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Small Prey Species' Behaviour and Welfare: Implications for Veterinary Professionals

E. Anne McBride, BSc, PhD, Cert.Cons., FRSA, HonMem BVNA
School of Psychology
University of Southampton
Highfield
Southampton
SO17 1BJ
Email: amcb@soton.ac.uk
Tel: 07771 625419 mob; Day time 02380 597483 / 02380 679445

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Summary

People have obligations to ensure the welfare of animals under their care. Offences under the UK Animal Welfare Act (HMSO 2006) are acts, or failures of action, causing unnecessary suffering. Veterinary professionals need to be able to provide current, scientifically-based prophylactic advice, and respect the limits of their expertise.

The ethical concept of a life worth living and the Five Freedoms are core to welfare (FAWC 2009; Broom and Fraser 2015). Behaviour is a central component, both influencing and influenced by physical health. Keepers of small prey mammals (SPM) frequently misunderstand their behaviour and how to meet their needs.

This review provides insight into the physical-social (external) and the cognitive-emotional (internal) environments of SPM, contextualised within an evolutionary perspective. This is extrapolated to captivity and practical suggestions given for meeting behavioural freedoms and enhancing client understanding and enjoyment of their animals, thereby improving welfare for both.

Keywords: Behaviour, Welfare, Medicine-General, Rodents, Rabbits, Exotics

1. Introduction

Understanding normal behaviour is central to veterinary diagnosis, patient monitoring, and provision of appropriate prophylactic advice and also enables keepers to meet welfare obligations (Fox 1970; Roshier and McBride 2012a; Payne *et al.* 2015; McBride 2016). Behaviour change is often the first sign of illness or injury as behaviour references the animal's emotional and physical state and how it is coping with its environment (Broom and Fraser 2015). Compromised welfare indicators are physical and behavioural (Poole 1997; Wűrbel 2001; Olsson *et al.* 2003), including behavioural inhibition, apathy, restlessness, changes in eating, grooming, repetitive and aggressive behaviours (Abou-Ismail and Mahboub 2011; Magnus and McBride 2017b). Yet, the layperson may mis-interpret such behaviours, inappropriately labelling them as 'amusing', 'wild' or 'unhandleable' character traits or vices (McBride 2000), or as normal behaviour (Packer *et al.* 2012). Welfare concerns may only be detected when behaviour becomes problematic for the human, if they then seek help. However, keepers may not seek help. For Small Prey Mammals (SPM) kept in cages, the response may be to minimise interaction, resulting in further reduced care (Magnus and McBride 2017a).

The SPM of interest herein are the domestic (European) rabbit (*Oryctolagus cuniculus*) and rodents. Over 2 million are kept as pets in the UK and 29.3 million across Europe (PFMA 2014). Millions more are kept as Use animals (laboratory, breeding or farmed) (Home Office 2015; Wilkins *et al.* 2015).

For decades, SPM have contributed extensively to medical and behaviour research (see e.g. Watson 1913) including developmental, aging and Alzheimer's disease (Ingram 1988; Crystal 2009; Chaby *et al.* 2015, Hawkins *et al.* in press) and testing of emotional and behavioural effects of psycho-pharmacological products (De Boer and Koolhaas 2003) including anti-depressants (Cryan and others, 2002). More recent is the growing body of research into their welfare needs, preferences, emotional lives, learning and cognitive abilities (Wemmer and Fleming 1975; Panksepp 1998; Pearce 2008; Mench 2012; Wynne and Udell 2013).

Evidence shows we underestimate SPM sentience, individuality and the effects of methods used in their husbandry, management and human interactions; with implications for welfare and the validity of research utilising animal models (Wűrbel 2001; Olsson *et al.* 2003; Hubrecht 2014). For example, it is a common perception that traditional handling practices do not present a problem in respect of the animal's welfare. However, recent research reveals that the method used can radically alter the level of distress an animal suffers. Stuart and Robinson (2015) showed that the stress of being injected is significantly reduced if the rat's (*Rattus norvegicus*) body is fully supported, with the head inclined upwards. Roughan and others (2015) found carrying mice (*Mus musculus*) by their tails, as opposed to cup handling, compromises recovery from surgery. Future research may highlight other areas where current methods can be improved and made less aversive. Meeting welfare needs and thereby avoiding future health and behaviour issues, means applying knowledge of normal organic and behavioural functioning to all aspects of husbandry and management.

Knowledge alone does not engender behaviour change (Ajzen 2005). Motivation to change behaviour, in this case to undertake appropriate husbandry and management, requires consistency between a person's cognitive (belief/knowledge) and emotional aspects of their attitudes (Bohner and Wänke 2002). The cognitive aspect encompasses education; increasing knowledge of, and thus belief in, animal sentience. This facilitates an emotional (empathic) understanding of the ***animal's*** perspective (Coleman *et al.* 1998, Coleman *et al.* 2000; Hemsworth 2004; Crawford 2011; Wilkins *et al.* 2015), important for assessing and maintaining welfare (Morton *et al.* 1990; Nuffield Council of Bioethics 2005). Finally, actual and sustained behaviour change only occurs if the person considers it feasible, relatively easy, and will be successful (Ajzen 2005). Regarding welfare provision, success may be evidenced by improvements in the animal's health and behaviour, which reinforces the keeper's attitude and behaviour (Hemsworth and Barnett 2000). Thus, when suggesting welfare improvements, the keeper's goals and constraints need to be considered.

This review introduces SPM via the inextricably linked physical-social (external) and the cognitive-emotional (internal) environments. Comparing natural, free-living with 'captive' conditions enhances comprehension of animal needs, enabling knowledge-based, pragmatic approaches to improving welfare. Where known, research evidence is referenced, otherwise proposals are based on critical, parsimonious synthesis of current knowledge (Morgan, 1906). The basic principles discussed can be extrapolated across the SPM to other vertebrates (Yeates 2017), and probably beyond (Gherardi 2009; Hovarth *et al.* 2013). The aim is to assist professionals in providing appropriate advice, often to lay persons of various ages and backgrounds, and thereby stimulate further interest and understanding of SPM.

