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Catalogue of the behaviour of *Meriones unguiculatus* f. dom. (Mongolian gerbil) and wild conspecies, in captivity and under natural conditions, based on a systematic literature review

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Abstract Despite *Meriones unguiculatus*' long history and popularity as an animal model in a wide range of research on topics from gastric and neurological diseases to animal cognition, there is no single comprehensive and detailed source of information about this animal's behaviour in nature or captivity. Instead, partial and heterogeneous descriptions of several aspects of behaviour can be found throughout a vast and dissimilar literature. Recognising the relevance of having available detailed and standardised terminology for animal models used in basic, applied, and translational behavioural research, we developed a comprehensive catalogue of the behaviour of *Mongolian gerbil* (*M. unguiculatus* f. dom) and wild conspecies, in captivity and under natural conditions, by adapting methodology currently widely accepted for conducting and reporting systematic literature reviews. As a result, 116 behavioural traits were compiled and classified. We expect several positive outcomes from this first version of the glossary: (1) improved interpretation of *M. unguiculatus*' behavioural data; (2) encouragement of laboratories to provide more systematic and standard descriptions of behaviour; (3) an increase in cross-species comparisons and behaviour modelling; and (4) saving researchers the substantial time and effort required to

develop their own definitions of behaviour. Overall, we believe this catalogue, by contributing to our comprehension of the repertoire of behaviour of an extremely versatile animal model, will favour understanding of related phenomena within and across species, including normal and pathological human brain functioning. We conclude by discussing additional efforts related to development of the catalogue and suggesting lines of research that may benefit from incorporating its definitions (e.g., behavioural differences between strains of Mongolian gerbils).

Keywords *Meriones unguiculatus* · Mongolian gerbil · Animal behaviour · Natural and seminatural settings · Captivity · Catalogue · Glossary · Systematic review

Introduction

Expanding, refining, and disseminating knowledge about animal models are important endeavours in basic, applied, and translational research in diverse scientific fields, for example medicine, biology, psychology, and neuroscience (Araujo et al. 2013; Ergorul and Levin 2013; Levin and Danesh-meyer 2013). Crucial to these efforts is the development and implementation of standard terminology for animal models because achievement of highly relevant objectives depends heavily on the availability and use of such uniform terminology, e.g., effectively communicating methods and findings throughout communities of researchers and non-specialists (laboratories, research groups, and newcomers to a given field), replicating methods developed in other laboratories, conducting collaborative efforts, and comparing and deciding which particular animal model to use in a given research program.

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Meriones unguiculatus (Mongolian gerbil) is a popular animal model for a wide range of research from gastric and neurological diseases to animal cognition (recently reviewed by Batchelder et al. 2012). This rodent, of the family Muridae, subfamily Gerbillinae, is a native of Mongolia and northern China. *M. unguiculatus* ranges in size between rats and mice and lives in family groups in burrows that they dig in different types of dry steppe soil or fields used for agriculture. During the summer, *M. unguiculatus* eats mainly green vegetation, including *Chenopodium album*, different grasses, and some agricultural plants. During winter, they eat mainly grain, seeds, and roots from their food stores (Agren et al. 1989; Grovov 2011). Although the generic word “gerbil”, as used in the literature, may refer to any of 12 genera with over 300 forms, the names “gerbil” and “Mongolian gerbil” usually refer to *M. unguiculatus* (extensive information about this species, e.g., distribution, form, function, and ecology, is given by Agren et al. 1989; Batchelder et al. 2012; Gulotta 1971; Rich 1968; Schwentker 1963; Stuermer et al. 2003).

Despite *M. unguiculatus*' long history, current popularity, and versatility as an animal model (more than 50 years—Schwentker 1963), a review of the literature indicates the lack of a single comprehensive and detailed source of information about its behaviour under natural, semi-natural, and laboratory conditions (notwithstanding outstanding efforts; e.g., Thiessen and Yahr's 1977). Instead, partial and heterogeneous descriptions of behavioural aspects in different domains (e.g., social, sexual, and parental) can be found throughout the vast and dissimilar literature. A serious issue results from this situation: comparisons of behavioural data across such literature require the consideration of not only the frequently recognised sources of variation (e.g., housing conditions, animal-related aspects, and environmental aspects) but also observational factors, for example the consistency of data collected in different laboratories (Moons et al. 2012; Lewejohann et al. 2006; Marsh and Hanlon 2004). As Moons et al. (2012) discuss:

“...the use of even slightly different descriptions of the same behaviour by different scientists could lead to different findings. Because this divergence in results is often not recognized as stemming from a classification dissonance, the differences could falsely be attributed to other factors.” (p. 170)

Accordingly, although intra-laboratory research is usually highly standardised, efforts to generate homogeneous data can be entirely lost when other laboratories attempt to replicate procedures when important experimental details are unavailable because they are not reported; a good example is the use of comprehensive and consistent definitions of behaviour (Moons et al. 2012).

As part of an ongoing effort in our laboratory, the purpose of which is to characterise several dimensions of the behaviour of *M. unguiculatus* under different housing conditions and in different experimental procedures (e.g., appetitive and aversive learning tasks), after recognising the difficulties of finding detailed and consistent sources of information about the behaviour of this species, we decided to develop a comprehensive catalogue of *M. unguiculatus* behaviour under natural, semi-natural, and captivity conditions on the basis of a systematic literature review. For this purpose, we adapted methodology designed for conducting and reporting systematic literature reviews which has gained substantial recognition in basic, applied, and translational research conducted in diverse scientific fields (Petticrew and Roberts 2006; PRISMA statement—Liberati et al. 2009; Moher et al. 2009).

As the first attempt to consolidate a glossary of the behaviour of *M. unguiculatus*, we expect this refined and standardised terminology will:

1. help improve interpretation of published findings; and
2. encourage more research groups or laboratories that are currently using or are considering using *M. unguiculatus* for their research to provide more systematic descriptions of behaviour.

On the basis of our experience when we initiated our research program and encountered substantial difficulties finding clear definitions of *M. unguiculatus*' behaviour throughout the scattered and inconsistent literature, we expect this glossary will save the time and efforts of researchers who are beginning to work with this species and are considering studying its behaviour.

In what follows, we first present details of the literature search conducted to find descriptions of the behaviour of intact and healthy *M. unguiculatus* under different housing conditions (natural, semi-natural, and captivity) and the catalogue that was consolidated after this search. For convenience, each of the 116 catalogue entries was classified into two major categories (individual and social behaviour) and different subcategories (communication, construction and maintenance of the nest and/or burrow, maintenance activities, locomotor behaviour, stereotyped behaviour, agonistic behaviour, encounters between individuals, sexual behaviour, parent and offspring behaviour, and miscellaneous) using a system that is similar to the system used by Roper and Polioudakis (1977). Each glossary record includes the following information:

1. a numeric identifier;
2. different names used in the literature to label the same type of behaviour (e.g., “nasal sniff”, “nose sniff”, “nose/nose contact”, and “nose to nose”);

3. a comprehensive description of a unit of behaviour based on all the information provided by the sources identified by the review; and
4. citations of the sources that provided information regarding that unit of behaviour.

In addition, supplementary information is included when available. For instance, information such as how a unit of behaviour is related to other forms of behaviour (e.g., if a unit of behaviour belongs to a known sequence or pattern or if functional differences have been identified), the incidence of a particular type of behaviour among males or females, or developmental characteristics (e.g., typical moment of appearance) have been included.

Materials and methods

Search strategy

Our search procedures generally followed the recommendations of Petticrew and Roberts (2006) for conducting systematic literature reviews and complied with the relevant items of the PRISMA statement (preferred reporting items for systematic reviews and meta-analyses guidelines—Liberati et al. 2009; Moher et al. 2009).

First, the following list of relevant search terms and phrases was determined by use of thesauruses available in the PsycINFO (American Psychological Association—APA) and MeSH (National Center for Biotechnology Information—NCBI) databases and using keywords that were found in a preliminary list of pertinent references (Agren et al. 1989; Gallup and Waite 1970; Gulotta 1971; Roper and Polioudakis 1977): *M. unguiculatus*, *M. gerbil*, living conditions, captivity, natural environment*, habitat, semi-natural environment, laboratory conditions, surrounding environment, behavior* pattern, behaviour* pattern, (asterisks denote truncation). Next, using these key terms and phrases, a comprehensive, systematic, and unrestricted computer-based search was conducted using the databases (June 2013) SCOPUS (Elsevier), Web of Knowledge (Thomson Reuters), and PsycINFO (APA—ProQuest search engine). Key terms and phrases were sought in the title, abstract, and keywords fields of the databases, and no language, date, or study type limiters were implemented. One-hundred and eighty-seven records found in the three databases (details are given in the first level of the flow chart in Fig. 1) were exported to reference manager software (Mendeley® 1.8.4; Elsevier, New York, US) for further processing. As will be described in detail below, another 199 records were later added to the database as a result of use of supplementary methods recommended by Petticrew

and Roberts (2006), for example contacts with experts and citation searching.

