FISEVIED

Review

Contents lists available at SciVerse ScienceDirect

Applied Animal Behaviour Science



journal homepage: www.elsevier.com/locate/applanim

The welfare of ferrets (*Mustela putorius fur*o T) A review on the housing and management of pet ferrets

Claudia M. Vinke^{a,*}, Nico J. Schoemaker^b

^a Department of Animals in Science & Society, Faculty of Veterinary Medicine, University of Utrecht, The Netherlands
^b Division of Zoological Medicine, Department of Clinical Sciences of Companion Animals, Faculty of Veterinary Medicine, University of Utrecht, The Netherlands

ARTICLE INFO

Article history: Accepted 22 March 2012 Available online 8 May 2012

Keywords: Ferret Welfare Housing Behaviour Diseases

ABSTRACT

Ferrets are very agile and lively animals, and their behavioural needs are not easily met in housing conditions like our living rooms. Nevertheless, ferrets are increasingly popular as pets. The present paper aims to review and discuss the available knowledge on our pet ferret. Topics are discussed like ferrets' behaviour priorities, common housing conditions and management conditions. Behaviour problems, as well as medical topics that are considered important to optimise the welfare of pet ferrets, are elucidated. The topics are discussed in consideration of ferrets' behavioural priorities, physical and physiological needs and/or capacities.

We conclude that the main points of interest in a pet ferrets' behaviour in relation to welfare are: (1) their high motivation to explore and forage, (2) the necessity of available adequate resting opportunities, (3) play opportunities, and (4) their social organisation with respect to interspecies aggression and territoriality. Therefore, good socialisation is of the utmost importance to prepare a young ferret for its life in a human surrounding. The provision of a daily activity program, variable (food) enrichments and comfortable hiding and resting places, might be helpful to fulfil ferrets' behaviour priorities to a higher extent and may prevent behavioural disorders and problems for the owner. Social matching in ferrets should always be carefully done.

The focus of the medical topics is on those for which potential preventive measures can be taken, such as routine annual examination by a veterinarian and subsequent treatment of parasites, vaccination against viruses and prevention of endocrine disorders through preventive (chemical) neutering. Referring to medical issues, the main points of interest for the pet ferrets' welfare are nutrition, hyperoestrogenism, hyperadrenocorticism, insulinoma and Helicobacter infection and gastric ulcers. The latter infection appears to be often associated to the presence of stress in the ferret's environment.

© 2012 Elsevier B.V. All rights reserved.

Contents

1.	Introduction	156
2.	The domestication of ferrets	157
3.	Regular housing of pet ferrets	157
4.	Behavioural priorities as a background for ferrets' main behavioural problems?	158

Corresponding author at: Department of Animals in Science & Society, Faculty of Veterinary Medicine, University of Utrecht, P.O. Box 80166, 3508 TD Utrecht, The Netherlands. Tel.: +31 30 2534373; fax: +31 30 2539227.
E-mail address: c.m.vinke@uu.nl (C.M. Vinke).

^{0168-1591/\$ -} see front matter © 2012 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.applanim.2012.03.016

	4.1.	Theoretical framework: behavioural priorities	58
	4.2.	In search for ferrets' habitats	58
	4.3.	Ferrets' territoriality and social organisation	58
	4.4.	Active behaviour: motivation to explore and forage	59
	4.5.	Sexual behaviour and behavioural development	50
		4.5.1. Sexual behaviour	50
		4.5.2. Behavioural development: socialisation and mother-child relationship	50
	4.6.	Ferret vocalisations to observe emotional states	50
5.	Play b	haviour as a positive welfare indicator and the provision of environmental enrichments	50
	5.1.	Play behaviour	50
	5.2.	Environmental enrichment	51
6.	Main 1	edical problems in our pet ferrets	52
	6.1.	Preventive care	52
	6.2.	Gastrointestinal diseases	52
		6.2.1. Gastrointestinal parasites	52
		6.2.2. Helicobacter and gastric ulcers	52
		6.2.3. Intake of foreign objects	53
	6.3.	Endocrine diseases	<u> </u>
		6.3.1. Hyperoestrogenism due to persistent oestrus	53
		6.3.2. Hyperadrenocorticism	<u> </u>
		6.3.3. Insulinoma	54
	6.4.	Influenza 16	54
	6.5.	Canine distemper virus infection	54
7.	Conclu	sions 16	35
	Ackno	vledgements	35
	Refere	nces	55

1. Introduction

Ferrets are quite popular pets in western countries. However, estimations of the extent of pet ferret populations in each country are scarce and vary between sources. A report from the Dutch Organisation for the Protection of Animals (Anon., 2004) mentioned an estimated 40,000–50,000 ferrets in the Netherlands. This figure includes pets as well as ferrets used for hunting purposes. In the United States, approximately 800,000 domestic ferrets are reported being kept as pets (Jurek, 1998). Another source estimated pet ferret possession in different countries as: U.S.: 5,000,000 ferrets; U.K.: >100,000; Germany: 115,000; Italy: 105,000 and France: 300,000 (Dr. N. Chai, 2010, personal communication).

Ferrets are very agile and lively animals and their behavioural priorities are not easily met in captivity. This is especially true when ferrets spend the majority of their life in their cages. Ferrets need various physical and mental challenges in their environment to fulfil their behavioural priorities. In veterinary practice, inter- and intraspecies aggression, fearfulness, urinating outside the litter box, and destructive behaviours (excavation of plant troughs) are regularly reported behavioural problems in pet ferrets (e.g. Applegate and Walhout, 1998; Staton and Crowell-Davis, 2003; Quesenberry and Carpenter, 2004, p. 83; Bays et al., 2006; Bulloch and Tynes, 2010). These problems may result into repetitive outplacement, or even euthanasia: all serious consequences for the ferrets' welfare. Information on the outplacement in shelters and rescue centres, however, is scarce. Approximately 440 ferrets per year are received from private owners in five out of ten shelters that accept ferrets in the Netherlands

(Van Leeuwen, 2010). This would be equivalent to approximately 1–2% of the Dutch ferret population, which is relatively low compared to the average percentage of mammal species within shelters in general (i.e. 7% sheltered versus total possessed population: Vinke et al., 2011, p. 132).

Ever since the international Brambell committee launched their five freedoms in 1965, which was initially applied to farm animal species, these criteria are commonly used as guidelines to assess animal welfare in practice: (1) Freedom from Hunger and Thirst; (2) Freedom from Discomfort; (3) Freedom from Pain, Injury or Disease; (4) Freedom to Express Normal Behaviour and (5) Freedom from Fear and Distress. Subsequently, several index systems for welfare assessment have been developed for farm animals (Bartussek, 2001; Bracke, 2001), with the Animal Welfare Quality Project® being the most recent initiative in this area (Botreau et al., 2007; Veissier et al., 2008). On a national level, the Dutch Law on Animal Health and Welfare (Gezondheids-en welziinswet voor dieren, 1992) provides a general framework for the welfare of animals. In the United Kingdom, animal welfare has been protected by the Animal Welfare Act (DEFRA, 2008).

Based on the commonly used topics in welfare assessment, the present paper aims to review the available knowledge on ferrets' behaviour priorities (freedoms 1 and 4), regular housing and management conditions (freedoms 1–5), and aims to discuss some behaviour problems and medical topics (freedoms 2, 3 and 5) that might be important to optimise the welfare of pet ferrets.

To understand more about the background of the ferret, this paper begins with describing the modern ferrets' ancestors, possible domestication processes and the ferret ancestors' natural habitat.

2. The domestication of ferrets

Ferrets (Mustela putorius furo) belong to the carnivore family of the Mustelidae. Other representatives of this family are e.g. the mink, stoat, ermine, polecat and the otter. Ferrets are sexually dimorphic, whereby the males' (hobs) bodyweight varies from 1200 to 2100 g, whereas the females' (jills) bodyweight is between 700 and 1200 g (Fox and Bell, 1998), but exceptions exist (Bulloch and Tynes, 2010). Just like in other mustelids (e.g. American mink_ wild, feral and farmed: Dunstone, 1993, p. 8), the bodyweight of pet ferrets may vary 30-40% over the seasons due to the increased amount of fat during the autumn, followed by a decrease during spring (Moorman-Roest, 1993). In captivity, the average lifespan of a ferret is approximately 6–8 years (Fox and Bell, 1998), but some live to be over 10 years of age (Moorman-Roest, 1993). The most common colour types of ferrets are wild colour (Polecat type), albino, and sandy colour (light-brown paws and tail). Many other colour types, however, exist (American Ferret Association, 2008).

The ferret is a fully domesticated species of which no wild counterpart exists. The most probable ancestors of the ferret are the European polecat (*Mustela putorius putorius*) and the Steppe polecat (*Mustela eversmanni*) (Ashton et al., 1965; Tetley, 1965; Fisher, 2006). Poole (1972) describes the behaviour of ferrets as less alert, less fearful for humans, more tolerant to environmental changes and less neophobic, than the polecat. The history of ferret domestication is uncertain, but it is likely that ferrets have been domesticated for at least 2000–3000 years (Bulloch and Tynes, 2010). Pet ferrets have been described in the classic literature more than a thousand years BC in the area of North Africa (Fisher, 2006).

Just like the house cat, it is likely that ferrets were domesticated to protect stored grains and other food from rodents (Price, 2002). For ages, the main purpose of keeping ferrets was hunting, such as for rabbits, mice and rats. Hunting with ferrets is called *ferreting* (Thompson, 1951). With their lean bodies, ferrets can chase their prev easily out of their burrows (Kaufman, 1980). In most countries, this hunting technique is only permitted with a licence enacted by law. Other uses of ferrets by humans are cabledragging jobs, such as for oil, electricity and telephone companies (BBC News, millennium concert, 1999). For this purpose, the ferret wears a small harness to which a small nylon string is attached that can easily be dragged through narrow circuitries and excavates (Brown, 2007). Incidentally, ferrets are used for entertainment: a disputable public amusement is the so called *ferret legging* (http://en.wikipedia.org/wiki/Ferret_legging): during this competition it is the challenge to keep a ferret as long as possible in the trousers (Slayton, 2009). Furthermore, ferrets are used as biomedical model for human influenza virus, especially after the pandemic of H5N1 influenza, and they are used in toxicology, pharmacology, reproductive physiology, and endocrinology research, mostly in American laboratories (Brown, 2007). Internationally, ferrets are also bred for their fur (fitch coat). In Europe no specialised farms are registered for *Fitch* pelts: the farming of ferrets is mostly combined with the farming of American mink (*Mustela vison*). In the year 2000, approximately 1700 Fitch skins were produced in Europe (200 pelts in Norway and 1500 pelts in Poland); 79 breeding stock were registered in Denmark in 2001 (Anon.: EU report, 2001).

