesh created a barrier between two conspecifics. This was a function of two separate colony cages being permanently positioned directly adjacent to one another throughout the course of data collection. Animals could see, hear and smell one another but had no physical contact.
- (b) Meeting unfamiliar and dispute involving unfamiliar – a degu from a different colony group was allowed to freely approach the subject degu. This context occurred only during breeding season (November-April) when males and females were introduced for breeding purposes.

Data analysis

The recorded sound files were transferred onto PC and saved in uncompressed .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. Since degus were not acoustically isolated at the time of recording, only vocalisations that were emitted singularly by the degu under observation were used for analysis (i.e. the spectrograph contained only the vocalisation from one degu). 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. 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.

Data compression

Data was saved to MiniDisc using ATRAC compression. All equipment was tested by recording tones of known frequency to determine the effects (if any) of this. Both the MiniDisc and MiniDisc/microphone combination were found to be accurate at detecting test frequencies of 500, 1000, 5000, 10000, 15000, 20000 and 21000 Hz with a small average error of ± 99 Hz. This value includes an error of ± 78 Hz which is a result of the accuracy of the software used for analysis.

RESULTS

In total, 3535 vocalisations were recorded and analysed. A detailed description of each vocal category, using their profile and expression, is provided below. The likely function of each vocalisation is deduced based on their behavioural context and effect on other degus in hearing range. Note that where percentage use of each vocalisation type according to degu sex and age range are given, percentages have been adjusted to take into account skew due to female bias (male $n=7$, female $n=10$). Example sonograms are provided in Figure 1, using a common timescale to facilitate comparison. Histograms of the harmonic qualities of all vocalisations are provided in Figure 2. A summary of the typical properties of each vocal category is listed in Table 1, including sample sizes, mean durations, mean maximum and minimum frequencies, mean units in succession, most common harmonic quality and most common frequency modulation, along with the type of behavioural context.

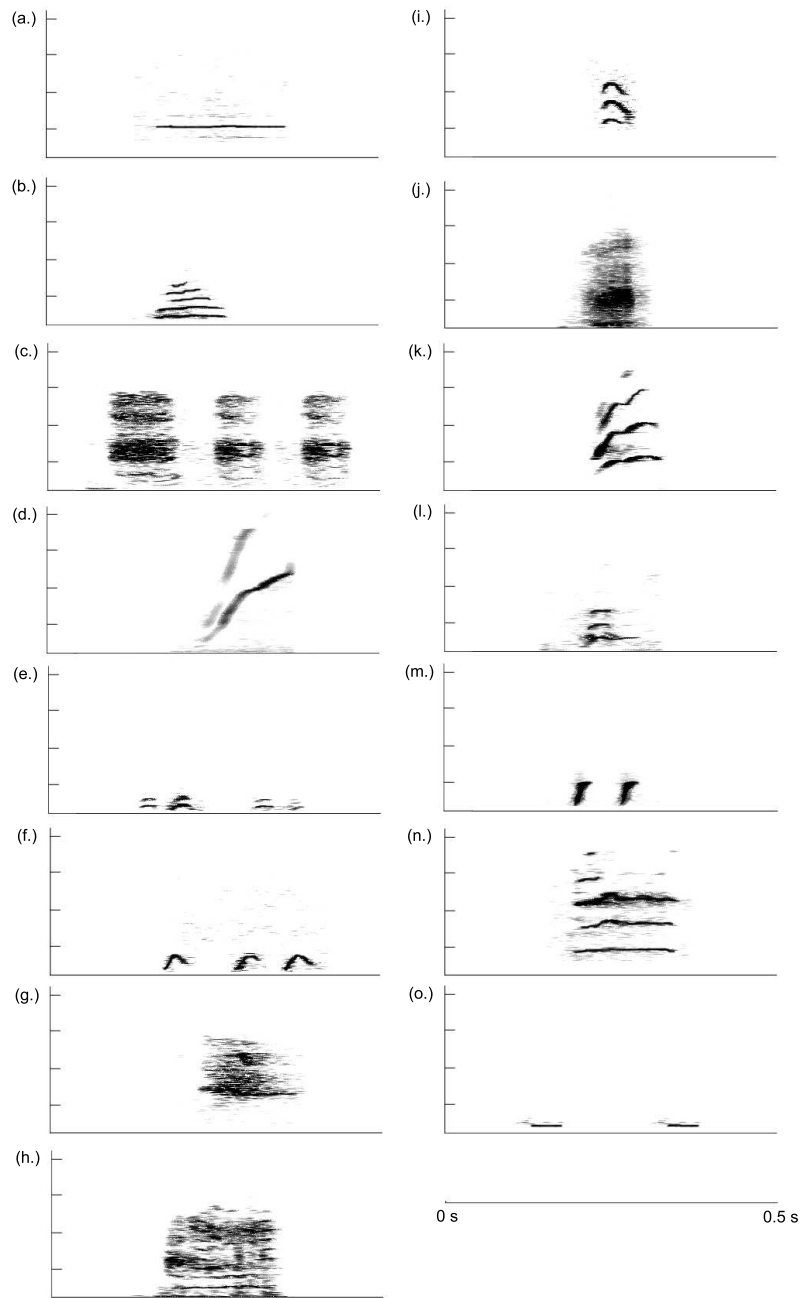
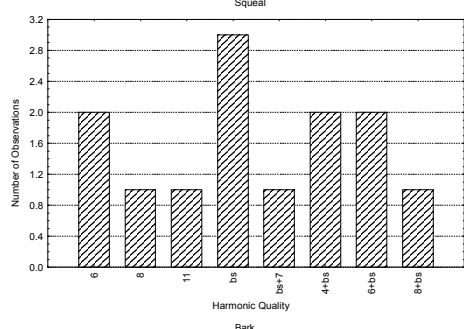
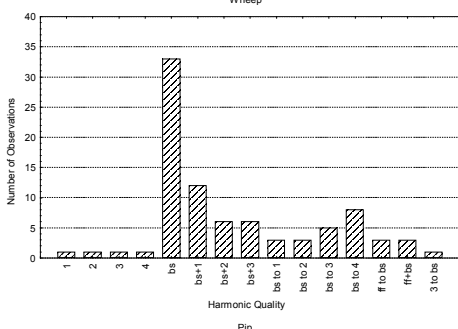
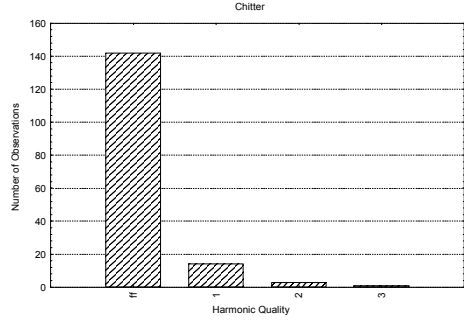
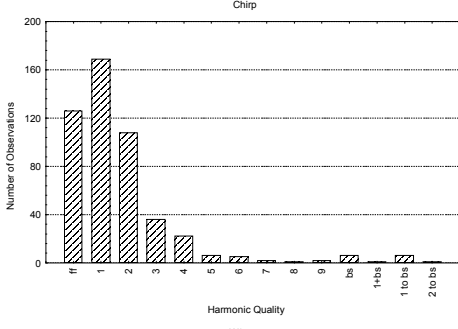
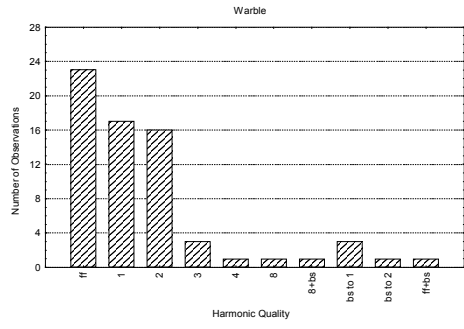
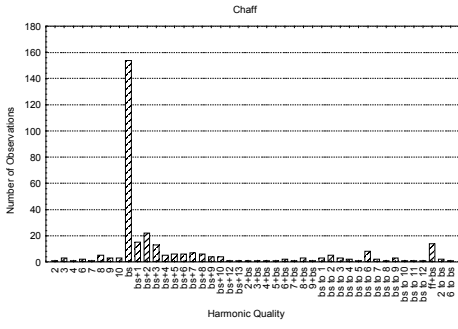


