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# Mammalian pheromones – new opportunities for improved predator control in New Zealand

B. Kay Clapperton, Elaine C. Murphy and Hussam A. A. Razzaq



Cover: Stoat in boulders in the Tasman River bed, Mackenzie Basin. *Photo: John Dowding.*

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# Mammalian pheromones – new opportunities for improved predator control in New Zealand

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## Abstract

To improve conservation outcomes and move towards a ‘predator-free New Zealand’, we need new pest control technologies. Our growing knowledge of the chemistry, behaviour and neuro-endocrinology of mammalian scents that affect other individuals (semiochemicals) provides an opportunity for these to be used in various ways to help to control pest species. In this report, we summarise current knowledge of attractant semiochemicals (pheromones) of rodents, mustelids, cats and possums in New Zealand, to find potential avenues for the development of lures and other control strategies. Putative pheromones have been identified in all these species, and the major urinary proteins (MUPs) and peptides derived from the major histocompatibility complex (MHC) have been shown to play a role as pheromone carriers in the house mouse (*Mus musculus*), Norway rat (*Rattus norvegicus*) and ship rat (*R. rattus*). In addition, attractant compounds have been identified in the urine and glands of cats (*Felis catus*), mustelids (stoats – *Mustela erminea*, weasels – *M. nivalis* and ferrets – *M. furo*) and brushtail possums (*Trichosurus vulpecula*), and the calming effect of the feline facial pheromone has been explored. There are several potential applications for pheromones in mammalian pest management, including in trap and lure-and-kill systems; toxic baits; immunocontraception or chemosterilisation delivery systems; monitoring for incursions; interruption of breeding behaviour; and enhancement of biological control. The learned component of responses to pheromones and the role of MUPs in that learning suggest a complex system and it is unlikely that there will be a single ‘magic bullet’ solution for all pest species, but some potential for inter-species attractants. The use of novel control strategies based on a sound understanding of animal behaviour and neurophysiology could see pheromones and MUPs being combined to help improve predator control in New Zealand.

Keywords: semiochemical, pheromone, sex attractant, pest control, major urinary proteins, mouse *Mus musculus*, rat *Rattus* spp., cat *Felis catus*, mustelid *Mustela* spp., brushtail possum *Trichosurus vulpecula*.

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# 1. Introduction

## 1.1 The potential roles of pheromones in New Zealand predator control

### Predator control in New Zealand

New Zealand has no native terrestrial mammals (other than bats), and introduced predatory mammals have been implicated in the demise or decline in the populations of a range of native birds, reptiles, amphibians and invertebrates (King 2005; Innes et al. 2010). The predators include stoats (*Mustela erminea*), weasels (*Mustela nivalis*) and ship (black) rats (*Rattus rattus*) whose arboreal habits make them a threat to many forest-dwelling prey species (O'Donnell 1996; Innes et al. 2010). Cats (*Felis catus*), ferrets (*Mustela furo*) and Norway (brown) rats (*R. norvegicus*) have more impact on ground-nesters and inhabitants of grassland, riverbed and swamp habitats (Alterio & Moller 1997; Murphy et al. 2005; O'Donnell et al. 2015). Rats can have a major impact on offshore island ecosystems (Bellingham et al. 2010). House mice (*Mus musculus*) predate nestling seabirds (Angel et al. 2009) and lizards (Newman 1994). The common brushtail possum (*Trichosurus vulpecula*) is not only a destructive forest herbivore but also predate native birds' eggs and is a carrier of bovine tuberculosis (Clout 2006; Innes et al. 2010). European hedgehogs (*Erinaceus europaeus*), although not covered in this review, are minor egg predators of ground-nesting birds and are considered a threat to indigenous invertebrate populations (Jones & Sanders 2005). The fight to control the damage that these introduced mammalian predators cause to the New Zealand biota has been under way for more than a century. To date, this has mostly targeted individual pest species in discrete areas of the country, because of limited monetary, labour and technological resources. However, there is a growing movement in New Zealand to tackle the pest issue at a larger scale on the mainland (Russell et al. 2015). Islands will continue to play important roles as refugia for the rarer native species and must maintain their pest-free status.

Trapping and poison baiting remain the standard methods for controlling small mammalian pests in New Zealand (O'Donnell & Hoare 2012; Fisher et al. 2014; Brown et al. 2015). However, despite recent developments in trap design (e.g. Morriss & Warburton 2014; <http://goodnature.co.nz/index.php>), toxins and toxin delivery systems (e.g. Pitt et al. 2011; Blackie et al. 2014, 2016; Eason et al. 2014; Murphy et al. 2014), current control techniques are not cost effective on the mainland for the removal of the last few individuals, which is required for the complete eradication of a pest species, nor are they guaranteed to detect any incursions into pest-free areas (McMurtrie et al. 2011; Dowding & O'Connor 2013; Prada et al. 2014; Brown et al. 2015; Campbell et al. 2015). There have been recent examples of where more attractive lures could have considerably aided conservation efforts. In 2009, a pregnant female stoat arrived on the mammalian pest-free nature reserve Kapiti Island, northwest of Wellington, and was not detected for over a year, after she had given birth and her young were independent (Prada et al. 2014). In November 2011, a rat was videoed at a shore plover (*Thinornis novaeseelandiae*) nest on Mana Island, near Wellington, after the plover population had crashed (Dowding & O'Connor 2013), despite there being monitoring stations and tracking tunnels across the island to monitor for rodent signs; and in November 2012, the shore plover population on Waikawa Island rapidly declined, but no predator sign was detected by traps, tracking tunnels and trail cameras, or by rat-, cat- and stoat-tracking dogs that worked the island (Anon. 2013). Scats were finally located by a rat-tracking dog in a litter sample containing the remains of dead birds (Ritchie 2013), which were identified as rat droppings (E. Murphy, unpubl. data).

Lures can attract an animal to a control or monitoring device and/or increase consumption of a poison bait (O'Connor & Eason 2000). However, discovery of the 'Holy Grail', i.e. an attractant that would lure all individuals to control devices, remains elusive (Brown et al. 2015). There has been little advance in the development of food-based lures (Witmer et al. 2008), although

there have been some improvements on the use of peanut butter for rats (Jackson et al. 2016a,b). However, when food is abundant, such as on pest-free islands or in areas that have been cleared of pests on the mainland, it is difficult to detect pest incursions using food-based lures. Furthermore, it is important to have techniques that will be attractive to pests even at low population densities (Dilks & Towns 2002; Russell et al. 2008). Thus, a lure other than food, such as a sex lure, may be more effective. Linklater et al. (2013) suggested that 'super-lures' that attract animals from great distances and ensure higher interaction rates with control devices have the potential to provide major gains in mammalian pest control. Also, since modern re-setting traps and devices that are equipped with computerised systems to record captures require fewer inspections, long-life lures are essential (Murphy et al. 2014; Carter et al. 2016).