Nowadays, the ferret is a popular pet. Pet ferrets can be bred by small-scale private breeders, but they can also be bred on commercial ferret farms (USA: Fisher, 2006). Some mink farmers also breed ferrets for pet trade. It is not uncommon that pet shops acquire their ferrets from international (commercial) breeders. With the importation of ferrets, however, new diseases can be introduced, for example a virulent strain of Aleutian disease virus, canine distemper virus or juvenile lymphoma, and should therefore be avoided. Private breeding is mostly small scale and predominantly done as a hobby. Although there are no statistics which support a hypothesis that either private or commercial breeding will more likely cause behavioural or health problems, there are some indications that shelter ferrets are more likely to originate from pet shops (i.e. commercial breeding) (Dutch Ferret shelters, 2010, personal communication). Many people impulsively buy a ferret, without seriously considering the complexity of having such an animal as a pet. This impulsive buying phenomenon is most commonly seen at pet shops and garden centres (Vinke, 1998; Vinke et al., 2011).

3. Regular housing of pet ferrets

Ferrets can be kept both indoors as well as outdoors (Hillyer, 1995). Most pet ferrets are kept in cages, whereby they are housed solitary or together with more conspecifics. The recommended minimum cage size for 1-2 ferrets is at least 1½-2 m². An additional ½ m² should be added per additional animal (Anon., Huisdierbijsluiter fret, LICG, 2010; MacKay, 2006), however, most authors advise and prefer larger sizes if possible. This additional advice is absolutely understandable if one considers one of the ferrets' possible ancestors, like the wild polecats, which average home ranges are approximately 12.4 ha for females and 31.4 ha for males (Blandford, 1987). Though travel distances and wide home ranges are found as the best predictors of stress and psychological dysfunction in captivity (Clubb and Mason, 2003), it remains unclear to what extent this dictates the pet ferrets' cage size to fulfil their behavioural priorities.

An aquarium is inadequate for housing ferrets because of its poor ventilation properties and the potential risk of overheating due to high temperatures (the preferred ambient temperature for ferrets should be 15–21 °C and should not exceed 29 °C: Bulloch and Tynes, 2010). Due to the sensitivity of the ferrets' respiratory track, it is not advised to use saw dust or straw as bedding material (Jenkins and Brown, 1993).

Ferrets mostly eliminate in one or two favourite areas in their cages (Schilling, 2000). This behavioural characteristic can be used to potty train them. Nevertheless, they are not very tidy and can avoid their litter boxes if they are not clean enough. They can also mark their territories in the corners of their cages, or in living rooms. This latter elimination type has a motivational back ground of territoriality and/or sexuality (anal scent glands: Woodley and Baum, 2003).

Ferrets need safe places to rest and sleep: reportedly a healthy ferret may sleep between 18 and 20 h a day (Fisher, 2006). It is important to provide a good resting place which may vary from a special nest/cardboard box to a closed hammock. Ferrets appear to have an extreme need for variable environments (Bays et al., 2006): in his study on enrichments in ferrets, Korhonen (1992) found increased overall health (body weight and fur quality) in cases of increased floor space allowance, company of cage mates and play tools. Chivers and Einon (1982) observed hyperactivity in cases of deprivation of rough and tumble social play (isolation induced effects). It is therefore believed, that the provision of environmental (food) enrichments might be profitable for the pet ferrets' welfare, just like in many other captive species. These topics are thoroughly discussed in Sections 4 and 5.

4. Behavioural priorities as a background for ferrets' main behavioural problems?

The behavioural repertoire of ferrets is variable and may include specific body positions and vocalisations. Many patterns are comparable with that of the polecat. A few behaviours are discussed below. This information provides the background for what should be included in a suitable pet ferret environment and gives insight into the causation of some main behavioural problems in pet ferrets, such as inter- and intraspecies aggression, fearfulness, urinating outside the litter box, and destruction (e.g. Applegate and Walhout, 1998; Staton and Crowell-Davis, 2003; Quesenberry and Carpenter, 2004, p. 83; Bays et al., 2006; Bulloch and Tynes, 2010). Whereas aggression and fear can directly impair the welfare of the individual, the latter problems may urge owners to decide to bring their pets to a rescue shelter, or consider alternatives to get rid of their pet.

4.1. Theoretical framework: behavioural priorities

Behavioural needs, or what is indispensable to an animal, have been described in various ways in the literature on animal welfare. This topic is especially covered by the fourth freedom of the Brambell committee, The Freedom to Express Normal Behaviour - by providing sufficient space, proper facilities and company of the animal's own kind. The scientific discussion on behavioural priorities and what should be normal behaviour is still an ongoing process. One approach on behavioural priorities is to reflect on the wild or natural environment and suggest that all elements that are denied to animals in captivity can be described as either lacking or deprived (Thorpe, 1965; Martin, 1979). This approach has been largely rejected by animal welfare scientists, citing the organism's behavioural plasticity, and the effects of domestication and humans' selective breeding programs (e.g. Dawkins, 1980, 1983; Veasey et al., 1996; Price, 1999, 2002; Vinke, 2001). Preferably, the term behavioural priority might be used instead of behavioural needs as discussed by e.g. Mason et al. (2001) and Cooper and Albertosa (2003). The term behavioural priority takes into account a hierarchy of requirements, in line with different motivations, whereby the need to satisfy these particular motivations depends on internal and external circumstances, as well as previous experiences and current circumstances. Behavioural priority additionally addresses the motivational and emotional state of the particular individual (Cooper and Albertosa, 2003).

4.2. In search for ferrets' habitats

In fact, it is difficult to speak about *the natural* habitat of ferrets, as ferrets are the result of crossbreeding by man of animals with uncertain ancestry. Therefore, only information about possible ancestor species and studies on feral ferrets can give us some insight in the way ferrets live or may live under natural conditions, and what their behavioural priorities might be.

The European polecat, the most probable ancestor, lives in wooded and semi-wooded areas mostly near the water (Blandford, 1987; Lodé, 1999; Davison et al., 1999), feeding on small mammals, amphibians and birds (Kaufman, 1980). Furthermore, some useful information about social organisation, territoriality and prey choices is available from several studies on feral ferrets (e.g. MacKay, 1995; Norbury et al., 1998; Caley and Morriss, 2001). These feral ferrets have reliably proven their survival capabilities in the wild, even seriously harming native fauna (e.g. New Zealand: Dymond, 1991; Alterio et al., 1998; Byrom, 2002).

4.3. Ferrets' territoriality and social organisation

Studies on feral ferret populations show home ranges that are comparable to other *mustelidae* such as mink, weasels, stoats, and martens (Norbury et al., 1998). Feral ferrets live in home ranges that mostly exclude samesex conspecifics, whereas, the home ranges of the males and females may overlap extensively (Powell, 1979; intrasexual territoriality: Moors and Lavers, 1981). Total home ranges found in male adult ferrets were marginally larger that those of females $(102 \pm 58 \text{ ha vs } 76 \pm 48 \text{ ha}; \text{ average})$ 90 ± 55 ha, respectively [mean \pm S.D.]); though core ranges (24% of the total home range) of the males $(27 \pm 15 \text{ ha})$ were larger than that of the females $(16 \pm 8 ha)$ (Norbury et al., 1998). The ferrets in the latter study used at least 9.4 ± 3.2 different dens (mostly rabbit burrows) with an inter-den distance of 0.5-0.6 km. In a study by Cross et al. (1998), the abundance of feral ferrets was estimated at 6.0 animals/km². Juvenile male and female ferrets dispersed over large distances, up to 5.0 km; only a few juveniles may completely leave their natal area as observed in a study of Caley and Morriss (2001). Powell (1994) concluded that the level of territoriality of the feral ferret might relate to the abundance of prey.

During the breeding season, males begin to search for mating partners, guided by olfactory cues (Baum, 1976; Baum et al., 1983; sex steroid hormones: Moors and Lavers, 1981). Ferrets can recognise each other individually by the secretion of their anal glands (Clapperton et al., 1988). Urine and faeces also play a role in the recognition of known and unknown conspecifics and receptive partners, and may even give information on social status (Woodley and Baum, 2003; Berzins and Helder, 2008).

Many behavioural problems of our pet ferret, such as urinating outside the litter box, are quite probably related to ferrets' territorial natures: territorial animals communicate to potential competitors by scent-marking their territory carefully (Fisher, 2006). Other territorial behaviours that can be observed in pet ferrets are: wiping behaviour (wiping the preputial sebaceous gland over surfaces), anal dragging (dragging the peri-anal sebaceous gland over surfaces) and defecating on objects (Fisher, 2006). Alternative reasons for the aforementioned behavioural problems are training and management procedures: inadequate potty training of the juvenile might cause eliminating outside the litter box (Bulloch and Tynes, 2010). Stress-induced elimination, which is well-known in cats (e.g. Landsberg et al., 2003), cannot be excluded for pet ferrets, and incidences are known in practice (Moorman, 2011, personal communication). However, no literature on this topic was available for ferrets.

Just like other mustelidae, ferrets are solitary carnivores, and they can aggressively reject new conspecifics. Aggressive interactions in mustelidae can be violent with a high risk of injuries (Poole, 1966, 1973, 1974; Dunstone, 1993). Social moments in the lifetime of a solitary animal, are the breeding season and the period of the pups being with their mother. Day time resting of feral ferrets was observed to be mostly solitary (Norbury et al., 1998), though they observed some den sharing by adult males in May and August. The solitary life style and territoriality provide the main background of pet ferrets' most frequently mentioned behavioural problems of interspecies aggression. Aggressive incidences can be observed most often between unfamiliar adult individuals and within the sexes (Bulloch and Tynes, 2010). Staton and Crowell-Davis (2003) reported four influencing factors on aggressive behaviour: (1) familiarity, (2) season, (3) sexes and (4) neutering status. Frequent aggressive interactions between socially housed pet ferrets seriously decrease their welfare. In the Netherlands, experts recommend that when ferrets are kept in groups, the maximum number of animals should not exceed 4 (Moorman, 2011, personal communication). In their study to identify factors, e.g. familiarity, sex, neutering status, and time of year, associated with aggression between pet ferrets and to test a method for reducing aggression in cases of introducing new ferrets in groups, Staton and Crowell-Davis (2003) advise that all introductions should be monitored carefully to break up fights, and it would be the best for the owner to adopt ferrets in an established pair, with the best results with a male-female pair, or a two male pair. The success of matching highly depends on the animals' genetic predispositions and life histories, but little is described in the literature on socialisation of the ferret and the effects of these early life experiences (Staton and Crowell-Davis, 2003). Nevertheless, some individuals may suffer quietly with the presence of another ferret. The same phenomenon can sometimes be observed in our domestic cat: cats housed in social groups sometimes live withdrawn, whereas others may develop stress-induced behavioural problems (e.g. fear, aggression, alopecia, auto-mutilation:

Landsberg et al., 2003). In ferrets, too many animals in one household and/or mismatches between individuals can result in chronic stress (Banks et al., 2010), which may lead to increased vulnerability for diseases and infections. In these circumstances, Helicobacter infection with gastric ulcerations is not an uncommon observation in ferrets (Fox and Marini, 2001; Banks et al., 2010) (see further Section 6.2.2).