Study selection

A four-phased selection procedure was used (Fig. 1). First, duplicates were eliminated, which left 109 records for further processing. Second, five exclusion criteria were implemented, using information available in the title and abstract of each record:

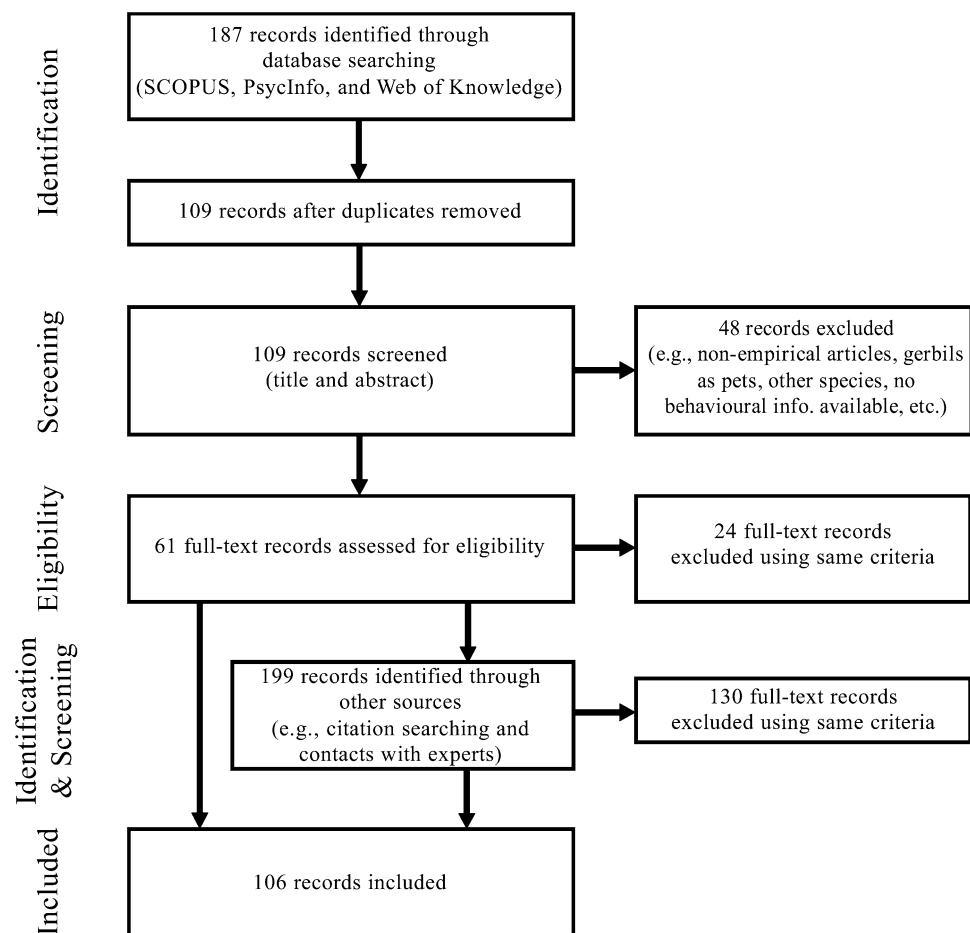
1. sources (e.g., articles or book chapters) that did not constitute original research (i.e., publications exclusively based on summaries, reviews, or synthesis of earlier publications);
2. sources that did not provide any information about the behaviour of healthy or intact *M. unguiculatus* (e.g., studies in which definitions of behaviour only applied to subjects exposed to chemical or pharmacological substances, pathogens, or surgical procedures);
3. studies in which the subjects were from a different species (e.g., other *Meriones*);
4. sources in which gerbils were referred to as pets; and
5. sources in a language other than English or Spanish (the latter because Spanish is the native language of the authors).

Forty-eight records were excluded on the basis of these criteria. Sources that could not be evaluated by use of the information provided in the title and abstract were assessed during the next stage of the selection process (i.e., when the full text of each record was obtained). It is worth noting that although major research on the behaviour of *M. unguiculatus* has been published in Russian and Chinese, use of English summaries or abstracts of these studies was not appropriate for the data extraction and compilation methods used for this catalogue (described below), because they did not provide detailed descriptions of behaviour.

The third phase of the selection process consisted of obtaining from different providers (e.g., PsycArticles® or ScienceDirect®) the full texts of the sources that were not excluded during the first two stages (61 records), and implementing the same exclusion criteria by screening the methods and results sections of these sources. Twenty-four records were excluded during this third phase. In the fourth phase, another 199 records were identified and added to the database by use of supplementary methods recommended by Petticrew and Roberts (2006), which included:

1. identifying references that authors of the articles used when labelling and/or defining any unit of behaviour (citation searching—an example is given in Appendix A and B; see supplementary material);
2. incorporating advice from experts in the behaviour and ecology of *M. unguiculatus* that helped with

Fig. 1 The flow of information through the different phases of the systematic review implemented for identifying sources of information for the catalogue of behaviour (in compliance with PRISMA guidelines—Liberati et al. 2009; Moher et al. 2009)



- identification of relevant sources (Professors V. Grovov and I. W. Stuermer and anonymous peer reviewers); and
- using annotated bibliographies (Schwentker 1974; Thiessen and Yahr 1977) to identify relevant sources published before the 1980s, which are very often not listed in electronic databases.

Of those 199 records, 130 were excluded after implementing the same exclusion criteria. Finally, 106 sources were deemed eligible for further analysis (Fig. 2 shows the distribution of these references over time). During a quality-control test, 98 % agreement on record exclusion was obtained between the research assistants who reviewed the sources.

Data extraction

The following information was systematically extracted from each of the selected sources (an example of an extraction table is given in Appendix A—see supplementary material):

- labels and descriptions of the specific behaviour mentioned and/or defined in detail throughout the

methods or results sections of the studies (i.e., units of behaviour); and

- references used by the author(s) of the article when labelling and/or defining any unit of behaviour.

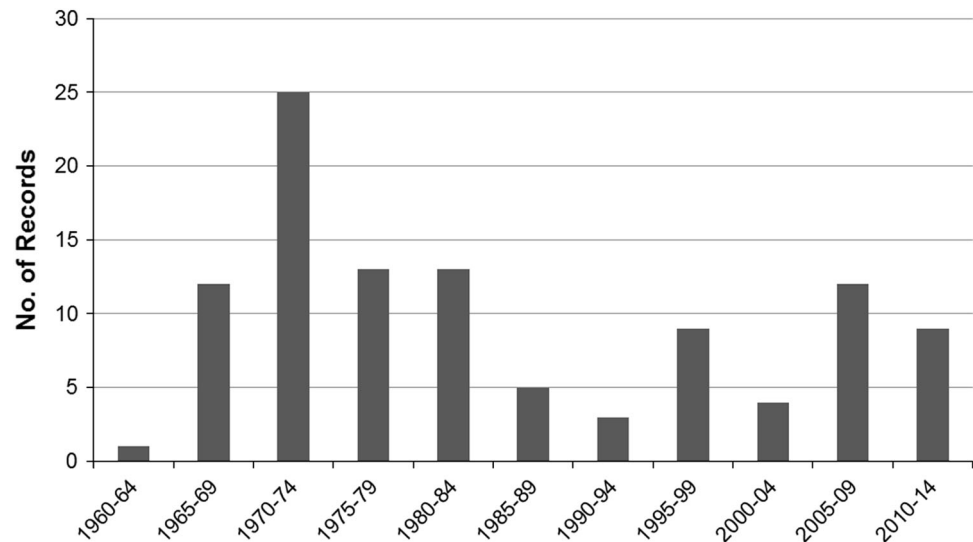
This latter referential information was used for citation searching (Petticrew and Roberts 2006). All the information extracted was saved in a Microsoft EXCEL[®] database.

Subsequently, each unit of behaviour that was found in each source was assigned to one of two major categories, social or individual, and to as many subcategories that applied (communication, construction and maintenance of the nest and/or burrow, locomotor behaviour, maintenance activities, stereotyped behaviour, agonistic behaviour, encounters between individuals, sexual behaviour, parent and offspring behaviour, or miscellaneous). An example of data extraction is presented in Appendix A (see supplementary material).

Data compilation and generation of comprehensive definitions

During the final stage of data processing, all labels and descriptions extracted from all of the sources were

Fig. 2 Distribution of the 106 references used for the catalogue over time (in five-year intervals)



compiled. During the first round, all units of behaviour from different sources that were labelled with the same or similar names were integrated to generate single comprehensive definitions, always trying to preserve as much as possible of the original descriptions provided by the authors (an example of the integration of different sources that described *nasal sniff* between individuals is given in Appendix B—see supplementary material). The most frequently used label across the sources was chosen as the heading for each unit of behaviour in the catalogue, whereas less-frequently used names were included as secondary or alternative labels. Units of behaviour that, for different reasons (e.g., no similar labels or coincidences were found in the database, ambiguous or conflicting descriptions were provided, or the information provided did not enable application of at least one of the subcategories) could not be compiled during this first round, were stored in a different database for later processing. During the final round, non-compiled units of behaviour were reviewed again by the principal investigator and by the research assistants and were integrated and classified by consensus when possible. An additional subcategory, “miscellaneous”, was created during this process for units that could not be classified during the two compilation/classification rounds. Finally, a subset of units of behaviour was excluded during this process when at least one of the following reasons applied:

1. the behaviour described was arbitrary (e.g., responses learned during an experimental procedure, for example pressing a lever in an operant conditioning chamber);
2. the descriptions of the behaviour were procedural refinements instead of actual definitions of behaviour (e.g., considering “food hoarding” as the amount of food pellets in the subject’s home cage);

3. the descriptions of the behaviour applied only to specific experimental conditions (e.g., jumping on and off a platform that was designed specifically for study of hearing thresholds of *M. unguiculatus*; Wagner et al. 2003);
4. the descriptions of the behaviour provided by the authors were ambiguous or imprecise (e.g., “losing fight”, which was defined as moving out of the way of the “advancing” dominant individual; Fisler 1977); or
5. a single source provided only a label of behaviour without any form of description.

Results

One-hundred and sixteen units of behaviour were compiled and classified by use of the above-mentioned methods, with 46 under individual behaviour and 70 under social behaviour. The glossary format provides a label for each definition of behaviour in boldface; this is followed by alternative names in italics and the corresponding entry. Citations for the sources that provided the information are included at the end of each unit, and cross-references to related unit of behaviour are in boldface and italics (these cross-references appear either throughout or at the end of each entry).

For convenience, the glossary follows a hierarchical numbering scheme that is related to the categories and subcategories that are used for systematising the unit of behaviour. For instance, “1.3.8.” is the numerical identifier assigned to the entry “Sleep”. The first digit (1.) denotes that this unit belongs to the “individual behaviour” category, the second digit (3.) indicates that this unit belongs to the subcategory “maintenance activities”, and the last digit (8.) indicates its corresponding position within the subcategory.