Figure 1. Example sonograms of each vocalisation type identified. Frequency range of all sonograms 20-22050 Hz; lines represent 5 kHz increments. Duration 0.5 seconds. (a) *Whine* (b) *Groan* (c) *Chaff* (d) *Warble* (e) *Chirp* (f) *Chitter* (g) *Wheep* (h) *Squeal* (i) *Pip* (j) *Grunt* (k) *Bark* (l) *Tweet* (m) *Trill* (n) *Loud Whistle* (o) *Low Whistle*.



Pip

Bark

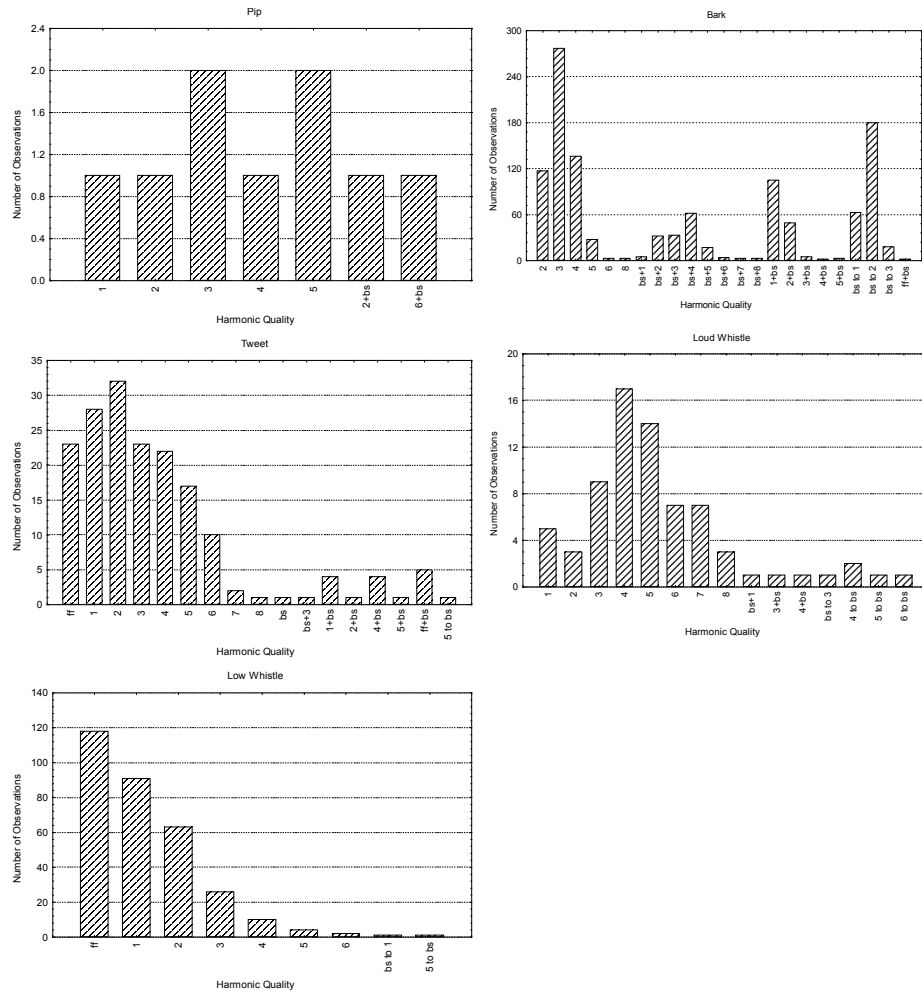


Figure 2. Histograms showing the common harmonic qualities of each vocal category (Key: *bs*- broad spectrum; *ff*- fundamental frequency; +- quality included for duration of sample; *to*- quality changes at some point in sample).

TABLE 1

Data summary for the 15 vocalisation categories identified. F_{\max} denotes maximum frequency, while F_{\min} denotes minimum frequency.

| Vocalisation category | Sample n | Mean duration (s) | Mean F_{\max} (Hz) | Mean F_{\min} (Hz) | Mean units in succession | Most common harmonic quality | Most common modulation | Behavioural context type |
|-----------------------|----------|-------------------|----------------------|----------------------|--------------------------|-------------------------------|------------------------|---------------------------|
| Whine | 228 | 0.288 | 6535 | 1775 | 1 | Fundamental frequency (28.9%) | Flat/none | Agonistic |
| Groan | 221 | 0.31 | 9156 | 761 | 1 | 4 or 5 harmonics (12.4%) | Flat/none | Agonistic |
| Chaff | 168 | 0.103 | 12051 | 2035 | 3 | Broad spectrum (47.8%) | N/a | Agonistic |
| Warble | 67 | 0.16 | 10870 | 3314 | 1 | Fundamental frequency (34.3%) | Positive | Affiliative |
| Chirp | 485 | 0.04 | 3239 | 697 | 3 | 1 harmonic (34.4%) | Positive-negative | Agonistic/ affiliative |
| Chitter | 160 | 0.03 | 3362 | 1112 | 4 | Fundamental frequency (88.8%) | Positive-negative | Affiliative |
| Wheep | 54 | 0.1 | 14891 | 4247 | 2 | Broad spectrum (37.9%) | N/a | Alarm |
| Squeal | 10 | 0.245 | 14755 | 1138 | 1 | Broad spectrum (23.1%) | N/a | Distress |
| Pip | 9 | 0.048 | 11388 | 1620 | 1 | 3 or 5 harmonics (22.2%) | Positive-negative | Affiliative |
| Grunt | 7 | 0.073 | 9839 | 416 | 3 | Broad spectrum (100%) | N/a | Agonistic |
| Bark | 1150 | 0.125 | 15797 | 2845 | 11 + | 3 harmonics (24.1%) | Positive-negative | Alarm |
| Tweet | 175 | 0.08 | 10360 | 2799 | 4 | 2 harmonics (18.2%) | Positive-negative | Agonistic |
| Trill | 412 | 0.03 | 4062 | 1268 | 5 | Fundamental frequency (100%) | Positive | Affiliative |
| Loud whistle | 73 | 0.225 | 15126 | 1834 | 2 | 4 harmonics (23.3%) | Flat/none | Distress |
| Low whistle | 316 | 0.094 | 3400 | 1118 | 3 | Fundamental frequency (37.3%) | Flat/none | Affiliative? |

Whine (Figure 1a)

Profile: A soft, drawn out sound of average duration $0.288 \text{ s} \pm 0.157 \text{ s}$. This vocalisation has a mean highest frequency of $6.5 \text{ kHz} \pm 2.9 \text{ kHz}$ and a mean lowest frequency of $1.8 \text{ kHz} \pm 1.0 \text{ kHz}$, consisting typically of an unmodulated fundamental frequency (28.9%). Most commonly used singularly (but was used up to 6 times in succession in this study) and followed by a 'groan' vocalisation.

Expression: No obvious physical characteristics but often accompanied by mildly agonistic behaviours such as forearm pushing, shouldering and back turning. Typically directed toward a conspecific. Used by males (40.8%) and females (59.2%) of all ages, most commonly during physical separation of observable conspecific (28.9%) and disputes involving food (28.5%).

Effect: Causes conspecific to back away, turn around or in some cases respond by 'whining' and shouldering or pushing.

Likely function: Mild threat or warning of further agonistic action intended to repel conspecific.

Groan (Figure 1b)

Profile: A harsh sound of average duration $0.31 \text{ s} \pm 0.171 \text{ s}$. This vocalisation has a mean highest frequency of $9.2 \text{ kHz} \pm 3.9 \text{ kHz}$ and a mean lowest frequency of $761 \text{ Hz} \pm 432 \text{ Hz}$, consisting typically of 4 and 5 unmodulated harmonics (12.4%). Most commonly used singularly (but was used up to 5 times in succession in this study) and preceded by a 'whine' vocalisation, may be interspersed with 'chirps'.