2 The Rodents and Rabbits

Of the 4000+ known mammal species, 24 are rabbits (Dickenson 2013) and 2000+ are rodents. Rodents have evolved on all continents, except Antarctica (UCMP n.d.). The few species kept in captivity originate from diverse habitats and therefore have diverse habits (Searle 1996). For example, the Syrian (Golden) hamster (*Mesocricetus auratus*) and Mongolian gerbil (*Meriones unguiculatus*) come from semi-desert conditions (hot days, cold nights); chinchilla (*Chinchilla chinchilla*) from high altitude, arid mountainsides; guinea-pig (*Cavia porcellus*) from temperate grasslands, and Siberian chipmunk (*Eutamias sibiricus*) and Siberian hamsters (*Phodopus sungorus*) from cold arctic forests and steppes respectively (Yeates 2017). The European rabbit, rat and mouse are particularly adaptable species. For millenia, they have exploited man-made habitats, travelling with us to various environments across the globe (Burt 2006; Dickenson 2013; Carroll 2015).

2.1 Evolution and Domestication

It is equally important to understand the natural origins of SPM considered as captive wild species (e.g. chipmunk (S*pps)*, degu (*Octodon degus*)) (Schuppli and Fraser 2000; CAWC, 2003) and of those 'highly domesticated' species, as domestication has caused little change to them physically or behaviourally (Berdoy 2002; Wolff and Sherman 2007; Meredith and Delaney 2010; Tynes 2010; Brandão and Mayer 2011).

Species evolve in response to environmental selection pressures; weather, substrate, predators and resource availability; food, mates, safe resting and nesting sites. This results in physical and behavioural phenotypes adapted to the ecological niche (Alcock 2013). Thus SPM species differ in size, sociality, mating strategies, young (precocial or altricial), and parenting system (Gubernick and Klopfer 1981; McBride 1986, 1988; Wolff and Sherman 2007). Within a species, variation in genotype and individual experience interact and enables population flexibility in a changing physical environment and longer term species' survival (Dawkins 1976, 1986; Pough 1989; Hastings 1996). For example, inherited predisposition to nervousness-confidence (Oddist *et al.* 1969; Broadhurst 1975; Crusio *et al.* 2013) may be modified by direct or vicarious learning (Boyd and Richerson 1990; Pearce 2008) and small differences can have substantial effects, as on brain development and cognitive ablities (Bredy *et al.* 2004). Indeed, studies of rodent development evidences how subtle differences in maternal care, such as the amount of licking of neonates, the social environment and human handling can profoundly effect adult behaviour and emotional reactivity (Cirulli *et al.*, 2010; Czerwinski *et al.* 2016). This has implications for the choice and care of breeding stock, whether offspring are destined as pets, labraotory animals or other, and having due regard for the rearing environment, transport and relocation, as from breeder to pet shop for example. There is a need here for further research to develop welfare friendly protocols.

Each species has specific dietary, physical and social environment requirements (Wolff and Sherman 2007), with individuals differing in their characters and preferences. For SPM, captivity is inevitably a compromise for welfare in terms of space, complexity and limiting the animal's opportunities to choose what to do, when and where (Broom and Fraser 2015; Yeates 2017). To try and ameliorate these constraints we need to consider what it is to be both small and a prey animal.

2.2. Implications of being a small prey species for welfare

Many SPM are only a few centimetres high when on all fours and even when rearing bipedally, at full stretch, they are approximately 100 times shorter than a UK adult (Hatton 2013). Larger rabbits may reach a metre, guinea pig or rat 30 -33cms (Reinhardt and Reinhardt 2002), and Golden hamsters 16cms (Kuhnen 2002). This means their perspective of the environment is different from ours, impacting on their experience of where and how they are housed and handled and how they may perceive humans. For example, the sights, sounds, light levels and scents reaching an animal caged near the floor may be quite different from those in cages located at human face height. We may not consider how objects in front of a cage may affect visibility or cast ultrasonic sound shadows (Hanson 2012), or how a human face or hand may not be seen as connected to the 'whole' person (McBride 1996).

Predation is the major selection pressure for SPM. They are hunted from the air, on the surface and below ground by birds, mammals and reptiles. Predation risk influences SPM behaviour. This is often mis-interpreted, as humans typically assess what is a threat from the human, not the animal's, perspective. Our intentions are irrelevant, from the animal's viewpoint a threat may be a fast-moving hand or a burst of laughter.

When SPM detect potential danger they freeze, blending into the surroundings to avoid attracting attention – predators being highly attuned to movement (Rochlitz 2007). If the threat comes closer, SPM will flee, ideally to a place of safety. If caught, they fight for their life, showing defensive aggression, or employ a final 'avoidance of death' strategy, namely tonic immobility or 'playing dead'. Being lifted, held around the back/neck area, or laid on their back are innately frightening experiences, associated with the predator's grasp.

In tonic immobility the animal appears dead, due to profound motor, not sensory, inhibition. It is highly stressed; very alert to any escape opportunity and able move rapidly (Thompson *et al.* 1981; Farabollini *et al.* 1990; McBride *et al.* 2006 ; Marx *et al.* 2008 ; McBride 2015). Also known as dorsal immobility response (Everitt 2014) this is often mistaken as a state of deep relaxation (e.g. Bunny Takes a Shower) and inappropriately advocated as a way of bonding. Hawkins *et al.* (2008) advise that it can be suitable for examination or non-invasive procedures, but not as a replacement for sedatives, analgesia or anaesthetics.

Except when neo-natal, SPM would only experience being moved in space in a dangerous situation; when caught by a predator, or if extreme weather moves the nest. Given that, it is not surprising that being transported in cages / carry-boxes is very stressful. Dallman *et al.* (2006) found that even moving rats in their home cage within and between rooms caused stress-induced hyperthermia lasting over an hour. They advise a miniumum one hour habituation period post transportation, applicable to patients coming to the veterinary surgery. Providing a consistent cue, such as a word or gentle tap on the cage prior to lifting it, may reduce the initial startle reaction and thus overall stress (Hawkins *et al.* in press), as will carrying and moving the cage as smoothly as possible. For larger animals, such as rabbits, where a separate transport cage is used, this should be part of the normal environment in order to increase familiarity with it and thereby reduce stress. For captive SPM handling is inevitable and doing so may be an important aspect of ownership, and appropriate methods can reduce stress (Bradbury and Dickens, 2016). It is not appropriate to lift animals by the neck scruff, tail or by grabbing/squeezing around the abdomen/diaphram. SPM can learn to associate hands with food and trained to climb onto and be gently lifted in cupped hands (Hurst and West 2010), larger species to approach to sit on a person's lap to be stroked, or lifted with the body weight fully supported and fingers gently preventing jumping should they be startled (O'Meara 1998; McBride 2000, 2014; Buseth and Saunders 2015). These methods are best employed from the beginning, but form the basis of behaviour modification to rehabilitate animals who are wary and/or aggressive when handled.