### **Pheromones overview**

Semiochemicals are chemicals that are emitted into the environment by living organisms to transmit information between individuals (Law & Regnier 1971). Thus, they differ from hormones such as oxytocin, arginine-vasopressin and the sex hormones, which work within the body to mediate social recognition responses between individuals (Ferguson et al. 2002; Bielski & Young 2004; Choleris et al. 2009; Gabor et al. 2012). Semiochemicals consist of pheromones and allelomones (Tirindelli et al. 2009). Pheromones were originally defined as molecules that act as innate signals to elicit specific, invariant behavioural or endocrinal reactions in conspecifics (Karlson & Lüscher 1959; Beauchamp et al. 1976), whereas allelomones are used to modify the behaviour of individuals belonging to a different species (Nordlund & Lewis 1976). Of these, pheromones are of the greatest interest in terms of the development of lures, and so are the focus of this review.

More recently, authors have investigated how the responses of mammals to pheromones can be modified by the context in which they are received and by experience of the receiver. Wyatt (2010; 2014a) differentiated between individual pheromones and the more complex mixes of scents through which individuals recognise each other and can change their responses with learning, which he referred to as 'signature mixtures'. Brennan & Keverne (2004) provided an overview of terminology relating to pheromones, and distinguished between single molecules or cocktails of a few molecules that elicit dramatic behavioural effects (releaser pheromones) and chemosignals that cause longer-term changes in neuroendocrine or developmental states (primer pheromones). Doty (2010) argued that there is probably a continuum of chemical/behavioural complexities within mammalian scent communication. Logan (2015, p. 96) stated that pheromones 'can be monomolecular or multi-component, and can provoke both hardwired and learned behaviour', so we include all semiochemicals that are used for intra-specific communication in this review.

Pheromones play major roles in sex attraction, social organisation, signalling between parents and offspring, and priming of the reproductive cycle (including oestrus synchronisation and puberty delay or acceleration). Indeed, the key roles that glandular secretions play in social communication in rodents and carnivores have been known for decades (e.g. Mykytowycz 1970; Johnson 1973; Doty 1976; Brown 1979; Halpin 1986; Merx et al. 1988).

Pheromones can be released to the environment via scent-marking behaviour. Mammals have an incentive to approach scent marks to avoid direct interactions with each other or to dictate appropriate responses to the scent markers during encounters (Gosling & Roberts 2001; Ferkin 2015). Several studies and reviews have investigated scent marking by mammalian pest species in New Zealand, including the use of scent marking for sex and individual recognition by Norway rats and mice (Brown 1975; Birke & Sadler 1984; Gosling & Roberts 2001; Johnston 2003; Hurst & Beynon 2004; Thom & Hurst 2004), mustelids (Erlinge et al. 1982; Clapperton et al. 1988; Erlinge & Sandell 1988; Clapperton 1989; Hutchings & White 2000; Berzins & Helder 2008), cats (Panaman 1981; Natoli 1985; Feldman 1994) and possums (Salamon 1994; Salamon et al. 1999). However, little is known about the scent marking of ship rats (Mallick 1992). Hedgehogs have a strong-smelling urine thought to be used in scent marking (Poduschka & Wemmer 1986) but there do not appear to have been any investigations into hedgehog pheromones, so this species is not included in the current review.

The flexibility in responses to mammalian pheromones mediated by learned responses (Beny & Kimichi 2014; Stowers & Liberles 2016) can affect the responses of pest mammals to baits and traps. Odours can make things seem more familiar. For example, Volfová et al. (2010) found that mice (particularly males) were more likely to enter bait stations that had been scented with odours from adult, sexually and socially experienced conspecifics than clean stations. A systematic approach to assessing the chemistry of signals has been advocated in the search for biologically active compounds (Clark & Shah 1991; Clark et al. 1991). However, when Apps et al. (2015, p. 1131) investigated the use of this approach to relate semiochemical compound properties with signal function, they found that overall relationships were ‘scarce and formed only small-scale patterns’. This may be due to the complex physiological and behavioural responses of mammals to semiochemicals (Logan 2015). Consequently, Jackson et al. (2016b) recommended that an integrated chemical image and response-guided approach be used to assess the potential of pheromones for use as olfactory lures. The potential of using mammalian semiochemicals as lures for pest species in New Zealand has been suggested (Christiansen 1976), and research has been initiated (Clapperton et al. 1989, 1994a,b, 1999; Edwards et al. 1997; Spurr et al. 2004). The emerging knowledge on the chemistry, physiology, genetics and learned behavioural responses related to pheromones may allow this research to reach its potential.

## 1.2 Aim of this review

The aim of this review is to summarise the current state of knowledge of pheromones of mammalian predator species in New Zealand, to find potential avenues for the development of lures and other control strategies. To do this, we begin in section 2 by summarising our current understanding of the identity and structure of pheromones and their carriers, and how they function and interact with other glandular secretions. We then briefly outline the role of mammalian odorant receptors in the chemical-detecting interface between the atmosphere and the nervous system, summarise the ways in which food intake is influenced by olfactory cues and metabolic status, and describe the role of the major histocompatibility complex in the control of odour expression in section 3. In section 4, we assess how this knowledge of mammalian odour communication might be used to improve pest control strategies and examine how the behavioural ecology of the various mammalian pest species defines how odours may be of use, putting this new knowledge into the context of what is already known about pest management and scent chemistry. Terms used frequently in this report, and their abbreviations, are listed in a glossary at the end of the report.

## 2. Pheromone identification and function in mammalian predator species

Various reviews have summarised recent information concerning semiochemicals and putative pheromones (Novotny 2003; Beynon & Hurst 2004; Brennan & Keverne 2004; Hurst & Beynon 2004; Burger 2005; Brennan & Kendrick 2006; Brennan & Zufall 2006; Müller-Schwarze 2006; Johansson & Jones 2007; Zufall & Leinders-Zufall 2007; Archunan 2009; Hurst 2009; Tirindelli et al. 2009; Doty 2010; Kaupp 2010; van der Hurk 2011; Apps 2013; Hurst & Beynon 2013), the vast majority of which has been conducted on mice and Norway rats (the 'lab rat'). Comprehensive information about pheromones and other semiochemicals from a wide range of taxa, including Rodentia and Carnivora, can be found in the freely accessible database Pherobase (El-Sayed 2012).

One of the key recent developments has been an increased interest in the role of high-molecular-weight, non-volatile peptides and proteins, including major urinary proteins (MUPs) (Touhara 2008; Wyatt 2014b).

Modern technologies have led to the identification of ever increasing numbers of hormone-dependent volatile compounds and binding proteins over the last 20 years. These techniques include stir bar sorptive extraction, element-specific detection combined with capillary gas chromatography, protein banding, peptide mass fingerprinting, electrospray ionisation/mass spectrometry, isoelectric focusing electrophoresis, X-ray crystallography, calcium imaging, metabolomics, pattern recognition analysis, and genetic and genomic tools, molecular docking and fluorescence analysis (reviewed by Gevaert & Vandekerckhove 2000; Scott & Scott-Johnson 2002; Talor et al. 2002; Stephens & Allan 2003; Lindon et al. 2007; Novotny & Soini 2008; Swaney & Keverne 2009; Tirindelli et al. 2009; Kaupp 2010; Paske et al. 2013b; Yu 2013; Yuriev & Ramsland 2013; Soso et al. 2014).