4.4. Active behaviour: motivation to explore and forage

In their active time, ferrets are very agile and lively animals that will continuously be stimulated. Under laboratory conditions, ferrets may sleep over 60% of the time; pet ferrets normally sleep 12-16 h a day, but their activityinactivity schedule typically reflects the schedule of human activity (Bays et al., 2006). Under natural circumstances, *mustelidae* spend a large proportion of their active time on foraging in wide home ranges (e.g. American mink: up to 3 h per day: about 35% of their active time: Dunstone, 1993, pp. 108-111). This may include patterns such as walking, running, jumping, nose pushing and digging, overseeing the area (appetitive patterns), and ends with finding food and eating (consummatory pattern: goal is achieved). As aforementioned, the precise habitat for ferrets might be hard to address, but referring to their possible ancestors and studies on feral ferrets, it is to be expected that ferrets may have a high motivation for diverse activities in a relative large area as well (Vinke et al., 2008b). Based on analyses of different carnivores, the wide ranging lifestyles in the wild were found as the best predictors for the development of stereotypy and the extent of infant mortality in captivity (Clubb and Mason, 2003, 2007).

Just as in many other pets, daily food is freely available for our pet ferret, whereby the animals' motivations to forage are often neglected. Foraging, as the appetitive pattern of feeding behaviour, is often mentioned as high priority behaviour and the deprivation to express these behaviour patterns is generally mentioned as a key feature for poor welfare of animals kept in captivity (Dawkins, 1988; Rushen et al., 1993). Mason and Mendl (1997) suggested that the timing of the occurrence of stereotypical behaviour might reflect the foraging strategy of the species: post-feeding stereotypies can be seen in pigs and chickens, whereas pre-feeding stereotypies are typical for farmed mink (see also: e.g. Vinke et al., 2002; Hansen and Møller, 2008). In farmed mink, it is described that the lack of fulfilling the animal's need to move and explore (patterns used for foraging and gathering environmental information) might be the most important factors inducing stress (e.g. Mason et al., 2001; Vinke et al., 2008b). Also, the ferret is highly motivated to spend a high percentage of its active time on exploration (foraging) behaviour (Fisher, 2006). This topic, addressing the fourth Freedom to Express Normal Behaviour, should be considered of importance for pet ferrets under chronically inadequate housing and/or management conditions. A good insight into ferrets' motivational backgrounds can be useful to choose adequate alternatives in environmental (food) enrichments and management (adequate activity programs).

4.5. Sexual behaviour and behavioural development

The early life environment is of the utmost importance to develop a *normal* species specific behavioural repertoire. For ferrets little has been published on the importance of behavioural development and socialisation periods.

4.5.1. Sexual behaviour

Starting with the ferrets' life cycles, ferrets' sexual behaviours are seasonal and the mating season extends from March till Augustus. A significant increase in light from 8 to 16 h per day is necessary to induce oestrus (Fox and Bell, 1998). The penis of the male ferret contains a Jformed bone. During copulation, hobs fixate the jills by a so-called neck bite. This neck bite has an important function in stimulating the jill to ovulate. Ferrets are induced ovulators, which mean that vaginal stimulation in combination with neck gripping will induce ovulation (Bibeau et al., 1991). On average, ferrets have one to two nests a year (mostly one), dependent on the oestrus cycle of the female (Marshall, 1904). The gestation time is 41-44 days with a mean of 42 days (Moorman-Roest, 1993). Female ferrets can give birth to about eight pups a year (Moorman-Roest, 1993).

4.5.2. Behavioural development: socialisation and mother–child relationship

Behavioural development starts directly after birth. For American mink (Mustela vison), Jonasen (1987) described the neonatal phase (birth to 3 weeks), motor phase (3-51/2 weeks), socialisation phase (51/2-8 weeks), exploration phase (8-13¹/₂ weeks) and the dispersal phase (13¹/₂-16 weeks). The sensitive period of ferrets is assumed to be between 4 and 10 weeks, just as mentioned for the polecat (Fisher, 2006, p. 178). In this period, the juvenile ferret has to learn many social skills and should learn and habituate to a variety of environmental cues. Though few investigations are available on ferrets specifically, Einon (1996) mentioned that by analogy to the rat, the social isolation of ferret pups during the first month of life might alter later social interaction, sexual behaviour, learning, drug tolerance, activity and body size. For pet ferrets, the juveniles must also be regularly handled by humans. Insufficient (positive) experiences with man will, just like in other animal species (e.g. dog, cat, and parrot: Seksel et al., 1999; Turner, 2000; Wanker, 1999; Landsberg et al., 2003), result in lifetime fear of humans with serious welfare consequences. Sometimes (fear) aggression can develop: the insufficient fulfilment of the sensitive period is considered one of the main reasons for aggression of ferrets to humans (MacKay, 1995; Fisher, 2006).

The bonding between mother and child is of the utmost importance to develop normal behaviour. In the Netherlands, it is advised to wean ferret juveniles not earlier than 8 weeks from their mothers (Anon., Huisdierbijsluiter *fret*, LICG, 2010; Meredith and Delaney, 2010). Just like other (carnivore) species, young ferrets have to learn many skills from their mother within the first weeks of life. It is mentioned in practice that the mother may play a role in the limits of play and aggression (canalising escalation), elimination places, and food

preferences. According to Apfelbach (1986), wild polecat juveniles have a sensitive period for the olfactory imprinting for the scent of their prey (60-90 days): prey species for which the smell is not learned in that sensitive period. will be refused. This may also explain ferrets' particular food preferences. It is therefore recommended that juvenile ferrets should always be offered a variety of foods during their first months of life to guarantee a variable diet acceptance in the future and so ensuring a better health (Fisher, 2006). Interestingly, Lodé's (1989) study on determined food preferences in juvenile polecats and the effects for food preferences later in life showed contrary results: group monotone hand-fed polecats kits did not show any differences in prey preference compared to a group kits that were variably fed by their own mother. A variety of prey species were accepted after a short time (seconds) of identification, which could be observed in both experimental groups. They concluded that this latency time may show the importance of olfactory stimuli as stated by Apfelbach (1986), but that no previous experience determination could be found.

4.6. Ferret vocalisations to observe emotional states

Ferrets' emotional states can easily be observed and heard by some particular behaviours, postures and vocalisations. A ferret in fear, (fear) aggression, frustration or pain will squeal and scream. Hissing is a vocalisation that is difficult to interpret. Hissing can indicate fear, but might also be heard during play patterns. The latter might only be heard in situations of play escalation. However, such a clear specification could not be found in the literature. Continuous screaming is an indication of being alert on a serious incidence (Fisher, 2006). If excited, which may be accompanied by fear, ferrets can produce a barking-like sound. In supposed positive excitement contexts, e.g. play behaviour, exploratory behaviour, a dook sound can be heard, also called chuckling (Schilling, 2000; Fisher, 2006; Bulloch and Tynes, 2010). The most prominent posture observed with emotional states in the ferret is piloerection of the tail (bottle brush tail) often accompanied with an arched back (Fisher, 2006). Piloerection can also be observed in other species, such as rats, cats and dogs, in states of excitement.

5. Play behaviour as a positive welfare indicator and the provision of environmental enrichments

5.1. Play behaviour

A specific behaviour that can be seen under relaxed conditions is play behaviour (e.g. Broom and Johnson, 1993; Vanderschuren, 2010). Like in other *mustelidae*, juvenile ferrets particularly frequently display playful patterns. The incidence of play is at a maximum level between 6 and 14 weeks of age, but can already be observed at four weeks of age and onwards (Bulloch and Tynes, 2010). Ferrets may *dance*, jerk, gallop, play fight with a partner, manipulate objects, and/or chase artificial prey (e.g. Poole, 1978; Fisher, 2006; Bulloch and Tynes, 2010). Object manipulation often starts by exploration with the mouth (Moorman-Roest, 1993), also called *mouthing* behaviour. Ferrets' play is largely comparable to that of the polecat which is thoroughly described by Poole (1978). Poole was among the first to describe the open mouth play face in *mustelidae*, as a ritualised pattern of inhibited biting, a *meta communication signal*, whereby all teeth are totally covered by the upper lips while the mouth is open. In aggressive circumstances, on the other hand, all teeth are clearly shown in the open mouth as a true and clear communication signal for an intention to bite.

Social play patterns may escalate under certain circumstances, which mean that patterns with a more aggressive motivational background may present themselves during play interaction. The interaction mostly stops by hissing and the fleeing of one of the interactors (Bulloch and Tynes, 2010). Whereas play in polecats decreases dramatically after 18 weeks of age, the period that they leave the nest, domestic ferrets' play frequencies continue. Bulloch and Tynes (2010) mentioned two explanations, namely early gonadectomy of pet ferrets and/or juvenilization of behaviour due to domestication processes. The latter is thoroughly described for ferrets by Church (2007). Since intact hobs can be seen playing outside the mating season (personal observation: Schoemaker, 2011), it is likely that domestication is the most important reason for continuous play behaviour in ferrets after the age of 18 weeks. In their research on the early behavioural development of the ferrets, Chivers and Einon (1982) found that deprivation of rough tumble social play caused hyperactivity that persisted in adulthood.

Generally, play behaviour of juveniles can be functionally seen as a preparation for developing motor and cognitive skills, social functioning, fight-, flight- and predatory behaviours, and it may enhance the animal's adaptive capacity later in life (e.g. Morgan, 1973; Fagen, 1981; Byers and Walker, 1995; Bekoff and Byers, 1992, 1998; Hall, 1998; Siviy, 1998; Thompson, 1998; van den Berg, 1999; van den Berg et al., 1999; Špinka et al., 2001). Presently, there is increasing interest in play behaviour as an additional parameter in welfare assessment methodology (Boissy et al., 2007, p. 387; Oliveira et al., 2010) due to the facts that: (1) play will mostly be displayed under familiar and relaxed motivational conditions (Fagen, 1981; Grier and Burk, 1992; Broom and Johnson, 1993), (2) play does not occur under severe stress (Hinton and Dunn, 1967; Müller-Schwarze et al., 1982; McCune, 1992; Thornton and Waterman-Pearson, 2002), (3) the presence of play may indicate that the primary behavioural priorities of the individual are met at that moment (Boissy et al., 2007) and (4) playing is rewarding for an animal as endorphins are released during play sessions (Vanderschuren, 2010). As the ferret is a very playful species, the observation of play patterns can be a useful indicator to assess a ferret's welfare status: a ferret that suddenly stops playing might be unwell, in pain and/or is stressed due to unfulfilled needs or social stress as discussed above. On the other hand, the stimulation of play may help the ferret to develop motor, cognitive and social skills and to fulfil its motivations. The delivery of sufficient enrichments and play tools can easily elicit play in ferrets (see further Section 5.2).