When educating keepers about SPM welfare, an understanding of their sensory abilities is an important component.

2.3 Sensory Abilities

The senses are essential to survival, enabling the detection and avoidance of danger and the location of resources. Information gathered about the physical and social environment form the basis of behavioural choices; to remain in the same behavioural state, or interact with pleasant, appetitive stimuli, or avoid / escape from unpleasant or dangerous stimuli (Pearce 2008). In this way physical and psychological homeostatsis is maintained. Anxious and frightening situations are avoided and energy is spent in pleasureable and relaxed activities such as foraging, socialising, playing, sleeping, eating and grooming (Panksepp 1998).

Senses facilitate communication, informing others about the environment and about oneself, transmitted through various media, notably sight, sound, touch and scent. Though clearly important to SPM communication, there is limited research into touch and scent (e.g. Barnett 1963; Berdoy 2002;

Wolff and Sherman 2007) with more into the role of sound, particularly ultrasound (e.g. Sales and Pye 1974; Long 2007, 2009; Panksepp 2007) and visual signals. For example, recent work into pain and analgesia has revealed clear visual signals and the development of reliable species-specific Facial Grimace Scales (Langford *et al.* 2010; Keating *et al.* 2012; Oliver *et al.* 2014; Miller and Leach 2015); useful resources for both owners and professionals.

SPM senses are adapted to their natural environment and associated pressures. Understanding SPM perception and communication is crucial to improving housing and management. There are several useful sources regarding SPM senses including for mice (Sherwin 2002; Olsson *et al.* 2003), rats (Burn 2008), gerbil (Waiblinger and König 2004), rabbit (Manning *et al*, 1994; Knott 2014). Here only general points are noted.

2.3.1 Vision

SPM eyes are located laterally, slightly above the midline (see Figure 1), giving a visual field of approximately 300^o (lateral) and 180^o (dorsal) (Knott 2014). This wide visual field compromises binocular depth perception. SPM judge depth and distance using motion parallex, moving their head to provide different retinal images (Legg and Lambert 1990). Bulging eyes is a sign of stress and Knott (2014) postulates this may extend the binocular field improving judgement of threat location. Wallace *et al.* (2013) placed minaturised cameras on rats' heads, discovering that, irrespective of head movements, rats' eyes move separately in opposing directions in both horizontal and vertical planes, giving constant visibility above the head. This adaptation probably evolved to detect aerial predators and is likely common across SPM. Of course, it enables detection of other threats from above; falling objects or a human hand. It is worth noting that, as in dogs (*Canis lupus familiaris*), the visual field is compromised by excessive hair around the head and/or a flattened (brachycephalic) skull shape, as seen in some rabbit breeds (Miller and Murphy 1995; McGreevy *et al.* 2003).

Predation affects daily activity rhythms. Most SPM are crepuscular or nocturnal, spending daylight hours in comparative safety below ground, in the dark, or in places of deep shade, where they are camouflaged. They see in the ultra-violet range, but have little need for colour vision, though rats can see green and mice are affected by red light (Wersinger and Martin 2008). All SPM so far studied are light-sensitive. Light over 100 lux is aversive to pigmented rats, and albino rats avoid light of 25 lux (Lockard 1963; Schlingmann *et al.* 1993; Van den Broek *et al.* 1995) and can suffer retinal damage from light levels of 60 lux (Semple-Rowland and Dawson 1987; Castelhano-Carlos and Baumans 2009). Bright light detrimentally affects play behaviour. Daily exposure of several hours supresses circadian sleep-wake rhythms and increases corticosterone levels; keeping rats in such conditions is used as an experimental model of chronic stress (Castelhano-Carlos and Baumans 2009). Ideally, SPM nocturnal time would be truly dark, as even levels as low as 5 lux of white light have been shown to affect activity and cause increased anxiety and depressive behaviours in mice (Bedrosian *et al.* 2013). However, in order to coincide with and enable human activity, it is recommended that nocturnal species are kept on reverse daylight cycles, in conditions of around 210 lux to provide for human vision, with the animals having places to hide from the light source (Castelhano-Carlos and Baumans 2009). Sodium, not white, light seems to provide a suitable compromise between these human and SPM needs (McLennan and Taylor-Jeffs 2004). Abrupt changes between light and dark conditions also have been found to have aversive effects on daily activity rhythms, and it is recommened to use dimmer switches to simulate twilight and dawn (Kavanau 1969).

Diurnal species, for example the degu, have been shown to have more colour vision, seeing a wider range of the spectrum, and to tolerate more intense light levels. Indeed the shift from predominately rod (night) to cone (daylight) vision requires levels above 300 lux in this species (Jacobs *et al.* 2003).

Lights differ in wavelength and irradiance (Gehrmann 1987). Currently, little is known of the effects on SPM of ultra-violet (UV) and full spectrum lighting, though the latter is likely important for crepuscular and more diurnal species such as degu, guinea pig and chinchilla. Light-emitting diodes (LED) affect SPM, and can be detrimental to welfare depending on colour and when used (Dauchy *et al.* 2015; Dauchy *et al.* 2016).

A further important consideration is the effect of light flicker. The critical flicker fusion frequency (CFF) indicates how fast an eye can process a flash of light and thus how animals perceive visual changes in the environment. It is suggested that this is higher in species with high metabolic rates and small body size (Healy *et al.*2013). Other factors thought to be influential in contributing to inter-specific differences are the natural habitat, such as wooded or open environment, and whether the species is active in low or high light level conditions. A higher CFF means the animals see in 'slow motion'. What we percieve as the rapid movemet of our hand as we reach to catch them, they see in much slower time frame. Thus higher CFF gives SPM more opportunity of escape and is evolutionarily advantageous. There is limited data on CFF values for SPM, namely 24 Hz for rabbits (Schneider, 1968), 39 Hz for rats and 50 Hz for guinea-pigs (Healy *et al*. 2013). Of course, predators too have evolved to have high CFF to facilitate catching prey with CFFs of 55 Hz in the cat (*Felis catus*), 80 Hz in the dog and 45 Hz in the arial predator, the Great Horned owl (*Bubo virginianus*) (Healy *et al.* 2013).