### 2.1 Mice

#### Urine and preputial glands

Mouse urine scent marks contain information including social rank, individual recognition, maturity, diet and degree of stress (Hurst 1990; Schaefer et al. 2010). Mice can determine the age of a conspecific by the volatile profile of its urine (Beauchamp & Yamazaki 2003; Osada et al. 2003; Cavagioni et al. 2006, 2008) and can also identify individuals that have been infected by parasites or disease (Penn & Potts 1998a; Penn et al. 1998; Beauchamp & Yamazaki 2003). Moreover, mice can distinguish between conspecifics with the same and different odour genotypes (Yamaguchi et al. 1981). Preputial (also known in females as clitoral) glands release secretions into the urine (Bronson & Caroom 1971; Brown & Williams 1972), while the urine itself is a source of even more compounds (Hurst et al. 1998). A large number of pheromones from mouse urine were identified during the 20th century (Novotny et al. 1986; Schwende et al. 1986; Archunan 2009) but these have not been used in pest control. Additional putative pheromones have been identified in the last 17 years, and the structure and function of previously identified compounds have been further investigated (Koyama 2016). Earlier studies suggested that there may need to be a learned association between the odour producer and the odour, to induce odour preference in female mice (Jemiolo et al. 1991; Wilson & Stevenson 2003). More recent research has confirmed this, showing that sex attractant volatiles do indeed need a learned association to induce the attractant effect, and that this requires direct contact with the non-volatile components of male scent (Moncho-Bogani et al. 2002, 2005; Martínez-García et al. 2008, 2009; Ramm et al. 2008). This is in line with an earlier finding by Sipos et al. (1992) that the ability of female mouse urine to elicit vocalisations in male mice depends on the presence of both a volatile pheromone and a stable non-volatile chemical. Over 50 volatiles identified

from mouse urine and preputial glands are listed in Appendix 1. Six of these compounds have long been known as prospective mouse pheromones: 2,5-dimethylpyrazine, 2-sec-butyl-4,5-dihydrothiazole (SBT), farnesene (a mixture of E,E- $\alpha$ -farnesene and E- $\beta$ -farnesene), 2,3-dehydro-exo-brevicommin (DHB), 2-heptanone, and 6-hydroxy-6-methyl-3-heptanone, although only the first three are highly odiferous (Novotny 2003). They are detected by different vomeronasal neurones at very low concentrations (Leinders-Zufall et al. 2000). SBT and DHB are produced by all adult males (Novotny et al. 1990; Hurst & Beynon 2004). They induce aggression in other males when presented in the urine (Novotny et al. 1985) and in combination are also attractive to female mice (Jemiolo et al. 1985, 1991). 3,4-Dehydro-exo-brevicommin (DEB) and SBT also attract female mice (Musso 2016), as do E,E- $\alpha$ -farnesene and E- $\beta$ -farnesene (Jemiolo et al. 1991), which can also induce the oestrus cycle (Ma et al. 1999). Responses to these urinary odours can be very specific. For example, Novotny et al. (1995) found that the absolute configuration of DHB and SBT is related to their stereospecific biological activity; and Cavaggioni et al. (2003) also noted that the S and R configurations of SBT induce different responses. SBT is now thought to act as an alarm pheromone in mice. This pheromone is released by both males and females, and has a similar structure to the heterocyclic sulphur-containing compounds present in stoat and ferret anal sac secretions (Brechtbühl et al. 2013). 6-Hydroxy-6-methyl-3-heptanone has also been shown to accelerate puberty in female mice (Novotny et al. 1999a), and three other volatiles (3-amino-s-triazole, 4-ethylphenol and 3-ethyl-2,7-dimethyl octane) of male mouse urine appear to act as attractants of the opposite sex (Achiraman & Archunan 2002a), while 3-cyclohexene-1-methanol attracts other males (Achiraman & Archunan 2005). In addition, Zhang et al. (2007) identified 1-hexadecanol and 1-hexadecanol acetate as potential male pheromones. Manipulating the odour profile of castrated male mice indicated that hexadecanol and hexadecyl acetate are components of male preputial gland secretions that attract females and are also attractive to males at low concentrations (Zhang et al. 2008a).

Achiraman & Archunan (2006) used gas chromatography–mass spectrometry to identify compounds in female mouse urine, searching for a putative oestrous-specific chemo-signal. They found that 1-iodo-2-methyl undecane (1I2MU), 1-H-cyclopentane, caryophyllene and copanene are present in the urine during oestrus, but only 1I2MU is also present in the pre-oestrous stage and absent in all other stages. They also conducted a behavioural assay, which showed that 1I2MU is attractive to male mice, but not as attractive as oestrous urine, suggesting that additional compounds contribute to its attractiveness; while in an investigation of pre-mating behaviour, Achiraman et al. (2010a) found that 1I2MU was the compound most preferred by males.

Trimethylamine, which is found in the urine of a range of mammals, is produced in high concentrations by *Mus musculus* and *M. domesticus* (Li et al. 2013; Stensmyr & Maderspacher 2013). However, this production is sex-dependent, with male urine containing c. 20 times the concentration of female urine. Both male and female *M. musculus* are attracted to trimethylamine at concentrations naturally found in mouse urine (Li et al. 2013).

Lin et al. (2005, p. 470) demonstrated that the main olfactory bulb of mice responded to male mouse urine, including a 'potent, previously unknown semiochemical', which was identified as (methylthio)methanethiol.

Some urinary compounds are thought to indicate the age or dominance status of the mouse, and this information may be used by females in mate selection (Osada et al. 2003, 2008; Liu et al. 2008). Furthermore, 2,5-dimethylpyrazine is a unique female compound that suppresses oestrus (Thompson et al. 2013). Isobutylamine and isoamylamine from the urine of male mice act as puberty accelerants (Archunan & Achiraman 2006; but also see Liberles & Buck 2006), and isobutylamine also acts as a vomeronasal agonist (Rodriguez & Boehm 2009).

Finally, Zhang et al. (2007) confirmed that various mouse urinary compounds vary in quantity according to strain, sex and/or individual identity.

## Other odour sources

Sex-specific peptides are found in other bodily secretions (Kimoto et al. 2005). For example, 7-kDa peptide from the lachrymal and submaxillary glands of male mice, exocrine-gland secreting peptide 1 (ESP1; Abe & Touhara 2014) induces females to adopt the lordosis (curved back) position for mating (Haga et al. 2010; Yoshinaga et al. 2013; Cavaliere et al. 2014) via stimulation of the vomeronasal organ (Kimoto et al. 2005). Young mice secrete another peptide from the lachrymal gland, ESP22, which inhibits the sexual behaviour of adult mice towards the pheromone producer (Ferrero et al. 2013). Based on Luo et al.'s (2003) trials investigating the responses of single neurons of the accessory olfactory bulb, Hurst (2009) considered that these ESPs provide distinct scent signals, playing a role in signalling individual identity.

The general body scent of mice comprises mostly aliphatic aldehydes but also a range of other compounds (Appendix 1; Röck et al. 2006). It arises not only from the volatiles found in urine, but also from other undetermined sources. Nitromethane, propanoic acid, dimethylsulphide, 1-octene, 1-hexanol, hexanoic acid, indole, and  $\alpha$ - and  $\beta$ -farnesene were collected in the air surrounding live mice. The abundance of 1-methoxy-2-propane, 6-hydroxy-6-methyl-3-heptanone, phenol and 4-methylphenol compounds found in both body scent and urine can vary by 10- to 100-fold (Röck et al. 2006).