5.2. Environmental enrichment

Captive animals are often provided with cage enrich*ments* to enable them to (at least partly) fulfil behavioural patterns that they are strongly motivated for: e.g. foraging, affiliative patterns, play, and to stimulate alertness and cognition (e.g. Newberry, 1995; Appleby, 1997; Torasdotter et al., 1998; Pham et al., 1999; Varty et al., 2000; Larsson et al., 2002). Many play toys and food puzzles are commercially available, aiming to enhance the welfare of our pets and to increase human-animal bonding. The types of enrichments offered to animals may vary depending the species (nesting material, cylinders, platforms, balls: Jeppesen and Falkenberg, 1990; Einon, 1996; van de Weerd et al., 1997) and aim to meet species specific motivations as much as possible. Environmental enrichments may include food enrichment (e.g. food puzzles, chewing material), which address the *appetitive part* of feeding (foraging) and is so often neglected in animal husbandry.

Enrichment in socially housed animals, however, can be complex. Whereas enrichments can decrease aggressive interactions due to compartmentalisation, reduced chances of unintentional physical contacts and increased refuge opportunities (Abou-Ismail, 2011), competition over the provided resources can elevate aggression in the socially housed animals (e.g. Honess and Marin, 2006; Howerton et al., 2008; Akre et al., 2011). However, clever management procedures, such as providing more than just one enrichment and by arranging the valuable resources in a dispersed way (*easy to share and hard to monopolise*: Akre et al., 2011), may overcome this problem.

Another topic of attention in case of environmental enrichment is *habituation*: the novelty of an object will change if provided for a longer period and may lose its attractive value over time (Zimmerman et al., 2001; Trickett et al., 2009; Anderson et al., 2010). In order to effectively manage the use of cage enrichment, it is assumed that it is necessary to change objects regularly or to arrange intermittent presentation in order to avoid habituation (e.g. minks: Jeppesen and Falkenberg, 1990; foxes: Pedersen, 2003; bears: Anderson et al., 2010).

For ferrets, ample literature is available on what kind of enrichments is best applicable to conform to the ferrets' behavioural priorities. In practice, healthy ferrets are sometimes fed intact prey animals, such as complete mice. Aside from a valuable nutrient source, feeding intact prey also allows some parts of natural feeding behaviour. The provision of enriching objects, e.g. play tools, can prevent the pet ferret from chewing on the carpet and digging out plants, and should be the first focus in behavioural therapy in case of destruction problems (Bulloch and Tynes, 2010). In order to prevent blockage of the digestive track, the material of the ferret's play tools should always be chosen carefully, e.g. hard rubber toys, but soft foam rubbers and toys with small parts should be avoided (Bulloch and Tynes, 2010, p. 66) (see also Section 6.2.3). Digging opportunities are highly preferred by the ferret and the provision of tubes, which are sometimes used in farmed mink as well (e.g. Vinke et al., 2002, 2004), might be suitable for pet ferrets to fulfil their motivations to play and hide. Complexes of tubes can be used to construct pipe lines that might be compared to mustelids' natural den constructions (i.e. rabbit burrows: Norbury et al., 1998). Debates exist if ferrets want water for swimming. Just like in farmed mink, it is debatable if swimming is a behavioural priority for ferrets (see Vinke et al., 2008b). Personal communications with many ferret owners and caretakers have clarified that there is a high individual variability in the use of water for swimming by pet ferrets.

6. Main medical problems in our pet ferrets

Diseases are inextricably connected to the concept of wellbeing and welfare, as described in the concept of five freedoms by Brambell (1965). Many diseases are known to affect ferrets. The most common infectious diseases and those affecting the gastro-intestinal tract and the endocrine system will be discussed here. We will predominantly focus on the influence the disease has on welfare and the available preventive options. A veterinarian who commonly sees ferrets should be consulted in case of actual disease, but can also play an integral part in maintaining the welfare of the pet ferret.

Assessing the level of discomfort in ferrets is not always easy. Reported signs of discomfort or pain in a ferret include reluctance to move, weight loss, anorexia, trembling, collapse, crying, whimpering, and teeth grinding (Johnson-Delaney, 2009; Brown, 2004).

When pain is suspected, it is generally advised to address the underlying cause as much as possible. In addition, use of non-steroidal anti inflammatory drugs (NSAIDs) such as meloxicam and carprofen can be used to alleviate the pain. It is important, however, to realise the potential side effects these drug may have on the sensitive stomach of ferrets which may harbour Helicobacter-related disease. Opioid drugs, such as butorphanol, buprenorphine and morphine, are considered safer for administering pain relief (Carpenter et al., 2001; van Oostrom et al., 2011).

6.1. Preventive care

Preventative care is a great tool to enhance welfare for ferrets. Besides controlling ectoparasites, such as fleas (*Ctenocephalides felis*) and ear mites (*Otodectes cynotis*), it is essential that every ferret is vaccinated yearly against canine distemper. In countries where rabies is prevalent, it is also necessary to vaccinate against this disease. Dental disease is fairly common in ferrets. Preventive health examinations, including inspection of the oral cavity is therefore recommended on a yearly basis.

Good nutrition is the basis of well being in all species. Ferrets are obligate carnivores. The crude protein component of the diet should range between 30 and 40% and is preferably meat based (Brown, 2004; Wolf and Hebeler, 2001). The recommended fat content should range between 18 and 30% depending on the stage of life. The diet for non-breeding adults should contain between 15 and 20% fat (Banks et al., 2010; Brown, 2004). Lactating females and pre-weaned kits should receive a diet containing over 25% fat (Brown, 2004; Wolf and Hebeler, 2001). The intestinal flora is relatively simple and the colon is short (appr. 10 cm); therefore fermentation does not take place. The digestion of fibres is therefore minimal (Andrews and Illman, 1987; Brown, 2004). Feeding prey species has been recommended, and is becoming fairly popular in the Netherlands, where prey species can easily be purchased through the internet (www.prooidier.nl). One of the authors (Schoemaker) also recommends feeding prey animals to ferrets when there is an indication that prolonged diarrhoea could be due to food intolerance.

Feeding patterns can be adapted and are related to the amount of food available, group size and caloric value of given diet. When food is ample and freely available, ferrets will typically eat 9–10 meals per day (Kaufman, 1980).

Deficiencies in the diet (i.e. increased amount of carbohydrates, decreased amount of high quality protein) have been associated with a number of diseases such as weight loss, poor coat condition, pancreatic endocrine disorders and urinary calculi (Bell, 1999).

Feeding a diet composed of just muscle meat makes an incomplete diet: the lack of calcium in such a diet and the relative surplus of phosphorus can give rise to the All Meat Syndrome (secondary nutritional hyperparathyroidism), leading to decalcification of bones with increased risk of bone fractures (Kronfeld, 1985).

Based on the above information, the authors recommend to feed either a commercial, balanced ferret diet or prey animals to their pet ferrets. Water intake is around 50 ml/kg body weight per day (Kaufman, 1980; Banks et al., 2010).

6.2. Gastrointestinal diseases

Gastrointestinal diseases are frequently seen in ferrets. The infectious causes of gastrointestinal disease are most frequently seen at a young age, while non-infectious causes are frequently associated with management failure or are immune-mediated.

6.2.1. Gastrointestinal parasites

Usually ferrets are free of parasitic worm infections, although infections with *Toxocara cati* have been reported (Morrisey, 1996). Routine deworming is therefore not recommended. The most common parasitic gastrointestinal disease in young ferrets is coccidiosis which can be caused by *Isospora* and *Eimeria* species. The most common symptom of this disease is diarrhoea, but can be more debilitating and even lead to death of the ferret. Supportive care (i.e. plenty of fluids and feeding) along with the use of a sulphonamide is usually effective as treatment (Morrisey, 1996). When introducing young ferrets to a new group, it is important to know where they came from and whether they could be infected. Preventive treatment is not recommended, but when diarrhoea occurs, immediate consultation with a veterinarian is recommended.

6.2.2. Helicobacter and gastric ulcers

Aetiological causes for gastric ulcers may be the use of NSAIDs for pain relief, gastric tumours, renal failure or a *Helicobacter mustelae* infection (Laporte et al., 1991; Fox and Marini, 2001). The latter is frequently reported to occur after stressful situations, such as dietary change, overcrowding or addition of a new animal in the group (Banks et al., 2010). Overcrowding is considered one of the most common triggering factors for Helicobacter mustelae associated disease in ferrets in the Netherlands (Moorman. 2011, personal communication). Confirmation of a H. mustelae infection, however, is very difficult as up to 100% of ferrets over one year of age are carriers of this bacterium (Solnick and Schauer, 2001). It is thought that ferrets are infected at an early age and remain infected until they are treated (Fox and Marini, 2001; Morrisey, 2004). The infection leads to colonisation of the bacterium in the stomach (Fox et al., 1991). During immunosuppression, especially stressful situations, infection can lead to gastric and duodenal ulceration (Fox and Marini, 2001). Clinical signs include lethargy, diarrhoea, melena, muscle wasting, and abdominal pain. Since most ferrets carry H. mustelae bacteria within their gastrointestinal system it is important to minimise stress as much as possible in these animals.

6.2.3. Intake of foreign objects

As mentioned previously, ferrets are very explorative animals. Rubber toys are favoured by many ferrets. They pose a great threat, however, as ferrets love to chew on them and incidentally swallow (smaller) pieces of these toys (Plant and Lloyd, 2010). Intake of these foreign objects is most commonly seen in younger (under 2 years of age) animals. Ingestion of these objects can remain without symptoms. More frequently, however, the following symptoms can be seen: anorexia, salivation, vomiting, abdominal discomfort, diarrhoea, and/or melena (black faeces). In some cases, the foreign objects will pass on their own, but very frequently they need to be surgically removed (Brown, 2004; Lennox, 2005). It is therefore essential that all soft rubbery objects are removed from the enclosure or room in which the ferret is allowed to roam around.

Similar problems may be seen in ferrets with a trichobezoar. Just as in cats, ferrets may develop these hair balls in their stomach which may lead to obstructions (Moorman-Roest, 1993). Frequent grooming and the use of cat laxatives are recommended during heavy moult (Moorman-Roest, 1993).

6.3. Endocrine diseases

Endocrine related diseases are also frequently seen in ferrets. Hyperoestrogenism, due to persistent oestrus, is preventable by taking the necessary precautions which will be discussed later. Adrenal tumours and insulinomas are considered the most two common endocrine diseases in ferrets (Schoemaker, 2009). It has been suggested that with preventive measures the incidence of these diseases could be decreased, and will be discussed below. Proof for this, however, does not exist at this moment.

6.3.1. Hyperoestrogenism due to persistent oestrus

As previously mentioned, the ferret is an induced ovulator, which means that they need external stimulation to ovulate. Other companion animals, which are induced ovulators include rabbits and cats. In the ferret, a firm stimulation, in the form of dragging by the scruff of the

neck and mating, is necessary for ovulation (Bibeau et al., 1991). When ovulation does not occur, these ferrets will remain in oestrus for a period of 6 months. Besides having a swollen vulva during this entire period, oestradiol levels are elevated. The latter can lead to bone marrow suppression resulting in a pancytopaenia which is potentially lethal (Martin, 1995). Prolonged hyperoestrogenism can also lead to alopecia (Chitty, 2009). When ferrets are housed outdoors, the lack of protective fur may cause problems in thermoregulation. Proof of the latter, however, has not been published. The swollen vulva can be irritating to the jill as in some cases it is so large that it continuously makes contact with the floor. Minor lesions are sometimes seen on the surface of the vulva due to rubbing of the vulva over the floor. Before the pancytopenia becomes life threatening, the loss of red blood cells may contribute to a lack of energy.