Glossary

Individual behaviour

1.1 Communication

- 1.1.1. **Arched frequency-modulated syllable (discrete part of a vocalisation):** A *vocalisation* of long duration (~260 ms) in which the fundamental frequency tends to reach the maximum around the middle of the call. Most of these calls consist of two to four harmonic components, of which the first dominates with a peak frequency range from 7 to 22 kHz. These *vocalisations* seldom occur alone and are typically observed with other arched calls, *noise bursts*, or *downward frequency-modulated* calls. This type of call has been reported to be often accompanied by serious *fighting*, including *biting* and *chasing* (Kobayasi and Riquimaroux 2012).
- 1.1.2. **Build up signal heaps (marking with signal heaps):** An animal leaves a drop of urine where the substrate is sufficiently loose, often near *ventral marks*. Simultaneously, the gerbil can also leave one to three faecal pellets in the same place. By throwing substrate (e.g., sand) beneath its belly by use of the anterior legs, the animal builds up a conic hillock that covers the drop of urine and faecal pellets. It has been reported that such signal heaps serve as both visual and scent marks (Gromov 1997, 2011).
- 1.1.3. **Chin gland mark (chinning, chin marking):** An animal deposits secretions from its sebaceous gland located around the chin and neck (Thiessen and Rice 1976) by rubbing these areas against distinctive objects in the environment, e.g., wooden pegs specifically designed for registering this behaviour (Gromov 2011; Thiessen et al. 1971).
- 1.1.4. **Downward frequency-modulated syllable (discrete part of a vocalisation):** A multi-harmonic *vocalisation* consisting of three to six harmonic components, of which the second usually dominates. The fundamental frequency ranges from 5 to 8 kHz and tends to be downward frequency-modulated. The typical duration of these calls is 180 ms. Downward frequency-modulated and *long downward frequency-modulated* calls share common spectrotemporal features: simple harmonics, a fundamental frequency covering a similar frequency and downward modulation. The former, however, are, importantly, shorter in duration and lower in all four frequency characteristics. Downward frequency-modulated *vocalisations* occur alone or form simple phrases with other syllables of the same type or with *long downward frequency-modulated* calls. Finally, this type of *vocalisation* is most often observed when two animals have a minor conflict (Kobayasi and Riquimaroux 2012).
- 1.1.5. **Foot-stomp (foot-stomping; drumming; thumping; foot thumping; hind paw drumming):** An animal rhythmically pounds the substrate with rapid movements of one or both hind feet in brief repetitive bursts of approximately 5 or 6 movements with durations that range from one hundred milliseconds to a few seconds. Under natural conditions, foot-stomping is mainly used to warn or communicate and in situations of great arousal. This pattern has also been observed during *copulation*, including the post-ejaculatory interval, when a series of *mountings* or before *mounting* occurs (Burley 1980; Burley et al. 1983; Fisler 1970; Gallup and Waite 1970; Gulotta 1971; Hendrie and Starkey 1998; Holman and Hutchison 1982; Henrich-Noack et al. 2011; Holman 1981; Kuehn and Zucker 1968; Reynierse 1971; Roper and Polioudakis 1977; Routtenberg and Kramis 1967; Swanson 1974; Ter-Mikaelian et al. 2012; Wechkin and Cramer 1971).
- 1.1.6. **High-frequency upward frequency-modulated call:** A *vocalisation* composed of one to two harmonics and duration between 20 and 44 ms. Typically, the initial frequency of these calls is 25–32 kHz and their terminal frequency is 30–37 kHz. The characteristic terminal frequency of this call is the maximum frequency of the vocalisation, and the minimum frequency is usually distributed in the first half of the call (Nishiyama et al. 2011).
- 1.1.7. **Long downward frequency-modulated syllable (discrete part of a vocalisation):** A *vocalisation* of the longest duration, approximately 360 ms, with multiple harmonics (three to six harmonic components, of which the second dominates). The fundamental frequency of these calls range between 7

- and 10 kHz and tend to decrease in time. Typically, these calls do not have any rapid modulations or noisy components and are seldom observed alone (instead, they tend to occur with other long downward or *downward frequency-modulated* calls). This type of call correlates with *fighting* over such resources as food, water, or space in the nesting area (Kobayasi and Riquimaroux 2012).
- 1.1.8. **Low-frequency multi-harmonic frequency-modulated call:** A *vocalisation* composed of two to six harmonics of duration 175 ± 72 ms. The initial frequency of these calls is 6.9 ± 1.6 kHz and their terminal frequency 6.5 ± 1.9 kHz. The maximum frequency in these calls is typically located in the first half of the *vocalisation* whereas the minimum frequency is in the second half (Nishiyama et al. 2011).
- 1.1.9. **Noise burst syllable (discrete part of a vocalisation):** A *vocalisation* characterised by an extremely broad spectral composition with a width of >10% of the peak frequency measured 15 dB below the maximum. These calls last an average of 160 ms; they occur as single calls and with other noise burst or *quasi-constant frequency syllables* and happen in the same context as that for *quasi-constant frequency* calls, namely, minor and serious *fighting* (Kobayasi and Riquimaroux 2012).
- 1.1.10. **Quasi-constant frequency syllable (discrete part of a vocalisation):** A long *vocalisation* of approximately 150 ms in duration and multiple harmonics with an average of five to nine harmonic components, of which the third is strongest. Because the fundamental frequency changes relatively little and does not have a specific frequency-modulated pattern, for example *downward frequency-modulated* or *upward frequency-modulated* calls, this type of *vocalisation* has been categorized as a quasi-constant frequency call. Compared with *downward frequency-modulated* calls, quasi-constant frequency *vocalisations* have lower fundamental frequencies and prominent multi-harmonic structures. This type of call occurs in the context of minor and serious *fighting* (Kobayasi and Riquimaroux 2012).
- 1.1.11. **Upward frequency-modulated syllable (discrete part of a vocalisation):** A long *vocalisation* of approximately 160 ms without noisy spectral components. Typically, only the first harmonic is observed and ranges between 28 and 32 kHz. These *vocalisations* tend to rise in frequency, with the minimum frequency being observed in the first half of the call and the maximum frequency being observed in the second half of the call. They occur as single *vocalisations* and with other calls of the same type or *upward sinusoidal frequency-modulated* calls in the context of *mating* (Kobayasi and Riquimaroux 2012).
- 1.1.12. **Upward sinusoidal frequency-modulated syllable (discrete part of a vocalisation):** A *vocalisation* of long duration (approximately 130 ms) composed of quasi-sinusoidal amplitude and frequency oscillations or ripples but not noisy components. The average modulation frequency and modulation depth (in frequency) are 74 Hz and 4.8 kHz, respectively. The fundamental frequencies of these calls range between 30 and 50 kHz. Typically, they start at the minimum and terminate at the maximum frequency and seldom occur alone (instead, these calls frequently form simple phrases). This type of *vocalisation* is often observed in the context of *mating* (Kobayasi and Riquimaroux 2012).
- 1.1.13. **Short bent upward frequency-modulated syllable (discrete part of a vocalisation):** A *vocalisation* of short duration (approximately 34 ms) characterized by an upward frequency modulation with a slight upward bend in the middle of the spectrogram (in the absence of noisy or irregular spectral components). These calls cover frequency ranges between 30 and 35 kHz. The minimum frequency is usually produced within the first one-third of the call length, and the maximum frequency is typically made at the end of the call. *Vocalisations* of this form are most often observed while two or more animals are in non-conflict contact with each other (Kobayasi and Riquimaroux 2012).
- 1.1.14. **Vocalise (*squeal, call, vocalisation*):** An animal utters a sound produced by pushing air through the larynx and out of the nasal passages. *Vocalisations* of pups occur in bouts of regularly spaced calls, and among animals 4 to 8 days old are highly correlated with maternal behaviour, including *sniffing*

pups, *pup grooming*, and *building nest*. A decrease in the calls is observed for isolated neonates up to 20 days (after this age vocalisations are no longer detectable), which indicates that behavioural interactions induce calling among animals 20 days and older. Between the ages of 17 and 85 days, in social contexts, gerbils emit a varied range of ultrasonic vocalisations (i.e., high-frequency calls) that tend to increase as the animals become older. The incidence of vocalisations before the age of 56 days has been found to differ across sexes in paired encounters, with female–female being higher than male–male. Adults rarely vocalise except in social contexts, and their vocalizations are stimulated by olfactory cues from conspecifics and correlate with locomotion and specific body movements, which include *hops*, abrupt body turns, *fighting*, *ventral gland marking*, and *foot-stomping*. Vocalisations vary in spectrotemporal structure, which has resulted in different categorization: (1) Kobayasi and Riquimaroux (2012) broadly distinguished between *ultrasonic* (33 ± 5 kHz) and *non-ultrasonic* calls (below 10 kHz). More specifically, Kobayasi and Riquimaroux classified vocalizations into distinct types of “syllable” (a discrete part of a call, which is surrounded by periods of silence), namely *upward sinusoidal frequency-modulated (FM)*, *short bent upward FM*, *upward FM*, *arched FM*, *long downward FM*, *downward FM*, *quasi-constant frequency*, and *noise bursts*. (2) Nishiyama et al. (2011) identified two predominant types of vocalisation among adult gerbils, namely *high-frequency upward FM* and *low-frequency multiharmonic FM*. Last, (3) Holman and Seale (1991) differentiated vocalizations into *rectilinear* (drift from the horizontal no more than ± 0.8 kHz) and *curvilinear* (calls that tended to have an ascending sigmoid-shaped spectrographic trace). Alternatively, calls have also been classified depending on the context in which they occur: Holman (1980, 1981) distinguished *modulated*, *unmodulated*, and *upsweep vocalisations* in different stages of reproductive interactions; and Ter-Mikaelian et al. (2012) identified vocalisations associated with six different social contexts, namely aggression, alarm, food-dispute, disturbance, mating, and contact. (Broom

et al. 1977; De Gheff 1974; Elwood 1979; Holman and Seale 1991; Kaplan and Hyland 1972; Kelly and Potash 1986; Kleese and Hull 1980; Lerwill 1978; Motomura et al. 2002; Sewell 1970; Thiessen et al. 1978, 1980).