## 2.2 Rats

### Urine and preputial glands

The main sources of odours in rats are urine and the preputial glands (Appendix 2). Kannan & Archunan (2001a, p. 250) quoted earlier studies showing that 'In rat scent glands, pheromones exist as a mixture of alcohols, aldehydes, acids of saturated or unsaturated aliphatic or aromatic compounds'. Zhang et al. (2008b) found that squalene, 2-heptanone and 4-ethylphenol, all of which naturally occur in sexually mature male Norway rat urine, are attractive to female rats either alone or in combination. However, even the combination was not as attractive as real male urine, suggesting that other components (the authors suggested heptan-4-one and phenol) may also be needed to create a highly attractive odour. Takács et al. (2016) found that a synthetic mix of 2-heptanone, 4-heptanone, 3-ethyl-2-heptanone, 2-octanone, 2-nonanone and 4-nonanone was attractive for female rats. Osada et al. (2009) confirmed the attractive properties of 2-heptanone and 4-ethylphenol and also showed that 4-methylphenol may be an important component of the female-attractant mixture released by adult males. Meanwhile, Achiraman et al. (2011a) found that squalene is also produced in the female preputial gland, increasing in concentration during pre-oestrus and oestrus, and described it as a 'female-specific chemosignal that attracted males'. 2-Heptanone and 4-ethylphenol also occur in female preputial gland secretions/urine but at lower concentrations (Zhang et al. 2008b).

There has been some research on 6,11-dihydro-dibenz-b,e-oxepin-11-one, 2,6,10-dodecatrien-1-ol-3,7,11-trimethyl(Z) and 1,2-benzene dicarboxylic acid butyl(2-methylpropyl) ester, all of which are found in the clitoral gland of the Norway rat. Kannan & Archunan (2001a) found that the first compound attracted conspecifics of the opposite sex, whereas the second and third attracted both sexes. Furthermore, these are not unique to female rats - Kannan et al. (1998) described 2,6,10-dodecatrien-1-ol-3,7,11-trimethyl and di-*n*-octyl phthalate as compounds from the preputial glands of male Norway rats that were attractive to females, while 1,2 benzene dicarboxylic acid diisooctyl ester attracted other males.

Zhang et al. (2008b) found that E,E- $\alpha$ -farnesene and E- $\beta$ -farnesene occurred at higher concentrations in female than male Norway rat glands, and consequently suggested a sex-attractant role for these compounds. In addition, both compounds were present in higher concentrations in dominant than in subordinate males (Pohorecky et al. 2008).

Farnesols 1 & 2 have been identified from the preputial glands of Norway rats and ascribed female-attraction powers (Ponmanickam et al. 2010), along with geranyl linalool isomer, oxirane and lanosterol. By contrast, Rajkumar et al. (2010a) identified cyclohexene, beta-bisabolene, 1-pentene, hexadecatetraene, 3-cyclohexene, farnesol 1 and farnesol 2 from the preputial glands of the ship rat, among which only the farnesols were bound to MUP  $\alpha_{2\mu}$ -globulin, suggesting that these compounds are more likely to play roles as pheromones. Rajkumar et al. (2009, 2010a) also found that the volatiles 1-chlorodecane, 2-methyl-N-phenyl-2-propenamide, hexadecane and 2,6,11-trimethyl decane were bound by  $\alpha_{2\mu}$ -globulin in ship rat urine.

Components of male ship rat urine that attract females include ethanol, 2-(octylthio) and 1-chlorodecane (Selvaraj & Archunan 2002a), while 1,3,5-triazone-2,4-diamine attracts other males. Females in oestrus produce hydroperoxide, 1-nitropentane and 4-azidoheptane, all of which attract males, while 1-nitropentane also attracts females.

### Other odour sources

The cheek glands of rats also act as a source of odiferous secretions. Kannan & Archunan (2001b) identified a range of alkanes, aliphatic acids esters and alcohols that were produced by the cheek glands of laboratory rats. Those of males contained di-n-octyl phthalate, 1,2-benzene dicarboxylic acid butyl (2-ethyl hexyl) ester and 1,2 benzene dicarboxylic acid (2-methylpropyl) ester, the first of which was attractive only to females, while the latter two were attractive to both sexes. By contrast, the two main components of female cheek glands were 1,2-benzene dicarboxylic acid (2-methylpropyl) ester and 2,6,10 dedecatrien-1-ol, 3,7,11-trimethyl-(Z, E), both of which were attractive to both males and females.

Nielsen et al. (2011, 2013) searched for odours in Norway rat faeces that might indicate the oestrous state of females. Male rats responded to the odour of oestrous female rats by penile erection. Although no compounds were identified that were unique to female rat faeces, the male rats responded to a synthetic mixture of five carboxylic acids (propanoic acid, 2-methylpropanoic acid, butanoic acid, 3-methylbutyric acid and pentanoic acid) in a dose-dependent way, and to 6-methyl-5-hepten-2-one, albeit not as strongly as to the natural faeces odour. These compounds are also found in the faeces of foxes and horses, and male rats respond to the faeces of vixens and mares as well as to those of female rats (Rampin et al. 2006).

The general body odour of the ship rat has been investigated by Byrom et al. (2003), who identified more than 20 compounds using headspace analysis, including pyrazine, 2-ethyl pyrazine, 2-ethyl-5-methyl pyrazine, m- or p-cresol and sulphur-containing thiazole-type compounds. They then created a 'chemical rat' based on the concentrations of the first four of these compounds and found that it emitted a distinct 'ratty' odour.

Alarm pheromones are released from the whisker pad and provoke sniffing, rearing and locomotory activities in male rats (Kiyokawa et al. 2004a). Although we know that those from the perianal region are testosterone-independent (Kiyokawa et al. 2004b), volatile (Inagaki et al. 2009) and water soluble (Kiyokawa et al. 2005), little is known about their chemical structure. Recent research on rat and mouse alarm pheromones has focused on the role of the vomeronasal organ (e.g. Kiyokawa et al. 2007) and Grueneberg ganglion neurons (Brechtbühl et al. 2008), and the stress and startle responses of rats to alarm pheromones (Kiyokawa et al. 2006; Inagaki et al. 2008). Inagaki et al. (2014) have identified hexanal and 4-methylpentanal as components of stress-related odour in Norway rats. Kiyokawa (2015) described how this combinational pheromone activate the anxiety circuit.

Carbon disulphide is released from the breath of rodents and is detected by specialised olfactory sensory neurones (Munger et al. 2010). Rats learn which foods are safe to eat from other rats (Galef 1986a,b, 1987, 1991), by detecting CS<sub>2</sub> (Galef et al. 1988; Mason et al. 1988; Galef 1992).