To prevent persistent oestrus, it is mandatory that a preventive measure is taken in non-breeding jills prior to the breeding season, which in the Northern hemisphere starts in March. Some jills which are kept indoors already come into oestrus in January. Different preventive measures have been described. Mating jills with a vasectomised hob has been common practice in Great Britain for many years. Although mating is a natural behaviour, the act itself is very stressful for the jill as she will be dragged by her scruff to every corner of the cage. This method is therefore not recommended by the authors. Another option is giving injections with proligestone on a yearly basis. Over the past years, however, spaying has been considered the method of choice to prevent oestrus in jills. In recent years, a correlation has been found between spaying and the occurrence of hyperadrenocorticism in ferrets (Schoemaker et al., 2000). It is suggested that the increased plasma concentrations of luteinizing hormone (LH), which occur after neutering, play an important role in the development of alterations within the ferret adrenal gland (Schoemaker et al., 2002). The use of a slow release GnRH implant (Suprelorin[®], Virbac) containing deslorelin, causing decreased plasma concentrations of LH, has been proposed as an alternative treatment (Prohaczik et al., 2010), and appears to be a promising alternative to preventive surgery.

The following ethical question can now be postulated: "Should ferrets be kept as pets, if surgical or medical intervention (i.e. neutering) is necessary to maintain the welfare of this animal?" As mentioned before, ferrets are fully domesticated. Since no wild counterparts exist for this species, these animals should either be kept as pets or only allowed for use as research animal or hunting tool. For the latter purposes, welfare remains important, necessitating medical intervention to prevent hormonally induced disease. The application of hormonal implants induces so little harm, that this form of neutering has already been advocated for use in male ferrets (Vinke et al., 2008a).

6.3.2. Hyperadrenocorticism

Hyperadrenocorticism, also referred to as adrenocortical disease, is considered to be one of the most common diseases in ferrets, which was first described by Fox et al. (1987). The syndrome differs from hyperadrenocorticism in other species, such as humans and dogs, in that glucocorticoid excess is much less pronounced in ferrets (Rosenthal and Peterson, 1996b). Instead, excessive production of sex steroids is seen in ferrets (Rosenthal and Peterson, 1996b). The prevalence of hyperadrenocorticism in Dutch ferrets was found to be 0.55% (95% confidence interval: 0.2-1.1%) (Schoemaker et al., 2000). This means that at any time 1 in 200 ferrets in the Dutch population has an adrenal tumour. Signs of hyperadrenocorticism in ferrets include symmetrical alopecia, vulvar swelling in jills, recurrence of sexual behaviour after neutering in hobs, urinary blockage in male ferrets due to prostatic enlargement and cyst formation, and pruritus (Rosenthal et al., 1993). Welfare issues associated with alopecia and a swollen vulva have been described under hyperoestrogenism. Hyper sexuality results in restlessness within the group. Animals will start to drag each other by the scruff and attempts at mating may take place. Squealing may be heard during the dragging of a cage mate. Urinary blockage results in severe loss of welfare as it is associated with extreme discomfort. In addition, it is potentially life threatening (Rosenthal and Peterson, 1996a). Many veterinarians do not associate urinary blockage with an adrenal tumour and primarily focus on urolithiasis. Adequate knowledge of the veterinarian is therefore of vital importance to correctly diagnose this condition and to the long term welfare of these animals. Severe loss of welfare is also caused by the pruritus which is seen in ferrets with adrenocortical disease. The exact cause of the pruritus is unknown, and it does not respond to regular treatment protocols. Addressing the adrenal hormone production is the only option to alleviate the ferrets of the itchy sensation (Rosenthal et al., 1993).

As described under hyperoestrogenism, a correlation has been found between neutering and the occurrence of adrenocortical tumours (Schoemaker et al., 2000). One could therefore reason not to neuter hobs.

Castrating hobs, however, does result in increased welfare in the sense of less aggressiveness and more play behaviour: this was observed in surgically as well in chemically castrated hobs (Vinke et al., 2008a). Since deslorelin implants (long acting GnRH agonist) have been found to be a suitable alternative for surgical castration in hobs (Schoemaker et al., 2008) it can be speculated that these implants could also be essential in preventing adrenal cortical tumours in ferrets. Further studies are necessary to prove this hypothesis.

6.3.3. Insulinoma

Insulinomas are small tumours of the pancreatic beta cells. These micro-adenomas produce an excess of insulin, resulting in hypoglycaemia (Quesenberry and Rosenthal, 2004). There is an equal distribution of insulinomas among the sexes and the median age in which ferrets are affected is 5 years (range 2–8 years).

The severity of symptoms ranges from asymptomatic, a glazed look in the eyes, lethargy, weight loss, hypersalivation, pawing at the mouth, hind leg weakness (paresis posterior), seizures, coma or even death (Carpenter et al., 2001). Blood glucose concentrations lower than 3.4 mmol/l, after withholding food for 4 h, are considered diagnostic when ferrets display the previously mentioned signs (Quesenberry and Carpenter, 2004). Although adenocarcinoma of the pancreas have been reported in ferrets, the great majority of insulinomas are benign and do not metastasise (Weiss et al., 1998), although local metastases have been described (Banks et al., 2010). Both surgical, as well as medical treatment options are available. The choice of treatment depends on many factors and is greatly dependent on the choice of the owner.

Hypersalivation and pawing at the mouth are signs of nausea. Inabilities to walk correctly in combination with seizures are signs of poor welfare. It is therefore imperative to prevent these signs as much as possible.

Based on the natural carnivorous diet of mustelids, it has been suggested that diets high in carbohydrates contribute to the development of insulinoma in ferrets (Finkler, 2004). Diets that are high in protein, high in fat, low in carbohydrates, and low in fibre are therefore frequently recommended. Although the theory behind this advice sounds very plausible, there is no scientific evidence to back up any claims that these diets indeed would prevent the occurrence of insulinoma in ferrets (Schoemaker, 2009).

6.4. Influenza

Ferrets are highly susceptible to several strains of the human influenza virus. It is considered the most common primary cause for respiratory disease in ferrets. Humans can infect ferrets and vice versa (Orcutt and Malakoff, 2009). This is the reason why ferrets are currently used in scientific studies on high pathogenic influenza strains (Belser et al., 2008; Jackson et al., 2009).

Many of the symptoms of influenza are similar to those of canine distemper (see later) but less severe. Nasal discharge is mucoserous instead of mucopurulent, there is more sneezing and coughing, and the fever is usually over before the animal is presented to the veterinarian. Just as in humans, the infection is self-limiting and usually not fatal (Bell, 1995). Because of the zoonotic nature of the disease, owners, veterinarians and/or their staff with minor symptoms of influenza should not come close to ferrets or should wear a mask to prevent the spread of the virus.

6.5. Canine distemper virus infection

Canine distemper is a serious disease in ferrets, which always ends in the death of the animals. The incidence of the disease is low due to wide spread vaccination within the population. Importation of unvaccinated ferrets, however, has recently led to an outbreak in privately owned Dutch ferrets. These imported ferrets were introduced to unvaccinated Dutch ferrets, which subsequently developed the disease and died. It is therefore imperative that ferrets are vaccinated against canine distemper and that importation of ferrets is only allowed under strict regulation.

Typical signs of a canine distemper infection start with a mucopurulent nasal discharge, conjunctivitis, severe fever, and skin lesions (pruritic and erythematous rash under the chin), followed by neurological signs, such as hyperexcitability, seizures and coma. Eventually all ferrets die of the infection. Prevention of the illness is possible through vaccination with a modified live vaccine (Welter et al., 2000).

7. Conclusions

Fundamental knowledge on the behaviour of ferrets can be derived from studies on feral ferrets' behaviour and social organisation. In addition, information can be derived from knowledge on behaviour of some related species. Points of interest in ferrets' behavioural motivations in relation to pet ferrets' welfare are their high motivation to explore and forage at a high activity level, resting and play opportunities, and natural social organisation with aspects of interspecies aggression and territoriality. Solutions can be found in the areas of socialisation, housing, food and adequate management.

Early life experiences (socialisation) are of the utmost importance to have a ferret that is able to live without stress as a pet in a human surrounding, and also to live in the company of other ferrets. A well balanced activity program in and outside the cage, the providing of adequate and variable (food) enrichments and comfortable hiding and resting places, can be helpful in fulfilling ferrets' behavioural priorities and preventing some behavioural disorders and problems for the owner. Social matching should always be carefully done, and the preference for a solitary life style should sometimes be accepted for some individuals.

Knowledge of ferret medicine is increasing among veterinarians. An annual examination of pet ferrets by veterinarians can aid in the early diagnosis of many diseases, improving the welfare of ferrets. Referring to medical issues, the main points of interest for the pet ferrets' welfare are nutrition, hyperoestrogenism, hyperadrenocorticism, insulinoma and Helicobacter infections and gastric ulcers. The latter infections appear to be often associated with the presence of stress in the ferret's environment.

Generally, in conclusion, knowledge of ferrets' behavioural priorities is poorly described in the literature and research on ferret behaviour is scarce. This review could only be compiled with the help of information and studies on related species. Specific research on pet ferrets is urgently needed.

Acknowledgements

The authors wish to acknowledge financial support from the Royal Society for the Prevention of Cruelty to Animals (RSPCA), and want to thank Birgit van der Laan, Hanneke Roest and Nicky Pasmooij for their help and constructive discussions of the text. The authors would also like to thank Mrs. R.I. Fleis-Keesler for the critical reading of the manuscript.

References

- Abou-Ismail, U.A., 2011. Are the effects of enrichment due to the presence of multiple items or a particular item in the cages of laboratory rat? Appl. Anim. Behav. Sci. 134 (1–2), 72–82.
- Akre, A.K., Bakken, M., Hovland, A.L., Palme, R., Mason, G., 2011. Clustered environmental enrichments induce more aggression and stereotypic

behaviour than do dispersed enrichments in female mice. Appl. Anim. Behav. Sci. 131, 145–152.