Expression: Often vocalised with an open mouth, sometimes accompanied by pinning back of ears, typically directed toward a conspecific. May be followed by threatening agonistic behaviours such as lunging, scrabbling with forepaws and boxing. Used by juvenile to adult males (30%) and females (70%), most commonly during physical separation of observable conspecific (37.8%) and disputes over food (22.7%).

Effect: Causes conspecific to move away from subject. Sometimes triggers responding 'whine' and 'groan' vocalisations, accompanied by lunging and boxing.

Likely function: Strong threat or warning of further agonistic action intended to repel conspecific.

Chaff (Figure 1c)

Profile: A rasping sound of average duration $0.103 \text{ s} \pm 0.064 \text{ s}$. This vocalisation has a mean highest frequency of $12.1 \text{ kHz} \pm 3.0 \text{ kHz}$ and a mean lowest frequency of $2 \text{ kHz} \pm 1.4 \text{ kHz}$, consisting typically of broad spectrum frequencies (47.8%). Most commonly used three times in succession (but use ranged from singular up to 15 times in succession in this study), can be interspersed with 'chirps'.

Expression: Sometimes vocalised with an open mouth, this vocalisation is often used when the subject is some distance away from a conspecific, but typically directed toward them. Used by males (7%) and females (93%) of all ages, usually during physical separation of observable conspecific (87.3%), but also when meeting an unfamiliar degu (4.5%).

Effect: Chaffs are directed toward conspecifics which are then more likely to approach the subject.

Likely function: Encourages approach (and allows subsequent investigation) of a distant conspecific.

Warble (Figure 1d)

Profile: a soft, high-pitched sound of average duration $0.16 \text{ s} \pm 0.096 \text{ s}$. This vocalisation has a mean highest frequency of $10.9 \text{ kHz} \pm 4.2 \text{ kHz}$ and a mean lowest frequency of $3.3 \text{ kHz} \pm 1.4 \text{ kHz}$, consisting typically of a positively modulated fundamental frequency (34.3%). Most commonly used singularly (but was used up to twice in succession in this study), usually preceded by another vocalisation such as the 'chitter', 'trill' or 'chaff'.

Expression: Mouth may open towards end of vocalisation, sometimes accompanied by 'tail beating'. May be directed toward a conspecific or broadcast. Used by males (6.6%) and females (93.4%) of all ages, most commonly during physical separation of observable conspecific (40.3%) and during pup care (29.9%).

Effect: Can trigger 'chittering', tail beating and sometimes 'warbling' in conspecifics within auditory range, and can stimulate play behaviour.

Likely function: May outwardly indicate emotional states such as pleasure, arousal or excitement, which could trigger reciprocal behaviours such as play.

Chirp (Figure 1e)

Profile: A sound of average duration $0.04 \text{ s} \pm 0.038 \text{ s}$. This vocalisation has a mean highest frequency of $3.2 \text{ kHz} \pm 2.0 \text{ kHz}$ and a mean lowest frequency of $697 \text{ Hz} \pm 427 \text{ Hz}$, consisting typically of a single harmonic with positive-negative modulation (34.4%). Most commonly used three times in succession (but use ranged from singular to 16 times in succession in this study) and usually mixed between other vocalisations such as the 'whine', 'groan', 'chaff' and 'tweet'.

Expression: No obvious outward physical characteristics, typically directed toward a conspecific. Used by males (26.3%) and females (73.3%) of all ages, most commonly during physical separation of observable conspecific (50.1%) and during disputes involving unfamiliar degus (14.7%).

Effect: Has no obvious effect on conspecific but may be related

to a reduced tendency toward agonistic actions.

Likely function: May discourage conspecific against taking further agonistic action against subject.

Chitter (Figure 1f)

Profile: A soft, repetitive, high-pitched sound of average duration 0.03 s \pm 0.008 s. This vocalisation has a mean highest frequency of 3.4 kHz \pm 941 Hz and a mean lowest frequency of 1.1 kHz \pm 769 Hz, consisting typically of a fundamental frequency with positive-negative modulation (88.8%). Most commonly used 4 times in succession (but use ranged from singular to 11 times in succession in this study).

Expression: No obvious outward physical characteristics but usually accompanied by conspecific nose-nose contact, nose-mouth contact and/or grooming behaviours. More frequently heard between closely bonded group members upon encounter, typically directed toward a conspecific. Used by males (33.3%) and females (66.7%) of all ages, most commonly during meeting a familiar degu (39.4%) and during physical separation of observable conspecific (25%).

Effect: Often stimulates reciprocal chittering from conspecific and further nose-nose contact or allogrooming.

Likely function: Used as a greeting and encourages social bonding.

Wheep (Figure 1g)

Profile: A loud sound of average duration 0.1 s \pm 0.029 s. This vocalisation has a mean highest frequency of 14.9 kHz \pm 2.1 kHz and a mean lowest frequency of 4.2 kHz \pm 1.2 kHz, consisting typically of broad spectrum frequencies (37.9%). Most commonly used two times in succession (but use ranged from singular to 7 times in succession in this study), it is usually followed by periods of complete silence.