## 2.3 Rodent Major Urinary Proteins (MUPs)

Malone et al. (2001) provided an overview of 20th century knowledge of the role of volatile semiochemicals, MUPs and the MHC in the communication of social status and mate choice in mice, while Cavaggioni & Mucignat-Caretta (2000) outlined the odour-binding mechanisms of MUPs, and Mucignat-Caretta & Caretta (2014) described the roles played by MUPs in chemical communication in mice. Mice and rats excrete very high concentrations of MUPs in their urine (Beynon et al. 2001), which bind to volatiles including SBT, DHB, farnesenes, 6-hydroxy-6-methyl-3-heptanone and geraniol (Novotny et al. 1999b; Hurst & Beynon 2004) in a central cavity or on surface patch features (Timm et al. 2001). MUPs are also found in the salivary, mammary and lachrymal gland secretions of both mice and rats (Shahan et al. 1987; Beynon et al. 2008), but saliva does not induce the same strong intra-strain attractiveness in mice as urine does (Bímová et al. 2009). Sharrow et al. (2002) not only found evidence for MUPIV protein in the nasal mucus and vomeronasal organ, but also demonstrated that nasal MUPs sequester and transport pheromones.

While MUPs clearly play a role as ligand binders (Robertson et al. 1993, 2001; Sharrow et al. 2002), there is mounting proof that they are more than just pheromone deliverers (Beynon & Hurst 2003). Marchlewska-Koj et al. (2000) showed that oestrus-stimulating compounds were ineffective when not bound to MUPs. Furthermore, the combination of volatile pheromones with the less-volatile MUPs provides a slow-release odour system (Hurst et al. 1998; Armstrong et al. 2005), allowing animals to determine the freshness of a scent mark (Hurst & Beynon 2004; Hurst et al. 2001) and thus avoid direct conflict with territory holders. MUPs may also stop oxidation of the scent (Novotny et al. 1999b). Unlike volatile ligands that induce responses in animals from a distance, MUPs require direct contact of the nose onto the scent mark (Luo et al. 2003).

There is both behavioural and neurophysiological evidence that MUP/pheromone ligand complexes, or even MUPs on their own, act as signals of 'scent ownership' (Hurst & Beynon 2004; Kaur et al. 2014). Not only can mice use MUPs to distinguish between familiar and unfamiliar (Hurst et al. 2001) and between different genetic strains (Cheetham et al. 2007; Stopková et al. 2007; Bímová et al. 2009), but they can also use them as an individual recognition system to identify neighbours (Hurst et al. 2001; Nevison et al. 2003; Hurst & Beynon 2004). This is because mouse MUPs are highly polymorphic and the MUP profiles remain constant throughout adult life (Hurst & Beynon 2004). Both males and females use this system, described as a 'barcode' (Beynon & Hurst 2003), but MUP production is 3–4 times greater in males than in females (Beynon et al. 2001). In addition, MUPs can indicate competitive ability (Hurst & Beynon 2004), and Chamero et al. (2007) described a MUP-ligand pheromone complex that has aggression-promoting activity in male mice. However, MUP-borne odorants have also been shown to inhibit the response of male mice to attack mouse pups (Cavaggioni et al. 2001).

Armstrong et al. (2005) provided evidence for a second type of MUP that contributes to sex-specific scent in male mice. Furthermore, varying concentrations of MUPs in female mouse urine advertise their reproductive state (Stopka et al. 2007; Achiraman et al. 2011b), potentially explaining why male mice are more attracted to oestrous than non-oestrous females (Archunan 2009).

Recently, investigators have studied the structure of MUPs. Perez-Miller et al. (2010) showed that differences in cavity size allow very specific binding of SBT onto one isoform (MUP-IV) of a male mouse MUP that is expressed in the vomeronasal mucosa rather than the urine. In addition, one male-specific MUP named darcin (mass = 18 893 Da) has been identified from the urine of wild-stock mice (Roberts et al. 2010; Phelan et al. 2010), and proteins belonging to the same family are found in the urine of both Norway and ship rats (Linklater et al. 2013; Paske et al. 2013a). Darcin acts as an attractant to female mice, inducing them to spend more time near the odour source. Importantly, contact with darcin also stimulated a strong learned attraction to the associated airborne urinary odour of an individual male, such that females were subsequently attracted to the airborne scent of that specific individual but not to those of other males. This is consistent with earlier observations by Hurst (1986) that wild female mice return to sites to wait for a male when ready to mate. Martínez-Ricós et al. (2007) also found that involatile male sexual pheromones not only elicited investigation, but also induced learned place preference,

and Lanuza et al. (2014) showed that darcin could induce a learned attraction to neutral odours, allowing mice to identify and respond appropriately to an individual's olfactory signature. Furthermore, females can also learn to associate darcin with spatial cues in the environment (Roberts et al. 2014).

The behavioural effects of MUP-borne odorants are mediated through the vomeronasal organ neural pathway. While previous workers have suggested a need for main olfactory epithelium signalling (Wang et al. 2006), Chamero et al. (2007) argued that two separate pheromone-responsive circuits exist that respond to different cues. Mice have a particularly high number of V1R genes and pseudogenes compared with rats (Grus et al. 2005); all these authors cautioned that there had not been a comprehensive search for rat V1R pseudogenes.

The best known rat MUPs are the lipocalins, which help in pheromone transport (Bacchini et al. 1992; Flower 1996), prolonged release (Hurst et al. 1998), and have some sensory properties (Kreiger et al. 1999). The most documented rat MUP from the preputial gland of laboratory rats is the 18-kDa  $\alpha_{2\mu}$ -globulin (Ponmanickam & Archunan 2006; Ponmanickam et al. 2009; Rajkumar et al. 2009). Similarly, a 20-kD protein has been found in the urine of male ship rats (Kamalakkannan et al. 2006) and a proteomic study identified a 22.4-kDa protein in male ship rat urine as a rat MUP (Rajkumar et al. 2010b).

The expression of MUPs in rats is even more male-specific than in mice and is testosterone dependent (Achiraman & Archunan 2002b; Beynon et al. 2008). However, this does not mean to say that MUPs do not play a role in olfactory communication by female rats – a lipocalin has now been found in female ship rat urine, with the highest concentrations being recorded during oestrus and metoestrus (Muthukumar et al. 2013). The MUP oestrus urinary lipocalin protein from female ship rats bound with both farnesol and 2-isobutyl-3-methoxypyrazine (Rajesh et al. 2016). Furthermore, MUPs have also been found in the preputial glands of rat pups (Ponmanickam et al. 2009), with the proportions changing during puberty (Vettorazzi et al. 2013).

The MUPs of wild Norway rats exhibit less inter-individual variation than those of wild mice as they are less polymorphic (Beynon et al. 2008), which suggests that they might not act as an individual recognition system mediating social organisation in rats.

Other recent advances in the study of MUPs in rats have focused on the genetics and hormonal control of lipocalins (McFadyen & Locke 2000; Logan et al. 2008; Karn & Laukaitis 2012). Mucignat-Caretta et al. (2006) investigated whether rats responded differently to mouse or rat chemosignals and found that only rat-specific urine and  $\alpha_{2\mu}$ -globulin, and not mouse MUPs, stimulated the vomeronasal amygdala in female rats.