CFF is important, particularly where fluorescent lighting is used in animal housing. Human CFF is 50-60 Hz. We register lights that flicker above 50-60 times per second as continuous and constant. We find lights that flicker below 50 Hz stressful, and these can cause eye strain and headaches. Fluorescent lights start to flicker below 50Hz after about 7000 hours of operation, equivalent to 583 days at a 12:12 hour light:dark cycle (Brundrett 1974). Animals too can suffer chronic stress in conditions of light flicker below their CFF values (Evans *et al.* 2012). A parsimonious approach would be to consider alternative lighting, replace fluorescent lightbulbs regularly and ensure all animals have the opportunity to escape from light sources.

2.3.2 Hearing: Ears and Vibrissae

When young and healthy, humans hear between 20Hz to 20KHz at 60dB. At 10dB sensitivity decreases and the range narrows to 250Hz to 8.1KHz. Different SPM have different frequencies to which they are especially sensitive, that is hear particularly clearly at 10dB (Heffner and Heffner 2007). These reflect adaptations to the soundscapes of differing natural habitats, be that grasslands, woods, rocky areas or open desert spaces. SPM hearing ranges overlap ours but extend into the ultrasonic, with mice hearing up to 85 KHz, guinea-pig 50KHz and rabbit 42KHz (Sales and Pye 1974; Berryman 1976; Heffner and Heffner 2007; Long 2007, 2009).

Much SPM vocal communication is also ultrasonic. The SPM have upright movable ears and rotating these away from the sound source can decrease its intensity by several decibels. Hearing is used to detect danger, communicate with and locate conspecifics and ultrasonic echolocation to navigate around the environment (Thomas and Jalili 2004). Ultrasound is highly directional, but does not easily penetrate solid objects, which can provide sound shadows and places of relative quiet (Hanson 2012).

Vibrissae are also used in navigation and danger detection. Whiskers enable judgement of the width of openings thereby preventing an animal getting stuck. Whisker length increases anteriorally-posteriorally along the face, each length resonating at different sound frequencies, stimulating neural activity (Hartmann et al. 2003). As Neimark *et al*. (2003) explain, this enables animals to 'see' by providing "an efficient, spatially distributed representation" (pg. 6508) of object shape and surface textures, and probably enables SPM to trace air current vortices generated by moving objects. Whiskers are significantly more sensitive than our fingertips, and using a single whisker, blindfolded rats can differentiate surfaces varying by grooves of 30 microns depth and 90 microns apart (Carvell and Simons 1990)! Thus, whiskers should not be clipped, neither by veterinarians during facial surgery nor by owners for aesthetic reasons.Artificial selection has altered sensory structures in different breeds, as in ear shape and mobility in lop rabbits, and curled whiskers in Rex rats, rabbits and guinea-pigs. As with visual compromises, these artificially selected alterations detrimentally affect sensory input, potentially restricting exploratory / active behaviour and the ability to cope with stressors. For example, lop-eared rabbits are likely to be partially or even completely deaf. These rabbits are both less reactive and less active than rabbits with upright ears. It is commonly postulated that this is because they are intrinsically calmer animals. The alternative explanation is this 'calm' behaviour is really stress-related behavioural inhibition due to being aurally compromised.

2.3.3. Light, Sound and the Captive Environment.

SPM are active in low light, have light-sensitive eyes and acute hearing for sonic and ultrasonic sounds. Exposure to light or noise stressors can cause sleep disturbances that, within a couple of weeks, can detrimentally affect health and behaviour. Recommended laboratory practice includes setting lighting regimes to low light during the working day, thereby synchronising human and animal activity periods, controlling for external light leakage (Bedrosian *et al.* 2013) and testing ultrasound levels with a bat detector (Hubrecht and Kirkwood 2010). However, pets are often housed in rooms where people are active during the daytime and are brightly lit at night. Cages may be located near noisy, often flashing, objects like TVs and refrigerators. Most cages do not contain suitably dark, solid resting places or runway tunnels to significantly attenuate light and ultrasound. Thus, the role of sleep disturbance in health and behaviour problems, including aggression, is probably underestimated.

Educating owners of these issues can help them decide which room and cage 'furniture' is best for their pet. Metal cages are significantly more noisy when moved than polycarbonate versions, and likewise moving and filling of metal food/water containers also produces aversive noise levels (Voipio *et al.* 2006). Choosing materials that resonate less, both sonically and ultrasonically, and undertaking husbandry tasks slowly and calmly reduces noise, thereby reducing behavioural and physiological distress in animals (Voipio *et al.* 2006; Willott 2007). It may, therefore, be important to avoid placing SPM within acoustic range of ultrasonic dental machines or instrument cleaners in a veterinary practice. Likewise, owners could provide sound barriers, such as wooden screens and covers, when cleaning and vacuuming rooms where SPM are kept. Veterinary practices could use a bat detector to assess ultrasonic noise in their own premises and loan it to owners.

Owners should be advised to warn animals of their approach by gently talking/ whistling or using a cue word, and letting the animal see the hand before being stroked or picked up. Owners of animals whose vision or hearing is restricted by their physical conformation and/or coat length should be made aware of this and advised to be particularly careful to not startle them.

2.3.4 Scent and the Captive Environment

Olfaction is important for communication, predator detection and finding food on the surface and buried under the soil, (Vander Wall *et al.* 2003). We exploit this ability in training Gambian Pouched (*Cricetomys gambianus*) rats to detect landmines (Poling *et al.* 2011).

Scent deposits provide information in absentia, indicating status (e.g. Shimozuru *et al.* 2006) and territory boundaries, helping reduce intra and inter-group conflict (Gosling and McKay 1990; Alcock 2013). Hence, recommendations to leave some used bedding when cleaning cages to reduce the resident animal's stress (Sørensen *et al.* 2005; Hubrecht and Kirkwood 2010; NC3RS 2013).

Animals leave scent trails that weaken over time. Thus, predators do not have to be physically present to influence SPM behaviour (Burn 2008). Predator odours, e.g. from cat fur, inhibit maintenance behaviours; grooming, foraging and eating (Apfelbach *et al.* 2005) in favour of vigilance and defensive behaviours (Blanchard *et al.* 2003).