- Alterio, N., Moller, H., Ratz, H., 1998. Movement and habitat use of feral house cats *Felis catus*, stoats *Mustela erminea* and ferrets *Mustela furo* in grassland surrounding Yellow-eyed penguin *Megadyptes antipodes* breeding area in spring. Biol. Conserv. 83 (2), 187–194.
- American Ferret Association. Ferret Color and Pattern Standards. Internetsite: Ferret.org. http://www.ferret.org/events/colors/colorchart.html (not peer-reviewed publication) (retrieved 30.11.2008).
- Anderson, C., Arun, A.S., Jensen, P., 2010. Habituation to environmental enrichment in captive sloth bears. Effect on stereotypies. Zoo Biol. 29, 705–714.
- Andrews, P.L.R., Illman, O., 1987. The ferret. In: Poole, T.B., Robinson, R. (Eds.), The UFAW Handbook on the Care and Management of Laboratory Animals, 6th ed., Longman Group, UK Limited, Ch. 27, pp. 436–455.
- Anon., 2001. EU rapport. The welfare of animals kept for fur production. Report of the scientific committee on animal health and animal welfare. Adopted on 12–13 December 2001, Brussels, Belgium.
- Anon., 2004. Beleid van de dierenbescherming over fretten als gezelschapsdier. Groep Beleid, Dier en Maatschappij. Report of the Dutch Organization for the Protection of Animals, Den Haag, The Netherlands [Title: Policy of the Dutch Organization for the Protection of Animals on pet ferrets] (not peer-reviewed publication).
- Anon., 2010. Huisdierbijsluiter fret. LICG, Nederland. Internet site: http://www.licg.nl/wcs/lcg/nl/4137/fret.html (not peer-reviewed publication).
- Apfelbach, R., 1986. Imprinting on prey odours in ferrets (Mustela putorius F. Furo L.) and its neutral correlates. Behav. Process. 12 (4), 363–381.
- Appleby, M.C., 1997. Life in a variable world: behaviour, welfare and environmental design. Appl. Anim. Behav. Sci. 54, 1–19.
- Applegate, J.A., Walhout, M.F., 1998. Childhood risks from the ferret. J. Emerg. Med. 16 (3), 425–427.
- Ashton, E.H., Thomson, A.P.D., Zuckerman, F.R.S., 1965. Some characters of the skulls and skins of the European Polecat, the Asiatic Polecat and the domestic ferret. Proc. Zool. Soc. Lond. 125 (2), 317–333.
- Banks, R.E., Sharp, J.M., Doss, S.D., Vanderford, D.A., 2010. Exotic Small Mammal Care and Husbandry Ferrets. Wiley-Blackwell, USA, pp. 61–73.
- Bartussek, H., 2001. An historical account of the development of the animal needs index ANI-35L as part of the attempt to promote and regulate farm animal welfare in Austria: an example of the interaction between animal welfare, science and society. Acta Agric. Scand. 30, 34–41.
- Baum, J.M., 1976. Effects of testosterone propionate administered perinatally on sexual behavior of female ferrets. J. Comp. Physiol. Psychol. 90, 399–410.
- Baum, M.J., Canick, J.A., Erskine, M.S., Gallagher, C.A., Shim, J.H., 1983. Normal differentiation of masculine sexual behaviour in male ferrets despite neonatal inhibition of brain aromatase or 5-alpha-reductase activity. Neuroendocrinology 36, 277–284.
- Bays, T.B., Lightfoot, T., Mayer, J., 2006. Exotic Pet Behavior. Birds, Reptiles and Small Mammals. Saunders Elsevier Inc., St. Louis, Missouri, USA.
- BBC News, 1999. Ferrets save millennium concert. Wednesday, 29 December 1999, 14:57 (not peer-reviewed publication).
- Bekoff, M., Byers, J.A., 1992. Time, energy and play. Anim. Behav. 44, 981–982.
- Bekoff, M., Byers, J.A., 1998. Animal Play. Evolutionary, Comparative and Ecological Perspectives. Cambridge University Press, Cambridge, UK.
- Bell, J., 1995. Proven or potential zoonotic diseases of ferrets. J. Am. Vet. Med. Assoc. 195, 990–994.
- Bell, J.A., 1999. Ferret nutrition. Vet. Clin. Exot. Anim. 2, 169-192.
- Belser, J.A., Blixt, S., Chen, L.-M., Pappas, C., et al., 2008. Contemporary North American influenza H7 viruses possess human receptor specificity: implications for virus transmissibility. Proc. Natl. Acad. Sci. U.S.A. 105 (21), 7558–7563.
- Berzins, R., Helder, R., 2008. Olfactory communication and the importance of different odour sources in the ferret (*Mustela putorius f. furo*). Mamm. Biol. 73 (5), 379–387.
- Bibeau, C.E., Tobet, S.A., Anthony, E.L., Carroll, R.S., Baum, M.J., King, J.C., 1991. Vaginocervical stimulation of ferrets induces release of luteinizing hormone-releasing hormone. J. Neuroendocrinol. 3 (1), 29–36.
- Blandford, P.R.S., 1987. Biology of the polecat Mustela putorius: a literature review. Mamm. Rev. 17, 155–198.
- Boissy, A., Manteuffel, G., Jensen, M.B., Oppermann-Moe, R., Spruijt, B.M., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. Anim. Physiol. 92, 375–397.
- Botreau, R., Bonde, M., Butterworth, A., Perny, P., Bracke, M.B.M., Capdeville, J., Veissier, I., 2007. Aggregation of measures to produce an overall

assessment of animal welfare. Part 1: a review of existing methods. Animal 1, 1179–1187.

- Bracke, M.B.M., 2001. Modelling of Animal Welfare: the Development of a Decision Support System to Assess the Welfare Status of Pregnant Sows. Institute of Agricultural and Environmental Engineering. Wageningen, The Netherlands. PhD-thesis, P.150.
- Brambell Committee (Report). HC Deb 15 December 1965. 722, cc279-80W.
- Broom, D.M., Johnson, K.G., 1993. Stress and Animal Welfare. Chapman and Hall, London, UK.
- Brown, S.A., 2004. Basic anatomy, physiology and husbandry. In: Hillyer, E.V., Quesenberry, K.E. (Eds.), Ferrets, Rabbits and Rodents, Clinical Medicine and Surgery. W.B. Saunders Company, UK, pp. 3–14.
- Brown, S., 2007. History of the ferret. Small Animal health series. Internetsite: Veterinarypartner.com. http://www.veterinarypartner. com/Content.plx?P=A&A=496 (not peer-reviewed publication).
- Bulloch, M.J., Tynes, V.V., 2010. Ferrets. In: Tynes, V.V. (Ed.), Behaviour of Exotic Pets. Wiley-Blackwell Publishing Ltd., USA.
- Byers, J.A., Walker, C., 1995. Refining the motor training hypothesis for the evolution of play. Am. Nat. 146, 25–41.
- Byrom, A.E., 2002. Dispersal and survival of juvenile feral ferrets, *Mustela furo*, in New Zealand. J. Appl. Ecol. 39, 67–78.
- Caley, P., Morriss, G., 2001. Summer/autumn movements, mortality rates and density of feral ferrets (*Mustela furo*) at a farmland site in North Canterbury, New Zealand. N. Z. J. Ecol. 25 (1), 53–60.
- Carpenter, J.W., Mashima, T.Y., Rupiper, D.J., 2001. Exotic Animal Formulary, 2nd ed. W.B. Saunders Company.
- Chitty, J., 2009. Ferrets: biology and husbandry. In: Keeble, E., Meredith, A. (Eds.), BSAVA Manual of Rodents and Ferrets. BSAVA, UK, pp. 193–204.
- Chivers, S.M., Einon, D.F., 1982. Effects of social early experience on activity and object investigation in the ferret, *Mustela furo*. Dev. Psychobiol. 15, 75–80.
- Church, B., 2007. Ferret-polecat domestication: genetic, taxonomic and phylogenetic relationships. In: Lewington, J.H. (Ed.), Ferret Husbandry, Medicine and Surgery., 2nd ed, pp. 122–150.
- Clapperton, B.K., Minot, E.O., Crump, D.R., 1988. An olfactory recognition system in the ferret *Mustela furo L.* (Carnivora: Mustelidae). Anim. Behav. 36 (2), 541–553.
- Clubb, R., Mason, G.J., 2003. Captivity effects on wide-ranging carnivores. Nature 424, 473–474.
- Clubb, R., Mason, G.J., 2007. Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures. Appl. Anim. Behav. Sci. 102, 303–328.
- Cooper, J.J., Albertosa, M.J., 2003. Behavioural priorities of laying hens. Avian Poult. Biol. Rev. 14 (3), 127–149.
- Cross, M., Smale, A., Bettany, S., Numata, M., Nelson, D., Keedwell, R., Ragg, J., 1998. Trap catch as a relative index of ferret (*Mustela furo*) abundance in a New Zealand pastoral habitat. N. Z. J. Zool. 25, 65–71.
- Davison, A., Birks, J., Griffiths, H., Kitchener, A., Biggens, D., 1999. Hybridization and the phylogenetic relationship between polecats and the domestic ferret in Britain. Biol. Conserv., 155–161.
- Dawkins, M.S., 1980. Animal Suffering. The Science of Animal Welfare. Chapman and Hall, London, UK.
- Dawkins, M.S., 1983. Battery hens name their price: consumer demand theory and the measurement of ethological 'needs'. Anim. Behav. 31, 1195–1205.
- Dawkins, M.S., 1988. Behavioural deprivation: a central problem in animal welfare. Appl. Anim. Behav. Sci. 20, 209–225.
- Dunstone, N., 1993. The Mink. T and AD Poyser, London, UK.
- Dymond, S.J., 1991. Winter use by ferret (*Mustela furo*) of vegation buffer zones surrounding yellow-eyed penguin (*Megadyptes antipodes*) breeding areas. University of Otago Wildlife Management. Report no. 15.
- Einon, D., 1996. The effects of environmental enrichment in ferrets. In: Environmental Enrichment Information Resources for Laboratory Animals. 1965–1995: Birds, Cats, Dogs, Farm Animals, Ferrets, Rabbits and Rodents. AWIC Resource Series No. 2. U.S.A. Department of Agriculture/Universities' Federation for Animal Welfare (UFAW), Beltsville, MD/UK, pp. 113–126.
- Fagen, R., 1981. Animal Play Behaviour. Oxford University Press, New York, USA.
- Finkler, M.R., 2004. A nutritional approach to the prevention of insulinomas in the pet ferret. Exot. Mamm. Med. Surg. 2.2, 1–5.
- Fisher, P.G., 2006. Ferret behavior. In: Bays, T.B., Lightfoot, T., Mayer, J. (Eds.), Exotics Pet Behavior. Birds, Reptiles, and Small Mammals. Saunders, Elsevier Inc., Missouri, USA.