## 2.4 Cats

The scent-marking behaviour of domestic cats and the semiochemicals involved in this have been described by Bradshaw & Cameron-Beaumont (2000), and the responses of cats to scent marks have also been investigated. For example, Roesch (2003) found that female domestic cats respond to the urine of male cats, with the most interest being shown by oestrous females to the scent of dominant males. In addition, field trials have shown that cats respond to decomposed anal gland material mixed with urine, at least during the breeding season (Edwards et al. 1997), and possibly to fresh faeces and urine (Moseby et al. 2004). Hanke & Dickman (2013) further showed that cat urine was more successful than catnip or valerian extracts in attracting cats to hair snares. While this contrasts with the findings of Clapperton et al. (1994a), in the latter trial the captive cats may have been desensitised to the scent of cat urine, and only frozen urine samples were tested. These findings raise the possibility of identifying specific pheromonal attractants for cats. However, very few studies have reported on the semiochemicals of cats (*Felis* spp.) (Burger 2005). Despite 50 years of research into tiger pheromones (Brahmachary & Poddar-Sarkar 2015), the domestic/feral cat is not even listed in the pheromone database Pherobase.

## Urine

The sulphur-containing putative pheromone felinine (2-amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid) was identified in 1951, but there has been very little recent (post-2000) investigation of it (Appendix 3). Felinine is found in both the urine and blood of domestic cats (Hendriks et al. 2001; Rutherford et al. 2002) and is believed to be testosterone dependent and so is more abundant in male than female urine (Hendriks et al. 1995, cited in Roesch 2003). Synthetic felinine is more stable than the natural compound in cat urine (Rutherford et al. 2004). Recent interest has particularly focused on the precursors of felinine. For instance, Miyazaki et al. (2006b) described the chemistry of cauxin, a MUP that regulates the species-, sex- and age-dependent production of felinine (Miyazaki et al. 2008) and is itself regulated by testosterone (Miyazaki et al. 2006a). Miyazaki et al. (2008) also identified 3-mercapto-3-methyl-1-butanol, 3-mercapto-3-methylbutyl formate, 3-methyl-3-methylthio-1-butanol and 3-methyl-3-(2-methyl-disulphanyl)-1-butanol as cat-specific odorants that may be used as 'territorial markers for conspecific recognition or reproductive purposes by mature cats'. Rutherford et al. (2004) further suggested that whichever of these compounds create(s) the distinctive 'tom cat odour' is/are active at very low concentrations. 3-Mercapto-3-methylbutanol has since been described as the tom cat compound (Apps et al. 2014), and is found in the urine of the domestic cat, as well as some big cat species, but is absent from the strong-smelling urine of lions (Andersen & Vulpius 1999). No studies to date have investigated the behavioural responses of cats to these other breakdown components of tom cat urine.

## Other odour sources

The feline facial pheromone (FFP) is thought to be used in territorial marking and familiarisation of the cat in a new environment (Feldman 1994; Pageat 1998). Recent work on FFP has mainly focused on its calming effect on cats, thereby allowing easier handling by veterinarians (Kronen et al. 2006). It is also used to eliminate urine spraying in domestic cats (Mills & White 2000; Mills & Mills 2001). There is also a feline interdigital secretion that elicits a scratching response in cats (Pageat & Cozzi 2011; Cozzi et al. 2013).

Cats are known to produce lipocalin proteins from the submandibular salivary gland and skin, including the allergen Fel d 4, which was described by Smith et al. (2004) as the cat homologue of rodent MUPs. Other lipocalin proteins include Fel d 1, 7 & 8 and Fel d 3 (cat cystatin) (Ichikawa et al. 2001a,b; Smith et al. 2011). While these compounds act as warning signals for rats (Dielenberg & McGregor 2001; Papes et al. 2010), their roles in intraspecific communication remain unknown.

Kittens orientate towards and attach onto specific nipples on the mother cat and this response is thought to depend on learned olfactory cues (Arteaga et al. 2013).

Burger et al. (2008) and Soini et al. (2012) identified a range of pheromones from the cheeks and foreheads of large felines, including the Bengal tiger (*Panthera tigris*).

There have been no studies of the constituents of odour from the anal gland secretions of cats, although Preti et al. (1976) determined that they did not contain trimethylamine.

No one has pursued the suggestion by Bland (1979) that valeric acid, present in the vagina of female cats in oestrous, may be a sex pheromone. Van der Hurk (2011) lists valeric acid as a putative pheromone that attracts cats, makes males restless, and stimulates sexual behaviour in females.

## 2.5 Mustelids

Most preliminary work on potential mustelid pheromones has focused on the highly malodorous contents of anal sac secretions (Brinck et al. 1978; Crump 1978, 1980a,b; Crump & Moors 1985; Clapperton 1985; Clapperton et al. 1988). But scent-marking studies showed that urine depositing,

body-rubbing and chin-rubbing behaviours are also likely to transmit intraspecific information (Wheeler 1978; Erlinge et al. 1982; Wildhaber 1984; Clapperton 1989). The presence in ferrets of abdominal glands similar to rodent preputial glands that are larger in males than in females (Clapperton et al. 1987), and of numerous sebaceous glands in the ventral body skin (Clapperton 1985) offer other potential sources of scent, so the search for pheromones has moved to investigating urine and body fur odours (Garvey et al. 2016; Murphy et al. 2013; Murphy 2016).

## Urine

In an investigation of the urinary profiles of ferrets, Zhang et al. (2005) listed 48 peaks (7 of which were unidentified). Of these, 2-methylquinoline was male-specific and ten others were more abundant in male urine: 4-heptanone, 2-heptanone, 2,5-dimethylpyrazine, quinoline, o-aminoacetophenone, dimethoxyacetophenone and 4-methylquinazoline plus three unidentified compounds (Appendix 2). When ferrets can smell but cannot see a conspecific, both males and females are more attracted to the opposite sex (Wheeler 1978; Kelliher & Baum 2001, 2002). Furthermore, ferrets prefer to investigate areas that have been soiled by unspecified 'scent marks', urine and faeces of the opposite sex (Chang et al. 2000). However, sorting out which odours are generating which behavioural responses is no easy task. Berzins & Helder (2008) showed that female ferret urogenital and body odours attracted males, while females showed little interest in those of males, leading the authors to suggest a sex attractant role for female urogenital odours. By contrast, Woodley et al. (2004) found that female ferrets did respond to male urinary odours and preferred these to the odour of an oestrous female; and Cloe et al. (2004) also found that female ferrets preferred male urinary odour over female urinary odour, while males had no preference.

## Other odour sources

The anal sac secretions of stoats and ferrets contain a range of sulphur-containing compounds (Crump 1978, 1980a,b; Crump & Moors 1985). Zhang et al. (2005) provided a further chemical analysis of ferret anal sac secretions, confirming the findings of Clapperton et al. (1988) that 2,3-dimethylthietane and 3,4-dimethyl-1,2-dithiolane are more abundant in females, and that 2-propylthietane can be abundant in males. They also identified the previously unknown o-aminoacetophenone from male secretions, two aldehydes, five ketones, benzothiazole, 2-methylquinoline and 4-methylquinazoline from both sexes, and 3-ethyl-1,2-dimethyl-1,2-dithiolane from female secretions. Similar compounds have been found in the anal sacs of other members of the genus *Mustela* (Schildknecht et al. 1976; Brinck et al. 1978, 1983; Zhang et al. 2002, 2003; Setzer 2008). Berzins & Helder (2008) also confirmed the finding of Clapperton et al. (1988) that ferret anal odours are attractive to both males and females, supporting their proposed role as territorial markers that display individual identity. However, the fact that males prefer to approach female anal gland odours and vice versa for females (Cloe et al. 2004) suggests that ferrets may also use anal gland odours in mate recognition (Woodley & Baum 2003, 2004).