Expression: Usually vocalised with an open mouth and pinning back of the ears, typically broadcast. Used by juvenile to adult males (22.8%) and females (77.2%), typically during environmental concern or alarm (98.9%).

Effect: Followed immediately by periods of silence and vigilance in the subject, all other degus in hearing range respond immediately by fleeing/hiding and/or freezing.

Likely function: Used as an alarm call to warn conspecifics in auditory range of potential or immediate danger.

Squeal (Figure 1h)

Profile: A loud sound of average duration 0.245 s \pm 0.12 s. This vocalisation has a mean highest frequency of 14.8 kHz \pm 1.7 kHz and a mean lowest frequency of 1.1 kHz \pm 1.1 kHz, consisting typically of broad spectrum frequencies (23.1%). Most commonly used singularly,

it is usually preceded by vocalisations such as the 'groan', 'whine' and 'chirp'.

Expression: Usually vocalised with an open mouth and pinning back of the ears, may be directed toward a conspecific or broadcast. Used by juvenile to adult males (35.3%) and females (64.7%), most commonly during disputes involving an unfamiliar degu (38.5%) and during physical separation of observable conspecific (38.5%).

Effect: Rapid, simultaneous movement of the subject away from the cause (most typically mouth-body contact (biting) from a conspecific).

Likely function: Probably an involuntary vocalisation as the result of a painful experience, may also alarm conspecific or predator and allow subject to escape.

Pip (Figure 1i)

Profile: A soft sound of average duration 0.048 s \pm 0.02 s. This vocalisation has a mean highest frequency of 11.4 kHz \pm 3.5 kHz and a mean lowest frequency of 1.6 kHz \pm 905 Hz, consisting typically of 3 or 5 harmonics with positive-negative modulation (22.2%). Most commonly used singularly, it is sometimes preceded by 'chitter' vocalisations.

Expression: Sometimes vocalised with an open mouth, usually during grooming by a conspecific, typically directed toward a conspecific. This study only recorded female use (100%) in pups and adults, most commonly during pup care (66.7%) and also during grooming by conspecific (22.2%).

Effect: Causes conspecific to momentarily cease grooming. Grooming may continue after vocalising.

Likely function: May serve as an indication of over-enthusiastic grooming by conspecific, as a result of mild discomfort or pain.

Grunt (Figure 1j)

Profile: A harsh sound of average duration 0.073 s \pm 0.025 s. This vocalisation has a mean highest frequency of 9.9 kHz \pm 3.5 kHz and a mean lowest frequency of 416 Hz \pm 609 Hz, consisting of broad spectrum frequencies (100%). Most commonly used 3 times in succession (but use ranged from singular to 5 times in succession in this study), it is usually followed by vocalisations such as the 'whine' and 'groan'.

Expression: Usually vocalised with an open mouth, typically directed toward a conspecific. This study only recorded use in juvenile to adult males (100%), most commonly during disputes with a familiar degu (83.3%).

Effect: Causes conspecific to move or run away from subject.

Likely function: A strong threat or warning of immediate agonistic action intended to repel conspecific.

Bark (Figure 1k)

Profile: A loud, repetitive sound of average duration $0.125 \text{ s} \pm 0.033 \text{ s}$. This vocalisation has a mean highest frequency of $15.8 \text{ kHz} \pm 2.0 \text{ kHz}$ and a mean lowest frequency of $2.8 \text{ kHz} \pm 1.1 \text{ kHz}$, 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. More frequently used by juvenile to adult males (92.1%) after mating (73.7%), but also used by juvenile to adult females (7.9%) after disputes involving unfamiliar degus (15.5%) or during environmental concern (10.9%). Typically broadcast.

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. Females may also use the call as a territorial alarm after environmental concern/disturbance.

Tweet (Figure 1l)

Profile: A sound of average duration $0.08 \text{ s} \pm 0.029 \text{ s}$. This vocalisation has a mean highest frequency of $10.4 \text{ kHz} \pm 4.6 \text{ kHz}$ and a mean lowest frequency of $2.8 \text{ kHz} \pm 1.6 \text{ kHz}$, consisting typically of 2 harmonics with positive-negative modulation (18.2%). Most commonly used 4 times in succession (but use ranged from singular to 10 times in succession in this study).

Expression: Vocalised with an open mouth, usually during physical separation of observable conspecific (81.8%) but also shortly before or during mounting of subject by conspecific (11.9%). Typically directed toward a conspecific. Used by juvenile to adult males (83.9%) and females (16.1%).

Effect: No obvious effects, sometimes linked with dismounting.

Likely function: May be used to repel a conspecific as a consequence of the subject being mounted or to displays of dominance.

Trill (Figure 1m)

Profile: A soft, repetitive sound of average duration $0.027 \text{ s} \pm 0.008 \text{ s}$. This vocalisation has a mean highest frequency of $4.1 \text{ kHz} \pm 755 \text{ Hz}$ and a mean lowest frequency of $1.3 \text{ kHz} \pm 1.1 \text{ kHz}$, 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.

Expression: No obvious outward physical characteristics, typically directed toward a conspecific. In this study the 'trill' was used exclusively by lactating and non-lactating adult females (100%) during pup nursing and care (100%).

Effect: No obvious effects are visible.