- 1.1.15. **Ventral gland mark** (*marking, ventral rubbing, ventral scent marking*): An animal deposits secretions (sebum that is oily to the touch and musky in smell) from its mid-ventral sebaceous gland pad on a substrate and/or distinctive, low-lying objects in the environment, e.g., wooden pegs specifically designed for recording this behaviour (Arkin et al. 1999; Thiessen et al. 1971). This pattern consists of an animal slightly spreading its fore and hind legs, assuming a concave back position, lowering its mid-region, and then pressing its ventral scent gland on an object or the floor with a forward swing of its body from the tail to head in one stereotyped movement. In the natural habitat, the objects of this type of marking include burrow entrances, soil hammocks, small stones, and lumps of ground, both inside the protected territory and along its border (Gromov 2011). Occasionally, this response is followed by *rolling* in sequences that may be repeated several times. Finally, it has been reported that ventral gland marking is sex-dimorphic (males mark about twice as frequently as females) and androgen-dependent. In addition, when a male enters a territory already ventrally marked by another animal, its marking frequency is reduced (Arkin et al. 1999; 2000; 2003; Agren et al. 1989; Baran and Glickman 1970; Burley 1980; Burley et al. 1983; Eisenberg 1967; Lee and Estep 1971; Gromov 2011; Hendrie and Starkey 1998; Holman and Hutchison 1982; Owen and Thiessen 1973; Pendergrass et al. 1989; Rieder and Reynierse 1971; Roper and Polioudakis, 1977; Swanson 1974; Thiessen 1968, Thiessen 1973; Thiessen et al. 1968a; 1969a ; 1970, 1971, 1980; Yahr et al. 1977).

- 1.2. Construction and Maintenance of the nest and/or burrow

- 1.2.1. **Dig** (*digging, burrowing, scratching, sand digging*): An animal makes rapid back and forth movements with its front paws, which alternate with movements of its hind legs that are directed toward the floor, wall, or corner.

These movements can be made while the animal is hunched or standing upright (*rear*) against a vertical surface (e.g., the cage wall). A typical digging performance observed among animals housed under laboratory conditions consists of four to seven foreleg scratches followed by one or two hind leg kicks (Moons et al. 2012). When the floor of the enclosure has a smooth surface (e.g., a plastic cage), slipping of the hind legs is often followed by a quick restoration of balance toward the standing *upright posture*. When observed in natural or semi-natural environments, digging is typically used for excavation of tunnels, closing the entrances to nesting sites, or creating small pits by removing or throwing away substrate, e.g., sawdust or sand (Agren et al. 1989; Bauer 1970; Burley 1980; Deacon 2009; Eisenberg 1967; Elwood 1979; Gallup and Waite 1970; Hendrie and Starkey 1998; Kaplan and Hyland 1972; Moons et al. 2012; Prates and Guerra 2005; Roper and Polioudakis 1977; Shimozuru et al. 2008; Susić and Masirević 1986; Swanson 1974; Ter-Mikaelian et al. 2012; Walters and Glazer 1971; Waring and Perper 1979, 1980; Wiedenmayer 1996, 1997).

- 1.2.2. **Build nest** (*nest building*): A comprehensive pattern of activities concerned with nest construction, which includes shredding, *chewing*, manipulating, carrying, gathering, rearranging, and/or building of materials, for example wood, wood shavings, paper, cardboard, sawdust, or any other available bedding materials. Nest construction and maintenance have been observed among young gerbils aged 21–22 days. Finally, gerbils have been reported to use leaves of buckwheat, Graminaceae, and Cyperaceae to build round nests approximately 18–25 cm in diameter under natural conditions (Agren et al. 1989; Burley 1980; Elwood 1975, 1979; Glickman et al. 1967; Gromov 2009, 2010; Kaplan and Hyland 1972; Kleese and Hull 1980; Lee and Estep 1971; Roper and Polioudakis 1977; Waring and Perper 1980).

1.3. Maintenance activities

- 1.3.1. **Chew** (*gnaw, gnawing*): An animal grasps between its forepaws objects or pieces of material available in the surroundings (e.g., wood, wood shavings, paper, cardboard, or sawdust) and shreds them with its teeth. It has

been reported that young gerbils start chewing and shredding material (e.g., pine shavings and empty seed hulls) by days 17 and 18 (Bauer 1970; Glickman et al. 1967; Kaplan and Hyland 1972; McManus 1971; Swanson 1974).

- 1.3.2. **Chop**: An animal bites pieces of food (e.g., vegetable matter, stalks, roots, or pods) into small pieces, which are then cached. In natural or seminatural environments, an animal caches foodstuffs either in the burrow or in discrete locations within the animal's home range (Eisenberg 1967).
- 1.3.3. **Drink** (*drinking*): An animal takes liquid (e.g., water) into its mouth from anywhere liquid is available in the surroundings, e.g., an animal obtains water by licking spouts that are fitted to laboratory bottles (Roper and Polioudakis 1977; Susić and Masirević 1986; Waring and Perper 1980; Wright 1976).
- 1.3.4. **Eat** (*eating, feeding, hunting*): An animal brings its snout in contact with food (e.g., lab chow or sunflower seeds) available in a feeding tray, food hopper, or anywhere in the surroundings. The animal then advances its paws to grasp the food (bilaterally) and puts the food into its mouth and/or nibbles while *sitting*. Gerbils feed on insects. Both wild and domesticated gerbils are able to catch grasshoppers and manipulate the insect with their forepaws in a way that enables the gerbil to start feeding on the head section of its prey (Stuermer 2014, personal communication; Burley 1980; Elwood 1975, 1979; Kaplan and Hyland 1972; Roper and Polioudakis 1977; Ter-Mikaelian et al. 2012; Waring and Perper 1980; Whishaw et al. 1998).
- 1.3.5. **Food gathering** (*harvesting*): In the wild and under semi-natural conditions (e.g. outdoor enclosure at Berlin Zoo), wild gerbils and their offspring show a comprehensive pattern, clicking like clockwork, aimed at collecting or harvesting food and nesting material. It consists of the appearance of a gerbil at the burrow entrance, *rearing* to check the environment, running straight to a source of material (cereals, hay), picking up the material, running back straight to the burrow, and staying in the burrow for only a few seconds to store food or nesting material. After a few seconds, the gerbil appears again at the burrows entrance to

- perform a new “gathering cycle” (Stuermer 2014, personal communication).
- 1.3.6. **Groom** (*grooming, self-grooming, washing*): This action includes episodes of licking, biting, scratching, nibbling, and/or rubbing of an animal’s own body regions (using the mouth, forepaws, and/or hindpaws), except the genital region, which is a separate unit - see **Genital grooming**. It has been reported that the first indications of grooming appear among young gerbils aged 12 days. By day 19 or 20 (when pelage is well developed), the young engage in grooming periods similar to those observed among adults (Agren et al. 1989; Bauer 1970; Burley 1980; Crawford et al. 1981; Elwood 1975, 1979; Guimarães-Costa et al. 2007; Hendrie and Starkey 1998; Kaplan and Hyland 1972; Kleese and Hull 1980; Lejeune et al. 1998; McManus 1971; Roper and Polioudakis 1977; Reynierse 1971; Swanson 1974; Ter-Mikaelian et al. 2012; Waring and Perper 1980). See also **Mutual grooming** in the section “**Social behaviour**”.
- 1.3.7. **Sandbath** (*sand-rolling*): An animal scabbles sand on to the ventral surface with the forepaws, lowering the ventral surface on to the substrate while stretching and wriggling, rubbing the sides on the substrate, and rolling on to the dorsal surface and wriggling from side to side. Not all of these actions are always performed; the most frequent actions are scabbling and ventral wriggling. It has been suggested that this pattern serves some olfactory communicatory function, in addition to removing excess oil from the pelage (Bauer 1970; Burley 1980; Eisenberg 1967; Burley et al. 1983; Roper and Polioudakis 1977).
- 1.3.8. **Sleep** (*sleeping, quiet*): An animal has no body movement (*inactive*), its eyes shut, and may be in one of the following postures alone or in contact with other conspecifics (**huddling**): sitting with its head tucked down between the rear legs, resting on its back with legs in the air, or lying on one side of its body. It has been reported that these sleeping positions vary with temperature, e.g., at or above 30°C, an animal may sleep on its back, and above 25°C, an animal sleeps in a sitting position with its head tucked down (Burley 1980; Florez-Acevedo et al. 2010; Gulotta 1971; Kaplan and Hyland 1972; Kleese and Hull 1980; Roper and Polioudakis 1977; Waring and Perper 1980).
- 1.3.9. **Test the air**: An animal is in a bipedal standing posture (*rear*) while *sniffing* the air (Bauer 1970).
- 1.4. Stereotyped behaviour
- 1.4.1. **Gnaw bar** (*bar-gnawing, bar-chewing*): An animal grasps a bar from the enclosure (e.g., from the food hopper in the cage) between its teeth and moves its mouth up and down this bar while chewing. The animal is in a *rearing* posture and, usually, one hind leg is raised slightly and intermittently (Burley 1980; Elwood 1975, 1979; Moons et al. 2012).
- 1.4.2. **Stereotyped dig** (*digging stereotypy*): Two definitions of stereotypical digging have been coined: (1) Bouts of *digging* composed of more than 7 consecutive scratches with the front legs, which are potentially, but not necessarily, followed by or interspersed with hind leg kicks, or (2) bouts of *digging* that last longer than 12 s (Moons et al. 2012; Wiedenmayer 1996, 1997).
- 1.5. Locomotor behaviour
- 1.5.1. **Cliff behaviour** (*cliff responses, cliff-descending responses*): an animal engages in a relatively uniform sequence of responses before descending from a visual or tactual cliff. First, there are several orientation responses, which include flattening the body against the surface of the raised area (e.g., a platform) and extending the head over the edge and downward. Initial orientations are typically shallow (~0.5 in) and become deeper with time. If the animal descends, the initial shallow orientation responses are followed by deeper orientations until the nose (or vibrissae) touches the floor. Actual descent rarely occurs unless the animal touches the floor with its nose; conversely, contact with the floor is rarely made without immediate descent. Descent involves lowering the forepaws to the floor without raising the head from the deep orientation response. The deepest orientation response possible without falling from the elevated surface is approximately 2 in. Virtually all orientation responses are completed in less than 2 s. It has been reported that both visual and tactual cues regulate the descent response. On cliffs differing only in visual cues, latencies to descend are significantly lower from the shallow cliff. When cliffs differ in tactual cues only, younger gerbils show slight