This has implications for owners keeping SPM and predators, including cats, dogs, ferrets (*Mustela putorius furo*), snakes and birds of prey, and for veterinary practices. Odour transfer should be minimised. Hospital accomodation should be separate from that used for any predators, and much helpful advice for the rabbit-friendly practice is applicable to SPM in general (Varga 2014). If predators or any equipment/cageing used for them has been touched, hands should be washed, if not tunic tops changed, before handling SPM (Wersinger and Martin 2008). It is advised to not wear perfume or scented deoderants which may contain volatiles shown to be anxiolytic to SPM and affect their immune response (Castelhano-Carlos and Baumans 2009). Ideally, the SPM patient should have access to its own carry cage or some used home bedding to provide familiar scents. As SMP use scent to identify people (Davis and Balfour 1992), a cloth impregnated with a familiar person's scent may reduce stress.

Scent is important in recognition of individuals, group and non-group members. For territorial species, like rabbit, chinchilla and gerbil, severe fighting (in both sexes) may result from introducing new animals (Mykytowycz *et al.* 1974). Altering an individual's scent profile, by placing it in a different environment for a short period, can mean it is no longer recognised and trigger fighting between previously amicable cagemates (Halpin 1976). Such situations can arise from visits to the veterinary surgery, associated handling and procedures such as anaesthesia. Attempted reintroductions are time-consuming and stressful to owners fearful of further fighting. Like introductions, reintroduction involves establishing group scent profiles through swapping bedding and body scents prior to monitored (re-)introductions (Campbell, 2010; Crowell-Davis 2010; Sobie 2010). Success is not guaranteed especially where a combatant has learnt to expect aggression and is now fearful of the other. In natural circumstances, one would simply emigrate. In captivity they are either kept separate or at least one is rehomed.

The evidence of the importance of scent recognition indicates that keeping the scent profiles of all group members similar will reduce potential for conflict. Thus, at least for rabbits, chinchilla and gerbil, it is advised that all members of the social group accompany any individual taken to a different environment, be that a show or the veterinary surgery. Where patients need to be separated, keeping the cagemates in a holding/carry cage in the same room means all are exposed to atmospheric volatiles, such as those in anaesthetics. Ideally this would include in the operating room, but certainly in the recovery room. Scents should be swapped prior to reintroducing cage-mates, by wiping a clean cloth over the patient and then over all the other group members, and vice versa, a separate clean cloth for each animal (McBride 2013b, 2014; Magnus and McBride 2017b). The scent of the Vet / Vet nurse can be transferred by this process, by handling all the animals or by rubbing their hands, or gloves if used, on a cloth to be placed into the group holding cage.

2.3.5. Stress, Vigilance and Diagnosis

The need for vigilance can override behavioural inhibition caused by pain or illness. An animal faced with the novel and thus threatening sounds, smells and handling at the veterinary surgery may appear alert, in contradiction to the owner's description of it being apathetic at home (Whittaker and Howarth 2014). A further complication is not attending to SPM signals of pain (Keating *et al.* 2012; Matsumiya *et al.* 2012; Oliver *et al.* 2014; Sneddon *et al.* 2014). Ignoring these factors may lead to mis-diagnosis. Owners should be asked to describe the patient's normal behaviour and how this has changed (McBride 2014).

3. Cognition

Brains have evolved to navigate individuals through the complexities of their physical and social environment; to find food, avoid injury, to communicate with others (MacLean *et al.* 2012) and to learn, classically and operantly, about experiences and the consequences of behaviour (Babb and Crystal 2006; Pearce 2008; Crystal 2009). SPM cognition research is relatively new, but has shown they can solve problems, use tools and have a sense of number and time (Janus *et al.* 2009; Wynne and Udell 2013). Indeed, Foote and Crystal (2007, 2012) showed that rats know when they do not know the answer to a problem, suggesting they have some degree of metacognition. Previously considered restricted to primates, metacogniton is the ability to reflect on one's own mental processes. Herein aspects of cognition relating to space, feeding and social living are considered.

All animals need to know where they are in relation to places of safety and resources, but weather and other disturbances alter the landscape. SPM learn and update spatial maps (Geva-Sagiv *et al.* 2015) using a variety of information sources (Maaswinkel and Whishaw 1999), an ability enhanced if reared in 'enriched' rather than 'barren' cages (Harris *et al.* 2009). However, enrichment in captivity is less complex than the natural environment, and thus we only partially understand their mapping skills.

3.1. Space

Animals use a small area as their core-territory, their 'home', where they rest, groom, play, sleep and breed. It is defended from non-group members. Animals also use a larger home-range which is shared with other groups, as we share our local area with other, unknown humans. The home-range is not a luxury but an essential part of their environment, used intensively for socialising and foraging. In the wild, home-range sizes vary depending on resource availablity. Where food is easily accessible, as in urban environments, rat home ranges may be only $80m^2$ compared to more than $2000m^2$ where resources are dispersed (Lambert *et al.* 2008).

In the natural environment useable space is not restricted to the ground surface, but includes opportunities for climbing and arial runways. Being on the ground is risky and objects, such as tall vegetation and rocks, act as lookout spots and immediately accessible cover from threats. Most SPM are crepuscular or nocturnal and light sensitive, and are semi-fossorial, spending daylight hours in the darkness of underground burrows.

Burrows enhance physical and psychological homeostasis. Underground, temperature is relatively constant and cool throughout the year (think of visiting a cave). Burrows enable escape from surface temperature extremes and provide safety from most predators (Miller *et al.* 1990). Burrows are extensive, even that of the solitary Golden hamster being 180 cm long (Gattermann *et al.* 2001). They are complex, comprising areas for socialising, sleeping, breeding and, for some SPM, food storage. In social species digging can be a cooperative activity (Ebensperger and Bozinovic 2000; Wolff and Sherman 2007). For rabbits, burrowing difficulty influences group size, being smaller where digging is easy but tunnels are prone to collapse, e.g. sandy soil (Cowan 1991). Burrow construction and maintenance, removing soiled bedding, rotten food and rectifying structural problems, account for a large part of the SPM daily activity budget.