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

Loud Whistle (Figure 1n)

Profile: A loud sound of average duration $0.225 \text{ s} \pm 0.105 \text{ s}$. This vocalisation has a mean highest frequency of $15.1 \text{ kHz} \pm 3.4 \text{ kHz}$ and a mean lowest frequency of $1.8 \text{ kHz} \pm 801 \text{ Hz}$, 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, typically broadcast. Used exclusively by male and female pups whilst playing away from the nest with a littermate (61.6%) or during isolation (28.8%). Its use decreases until pups are roughly two weeks old.

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

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

Low Whistle (Figure 1o)

Profile: A soft sound of average duration $0.094 \text{ s} \pm 0.06 \text{ s}$. This vocalisation has a mean highest frequency of $3.4 \text{ kHz} \pm 2.0 \text{ kHz}$ and a mean lowest frequency of $1.1 \text{ kHz} \pm 403 \text{ Hz}$, 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, typically directed toward a conspecific. Used exclusively by male and female pups more or less continuously from birth, most commonly during pup care (60.8%) and during isolation (28.2%). 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 (e.g. Ebensperger *et al.* 2004).

DISCUSSION

Of the 15 vocal categories determined in this study, the most common vocalisation in daily use was the 'chirp' (13.1%) (not including the 'bark' which was by far the most common during breeding season (30.8%)). The 'chirp' and its likely function holds significance for the degu as a social species, since reducing aggressive responses and the energy involved would be of high importance in regular social interactions. It has also been suggested that short sounds, such as the 'chirp', can be classified as syllables which may be incorporated into phrases (Eisenberg 1974). Their function of dividing up a string of different vocal sounds could also explain the frequency of use observed. The least common vocalisations were found to be the 'grunt' and the 'pip' (0.2%), the former of which is only used in highly agonistic situations, which occur infrequently in day-to-day life in captivity.

A comparison of the results of this study with previous findings leads to some interesting conclusions. The 'loud whistle' was found to be analogous to the 'distress whistle' (Braun *et al.* 2003; Monticelli *et al.* 2004) or 'isolation call' (Eisenberg 1974) in the sense that it is used exclusively by pups in response to parental separation/isolation. This study's 'loud whistle' frequency range and duration correlated with the findings of Braun *et al.* (2003); however the data shown by Eisenberg (1974) appeared to correlate more closely with the data for the 'low whistle' vocalisation identified in this study, which was found to be used by pups even when suckling from their mother in the nest. With regard to the analogous vocalisation in guinea pig pups identified by Monticelli *et al.* (2004), the mean frequency of the 'loud whistle' was found to be above the 3 kHz stated, but since it had an average of 4 harmonics it bore a small resemblance to this closely related species' call. It is worth noting that the relatively high maximum frequency of the 'loud whistle' and the interesting sonographic properties may indicate an ultrasonic component in this degu vocalisation.

The 'mothering call' outlined in Braun & Scheich (1996) 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', the former of which has been found by this study to be unique to this call. Braun and Scheich suggested that this sound (sequence) was 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 'maternal call' may not be used for identification by pups, but could have some other function derived from its "soothing effect" (e.g. Ziabreva *et al.* 2003a). Support for the finding that pups do not identify lactating females in this way may

also be found in White *et al.* (1982) and, more recently, Ebensperger *et al.* (2006).

Upon comparing the results of the current study with the other vocal sounds identified by Eisenberg (1974), it was found that the 'warning squeak', which was expected to be analogous (based on behavioural context) to the sound classified as the 'wheep' in this study, had frequencies that were significantly higher (12-24 kHz as compared to 4.2-14.9 kHz in this study), although the durations were similar. The Eisenberg data has frequencies well into the ultrasonic range (20 kHz upward), although it is stated that the maximum range of the equipment used was 18 kHz, which may indicate that this is a typographical error. The equipment used in the current study is capable of recording up to 22 kHz, so this difference is surprising, and although an ultrasound detector was briefly used to test this (with negative results) further ultrasonic exploration will form part of future studies. Eisenberg's 'protest squeak' and 'protest growl' were expected to correlate to agonistic vocalisations such as the 'whine', 'groan', 'squeal' or 'grunt'. With dominant frequencies at 2-4 kHz and a duration of 0.23-0.48 s, the 'protest squeak' was identified as analogous to the 'whine' in this study, however Eisenberg's 'protest growl' with dominant frequencies below 4 kHz and a rather lengthy duration of 0.69 s was found to relate only vaguely to one vocalisation identified by this study, the 'groan' (where the longest average duration was 0.31 s). The Eisenberg 'cluck' was found to correlate with the 'chirp', 'chitter' and 'trill' vocalisations of this study, and given Eisenberg's context of "during an encounter and allogrooming" this could be further defined as being analogous to the 'chitter'. The 'post copulatory cry' was assumed to be analogous to the 'bark' and both studies demonstrated similar durations, although Eisenberg's dominant frequency figure of below 5 kHz fell slightly below this study's findings of dominant frequencies around 5-6 kHz. It is of significant interest that the current study found the 'bark' to be used not only by males after copulation, but also by females as a territorial alarm. The data occasionally exhibited more than one subtly different frequency peak that may suggest individual components, or possibly subtle male-female differences, which requires further investigation. Eisenberg also lists a 'pup gurgle' sound, which is within the frequency range for this study's 'low whistle', but of shorter duration. Since Eisenberg's 'isolation call' is believed to be analogous to the 'low whistle', it is difficult to categorise without context.