- discrimination, and older animals much greater, discrimination. Finally, exposure to flat and cliff surfaces during early life (30–51 days) modify visual cliff behaviour in later stages (Collins et al. 1969; Routtenberg and Glickman 1964; Thiessen et al. 1968b; 1969b)
- 1.5.2. **Escape:** An animal's response to a given stimulus (e.g., sudden overhead visual stimulation) characterised by startle and a brief burst of high-speed running and manoeuvres that follow the onset of such stimulus, with a very short latency. It has been reported that *Mongolian gerbils* captured in the wild and disengaging themselves from restraining conditions sometimes make extreme *jumps* to escape their cages or the grip of a scientist to reach nearby cover under scrub, a tarpaulin, or in a hole, within seconds. Covered, the gerbil remains *immobile* for minutes (Stuermer 2014, personal communication; Bauer 1970; Ellard 1993, 1996; Ellard and Goodale 1988; Guimarães-Costa et al. 2007). For social interactions, see *Flee*.
- 1.5.3. **Explore** (*exploring, patrolling*): An animal seems generally active, alert, and investigative, moving from place to place more quickly and more regularly than when foraging. For instance, it has been reported that animals that are exploring occasionally stop to *sniff* the ground or *mark with their ventral glands* places that are often visited by conspecifics. In natural or seminatural enclosures of 600 m² or above, such places are typically located along territorial borders (Agren et al. 1989; Susić and Masirević 1986; Ter-Mikaelian et al. 2012; Waring and Perper 1980).
- 1.5.4. **Jump** (*jumping*): An animal pushes itself off the ground with the hind legs in a “jump-like” vertical movement. This response is normally associated with *head bobs*. In addition, extreme and instant jumps are related to panic, *flee*, and/or *escape* from predators (Stuermer 2014, personal communication). A particular form of jumping occurs among young offspring of wild gerbils (4–8 week) and among domesticated gerbils prone to *seizures*, and can be initiated by opening of cages or ultrasound (e.g. shaking of a bunch of keys). This “bouncing” behaviour consists of several rapid jumps against the wall of the cage within a few seconds; it can merge into *seizures* or harm the animal. Among the wild strain, it gradually disappears at the end of the 2nd postnatal month (Stuermer 2014, personal communication). Finally, jumping is also part of agonistic encounters - see *Offense* (Ellard 1993; Goodale et al. 1990; Henrich-Noack et al. 2011; Crawford et al. 1981; Lejeune et al. 1998; Nishiyama et al. 2011; Stuermer and Wetzel 2006; Swanson 1974; Wechkin and Cramer 1971).
- 1.5.5. **Hop:** An animal moves rapidly in short jumps. Very often, all four feet leave the ground. It has been reported that emission of ultrasonic *vocalisations* correlates with the moment at which the forepaws touch the ground. It has been reported for young gerbils that the first indication of the hopping response of adults is apparent by day 16, although movement of the hind feet is not entirely synchronous. Hopping movements become common by day 19 (McManus 1971; Thiessen et al. 1980).
- 1.5.6. **Inactive** (*immobile, freezing*): An animal has all four paws on the ground with complete cessation of movement or no gross body movement, apart from movements required for respiration, for more than 10 seconds. In defensive interactions, freezing typically lasts several seconds and is accompanied by autonomic reactions, for example defecation, exophthalmia, and/or micturition (Burley 1980; Elwood 1975; Guimarães-Costa et al. 2007; Henrich-Noack et al. 2011; Waring and Perper 1980). For encounters between conspecifics, see *Immobile-in-contact*.
- 1.5.7. **Rear** (*rearing, rear up, erect on hind legs*): An animal stands upright on its hind legs with a straight back, and both of its front paws are off the floor and may be or not in contact with a vertical surface (e.g., the wall of a cage or an arena). It has been reported that this activity sometimes occurs in a non-social context when an animal is alarmed. This behaviour often involves a more fully erect and more stable posture, and the animal may remain alert for several minutes surveying the surroundings and *sniffing* the air (Bauer 1970; Bols and Wong 1973; Crawford et al. 1981; Guimarães-Costa et al. 2007; Hendrie and Starkey 1998; Kaplan and Hyland 1972; Kleese and Hull 1980; Lejeune et al. 1998; Roper and Polioudakis 1977; Shimozuru et al. 2008; Ter-Mikaelian et al. 2012; Wechkin and Cramer 1971).

1.5.8. **Walk** (*walking, walks*): An animal moves or locomotes from one place to another. This movement is sometimes measured by the number of steps that are taken by the animal's hind legs (Crawford et al. 1981; Susić and Masirević 1986; Kaplan and Hyland 1972; Shimozuru et al. 2008).

1.6. Miscellaneous

- 1.6.1. **Alert posture** (*attention posture, sit alert*): An animal suddenly interrupts ongoing behaviour, comes to an erect position, and *sits* on two or three legs with its body tense, ears cocked, and one or two forepaws hanging in the air. This posture is typically retained for several seconds and is often accompanied by *sniffing* of the surrounding air. In some cases the head is raised and/or the posture changes to an extended *upright posture*. (Guimarães-Costa et al. 2007; Kaplan and Hyland 1972; Lerwill 1978; Walters and Glazer 1971).
- 1.6.2. **Body shake** (*wet dog shake*): An animal jerks briefly from side to side with rapid and forceful movements (Hendrie and Starkey 1998).
- 1.6.3. **Crouch**: An animal has its front paws off the ground and assumes a hunched posture, usually accompanied by lowering of the head and eye closure. In parental interactions, the males or female crouch over the pups, which usually takes the form of a dyadic interaction, i.e., female or male with pups, but not both *huddled* together with pups (Crawford et al. 1981; Prates and Guerra 2005; Hendrie and Starkey 1998; Reynierse 1971; Saltzman et al. 2006).
- 1.6.4. **Head bob** (*head movement*): Consecutive upward or downward movements of the head (having the animal's eye as a reference point for these movements) that occur in the period before an animal initiates a *jump*. Such individual movements of the head are typically separated by pauses (Ellard et al. 1984; Goodale et al. 1990).
- 1.6.5. **Object-directed**: An animal touches or manipulates an object that is available in its surroundings with its head or front paws or *sniffs* the object with its nose 1 cm or less from the object (Crawford et al. 1981).
- 1.6.6. **Roll** (*rolling*): A rapid action in which an animal rolls over on its back and makes a complete turn back to its belly. It has been

reported that rolling occasionally follows *ventral gland marking* in a sequence that may be repeated several times (Swanson 1974).

- 1.6.7. **Seizure** (*fit, convulsion*): A pattern that typically begins with cessation of ongoing activity, together with vibrissae twitching, eye blinking, flattening of ears against the head, and small muscle twitching. This initial state is followed by contractions of the anterior part of the body, crouching (often with front paws pushing against the substrate), and, later, immobility. This immobility sometimes occurs in unusual postures, for example with limbs spread out laterally or with the tail curved up over the body. Subsequently, the animal may roll over on to one side, which is often accompanied by spasms that result in random movements, for example pawing the air, slow head turns, and jerky movements of the head, limbs, and torso. At the beginning of the recovery period, animals are flexy-cataleptic, and their extremities can be moulded into permanent positions. The remaining of the recovery period is characterized by copious, sometimes bloody, salivation, Straub tail, statuesque postures, immobility, coughing and choking, repeated pawing at the nose and face, slow turnings of the head, motor arrest, retropropulsive circling, and uncoordinated locomotion. Finally, an animal may make large muscular movements that result in unusual behavioural sequences, for example *grooming, chewing, walking, circling, running, and jumping*, which are often interspersed with periods of *inactivity* and are distinguishable from normal behaviour in that the movements are irregular, violent, or abortive. Although these patterns predominate during seizures, variability has been reported in respect of the occurrence or non-occurrence of specific items, the sequence in which items occur, and the severity of the episodes (Loskota et al. 1972, 1974 provided a seizure rating based on the extent of motor involvement and the duration of the seizure and of recovery), and in respect of differences between spontaneous and provoked or induced seizures. It has also been reported that multiple seizures can occur (mild seizures usually are

- preceded or are interrupted by a severe seizure) and seizures are sometimes preceded by *vocalisations* and/or *foot-stomping* (Bertorelli et al. 1995; Buckmaster 2006; Kaplan and Miezieski 1972; Loskota et al. 1972; Loskota et al. 1974; Robinson 1968; Thiessen et al. 1968c).
- 1.6.8. **Sit** (*sitting on hind legs*): An animal rests on its hind legs, using its tail as a prop. This posture is sometimes described as sitting “spermophile-like” (Gulotta 1971; Lejeune et al. 1998).
- 1.6.9. **Sniff** (*sniffing*): Nasal investigation of any physical feature in the enclosure or surroundings or of a peer mate (e.g., during *mating*), usually accompanied by head movements (Crawford et al. 1981; Prates and Guerra 2005; Hendrie and Starkey 1998; Reynierse 1971).
- 1.6.10. **Stretch**: An animal moves its fore legs away from its hind legs with a concave back; this movement is often accompanied by yawning (Hendrie and Starkey 1998; Thiessen et al. 1980).