Some component(s) of the odours found in bedding material may hold promise as lures for mustelids. The male stoat caught on Kapiti Island in the 2010 incursion was caught in a trap lured with bedding from a female stoat (Prada et al. 2014), and in captive trials, both male and female stoats are attracted to bedding material from oestrous stoats year-round (E. Murphy et al., unpubl. data). Bedding material collected from oestrous stoats is also more attractive to both male and female stoats than stoat urine and scats (Murphy 2016). Garvey et al. (2016) found that the body odour of ferrets acts as an attractant to stoats.

## 2.6 Possums (with reference to other marsupials)

Marsupials have the neurological potential for sophisticated pheromonal communication, not unlike that of rodents (Takami 2002; Grus et al. 2005). Both male and female possums respond to the scent of female urine, and components of female urine improve the capture efficiency of both male and female possums by increasing the time animals spend near devices (Duckworth et al. 2016). So the search is on to identify these key semiochemicals and the most effective formulations (Walker & Croft 1990; Duckworth et al. 2013) and it may be informed by research on other marsupials.

### Urine

Toftegaard et al. (1999) identified ten volatile urinary compounds of the brown antechinus (*Antechinus stuartii*), and demonstrated that the main components were homologous methylketones in both male and female urine, and aldehyde in female urine. Furthermore, a distinctive characteristic of the urine of sexually active males was high concentrations of two pyrazine derivatives and four methylketones. Brown antechinus scent mark using cloacal glands, so these compounds could be released into the environment. Furthermore, male urine stimulates activity of the accessory olfactory bulb (Toftegaard et al. 2002), which also indicates semiochemical activity (Toftegaard & Bradley 2003).

Male but not female grey short-tailed opossums (*Monodelphis domestica*) respond to conspecific urine; male scent is thought to related to territorial defence, and female urine indicates mating availability (Zuri et al. 2007).

### Other odour sources

The sternum gland of the brown antechinus also produces volatile chemicals that Toftegaard & Bradley (2003) suggested may act as status symbols. Acetic acid, short-chain (C6-C10) aldehydes, long-chain (> C15) hydrocarbons and 1,1-bis-(p-tolyl)-ethane are common components of the sternum glands of Australian marsupials (Zabaras et al. 2006).

Grey short-tailed opossums use semiochemicals from the suprasternal and submandibular glands and body odour more than urine for intraspecific communication (Poran et al. 1993; Zuri et al. 2003; Zuri et al. 2005). Zuri & Halpern (2005) showed that the vomeronasal system was used to decode these olfactory signals.

The paracloacal glands of brushtail possums contain triacylglycerol estolides and various sulphur-containing compounds (McLean et al. 2012, 2015), which could play a role in social communication. Possum sternal gland scent has been trialled as a lure but the sample size was too small to determine if it was attractive (Kreigenhofer 2011).

### 3. Odour perception and expression

Recent work has also focused on how behavioural, neurological and hormonal responses are mediated by the vomeronasal organ, the main olfactory epithelium, olfactory neurons of the main olfactory bulb and accessory olfactory bulb, and the interactions between these sensory systems. An in-depth review of the neurological literature is outside the scope of the current study; however, such information is available elsewhere (Tirindelli et al. 1998; Novotny 2003; Wyatt 2003; Brennan & Keverne 2004; Rodriguez 2004; Lin et al. 2005; Kelliher 2007; Keller & Vosshall 2008; Brennan 2009; Ponmanickam et al. 2010, 2013; Baum 2012; Chamero et al. 2012; Mucignat-Caretta et al. 2012; Apps 2013; Dey et al. 2013; Liberles 2014; Mucignat-Caretta 2014; Li & Liberles 2015; Stowers & Kuo 2015). Likewise, the genetic basis of pheromones is more thoroughly reviewed elsewhere (Dulac 2000; Dulac & Wagner 2006; Kam 2013; Ganem et al. 2014). The potential for the development of bioassays of pheromones based on the responses of neurons in the vomeronasal organ and/or the main olfactory bulb make this area of research of interest in the development of mammalian pest control lures (Linklater et al. 2013).

#### 3.1 How do animals perceive odours?

The findings presented in section 2 highlight the difficulty of naming a single chemical compound or group of compounds that would produce the required response from all animals. This can be attributed to the nature of the chemicals forming the compound(s), such as the percentage of each component (i.e. effective concentration) and the isomer form; and/or factors related to the olfactory physiology of the species.

The mammalian olfactory system is capable of detecting a wide range of volatile chemical compounds that may be translated into varying instinctive responsive behaviours (Buck & Bergman 2012). Mammalian odorant receptors (ORs) form a chemical-detecting interface between the atmosphere and the nervous system, but very little is known about the mechanisms of molecular recognition binding and discrimination between small molecule odorants. The ORs work in combination or inter-related fashion to detect/identify the odorant chemicals through the odorant's structural characteristics (Nara et al. 2011). Let us use aldehydes as an example of the role of molecular shape. Aldehydes are found in a variety of natural sources, such as herbs, flowers and fruits, and are typically fresh-smelling chemicals, with synthetic aldehydes being important in the flavour and fragrance industries. However, some of the nose's many aldehyde receptors do not detect an aldehyde by its structure and shape directly, but rather recognise it according to its ability to undergo a chemical reaction with water, probably after entering the nose. Once exposed to air, aldehydes have a limited lifetime, as oxygen slowly converts them into less-savoury or even malodorous chemicals. Thus, the human nose is adapted to detecting aldehydes and distinguishing them from structurally similar chemical groups (Li et al. 2014).

Many ORs that detect the eight-carbon aldehyde octanal recognise the portion of the aldehyde molecule by its ability to morph into a completely different chemical group, known as a gem-diol. Since this reaction is unique to aldehydes, it serves to discriminate them from similarly shaped chemical groups. These odorant molecules might be able to alter fragrance mixture odours in two ways: by muting the activity of flexible odorants present in a mixture, and by activating a smaller subset of olfactory sensory neurons than chemically related flexible odorants do (Li et al. 2014).

Humans possess approximately 400 different types of specialised sensors (known as olfactory receptor proteins) which somehow work together to detect a large variety of odours (Trimmer et al. 2014). However, each individual has a unique set of genetic variations that leads to variation in olfactory perception (Mainland et al. 2014), though it is still unknown how the activity patterns are translated into a signal that our brain registers as the odour (Monell Chemical Senses Center 2013). According to Gertrude Stein, 'A rose is a rose is a rose'; however, new research indicates that this may not be the case when it comes to the rose's scent. Researchers from the Monell Chemical

Senses Center (Philadelphia, USA) and collaborating institutions have found that as much as 30% of the large array of human ORs differs between any two individuals (Mainland et al. 2014), which, in turn, translates into variability in how each person perceives odours (McRae et al. 2012; Monell Chemical Senses Center 2013). Furthermore, the perception of flavours (e.g. *cis*-3-hexen-1-ol in humans) can be linked to activation of a few receptors on single nucleotide polymorphisms by just a single odorant component (Wetzel et al. 1999; McRae et al. 2012).