Of the vocalisations described, the 'chitter' and 'trill' were found to have a very similar spectrographic appearance and required a more detailed statistical comparison to validate independent classification. This was analysed based on the duration, maximum frequency, minimum frequency and units in succession of each call with an unpaired T-test. It was found that although the minimum frequencies

and units used in succession were not significantly different, the differences between the maximum frequencies and durations in the 'chitter' and 'trill' were statistically significant ($p < 0.005$; d.f. 570; t -value for duration and F_{\max} 4.46 and -9.27 respectively). This, coupled with the differences in behavioural contexts (unique to pup care for the 'trill' and during greeting/playing for the 'chitter') and frequency modulations (mostly positive for the 'trill' and positive-negative for the 'chitter') justified their classification as two independent vocal categories.

An area which remains unstudied is the hearing range of the degu. It is reasonable to assume that this will fall within the frequency range of vocalisations used by this species. This study's estimation places the hearing range in the region of 71 Hz to 21.7 kHz, as defined by the lowest and highest frequencies observed in the individual vocalisations (71 Hz in the 'grunt' and 21728 Hz in the 'bark'). This figure is very similar to that of the chinchilla as described by West (1985). The limit of the recording range, however, was set to 22 kHz, and since this figure is so close to the upper limit a further study will be carried out to investigate possible ultrasonic components of degu vocalisations.

Several of the vocal categories such as the 'whine', 'groan', 'chaff' and 'warble' were used more by females than males, even when values were adjusted to take into account the female bias of the data set. It is possible that females could generally be more vocal than males of the species, which may be related to the fact that wild degu communities consist predominantly of female groups with only one or two males present (e.g. Ebensperger & Caiozzi 2002). It is interesting to note that some vocal categories, such as the 'groan', 'squeal', 'grunt' and 'wheep', were not used by pups. In the case of the former three this could be a result of an undeveloped concept of social hierarchy and hence fewer requirements for agonistic expressions, although use of the 'whine' was commonplace. In the case of the latter, it may be that pups have a reduced perception of danger in early life, or rely more on parental protection. As a behavioural category, the physical separation of observable conspecifics produced the majority (and broadest range) of vocalisations (excepting after mating attempt, relating to the 'bark', which gave the most data samples due to its repetitive nature). It is unlikely that this situation is encountered by wild degus, and it is hypothesised that the lack of physical contact with a conspecific that the subject degu can see leads to a greater number of vocalisations due to enhanced neural stimulation, and emotional arousal states such as those expressed during frustration and excitement. This is demonstrated by the frequent use of the 'chaff' to encourage the conspecific to move closer to the subject when (due to the physical barrier) they cannot; 'chattering' to greet the conspecific; 'whines', 'groans' and 'chirps' resulting from agonistic behaviours and

possibly frustration where the conspecific is a familiar degu; 'warbles' due to excitement and neural stimulation; 'tweeting' possibly to initiate displays of dominance where mounting and fighting are not possible. The 'pip' was found not to be used by males or juveniles of either sex in this study, however this is likely to be a result of the scarcity of its use and hence lack of recorded examples. The 'grunt' had similarly few data points and could explain why it was found to be used only by males in this study, rather perhaps than being sex-specific.

The adult vocalisations of the degu can be compared with those of another caviomorph species; the guinea pig. Three of the 11 categories outlined by Berryman (1976) appear to correspond to those used by the degu. The guinea pig 'chut' is assumed to be analogous to the degu 'chitter', in that it is used during greeting conspecifics and socialising. While the 'chut' is of similar duration and maximum frequency, the minimum frequency is much lower (250 Hz) and has 1-2 harmonics. The guinea pig 'squeal' is analogous to the 'squeal' of the degu in that it is used in response to pain. The duration and minimum frequency of both calls are very similar, however the maximum frequency of the guinea pig 'squeal' is higher at 18 kHz and it contains 3-12 harmonics rather than being broad spectrum as in the degu 'squeal'. The guinea pig 'drrr' call is given in response to environmental disturbance and is assumed to be an alarm call, analogous to the 'wheep' of the degu. However the sonogram of the 'drrr' is entirely dissimilar to that of the 'wheep', and indeed contains no features consistent with the 'wheep'. The fact that two members of the same sub-order have such a broad yet divergent vocal repertoire is of interest, particularly when the motivation-structure rules proposed by Morton (1977) are considered. Under these rules, it is to be expected that highly social animals such as guinea pigs and degus express a wide vocal repertoire due to the complexity of social interactions. Both guinea pigs and degus have vocalisations that are positively modulated and related to low hostility or alarm (such as the degu 'warble' or guinea pig 'whistle'), which fits with such rules.

A further point to be considered is whether the vocalisations defined in this study are directly comparable to those used by wild degus. Not only do the environmental conditions differ, but also it is not known exactly how far removed genetically the degus in this study are from their wild counterparts, and whether this would affect their vocal behaviour. It may be interesting to extend this study to wild-born degus, both in captivity and in their natural habitat.

CONCLUSIONS

In this study I identified, categorised and gave parameters to 15 unique vocalisations of the degu, providing a much needed reference

point for future studies in this area, and demonstrating that degus use a much wider and more complex repertoire of vocal sounds than was previously assumed. Certain categories of degu sounds were found to be specific to both age and gender, while varying widely with season and behavioural context, as expected in a complex social hierarchy. In particular, 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', 'wheep' and 'bark' 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 (predicted to be around that estimated in this study; 71 Hz to 21.7 kHz). In addition, further studies may look into the possibility of individual components of calls, particularly relating to male-female use in vocalisations such as the 'bark', 'groan' and 'wheep'.