- Fox, J.G., Bell, J.A., 1998. Growth, reproduction, and breeding. In: Biology and Diseases of the Ferret, 2nd ed. Lippincott Williams & Wilkens, London, pp. 211–227.
- Fox, J.G., Marini, R.P., 2001. Helicobacter mustelae infection in ferrets: pathogenesis, epizootiology, diagnosis and treatment. Seminars in Avian and Exotic Pet Medicine. Bact. Dis. 10 (10), 36–44.
- Fox, J.G., Otto, G., Taylor, N.S., Rosenblad, W., Murphy, J.C., 1991. Helicobacter mustelae-induced gastritis and elevated gastric pH in the ferret (*Mustula putorius furo*). Infect. Immun., 1875–1880.
- Fox, J.G., Pequet-Goad, M.E., Garibaldi, B.A., Wiest, L.M., 1987. Hyperadrenocorticism in a ferret. J. Am. Vet. Med. Assoc. 191, 343–344.
- Grier, J.W., Burk, T., 1992. Biology of Animal Behaviour, 2nd ed. Mosby-Year Book Inc., Missouri, USA.
- Hall, F.S., 1998. Social deprivation of neonatal, adolescent, and adult rats has distinct neurochemical and behavioral consequences. Critical Reviews in Neurobiology 1, 129–162.
- Hansen, S.W., Møller, S.H., 2008. Diurnal activity patterns of farm mink (*Mustela vison*) subjected to different feeding routines. Appl. Anim. Behav. Sci. 111 (1–2), 146–157.
- Hillyer, E.V., 1995. Ferret preventive medicine and clinical techniques. In: Exotic Animals: A Veterinary Handbook. Veterinary Learning Systems Co. Inc., New Jersey, USA (originally published in TNAVC 1994 Proceedings, vol. 8, 7–9).
- Hinton, H.E., Dunn, A.M.S., 1967. Mongooses: Their Natural History and Behaviour. Oliver and Boyd Ltd., London, UK.
- Honess, P.E., Marin, C.M., 2006. Enrichment and aggression in primates. Neurosci. Biobehav. Rev. 30, 413–436.
- Howerton, C.L., Garner, J.P., Mench, J.A., 2008. Effects of a running wheeligloo enrichment on aggression, hierarchy linearity, and stereotypy in group-housed male CD-1 (ICR) mice. Appl. Anim. Behav. Sci. 115, 90–103.
- Jackson, S., van Hoeven, N., Chen, L.M., Maines, T.R., Cox, N.J., Katz, J.M., Donis, R.O., 2009. Reassortment between avian H5N1 influenza viruses in ferrets: a public health risk assessment. J. Virol. 83 (16), 8131–8140.
- Jenkins, J.R., Brown, S.A., 1993. A practitioner's guide to rabbits and ferrets. Amer Animal Hospital Assn, USA.
- Jeppesen, L.L., Falkenberg, H., 1990. Effects of play balls on pelt-biting, behaviour and level of stress in ranch mink. Scientifur 14(3), 179–186.
- Johnson-Delaney, C.A., 2009. Ferrets: anaesthesia and analgesia. In: Keeble, E., Meredith, A. (Eds.), BSAVA Manual of Rodents and Ferrets. BSAVA, UK, pp. 245–253.
- Jonasen, B., 1987. Ontogeny of mink. Scientifur 11 (2).
- Jurek, R.M., 1998. A review of national and California population estimates of pet ferrets. Calif. Dep. Fish and Game, Wildl. Manage. Div., Bird and Mammal Conservation Program Re 98-09. Sacramento, CA, USA, 11 pp.
- Kaufman, L.W., 1980. Foraging cost and meal patterns in ferrets. Physiol. Behav. 25 (1), 139–141.
- Korhonen, H., 1992. The effects of environmental enrichment in ferrets. In: Smith, C.P., Taylor, V. (Eds.), Environmental Enrichment Information Resources for Laboratory Animals: Birds, Cats, Dogs, Farm Animals, Ferrets, Rabbits and Rodents. AWIV Resource Series (2), Beltsville, MD, US.
- Kronfeld, D.S., 1985. Nutrition in orthopaedics. In: Newton, C.D., Nunamaker, D.M. (Eds.), Textbook of Small Animal Orthopaedics. IVIS Ithaca, NY, USA.
- Landsberg, G., Hunthausen, W., Ackerman, L., 2003. Handbook of Behaviour Problems of the Dog and Cat. Saunders, an imprint of Elsevier Limited.
- Laporte, J.R., Carné, X., Vidal, X., Moreno, V., Juan, J., 1991. Upper gastrointestinal bleeding in relation to previous use of analgesics and non-steroidal anti-inflammatory drugs. Lancet 337 (8733), 85–89.
- Larsson, F., Winblad, B., Mohammed, A.H., 2002. Physiological stress and environmental adaptation in enriched vs. impoverished housed rats. Pharmacol. Biochem. Behav. 73 (1), 193–207.
- Lodé, T., 1999. Comparative measurements of terrestrial and aquatic locomotion in Mustela lutreola and Mustela putorius. Zeit. Saugertier. 64, 110–115.
- Lodé, T., 1989. Ontogenese des comportements de predation et role de l'experience alimentaire precoce chez *Mustela putorius* (Ontogenesis of predatory behaviour and early feeding experience in *Mustela putorius*). Mammalia 53 (4), 497–509.
- Lennox, A.M., 2005. Gastrointestinal diseases of the ferret. Vet. Clin. North Am.: Exot. Anim. Pract. 8 (2), 213–225.
- MacKay, J., 1995. Complete Guide to Ferrets. Swan Hill Press, an imprint of Quiller Publishing Ltd, Shrewsbury, UK.
- MacKay, J., 2006. Ferret Breeding. Swan Hill Press, an imprint of Quiller Publishing Press, Shrewsbury, UK.

Marshall, F.H.A., 1904. The estrous cycle in the common ferret. Q. J. Microsc. Sci. 48, 323–345.

- Martin, G., 1979. Zur K\u00e4fighaltung von Legehennen. Eine Stellungnahme aus der Sicht der Verhaltenswissenschaft. In: Yeutsch, G.M., von Loeper, E., Martin, G., M\u00fcller, J. (Eds.), Intensivhaltung von Nutztieren aus ethischer, rechtlicher und ethologischer Sicht. Birkh\u00e4user, Basel, pp. 101–122.
- Martin, D.A., 1995. Bone marrow depression associated with prolonged oestrus in the European polecat and fitch ferret. In: Exotic Animals: A Veterinary Handbook. Veterinary Learning Systems Co. Inc., New Jersey, USA, pp. 10–13.
- Mason, G.J., Mendl, M., 1997. Do the stereotypies of pigs, chickens and mink reflect adaptive species differences in the control of foraging? Appl. Anim. Behav. Sci. 53, 45–58.
- Mason, G.J., Cooper, J.J., Clarebrough, C., 2001. Frustrations of fur-farmed mink. Nature 410, 35–36.
- McCune, S., 1992. Temperament and the welfare of caged cats. PhD Thesis, University of Cambridge, UK.
- Meredith, A., Delaney, C.J. (Eds.), 2010. BSAVA Manual of exotic pets, 5th ed. British Small Animal Veterinary Association, UK.
- Moorman-Roest, J., 1993. De fret. In: Diergeneeskundig memorandum. Handleiding voor bijzondere dieren. Gezamelijke uitgave van Mycofarm, Janssen Pharmaceutica en Solvay Duphar, pp. 82–88.
- Moors, P.J., Lavers, R.B., 1981. Movements and home range of ferrets (*Mustela furo*) at Puke puke lagoon. N. Z. J. Zool. 8 (1981), 413–423.
- Morgan, M.J., 1973. Effects of post-weaning environment on learning in the rat. Anim. Behav. 21, 429–442.
- Morrisey, J.K., 1996. Parasites of ferrets, rabbits and rodents. Seminars in Avian and Exotic Pet Medicine. Avian Exot. Parasitol. 5 (2), 106–114.
- Morrisey, J.K., 2004. Ferrets: therapeutics. In: Keeble, E., Meredith, A. (Eds.), BSAVA Manual of Rodents and Ferrets. BSAVA, UK, pp. 237–244.
- Müller-Schwarze, D., Stagge, B., Muller-Schwarze, C., 1982. Play behavior: persistence, decrease, and energetic compensation during food shortage in deer fawns. Science 215, 85–87.
- Newberry, R.C., 1995. Environmental enrichment: increasing the biological relevance of captive environments. Appl. Anim. Behav. Sci. 44, 229–244.
- Norbury, G.L., Norbury, D.C., Heyward, R.P., 1998. Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). N. Z. Ecol. 22 (2), 149–159.
- Oliveira, A.F.S., Rossi, A.O., Silva, L.F.R., Lau, M.C., Barreto, R.E., 2010. Play behaviour in nonhuman animals and the animal welfare issue. J. Ethol. 28, 1–5.
- Orcutt, C., Malakoff, R., 2009. Ferrets: cardiovascular and respiratory system disorders. In: Keeble, E., Meredith, A. (Eds.), BSAVA Manual of Rodents and Ferrets. BSAVA, UK, pp. 282–290.
- van Oostrom, H., Schoemaker, N.J., Uilenreef, J.J., 2011. Pain management in ferrets. Vet. Clin. Exot. Anim. 14, 105–116.
- Pedersen, V., 2003. Gnawing Objects to Farm Foxes: Effect of Renewal, Sharing and Deprivation. Zoological Institute, Department of Animal Behaviour, University of Copenhagen, Denmark, Report Fur Animal Welfare Committee (report reference: FA009).
- Pham, T.M., Ickes, B., Albeck, D., Soderstrom, S., Granholm, A.C., Mohammed, A.H., 1999. Changes in brain nerve growth factor levels and nerve growth factor receptors in rats exposed to environmental enrichment for one year. Neuroscience 94 (1), 279–286.
- Plant, M., Lloyd, M., 2010. The ferret. In: Hubrecht, R., Kirkwood, J. (Eds.), The UFAW Handbook on the Care and Management of Laboratory and Other Research Animals., 8th ed. Wiley-Blackwell, pp. 418–432.
- Poole, T.B., 1966. Aggressive play in polecats. Sym. Zool. Soc. Lond. 18, 23-44.
- Poole, T.B., 1972. Some behavioural differences between the European polecat, *Mustela putorius*, the ferret, *Mustela Furo* and their hybrids. J. Zool. 166 (1), 25–35.
- Poole, T.B., 1973. The aggressive behaviour of individual male polecats (*Mustela putorius, M. furo* and hybrids) towards familiar and unfamiliar opponents. J. Zool. Lond. 170, 395–414.
- Poole, T.B., 1974. Detailed analysis of fighting in polecats (Mustelidae) using ciné-film. J. Zool. Lond. 173, 369–393.
- Poole, T.B., 1978. An analysis of social play in polecats (Mustelidae) with comments on the form and evolutionary history of the open mouth play face. Anim. Behav. 26, 36–49.
- Powell, R.A., 1979. Mustelid spacing patterns: variations on a theme by Mustela. Z. Tierpsychol. 90, 153-165.
- Powell, R.A., 1994. Structure and spacing of Martes populations. In: Buskirk, S.W., Harestad, A., Raphael, M., Powell, R. (Eds.), Biology and Conservation of Martens, Sables and Fishers. Cornell University Press, Ithaca, NY, USA, pp. 101–121.