Social behaviour

2.1. Agonistic behaviour

- 2.1.1. **Appeasement**: An animal licks the mouth of an aggressor and rubs its rear on his/her ventral gland (Scheibler et al. 2005a, b, 2006).
- 2.1.2. **Bite** (*biting*): One animal *attacks* or hurts another with its teeth. Bites are often directed toward the neck of the conspecific and tend to occur during *fighting* and *chasing* (Roper and Polioudakis 1977; Reynierse 1971; Scheibler et al. 2005a, b, 2006; Ter-Mikaelian et al. 2012).
- 2.1.3. **Box** (*boxing, upright boxing, sparring, mutual upright*): Two animals face each other standing in an upright posture (*rear*) on their hind legs with their front paws and vibrissae in contact and push each other by means of rapid movements of the forepaws, i.e., sparring movements (Burley 1980; Halpin 1976; Hendrie and Starkey 1998; Shimozuru et al. 2008; Nyby et al. 1970; Reynierse 1971; Roper and Polioudakis 1977; Ter-Mikaelian et al. 2012).
- 2.1.4. **Chin-over**: An animal reacts to threat gestures of a dominant conspecific by placing its chin over the head of the other male (Thiessen et al. 1978).
- 2.1.5. **Close eyes**: Complete or partial closure of one or both eyes occurring in conjunction with either a submissive *crouch* or *turning away* responses (Reynierse 1971).
- 2.1.6. **Defence** (*defensive reactions/responses*): A comprehensive pattern of behaviour in reaction to threat gestures of a dominant conspecific. It includes *fleeing*, *crouching*, *vocalising*, use of *chin-over* responses, protective *rearing* postures and defensive sideways, or thrusting of forepaws toward the opponent (Hendrie and Starkey 1998; Shimozuru et al. 2008; Thiessen et al. 1978).
- 2.1.7. **Dominance**: In the context of *fighting*, an animal *chases* a conspecific and exhibits threat reactions while the other assumes submissive postures, for example *huddling* and *closing eyes* (Gallup and Waite 1970; Thiessen et al. 1970).
- 2.1.8. **Dominance-approach**: An animal *approach* is followed by submissive responses by another animal, which include *crouching*, *turning away*, and *closing eyes* (Reynierse 1971).
- 2.1.9. **Evade**: An animal turns and moves away from a conspecific that *approaches* to within one body length before physical contact is made (Hendrie and Starkey 1998). In heterosexual interactions, it has been reported that females evade male mounting attempts by running away or by adopting a *boxing* posture (Burley 1980).
- 2.1.10. **Fight** (*aggression, fighting, locked fight/fighting*): A comprehensive pattern in which two animals grip each other’s flanks in vibrissae/vibrissae and ventro/ventro contact, together with *biting*, *boxing*, pinning, pushing, kicking, rolling over, and/or leaping into the air. It has been reported that fighting is often preceded by *anogenital sniff* and/or *side-to-side* responses (Berg et al. 1975; Dunstone et al. 1972; Fisler 1977; Gallup and Waite 1970; Halpin 1976; Hendrie and Starkey 1998; Kaplan and Hyland 1972; Nyby et al. 1970; Roper and Polioudakis 1977; Ter-Mikaelian et al. 2012; Swanson 1974; Yahr et al. 1977).
- 2.1.11. **Flee**: An animal runs away from a conspecific (Ter-Mikaelian et al. 2012; Wechkin and Cramer 1971).

- 2.1.12. **Food or water restriction** (*exclusion from food or water*): An animal (aggressor) keeps another animal away from food or water by **biting** and **chasing** (Deacon 2009; Scheibler et al. 2005a, b, 2006).
- 2.1.13. **Immobile-in-contact**: An animal becomes motionless (freezes) in response to physical contact that is initiated by a conspecific (Hendrie and Starkey 1998; Shimozuru et al. 2008).
- 2.1.14. **Nose push**: An animal shoves another with the snout, which may or may not be successful in displacing or moving the other animal. If the receiver moves away, this tends to indicate that the other animal is dominant (Fisler 1970).
- 2.1.15. **Offense** (*attack*): A comprehensive pattern that includes **chasing**, grasping, **biting**, and **jumping** on a conspecific, which is sometimes alternated with attacking sideways and **boxing** postures. It has been reported that before an attack animals typically sniff the anal-genital region of their conspecific (**anogenital sniff**), exhibit piloerection, and assume a **rear** posture (Ginsburg and Braud 1971; Hendrie and Starkey 1998; Shimozuru et al. 2008; Susić and Masirević 1986; Scheibler et al. 2005a; Swanson 1974).
- 2.1.16. **Turn away**: An animal displays a turning movement away from and presenting the side of the body at an angle to the other animal (Reynierse 1971).
- 2.1.17. **Side-to-side** (*sideway posture, sideways offensive posture, sidling*): One animal turns sideways to a conspecific; the two animals stand parallel to each other in a “tense posture” with flanks pressed together. Animals usually assume a slightly concave or hunched position with the head tilted downward away from the opponent and the forepaws slightly off the ground (Burley 1980; Roper and Polioudakis 1977; Halpin 1976; Nyby et al. 1970; Swanson 1974).
- 2.1.18. **Watch**: Two animals remain motionless and face-to-face at a distance less than approximately 5 cm, which is often accompanied by conspicuous erection of the body hairs (Ter-Mikaelian et al. 2012).
- 2.1.19. **Wrestle** (*wrestling*): One animal lies over another conspecific in a supine position without **biting** (Shimozuru et al. 2008; Susić and Masirević 1986).
- 2.2. Encounters between individuals
- 2.2.1. **Anogenital sniff** (*nose/anogenital contact*): An animal **approaches** another, usually from behind, and actively sniffs its anogenital region (Halpin 1976; Hendrie and Starkey 1998; Roper and Polioudakis 1977; Shimozuru et al. 2008; Reynierse 1971; Ter-Mikaelian et al. 2012).
- 2.2.2. **Approach**: A rapid and sudden approach movement toward other animal (Reynierse 1971). See also, **dominance-approach** in agonistic behaviour.
- 2.2.3. **Chase** (*chasing, pursuit*): One animal rushes after another by more than one body length. In the context of agonistic encounters, the attacked animal **flees** by running while the aggressor follows closely behind. Chasing could be one-way (from location A to location B), two-way, and/or roles may change, e.g., animal 1 chases animal 2 from A to B, whereupon roles shift and 2 chases 1 back to A again (Agren 1984; Agren et al. 1989; Roper and Polioudakis 1977; Scheibler et al. 2005a, b, 2006; Swanson 1974; Wechkin and Cramer 1971; Yahr et al. 1977).
- 2.2.4. **Climb** (*climbing*): An animal puts its forepaw(s) on the back of a second animal and attempts to climb up, or may actually do so. It has been reported that this behaviour is related to hierarchical and sexual interactions, e.g., as part of **mount** (Agren et al. 1989; Holman and Hutchison 1982).
- 2.2.5. **Leave** (*move away*): After a period of physical contact, an animal **turns** and moves to more than one body length away from the stimulus animal (e.g., cage partner). Unlike **chase**, the stimulus animal does not follow the other gerbil (Burley 1980; Burley et al. 1983; Hendrie and Starkey 1998; Ter-Mikaelian et al. 2012).
- 2.2.6. **Mutual grooming** (*grooming other, allogrooming*): Episodes of licking, biting, scratching, and/or rubbing (**grooming**) between conspecifics in which the grooming animal makes characteristic bobbing movements of the head while its lower incisors are run through the fur of the groomee (frequently around the area of the head). The responsibility for the initiation of mutual grooming could be assigned to (1) the groomer, who commences unsolicited