3.1.1. Space and the captive environment

Many commercial pet cages are based on floor size requirements set for laboratory animals, which are minimum and not designed with welfare as a top priority. They are approximately 1000x smaller than normal home ranges (Table 1), and do not allow animals to perform basic locomotor behaviours of moving rapidly, jumping or standing fully upright on hind legs (see Figure 2). Research shows that being unable to stand fully upright, climb and burrow compromises welfare (Makowska and Weary, 2016). SPM cages should allow free movement and contain shelters, lookout places and species appropriate climbing and burrowing opportunities. The floor should be solid, but not slippery and contain a good depth of absorbent substrate (Yeates, 2017). This is also true for animals allowed to roam indoors, such as house rabbits (and dogs and cats), where flooring is polished and slippery. Fixed carpet runners are essential to give traction and avoid injury through skidding and slipping as the animal moves within and between rooms. Unless there is no alternative, animals will not use areas with slippery substrate. This may mean they are space-restricted and unable to display their full locomotor repertoire, and potentially have reduced access to companions, food or water. Owners should be advised to watch their animals to see how they use the space available to them and amend the environment accordingly.

Owners should be encouraged to provide as much space as possible and, ideally ad libitum, access to digging pits, such as ventilated terrariums (compare Figure 3 with Figures 4a and 4b). Digging substrate should be a mixture of children's sandpit sand and sterilised (microwaved) soil (McBride 2010, 2013a). The normal cage litter should also be deep enough for digging and foraging opportunities (see 3.2). Placing cages on trays or plastic sheets reduces any mess from digging.

Tunnels provide safe entrances to rest areas. Even a short, dark, artifical tunnel reduces stress (Figure 5; Waiblinger and König 2004). Many SPM cages have nest boxes, and some connecting tunnels, made from clear or light coloured translucent plastic. These materials do not provide protection from bright light (see 2.3.3), nor burrowing opportunities.

Cage manufacturers and retailers should be encouraged to improve cage size and design to be more accommodating of SPM needs. Veterinary professionals need to raise owner awareness regarding cage design, what to look and ask for, as well as advise how to modify current caging to improve the welfare of their pets.

3.2 Foraging and Feeding in the Captive Environment

Foraging is time consuming and animals have a strong motivation for exploring and expending physical and mental energy on food acquistion (Forkman 1996). In nature, food is seasonal, patchily distributed and availablility unreliable. Animals must search across the home range or explore further to find new sources if usual sources are unavailable, whether due to flooding, drought, or human activity. Hence, the importance of spatial mapping. SPM learn about the what, where and how of food from individual experience and culturally from information communicated both within and across generations (Kalat and Rozin 1973; Galef and Aleen 1995; Berdoy and Drickamer 2007).

Individuals have to decide where and for how long to forage, these decisions are known as Optimal Foraging Strategies (Kotler *et al.* 1991; Arcis and Desor 2003). When activily engaged in behaviours, such as foraging, eating or socialising, an animal is less vigilant and more vulnerable to predation. How time is divided between vigilance and other behaviour is influenced by the landscape (e.g. visual range, wind currents, availability of cover), predator activity and the number of other animals in proximity who can alert to any threat (Beauchamp, 2007; Favreau *et al.* 2010). More solitary species, such as the Golden Hamster, gather food to eat in the safety of the burrow, spending a minimum amount of time above ground.

Rabbits, guinea-pigs, chinchilla and degu are obligate herbivores. They graze selectively, actively searching for variety of plants that provide a nutritionally balanced diet. Fields, mountainsides and roadside verges comprise a range of different flora, providing an array of both tastes and textures; as found in commercially available meadow hay. Other hay products may contain only a single grass species, such as Timothy hay. This dietary monotony can lead to sensory-specific satiety with the animals finding the food increasingly aversive and reducing intake (Rolls, 1986). This may explain owner comments that their pet does not ‘like / eat much hay’, which can impact health if they are not ingesting sufficient digestible and indigestible fibre (Johnson-Delaney, 2009). For omnivores, like rats, the diet embraces an even wider range of foodstuffs, including seeds, berries, eggs, insects, carcasses, human leftovers. Obtaining these may pose problems, solved by feats of climbing and acrobatics, or ingenuity, including tool use as shown in degu (Okanoya *et al.* 2008). For both herbivores and omnivores offering a variety of appropriate foods with different sensory characteristics is of welfare importance in reducing stress and enhancing learning (Rolls, 1986; Favreau-Peigné *et al.* 2013).

Diet and eating is more than simply nutrition; it comprises active exploration, finding and choosing and manipulation, and feeling safe to undertake these activities. It involves movement, scent, taste and texture – a veritable feast for the senses, body and brain. Providing choice and variety of suitable foodstuffs is important for both herbivores and omnivores. Equally important is providing exploration and problem solving opportunites through giving new objects to investigate, scattering food on or burying in the cage litter and using commercial or home-made puzzle feeders, at least one per animal to prevent competition (Hopping Mad and McBride 2011). These measures reduce stress, frustration, aggression, repetitive behaviours, pica, overeating and obesity (Meehan and Mench 2007, Magnus and McBride 2017a).

Encouraging such activity makes the animal more interesting to watch, thereby enhancing the owner's relationship. Training also links feeding, mental stimulation and owner interaction. SPM can be trained using clicker training, shaping and targetting. Using part of the daily food ration as positive reinforcement, behaviours can be taught to be perfomed on cue, and can contribute directly to the animal's physical and mental health and indirectly through enhanced human interest and care. These include coming when called, putting out a paw, entering their carry box, stretching and completing obstacle courses (Johnson 2003; Orr and Lewin 2006).

3.3 Sociality and the captive environment.

Most captive SPM are social, needing companionship of amicable others throughout their life. Many live in multi-age groups (Wolff and Sherman 2007). Being reared in species-appropriate groups buffers against later anxiety-states (Cirulli *et al.* 2010) and intra-specific aggression (Sachser and Prove 1984; Sachser and Renninger 1993). Inappropriate rearing conditions, isolation or over crowding, can have deleterious effects on adult ability to cope with even moderate stress (Gamallo *et al.* 1986), let alone the many substantial stresses associated with captivity. Keeping social animals as singletons causes chronic stress as it denies normal intra-specific communication and behaviours, including play, allo-grooming and group vigilance (Trocino *et al.* 2013; Yeates 2017). Likewise, overcrowding or incompatible grouping is stressful (Brown and Grunberg 1995; Yeates 2017).