- Price, E.O., 1999. Behavioural development in animals undergoing domestication. Appl. Anim. Behav. Sci. 65, 245–271.
- Price, E.O., 2002. Animal Domestication and Behaviour. CABI Publishing, CAB International, Wallington, Oxon, UK.
- Prohaczik, A., Kulcsár, N., Trigg, T., Driancourt, M.A., Huszenicza, G., 2010. Comparison of four treatments to suppress ovarian activity in ferrets (*Mustula putorius furo*). Vet. Record 166, 74–78.
- Quesenberry, K.E., Carpenter, J.W., 2004. Ferrets, Rabbits and Rodents: Clinical Medicine and Surgery, 2nd ed. WB Saunders Co., Philadelphia, USA.
- Quesenberry, K.E., Rosenthal, K.L., 2004. Endocrine Diseases. In: Hillyer, E.V., Quesenberry, K.E. (Eds.), Ferrets, rabbits and rodents, clinical medicine and surgery. W.B. Saunders company, UK, pp. 79–90.
- Rosenthal, K.L., Peterson, M.E., 1996a. Stranguria in a castrated male ferret. J. Am. Vet. Med. Assoc. 209, 62–63.
- Rosenthal, K.L., Peterson, M.E., 1996b. Evaluation of plasma androgen and estrogen concentrations in ferrets with hyperadrenocorticism. J. Am. Vet. Med. Assoc. 209, 1097–1102.
- Rosenthal, K.L., Peterson, M.E., Quesenberry, K.E., Hillyer, E.V., Beeber, N.L., Moroff, S.D., Lothrop Jr., C.D., 1993. Hyperadrenocorticism associated with adrenocortical tumor or nodular hyperplasia of the adrenal gland in ferrets: 50 cases (1987–1991). J. Am. Vet. Med. Assoc. 203, 271–275.
- Rushen, J., Lawrence, A.B., Terlouw, C.E.M., 1993. The motivational basis of stereotypies. In: Lawrence, A.B., Rushen, J. (Eds.), Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare. CAB International, Wallingford, Oxon, UK, pp. 41–64.
- Schilling, K., 2000. Ferrets for Dummies. IDG Books Worldwide Inc., CA, USA.
- Schoemaker, N.J., Schuurmans, M., Moorman, H., Lumeij, J.T., 2000. Correlation between age at neutering and age at onset of hyperadrenocorticism in ferrets. J. Am. Vet. Med. Assoc. 216, 195–197.
- Schoemaker, N.J., Teerds, K.J., Mol, J.A., Lumeij, J.T., Thijssen, J.H., Rijnberk, A., 2002. The role of luteinizing hormone in the pathogenesis of hyperadrenocorticism in neutered ferrets. Mol. Cell. Endocrinol. 197, 117–125.
- Schoemaker, N.J., Van Deijk, R., Muijlaert, B., Kik, M.J.L., Kuijten, A.M., De Jong, F.H., Trigg, T.E., Kruitwagen, C.L.J.J., Mol, J.A., 2008. Use of gonadotropin releasing hormone agonist implant as an alternative for surgical castration in male ferrets (*Mustela putorius furo*). Theriogenology 70 (2), 161–167.
- Schoemaker, N.J., 2009. Ferrets: endocrine and neoplastic diseases. In: Keeble, E., Meredith, A. (Eds.), BSAVA Manual of Rodents and Ferrets. BSAVA, UK, pp. 320–330.
- Seksel, K., Mazurski, E.J., Taylor, A., 1999. Puppy socialization programs: short term and long term behavioural effects. Appl. Anim. Behav. Sci. 62, 335–349.
- Siviy, S.M., 1998. Neurobiological substrates of play behaviour. In: Bekoff, M., Beyers, J.A. (Eds.), Animal play. Evolutionary, comparative and ecological perspectives. Cambridge University Press, Cambridge, UK, pp. 221–242.
- Slayton, J., 2009. Ferret legging among the activities at Celtic festival. Richmond Times-Dispatch, 26 October, 2009 (popular publication).
- Solnick, J.V., Schauer, D.B., 2001. Emergence of diverse *Helicobacter* species in the pathogenesis of gastric and enterohepatic diseases. Clin. Microbiol. Rev. 14, 59–97.
- Špinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. The Quarterly Review of Biology 76 (2), 141–168.
- Staton, V.W., Crowell-Davis, S.L., 2003. Factors associated with aggression between pairs of domestic ferrets. J. Am. Vet. Med. Assoc. 222 (12), 1709–1712.
- Tetley, H., 1965. Notes on British polecats and ferrets. Proc. Zool. Soc. Lond. 155 (1–2), 212–217.
- Thompson, A.D., 1951. A history of the ferret. J. Hist. Med. Allied Sci. 6 (4), 471–480.
- Thompson, K.V., 1998. Self assessment in juvenile play. In: Bekoff, M., Byers, J.A. (Eds.), Animal play: evolutionary, comparative and ecological perspectives. Cambridge University Press, Cambridge, U.K, pp. 183–204.
- Thornton, P.H., Waterman-Pearson, A.E., 2002. Behavioral responses to castration in lambs. Anim. Welfare 11, 203–212.
- Thorpe, W.H., 1965. The assessment of pain and distress in animals. Report of the Technical Committee to Enquire into the Welfare of Animals kept under Intensive Livestock Systems. Command Paper 2836, HMSO, London, UK, pp. 125–134.
- Torasdotter, M., Metsis, M., Henriksson, B.G., Winblad, B., Mohammed, A.H., 1998. Environmental enrichment results in higher levels of nerve growth factor mRNA in the rat visual cortex and hippocampus. Behav. Brain Res. 93 (1–2), 83–90.

- Trickett, S.L., Guy, J.H., Edwards, S.A., 2009. The role of novelty in environmental enrichment for the weaned pig. Appl. Anim. Behav. Sci. 116, 45–51.
- Turner, D.C., 2000. The human-cat relationship. In: Turner, Bateson (Eds.), The Domestic Cat. The Biology of its Behaviour., 2nd ed. Cambridge University press, UK.
- van den Berg, C.L., 1999. Play deprivation, long-lasting consequences of juvenile isolation in rats; involvement of opioid systems. PhD Thesis, University of Utrecht. Ponsen & Looijen BV, Wageningen, The Netherlands.
- van den Berg, C.L., Hol, T., Everts, H., Koolhaas, J.M., van Ree, J.M., Spruijt, B.M., 1999. Play is indispensable for an adequate development of coping with challenges in the rat. Dev. Psychobiol. 34 (2), 129–138.
- Vanderschuren, L.J.M.J., 2010. How the brain makes play fun. American Journal of Play. Winter 2010[®] by the Board of Trustees of the University of Illinois, USA.
- Van Leeuwen, M., 2010. Inventariserend onderzoek naar het aanbod en de welzijnsconditie van bijzondere huisdieren bij opvangcentra in Nederland (Inventory on Welfare Conditions of Exotic Animal Species in Dutch Animal Rescue Centers). Faculty of Veterinary Medicine, University of Utrecht, The Netherlands.
- Varty, G.B., Paulus, M.P., Braff, D.L., Geyer, M.A., 2000. Environmental enrichment and isolation rearing in the rat: effects on locomotor behavior and startle response plasticity. Biol. Psychiatry 47 (10), 864–873.
- Veasey, J.S., Waran, N.K., Young, R.J., 1996. On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. Anim. Welfare 5, 13–24.
- Veissier, I., Butterworth, A., Bock, B., Roe, E., 2008. European approaches to ensure good animal welfare. Appl. Anim. Behav. Sci. 113, 279–297.
- Vinke, C.M., 1998. Onderzoek naar de welzijnsomstandigheden van exotische dieren in de dierenhandel (Research into the Welfare Conditions of Exotic Pet Animals during Trade). In: Rapport Interfacultair Centrum Welzijn Dieren. Faculteit Diergeneeskunde, Universiteit Utrecht, The Netherlands, 107 pp. (Policy Report).
- Vinke, C.M., 2001. Some comments on the review of Nimon and Broom on the welfare of farmed mink. Anim. Welfare 10, 315–323.
- Vinke, C.M., Eenkhoorn, N.C., Fermont, P.C.J., Netto, W.J., Spruijt, B.M., 2002. Stereotypic behaviour and tail biting in farmed Mink (*Mustela* vison) in a new housing system. Anim. Welfare 11 (2), 231–245.

- Vinke, C.M., van den Bos, R., Spruijt, B.M., 2004. Anticipatory hyperactivity and stereotypical behaviour in American mink (*Mustela vison*) in three housing systems differing in the amount of enrichments. Appl. Anim. Behav. Sci. 89, 145–161.
- Vinke, C.M., van Deijk, R., Houx, B.B., Schoemaker, N.J., 2008a. The effects of surgical and chemical castration on intermale aggression, sexual behaviour and play behaviour in the male ferret (*Mustela putorius furo*). Appl. Anim. Behav. Sci. 115, 104–121.
- Vinke, C.M., Hansen, S.W., Korhonen, H., Mohaibes, M., Mononen, J., Bakken, M., Cooper, J.J., Spruijt, B.M., 2008b. An interpretation of farmed mink's motivation for a water bath: to swim or not to swim? Appl. Anim. Behav. Sci. 111 (1–2), 1–27 (review).
- Vinke, C.M., van Eijk, I.A.M., Boissevain, I., 2011. Inventarisatie en prioritering van welzijnsproblemen binnen de sector bijzondere dieren (Inventory and Priorities of Welfare Problems into the Area of Trade and Possession of Exotic Animal Species). Faculty of Veterinary Medicine, University of Utrecht, The Netherlands, ISBN 978-90-393-5632-6 (Dutch Policy Report).
- Wanker, R., 1999. Socialization in spectacled parrotlets (Forpus conspicillatus): how juveniles compensate for the lack of siblings. Acta Ethol. 2 (23), 23–28.
- van de Weerd, H.A., van Loo, P.L.P., van Zutphen, L.F.M., Koolhaas, J.M., Baumans, V., 1997. Preferences for nesting material as environmental enrichment for laboratory mice. Lab. Anim. 31, 133–143.
- Weiss, C.A., Williams, B.H., Scott, M.V., 1998. Insulinoma in the ferret: clinical findings and treatment comparison of 66 cases. J. Am. Anim. Hosp. Assoc. 34 (6), 471–475.
- Welter, J., Taylor, J., Tartaglia, J., Paoletti, E., Stephensen, C.B., 2000. Vaccination against canine distemper virus infection in infant ferrets with and without maternal antibody protection using recombinant attenuated poxvirus vaccines. J. Virol. 74 (14), 6358-6367.
- Wolf, P., Hebeler, D., 2001. Characteristics of the digestive physiology in ferrets. Kleintierpraxis 46 (3), 161–164.
- Woodley, S.K., Baum, M.J., 2003. Effects of sex hormones and gender on attraction thresholds for volatile anal scent gland odors in ferrets. Horm. Behav. 44, 110–118.
- Zimmerman, A., Stauffacher, M., Langhans, W., Würbel, H., 2001. Enrichment-dependent differences in novelty exploration in rats can be explained by habituation. Behav. Brain Res. 121, 11–20.