ACKNOWLEDGEMENTS

I would like to thank Drs. Paul Lepper and Jim Hague from the University of Loughborough, UK, for technical support and helpful discussions.

REFERENCES

- Berryman, J. (1976) Guinea-pig vocalisations: their structure, causation and function. *Zeitschrift Tierpsychol*, **41**, 80-106.
- Braun, K., Kremz, P., Wetzel, W., Wagner, T. & Poeggel, G. (2003) Influence of parental deprivation on the behavioural development of *Octodon degus*: Modulation by maternal vocalisations. *Developmental Psychobiology*, **42**, 237-245.
- Braun, K. & Poeggel, G. (2001) Recognition of mother's voice evokes metabolic activation in the medial prefrontal cortex and thalamus of *Octodon degus* pups. *Neuroscience*, **103**, 861-864.
- Braun, S. & Scheich, H. (1991) Learned relevance of species-specific vocalisations and their 14C-2-DG pattern in auditory cortex of the degu (*Octodon degus*). *21st Annual meeting of the Society of Neuroscience*, **2** (559.17), 1404.
- Braun, S. & Scheich, H. (1996) Influence of experience on the representation of the "mothering call" in auditory and other cortices of pups of the rodent *Octodon degus*: A FDG mapping study. *Journal of Comparative Physiology A*, **181**, 697-709.
- Ebensperger, L. (2001) No infanticide in the hystricognath rodent, *Octodon degus*: Does ecology play a role? *Acta Ethologica*, **3**, 89-93.
- Ebensperger, L. & Caiozzi, A. (2002) Male degus, *Octodon degus*, modify their dustbathing behaviour in response to social familiarity of previous dustbathing marks. *Revista Chilena de Historia Natural*, **75**, 157-163.
- Ebensperger, L., Hurtado, M., Soto-Gamboa, M., Lacey, E. & Chang, A. (2004) Communal nesting and kinship in degu (*Octodon degus*). *Naturwissenschaften*, **91**, 391-395.

- Ebensperger, L., Hurtado, M. & Valdivia, I. (2006) Lactating females do not discriminate between their own young and unrelated pups in the communally breeding rodent, *Octodon degus*. *Ethology*, **112**, 921-929.
- Eisenberg, J. (1974) The function and motivational basis of hystricomorph vocalizations. *Symp Zool Soc Lond.*, **34**, 211-247
- Fulk, G. (1976) Notes on activity, reproduction and social behaviour of *Octodon degus*. *Journal of Mammalogy*, **57**, 495-505.
- Lee, T. M., Hummer, D. L., Jechura, T. J. & Mahoney, M. M. (2004) Pubertal development of sex differences in circadian function: An animal model. *Annals of the New York Academy of Sciences*, **1021**, 262-275.
- Monticelli, P., Tokumaru, R. & Ades, C. (2004) Isolation induced changes in Guinea Pig *Cavia porcellus* pup distress whistles. *Annals of the Brazilian Academy of Sciences*, **76**, 368-372.
- Morton, E. S. (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Amer Natur.*, **111**, 855-869.
- Novak, R. (1999) *Walker's Mammals of the World* (6th ed.). Baltimore: Johns Hopkins University Press.
- Poeggel, G. & Braun, K. (1996) Early auditory filial learning in degus (*Octodon degus*): Behavioural and autoradiographic studies. *Brain Research*, **743**, 162-170.
- Reynolds, T. & Wright, J. (1979) Early postnatal and physical development of degus (*Octodon degus*). *Lab Animal*, **13**, 93-9.
- Shelley, E. & Blumstein, D. (2005) The evolution of vocal alarm communication in rodents. *Behavioural Ecology*, **16**, 169-177.
- Suta, D., Kvasnak, E., Popelar, J. & Syka, J. (2003) Representation of species-specific vocalisations in the inferior colliculus of the guinea pig. *Journal of Neurophysiology*, **90**, 3794-3808.
- Weir, B. J. (1974) Reproductive characteristics of hystricomorph rodents. *Symp Zool Soc Lond.*, **34**, 265-301.
- West, C. (1985) The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *Journal of the Acoustic Society of America*, **77**, 1091-1101.
- White, P., Fischer, R. & Meunier, G. (1982) The lack of recognition of lactating females by infant *Octodon degus*. *Physiol Behav.*, **28**, 623-5.
- Woods, C. & Boraker, D. (1975) *Octodon degus*. *Mammalian Species*, **67**, 1-5.
- Yáñez, J. (1976) Ecoetología de *Octodon degus*. Bachelor in Sciences Thesis, Universidad de Chile, Santiago: 67pp.
- Ziabreva, I., Poeggel, G., Schnabel, R. & Braun, K. (2003a) Separation induced receptor changes in the hippocampus and amygdala of *Octodon degus*: Influence of maternal vocalisations. *Journal of Neuroscience*, **23**, 5329-36.
- Ziabreva, I., Schnabel, R., Poeggel, G. & Braun, K. (2003b) Mothers voice "buffers" separation-induced receptor changes in prefrontal cortex of *Octodon degus*. *Neuroscience*, **119**, 433-441.

Received 5 March 2007, revised 8 May 2007 and accepted 1 June 2007