- grooming usually on the head of the groomee, or to (2) the eventual groomee, who solicits allogrooming from a conspecific, using **mutual grooming solicitation** postures (Burley 1980; Burley et al. 1983; Gromov 2009, 2010; Holman and Hutchison 1982; Kaplan and Hyland 1972; Reynierse 1971; Roper and Polioudakis 1977; Waring and Perper 1980).
- 2.2.7. **Mutual grooming solicitation** (*allogrooming solicitation*): An animal solicits **mutual grooming** from a conspecific. Two postures have been described: (1) an animal (-groomee) presents its head under that of the other animal (groomer). Its head is stretched forward and lowered, and the ears are flattened against the head and the eyes closed, or (2) an animal (groomee) rolls on to its side and presents the underside of the head and neck to the other animal (Burley 1980; Gromov 2009).
- 2.2.8. **Nasal sniff** (*nose-nose contact, nose-to-nose, nosing, nasal contact, mutual sniff*): Two animals face each other and briefly touch and sniff noses, buccal cavities and/or facial areas. Sometimes the ears are flattened and the eyes are partially closed (Gromov 2009; Halpin 1976; Hendrie and Starkey 1998; Roper and Polioudakis 1977; Shimozuru et al. 2008; Swanson 1974; Ter-Mikaelian et al. 2012).
- 2.2.9. **Sniff conspecific** (*olfactory investigation*): An animal **sniffs** any area of another animal's body (in the case of parental interactions, see **Sniff pup**). This comprehensive pattern may include an olfactory inspection of the head region (see **Nasal sniff**), the ventral gland area (see **Ventral gland sniff**), or the anogenital region (see **Anogenital sniff**) and the back of the other individual (Burley 1980; Burley et al. 1983; Halpin 1976; Reynierse 1971; Yahr et al. 1977).
- 2.2.10. **Territorial acquisition and defence**: A comprehensive pattern that overall follows three phases: (1) frequent **ventral gland marking**, attraction to the sebum left by the **ventral gland marking** of other animals, and social neutrality; (2) **fighting** and the establishment of property rights; and (3) social distinction. It has been reported in artificial and seminatural observations that territorial behaviour leads to repulsion and dispersal severe enough to force territorial subordinates across a geographical barrier (Thiessen and Dawber 1972; Thiessen 1973).
- 2.2.11. **Ventral gland sniff** (*nose/gland contact, gland sniff, ventral sniff*): One animal **approaches** another from the side or from the front, pushes its nose under the ventral surface and sniffs the area of the ventral sebaceous gland, which has been reported to be present in both sexes (Batchelder et al. 2012). An animal may also sniff at the gland of the animal that is in a **rear** posture (Halpin 1976; Roper and Polioudakis 1977; Swanson 1974).
- 2.3. Sexual behaviour
- 2.3.1. **Approach to partner** (*approaching*): A male or female proceeds toward its partner to within 2 cm and sniffs his/her face or flank. This approach may be reciprocated, in which case **nosing** is mutual, or may be avoided by turning to the side or **evading**. When a male approaches, this pattern often initiates **darting** by a female, particularly if this approach is combined with investigation of the female's anogenital region or investigation of the female's pelvic-lumbar area (Burley et al. 1983; Hendrie and Starkey 1998; Holman and Hutchison 1982; Swanson 1974).
- 2.3.2. **Copulation**: A comprehensive pattern that includes **lordosis** and **invitation** among females and **mounting** and **intromissions** by males, which may be preceded by **following**. It has been reported that males may interrupt the female's activity to copulate (Agren 1984; Agren et al. 1989; Burley 1980; Kuehn and Zucker 1968; Prates and Guerra 2005; Weinandy et al. 2001).
- 2.3.3. **Copulation avoidance** (*mount avoidance*): A female poses her head toward the male, **vocalises** and/or avoids the male, and her genitals and tail are directed away; e.g., turns her body 180° and maintains a face-to-face posture (Prates and Guerra 2005; Weinandy et al. 2001).
- 2.3.4. **Copulation trials**: A female presses her tail to her bottom and thwarts the male attempting to **mount** the female (Weinandy et al. 2001).
- 2.3.5. **Dart** (*darting*): A female moves away from a male in a fast, ritualised running or **hopping** movement that differs from normal locomotion in form and in speed. A female generally

- performs a single darting run moving away from the male; however, she may dart past the male in a circular path (Burley 1980; Burley et al. 1983; Holman and Hutchison 1982).
- 2.3.6. **Ejaculation:** see *Intromission*.
- 2.3.7. **Follow** (*following, sexual pursuit*): A male moves behind the female maintaining close proximity with her hindquarters. Male following commonly accompanies female *darting* and often precedes *mounting* attempts by the male (Agren 1984; Agren et al. 1989; Elwood 1975; Burley 1980; Hendrie and Starkey 1998; Ter-Mikaelian et al. 2012).
- 2.3.8. **Genital grooming:** An animal licks its own genital region. This pattern occurs among males after almost every intromission and quite infrequently before genital contact (Burley 1980; Holman and Hutchison 1982).
- 2.3.9. **Invite** (*invitation*): A female *approaches the partner*, typically sniffs his nose (*nasal sniff*), turns around and walks away a few steps (*darting*), then stops in *present posture*. If the male does not respond by *following* and *mounting*, the female might repeat this pattern (Agren 1984; Agren et al. 1989).
- 2.3.10. **Intromission:** A male's *mounting* of a female, which is accompanied by penetration of the vagina during a final, deep pelvic thrust, when one hind leg is often raised off the floor. The pattern is completed as the male dismounts with a forcible springing motion away from the female (often propelling the female forwards along the ground). Intromissions differ from *mounts* in that these movements include penetration of the vagina during the final deep pelvic thrust. In addition, *ejaculations* are distinguished from intromissions by the greater depth of the final thrust and by the longer duration of the ejaculatory penetration (Burley 1980; Kuehn and Zucker 1968).
- 2.3.11. **Jerk:** As part of *mating*, a female releases herself from the grip of the male by shaking her back in one quick motion and often turning 180° (Ter-Mikaelian et al. 2012).
- 2.3.12. **Lordosis:** A female remains in front of a male with bent hind paws, a lifted tail, marked elevation of the perineal region, and slight raising of her head, which gives rise to a characteristic concave outline along the spine. Lordosis is readily assumed from the *present posture* in response to *mounting* or *anogenital sniff* by a male (Burley 1980; Roper and Polioudakis 1977; Ter-Mikaelian et al. 2012; Weinandy et al. 2001).
- 2.3.13. **Mate** (*mating*): A comprehensive pattern that consists of short and frequent *mounting* attempts by a male, which are separated by periods of *genital grooming* and by sporadic periods of energetic *chasing*. The female usually resists the initial advances of the male; however, as the male becomes more active, the female allows copulation to occur. The female exhibits *lordosis* during copulation and permits the male to mount many times. A series of *intromissions* culminates in *ejaculation*, which is followed by a period of *grooming, genital grooming*, and sexual refractoriness (Gulotta 1971).
- 2.3.14. **Modulated vocalisation:** Low-intensity, modulated upsweep sounds (median duration, 56 ms) that begin at 28 kHz, extend up to 38 kHz and are produced during the *mounting* period (Holman 1980, 1981).
- 2.3.15. **Mount** (*mounting*): A male grips a female by placing his fore paws on her hindquarters while oriented posteriorly to her. During mounting, the male may rapidly palpate the female's flanks with alternate movements of the fore paws. Typically, males initiate a mounting episode by *following* females persistently and sniffing their genitalia (i.e., *anogenital sniff*). It has been reported that most mounts occur outside the nest (Burley 1980; Prates and Guerra 2005; Roper and Polioudakis 1977; Swanson 1974; Ter-Mikaelian et al. 2012).
- 2.3.16. **Piloerection posture:** A female's back faces a male, and the skin of her lumbar region moves to cause conspicuous erection of the hairs of the lower back (Burley 1980; Burley et al. 1983).
- 2.3.17. **Present posture:** A female assumes a low crouching posture, with all four feet firmly positioned on the ground. This posture is often adopted at the end of a *dart*; however, the female's hindquarters are oriented toward the male (Burley 1980; Burley et al. 1983).
- 2.3.18. **Unmodulated vocalisation:** long ultra-sounds tones (median 145 ms) of 26 kHz. These high intensity sounds are produced during the post-ejaculatory period, although these sounds are infrequently produced

during the mounting and the pre-mount period (Holman 1980, 1981).

- 2.3.19. **Upsweep vocalisation:** A low-intensity, short-duration (approximately 20 ms) vocalisation that begins at 26–28 kHz and ascends to 35 kHz. This vocalisation is emitted by the male intermittently throughout the sexual interaction but predominantly during the pre-mount phase (Holman 1980, 1981; Holman and Hutchison 1982).
- 2.4. Parent and offspring behaviour
- 2.4.1. **Attack pup** (*infanticide, cannibalize pup, harm pup*): a parent *bites* and/or dismembers a pup. It has been reported that, under laboratory conditions, once a pup is bitten, it is typically consumed (Elwood and Ostermeyer 1984a, b; Saltzman et al. 2006, 2008)
- 2.4.2. **Care of the offspring:** A comprehensive pattern that includes *nursing* and being *in contact with pups*, as well as periodic *pup grooming* that is composed of licking the region of genitalia and stomach, licking off urine, and licking the sides, back, head and other parts of the pup's body (Gromov 2009).
- 2.4.3. **Crouch over pups:** see *Crouch*.
- 2.4.4. **Huddle between pups:** A pup lies in contact with other pup(s) but is not *nursed* (Kaplan and Hyland 1972).
- 2.4.5. **In nest:** Any portion of the animal's body is in contact with the nest (Burley 1980; Elwood 1975, 1979; Kaplan and Hyland 1972; Kleese and Hull 1980).
- 2.4.6. **Leave pup** (*away from pup*): A parent moves and remains away from its pup(s) (Saltzman et al. 2006; Kaplan and Hyland 1972).
- 2.4.7. **Mutual grooming** (*grooming other, allogrooming*): Episodes of licking, biting, scratching, and/or rubbing (*grooming*) among parents and young. Specifically, in *pup grooming*, this behaviour includes licking the region of the genitalia and stomach, licking off urine, and licking the sides, back, head, and other parts of the pup's body. It has been reported that pup grooming, specially licking, only occurs in the nest, usually when the parent is in a *crouching* posture (Elwood 1975, 1979; Gromov 2009, 2010; Kaplan and Hyland 1972; Prates and Guerra 2005; Roper and Polioudakis 1977; Saltzman et al. 2006; Waring and Perper 1980).
- 2.4.8. **Nurse pup(s):** A female suckles one or more pups (Waring and Perper 1980).
- 2.4.9. **Nursed:** A pup lies under the mother in nursing position and feeds by sucking from her teat (Kaplan and Hyland 1972).
- 2.4.10. **Pup groom:** see *Mutual grooming*.
- 2.4.11. **Pup lick:** see *Mutual grooming*.
- 2.4.12. **Pup mouthing:** see *Mutual grooming*.
- 2.4.13. **Pup movement:** A pup changes position while being *nursed* or *huddling* (Kaplan and Hyland 1972).
- 2.4.14. **Pup vocalisation** (*pup squeal*): see *Vocalisation*.
- 2.4.15. **Retrieve:** An animal lifts and carries a pup in its mouth or pulls a pup with its paw (Elwood 1975; Kaplan and Hyland 1972).
- 2.4.16. **Sniff pup:** An animal moves and actively twitches its nose over a pup (Elwood 1975, 1979; Waring and Perper 1980).
- 2.4.17. **With pup** (*body contact, on pups*): An animal lies in contact with or right next to one or more pups (Elwood 1975; Kaplan and Hyland 1972).
- 2.4.18. **With mother:** A pup is in contact with or is adjacent to its mother (Kaplan and Hyland 1972).
- 2.5. Miscellaneous
- 2.5.1. **Disperse and hide:** A group of animals suddenly bolts and hides after an unexpected stimulus (e.g., a loud noise) and/or an alarm call that is produced by a conspecific, such as *squeals* or *foot-stomping* (Ter-Mikaelian et al. 2012).
- 2.5.2. **Huddle:** An animal nestles with one or more conspecifics (Gromov 2009). See also *Huddle between pups*.
- 2.5.3. **Orientate to conspecific:** Animal turns its head and body as necessary towards another animal that *approaches* to within one body length (Hendrie and Starkey 1998).