Social animals communicate extensively. Solitary species also communicate with others, be it to ward them off, to court or interact with offspring. Communication can be through scent, sound, touch and body movements. Communications indicates emotional state and behavioural intention. Scientists agree that mammals experience basic emotions (Panksepp and Watt 2011) and this is likely true for all vertebrates and many invertebrates (Panksepp 1998, 2003).

Emotional and motivational feelings help decisions, cognitive choices, such as “where to find food when hungry, water when thirsty, warmth when cold, and companionship when lonely or lusty” (Panksepp 2003, pp 6). Choices are not simply about avoiding aversive states and being in some neutral emotional space. Like us, animals, including SPM, experience and seek pleasure (Panksepp 1998, 2007; Balcombe 2007, 2009).

Research shows SPM can interpret the emotional state of another via auditory and/or scent signals (de Laat *et al.* 1989). Simply witnessing stressful procedures, such as restraint and injections, is stressful, especially during the light phase of the daily light/dark cycle (Abou-Ismail *et al.* 2015). Martin *et al.* (2014) review how social buffering, social stress, emotional contagion and vicarious learning affect pain in both rodents and humans.

SPM display empathy and altruistic behaviour (Panksepp 1991; Panksepp and Lahvis 2011; Panksepp and Panksepp 2013). Rats demonstrate empathy and altruisim to known and unknown rats. In a series of experiments, rats freed trapped rats and even saved desirable food treats to share with them (Ben-Ami Bartel *et al.* 2011, 2014). Analogous to human behaviour, the individual rat’s social experience modulated how altruistically it behaved to an unknown rat.

For social species, company of amicable conspecifics is of welfare importance, but grouping must appropriate for that species (Hubrecht and Kirkwood 2010; Yeates 2017; McBride and Magnus, 2017). Where these are mixed-sex, population control must be considered. SPM produce many offspring and it is unlikely that suitable homes would be found for all, and there are welfare implications for the future of these unplanned and unwanted animals. Neutering of one or both genders is the most appropriate solution (Yeates 2017). Further, neutering can have preventative health benefits including, but not restricted to, avoidance of testicular tumours in all species, ovarian cysts in guinea pigs, mammary tumours in rats and uterine adenocarcinoma in rabbits (Meredith and Delaney, 2010; Meredith and Lord, 2014). Neutering therefore should be recommended to pet owners.

Conclusion

An insight into the SPM literature available has been provided and practical suggestions made for welfare provision both in the veterinary clinic and day to day management by owners (Tables 2 and 3). SPM have long been used as models to emulate and thus enhance understanding of the human physical, psychological and emotional condition. This and other research endeavours demonstrate they have rich emotional and cognitive lives. Yet, we frequently ignore this and thus fail to provide fully for their needs, leading to physical and behavioural problems.

Veterinary professionals should endeavour to make their practices SPM welfare-friendly. They need to be cognisant of the effects of novelty, potential predator threat, moving cages and handling on stress, over-riding behavioural inhibition due to ill-health, on thermoregulation and on recovery from surgery (Dallman *et al.* 2006; Roughan *et al.* 2015; Stuart and Robinson, 2015). Further, veterinarians should educate owners about handling, moving cages and other stressors. Additional predictable and unpredictable stressors include bright light, loud noise, damp bedding, empty water bottle, presence of predators. Research into human depression and its treatment uses SPM as animal models. One means of inducing symptoms of chronic depression in SPM is short periods of intermittent exposure to such stimuli over a matter of a few weeks, causing various effects including fragmented sleep patterns and reduced sucrose intake (Willner 1997; Grønli *et al.* 2004) and potential long term effects for health and longevity.

Where behaviour is problematic, medical reasons must be excluded (McBride 2014) and husbandry and management regimes should be reviewed and brought in line with species' needs (Table 2 and 3). Where this does not resolve the issue, further expert behavioural help should be sought (ABTC n.d.). Worldwide, many SPM keepers wish and/or are legally obliged to provide for animal welfare, but do not know how. It is incumbent on veterinarians to provide current and appropriate advice.

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Table 1: Example comparison of natural home range and recommended laboratory cage size for adult animals: rat, Guinea pig and rabbit.

All sizes given in M^2. Note I hectare (2.47 acres) is 10,000 M^2, 1 M^2 = 10,000 cm^2

	Home range M^2		Laboratory Minimum floor area Guidelines M^2	
Rat	**80** – 2300 for males **44** - 62·0 for females	Lambert and others 2008	**0.08** for a 600g adult **0.045** per group housed animal	HMSO 2014
Guinea pig	**800**	Asher and others 2004	**0.25** for a 600g guinea pig **0.07** per group housed animal	HMSO 2014
Rabbit	**20,000** (i.e. 2Km^2 / 200 hectares)	Stodart and Myers 1964	**0.5** for two socially harmonious animals weighing 2.5 – 3 kg	HMSO 2014

Table 2: Summary of Key Points to Improve SPM Behavioural Welfare In Veterinary Practice

Action	
1	Have a separate part of the Waiting room for SPM, to reduce visual and auditory disturbance from predators.
2	Have a separate recovery room for SPM.
3	Have low light in recovery rooms, and test for and minimise ultrasound and sound levels, including baffling on doors to promote quiet closure.
4	Provide suitable cage furniture to provide retreat from lights and ultrasound in both recovery and transport cages
5	Provide shelters, lookout places and light proof nest boxes with access via a dark tunnel.
6	Avoid transmission of scents from predators into areas where SPM are held and before interacting with SPM.
7	Avoid transmission of scent between non-group members, especially in territorial species
8	Leave some used bedding in cleaned cages.
9	Advise owners to bring all cage mates to all visits to the surgery
10	Ensure group scent profiles remain similar should any animal need to be temporarily removed from the group.
11	Consider effects of stress on masking behavioural signs of ill-health
12	Gently tap cages before moving, and carry them steadily. Wherever possible allow recovery time after moving of at least an hour before examination or treatment.
13	Ask owners about the animal's normal behaviour, activity cycles, cage and wider environment, management and how handled and changes in any of these aspects
14	Ask owners if patient has been trained to any cues, including relating to handling and entering carry cages. These should be used if the animal needs hospitalising
15	When holding SPM ensure the body weight is supported and the head remains upright to prevent perceived loss of support.
16	Where appropriate to the individual's health status in hospital, provide free access to enough space to facilitate the full locomotor repertoire, including climbing and digging opportunities. Ensure surfaces are not slippery.
17	Provide variety in a species-suitable diet to encourage eating and natural movement
18	Ensure all staff are knowledgeable in SPM behaviour and Facial Grimace Scales
19	Ensure all staff are knowledgeable of SPM management and appropriate handling, and individual particulars such as cue words used by the owner.
20	Advise all current SPM owners how to meet their animal's welfare needs: its diet, a suitable environment, how to keep it physically healthy and mentally active and happy and how to detect if it is unwell or in pain, including normal behaviour and Facial Grimace Scales.
21	Encourage practice participation in outreach education to current and potential owners (including children), breeders, rescue and pet shop staff regarding SPM ethology, behaviour, Facial Grimace Scales, and how to meet their physical and behavioural welfare needs.
22	Design in house or use information leaflets regarding management available from credible sources such as the RSPCA, Rabbit Welfare Fund and freely distribute to all SPM owners; perhaps as species specific packs.
23	Encourage companies to supply better designed, species appropriate housing to meet welfare needs
24	Encourage all companies to use images in their publicity materials of breeds with natural conformations (head shape, upright ears, and appropriate fur length) in suitable