Discussion

The terminology presented here is an updated and standardised catalogue of many units of the behaviour of *M. unguiculatus* with a wide range of domains (communication, construction and maintenance of the nest/burrow, maintenance activities, locomotor behaviour, stereotyped behaviour, agonistic behaviour, encounters between individuals, sexual behaviour, and parent and offspring behaviour). These definitions were systematically developed by searching, identifying, and compiling information from

the varied research literature that has reported use of this species as a behavioural model during the last 58 years (references identified in the literature review ranged in date from 1964 to 2012).

Recognising the importance of detailed and standardised terminology in behavioural research and the lack of a comprehensive and detailed source of the behaviour of *M. unguiculatus* in different settings, the primary purpose of this catalogue is to provide comprehensive information about the behaviour of this species under natural and seminatural conditions and captivity on the basis of observations that many laboratories around the world have reported in different amounts of detail over the last five decades (irrespective of the wide range of research purposes). Although similar efforts have been successfully conducted for other popular animal models, for example zebrafish (Kalueff et al. 2013), this is, as far as we are aware, the first such attempt for *M. unguiculatus*. In this regard, we expect this catalogue to undergo regular revisions in the future as:

1. behavioural information regarding this species continues to grow;
2. the glossary begins to be adopted as a common reference guide for specialised literature; and
3. input from experts on the behaviour of *M. unguiculatus* (i.e., researchers with first-hand experience on different units of behaviour) is used to improve the current definitions or add units of behaviour not yet present.

We expect several positive outcomes from this glossary:

1. improved interpretation of *M. unguiculatus* behavioural data that have already been published and will continue to emerge from different research fields;
2. encouragement of laboratories that are currently using this animal model, or are considering this animal for their research, to provide more systematic and standard descriptions of the behaviour;
3. favouring of cross-species comparisons and behavioural modelling; and
4. helping researchers who are beginning to work with this species by saving much of the time and effort involved in developing their own definitions of behaviour.

We believe this catalogue, by contributing to our comprehension of the repertoire of behaviour of a versatile animal model, will promote understanding of other related phenomena within and across species, including normal and pathological human brain functioning.

We expect the research community currently using or planning to use *M. unguiculatus* as a behavioural model to benefit from additional efforts related to the development of the present catalogue.

- First, we have adapted this glossary for *JWatcher 1.0 + video*, highly versatile freeware designed by DT Blumstein, JC Daniel and CS Evans (University of California—Los Angeles & Macquarie University—<http://www.jwatcher.ucla.edu>—Blumstein and Daniel 2007) for scoring and analysis of behaviour. Thus, researchers interested in using the catalogue with this free software may obtain the necessary files (global and focal behavioural definition files), on request, without any charge.
- Second, the catalogue is currently being uploaded to <http://www.EthoSearch.org>, which is a joint initiative of the Institute of Museum and Library Services (IMLS), the Lincoln Park Zoo, and Binghamton University. The purpose of EthoSearch is to support efforts in comparing and contrasting species-specific ethograms (e.g., by promoting standardisation of data collection), to enable comparison of ethograms for different species, to serve as a repository for researchers to upload new ethograms for use by colleagues, and to enable database searching according to species/taxon, specific behaviour, categories of behaviour, or types of behaviour. More important, all of these resources are open-access.

We would like to suggest some lines of research that may benefit substantially from incorporation of this catalogue.

- First, considering the importance of evidence of behaviour when assessing and making decisions regarding animal welfare (Beaver 2010a, b; Broom 2010), this glossary could be used in research that focuses on the management and well-being of *M. unguiculatus* in captivity, specifically in terms of investigating relationships between a specific unit of behaviour and other normal and pathological biological functions (Waiblinger and König 2004).
- Second, a series of studies have reported important differences between the morphology (e.g., body length, weight, and brain mass) and behaviour (occurrence of seizures, stereotyped digging, arousal, hearing, and tameness) of wild *M. unguiculatus* trapped during an expedition in Mongolia in 1995 and a laboratory strain bred in captivity since 1935 (Eckrich et al. 2008; Gleich et al. 2000; Stuermer and Wetzel 2006; Stuermer et al. 2003, 2006). Although one of the most relevant implications of such findings is the possibility that the strain currently kept in most laboratories throughout the world has become domesticated, this research has, so far, encompassed only a few of the behavioural traits of *M. unguiculatus*. Accordingly, we suggest that a relevant endeavour across laboratories consists of the continued more systematic exploration

of behavioural differences between strains of gerbils. In this regard, a comprehensive catalogue of the type provided here is not only an excellent tool but also a basis for directing this type of effort.

- Finally, to the best of our knowledge this catalogue is the first time methodology designed for conducting and reporting systematic literature reviews (Petticrew and Roberts 2006; PRISMA statement—Liberati et al. 2009; Moher et al. 2009) has been adapted and implemented successfully for this type of research effort. On the basis of our experience, this approach seems to be versatile and could be implemented for developing similar comprehensive and updated sources of information for other animal models. Thus, we encourage researchers to consider the continued expansion of the possibilities of this methodological approach, which has gained substantial recognition across basic, applied, and translational research conducted in diverse scientific fields.

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Appendix A

Example of the table that was used for data extraction.

Article No.: 10		
Extracted by: Carlos		
Title: <i>Pair formation in the Mongolian gerbil.</i>		
Author(s) and year: Agren (1984)		
Source: <i>PsycINFO</i>		
Behaviours	Information to be extracted	Details
Behaviour 1	Name(s)/Label(s)	Chasing
	Description	One animal rushed after another.
	Source(s) cited	None.
Behaviour 2	Name(s)/Label(s)	Invitation
	Description	The female approached a male; she usually sniffed his nose (naso-nasal coronet), turned around and walked away a few steps (darting), then stopped in the present posture (Burley 1980). If the male did not respond by sexual pursuit and mounting, the female might repeat the actions.
	Source(s) cited	Burley 1980 (darting)
Behaviour 3	Name(s)/Label(s)	Sexual pursuit
	Description	The male followed the female.
	Source(s) cited	None.
Behaviour 4	Name(s)/Label(s)	Copulation
	Description	This behaviour included lordosis in females and mounting by males, preceded or not by sexual pursuit (Kuehn and Zucher 1968).
	Source(s) cited	Kuehn and Zucher 1968

Appendix B

Example of the compilation of different sources that described *nasal sniff* between individuals.

Category: <i>Social behaviour</i>		Subcategory: <i>Activities during encounters</i>
	Information	Description
Source 1	Name(s)/Label(s)	Nose/nose contact
	Description	... animals reaching tentatively towards one another. Sometimes the ears were flattened and the eyes partly

		closed...
	Source(s) cited	None.
	Reference:	Roper TJ, Polioudakis E (1977) The behaviour of Mongolian gerbils in a semi-natural environment, with special reference to ventral marking, dominance and sociability. <i>Behaviour</i> 61:207-237
Source 2	Name(s)/Label(s)	Nose-to-nose
	Description	...two animals face each other and briefly touch noses.
	Source(s) cited	None.
	Reference:	Halpin ZT (1976) The role of individual recognition by odors in the social interactions of the Mongolian gerbil (<i>Meriones unguiculatus</i>). <i>Behaviour</i> 58:117-130
Source 3	Name(s)/Label(s)	Nose-sniff
	Description	Sniffing at the nose and facial area of the unfamiliar male.
	Source(s) cited	None.
	Reference:	Shimozuru M, Kikusui, T, Takeuchi Y, Mori Y (2008) Effects of isolation-rearing on the development of social behaviors in male Mongolian gerbils (<i>Meriones unguiculatus</i>). <i>Physiol Behav</i> 94:491-500
Source 4	Name(s)/Label(s)	Nasal sniff
	Description	Nose-to-nose contact, often performed from a head-on approach. Sometimes the ears were flattened and the eyes partially closed.
	Source(s) cited	None.
	Reference:	Ter-Mikaelian M, Yapa WB, Rübsamen R (2012) Vocal behavior of the Mongolian gerbil in a seminatural enclosure. <i>Behaviour</i> 149:461-492
Source 5	Name(s)/Label(s)	Nose sniff
	Description	Sniffing at the nose and buccal cavity area of the stimulus animal.
	Source(s) cited	None.
	Reference:	Hendrie CA, Starkey NJ (1998) Pair-bond disruption in Mongolian gerbils: Effects on subsequent social behaviour. <i>Physiol Behav</i> 63:895-901
Source 6	Name(s)/Label(s)	Nose
	Description	Not reported
	Source(s) cited	None.

	Reference:	Swanson HH (1974) Sex differences in behaviour of the Mongolian gerbil (<i>Meriones unguiculatus</i>) in encounters between pairs of same or opposite sex. <i>Anim Behav</i> 22:638-644
Source 7	Name(s)/Label(s)	Naso-Nasal Contact
	Description	Not reported
	Source(s) cited	None.
	Reference:	Gromov VS (2009) Interactions of partners in family pairs, care of the offspring, and the role of tactile stimulation in formation of parental behavior of the Mongolian gerbil (<i>Meriones unguiculatus</i>) under laboratory conditions. <i>Biol Bull</i> 36:479-488