	environments. In this way welfare can be indirectly improved by influencing owner perception, attitudes and expectations.

Table 3: Summary of Key points to assist owners to meet SPM welfare needs

This table is written in owner friendly language to aid veterinarians who may wish to use the text for their clients.

Steps	20 Steps to healthy and happy small prey mammal (SPM) pets
1	Ask your veterinarian for advice and sources of further information about meeting your pet's welfare needs: its diet, a suitable environment, how to keep it physically healthy and mentally active and happy and how to detect if it is unwell or in pain.
2	Think about where is best to keep your small prey mammals: they need low light and quiet, away from lots of human activity, and from machines that emit ultrasound including computers, TVs and refrigerators. Keep, and interact with, SPM in quiet, low-light conditions with stable light-dark cycles. (Please note: pets kept outdoors, such as rabbits, will have natural daylight cycles).
3	Set up a suitable home for them, this should be as large as possible and give them free access to enough space to enable them to move slowly and run quickly, jump, stretch to full height, and give climbing and digging opportunities. Ensure surfaces are not slippery.
4	Suitable cage furniture enables your pet to escape from light and ultrasound and frightening stimuli, including shelters, lookout places and **light proof** nest boxes with access via a dark tunnel.
5	Provide lookout places and novel objects to provide exploration opportunities.
6	Provide variety in diet (suitable for the species) and mental stimulation in its presentation, such as homemade puzzle feeders.
7	Take time to learn how your pet communicates: you need to be able to recognise when it is happy, scared or in pain.
8	Keep small prey mammals in species appropriate groups and try to acquire all the animals at the same time, in this way they are more likely to be compatible. It is worth spending a bit of time watching them in the pet shop to choose an animal you particularly like, and the one with whom it already bonded, that it chooses to sit next to or groom.
9	When bringing new animals home, allow a day or two for them to settle before trying to interact with then
10	When approaching your pet talk softly or whistle so you do not startle them. Gently tap cages before moving, and carry them steadily. Simply being moved is stressful.
11	Using small pieces of food, train SPM to approach to sit on your hand or be picked up and to enter carry cages on cue.
12	When holding small prey mammals ensure the body weight is supported and the head remains upright to prevent it feeling it may fall. Science has shown this is less stressful for them.
13	Consider training your pet to do some tricks – this can be done with clicker training and can provide a lot of enjoyment for you and your pet.
14	Small prey mammals recognise cage mates and their owners by smell. They also detect danger by smell and recognise the scent of predators and intruders. Thus, it is very important to consider scent when we handle our pets in order to help them feel safe
15	Try not to wear perfumes or use hand creams before handling your pet, simply have your natural hand smell.

16	Avoid transmission of scent from predators (e.g. dogs, cats, ferrets, snakes, birds of prey), and non-group members by washing your hands (even changing your top) before handling your small prey mammals.
17	Leave some used bedding in cleaned cages, so it still smells of home when you put your pet back.
18	If your pet needs to go to the veterinary surgery, take all its cage mates along too. This reduces stress of being alone and helps to keep the group scent and prevent any fighting.
19	Ensure group scent profiles remain similar should any animal need to be temporarily removed from the group. This is done by scent swopping and your veterinary surgeon can advise how this is done. This is important to reduce the chance of them fighting when you re-introduce them.
20	As prey species, these animals do not like to attract attention and are subtle in showing when they are unwell. Be observant, if your animal shows any change from its normal behaviour it may be ill or in pain or otherwise stressed and need to see the vet, this includes aggression, chewing the cage/ cage bars; apathy or restlessness, over or under eating. Do not delay, by the time signs of illness are obvious, it may be too late to help your pet.

Figure 1. Lateral position of the eye in SPM, such as the gerbil, provides a wide field of vision to enable visual detection of terrestrial and aerial predators.

Figure 2. Animals need to be able to stretch to full height.

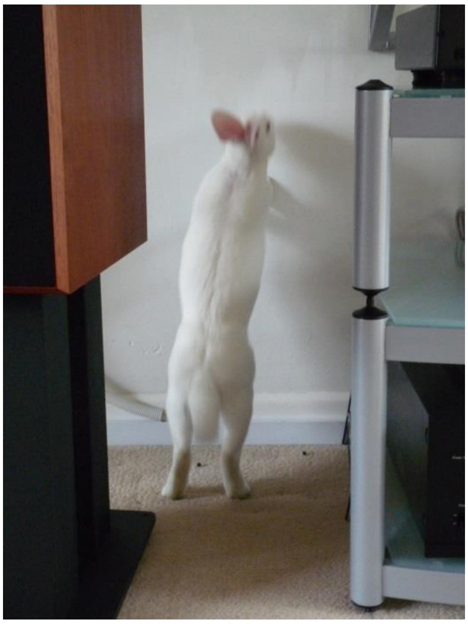

Figure 3. Standard laboratory cage for group-housed gerbils, containing a variety of bedding materials but providing very limited opportunity for burrowing.

Figure 4. Terrarium for group-housed gerbils with deep, burrowing substrate that allows the expression of normal burrowing behaviour. Note that access to water bottles must not be compromised by the animals' movement of the substrate and must be monitored.

Figure 5. Nest box with dark (red), translucent access tube. The tube allows visibility by the observer but is perceived as solid, and thus a safe access, by the rodent.