In most species, food intake is influenced by olfactory cues, and metabolic status can affect the olfactory function of animals and regulate feeding-related behaviours. In a study on four rat strains, Karine et al. (2014) observed that metabolic and behavioural changes were partly associated with variations in the transcription profiles of leptin, insulin and orexin and their receptors in the hypothalamus and olfactory system, indicating that variations in metabolic-related gene expressions along the olfactory pathways influence food-odour-driven behaviours. Thus, food-odour-driven behaviours are clearly affected by long-term metabolic status. Moreover, Mainland & Sobel (2006) argued that sniffs are necessary for olfactory perception, affect odorant intensity and identity perception, drive activity in the olfactory cortex, are rapidly modulated in an odorant-dependent fashion by a dedicated olfactomotor system, and are sufficient to generate an olfactory perception of some sort even in the absence of an odour.

Until recently, the olfactory epithelium in mice was thought to contain 1000 ORs. It was also thought that in addition to those ORs, mice possess approximately 14 trace amine-associated receptors (TAARs) (Saraiva et al. 2015), but a more recent study (Saraiva et al. 2016) identified 16 extra TAARs. The ORs and TAARs are each expressed by a different subset of olfactory sensory neurons (Saraiva et al. 2015); and the genes for encoding ORs and TAARs have different nuclear locations (Yoon et al. 2015). It has been suggested that TAARs may have a distinct function from that of the ORs, which was attributed to their ability for high-sensitivity detection of amines, and the TAARs may particularly induce innate aversion responses (Dewan et al. 2013). These findings suggest the presence of complex regulatory mechanisms, through which a sensed odour triggers the synthesis of signal-inducing molecules that are recognised by the brain, which in turn translates these signals into certain behavioural responses.

The existence of such mechanism(s) may be verified by the findings of the study by Saraiva et al. (2016), which identified 16 extra TAAR agonists in mice, all volatile amines. The study illustrated that a single odorant may activate 1–6 TAARs, confirming that some of them respond to more than one odorant. Half the tested TAARs induced behavioural responses; ten of them induced attraction, and three induced aversion. Also in that study, 54 different odorants were classified on the basis of their structure, and tested on mice. Many of the odorants induced either attraction or aversion behaviour, and the effects were concentration dependent, although some odorants maintained their effect, even after fading.

These findings demonstrate the difficult task of predicting/manipulating a predator's behavioural responses to a compound or a mixture of odorant compounds, especially if some compounds can override, cancel or block the function of other compounds. Achiraman et al. (2010b) suggested that in male mice the main and accessory olfactory systems work in synergy for the detection of oestrus in the urine of females; and Sam et al. (2001) reported that not only does the vomeronasal organ respond to specific pheromones, it also responds to general odorants. However, Kippin et al. (2003) showed that odours from oestrous female rats trigger different neural pathways in male rats from those triggered by neutral scents that had been paired with copulation, with only the former increasing Fos-like immunoreactivity in the accessory olfactory bulb/vomeronasal organ. Nodari et al. (2008) further showed that mouse vomeronasal organ sensory neurones particularly respond to sulphated steroids (Appendix 1), and Xu et al. (2005) found that 2-heptanone stimulates both the accessory and main olfactory bulb in mice. These findings also point out that behavioural responses are the result of a chain of reactions involving the olfactory receptors, the brain, and the genetic codons to produce the appropriate molecules that dictate the response behaviour.

Clearly, the responses of animals to individual or mixes of odorous compounds will vary from individual to individual and certainly among different species, and the complexity of these mechanisms and our lack of understanding of them explain why researchers in this field

experience so many setbacks. Therefore, more research is required to identify the most potent molecules or mixtures of molecules in the correct concentration ratios that result in the most attraction and longest lasting effect. In particular, the identification of olfactory stimulating molecules that are common between species would be of great significance for the formulation of multi-species lures and baits.-

### 3.2 Influence of the MHC

The role of compounds produced by the major histocompatibility complex (MHC) as pheromone carriers and stabilisers that extend the life of scent marks has been reviewed by Hurst et al. (1998), as has their influence on mating preferences (Penn & Potts 1998b). One of the main areas of recent research has focused on how the MHC genes control odour expression, as reviewed by Boyse et al. (1987), Penn (2002), Beauchamp & Yamazaki (2003), Dulac & Torello (2003), Hurst & Beynon (2004), Brennan & Kendrick (2006), Tirindelli et al. (2009) and Ruff et al. (2012). Peptides that are produced by the MHC genes are recognised by the main olfactory epithelium and vomeronasal organ (Leinders-Zufall et al. 2004; Kwak et al. 2009). Novotny et al. (2007) provided evidence for a quantitative link between the MHC genes and volatile compounds in mouse urine, including the testosterone-mediated pheromones SBT, DHB and dihydrofurans, various sulphur-containing compounds, and the carbonyl metabolites 2-heptanone and 5-hepten-2-one.

Studies on both trained and untrained mice show that mice prefer to mate with individuals with different MHC alleles, and that this is mediated by odour (Carroll et al. 2002; Spehr et al. 2006), providing a mechanism by which inbreeding can be avoided (Penn 2002). Willse et al. (2005) found that there were quantitative differences in the key pheromones (including 2,5-dimethylpyrazine and SBT) contained in the urine of two inbred strains of mice that differed only in their MHC gene composition.

The MHC of the Norway rat, Rt1, has been used as a model for MHC studies (Günthe & Walter 2001). Like mice, rats can distinguish kin from non-kin based on odours determined by the MHC (Hepper 1987; Thom et al. 2008). For instance, Zhang & Zhang (2011) found that female Norway rats of two different strains determined their preference to investigate male urine based on the ratios of the genetically determined volatiles heptan-2-one, heptan-4-one, dimethyl sulphone and 4-ethylphenol.

Both mothers and young mice can identify MHC odour types, allowing parent-progeny recognition (Yamazaki et al. 2000). The role of odours in the behavioural bonds between parents and offspring was reviewed by Corona & Lévy (2015).

However, the extent to which the MHC is involved in individual odour recognition remains controversial. While Schaefer et al. (2001) demonstrated that MHC-controlled odorants in mouse urine maintain spatial patterns that could act as 'an olfactory fingerprint', Hurst et al. (2005, p. 715) strongly argued that 'MHC odours are not required or sufficient for recognition of individual scent owners'; and Sherborne et al. (2007) agreed that in wild mice the reluctance to mate with mice of the same MUP haplotype was adequate to act as an inbreeding avoidance mechanism without evoking an MHC-controlled mechanism. Moreover, MHC-associated odours are affected by diet, indicating that they do not hold key information about the scent marker. Consequently, Overath et al. (2014, p. 2440) favoured the view that 'sensing the gestalt of the urinary peptidome as well as variability in MUPs and volatiles provides enough critical information for individual recognition without the requirement for the apparently minute MHC-dependent differences'. There may also be an interplay between MHC genes and 'background' genes, and the MUPs may moderate the effect of the MHC (Willse et al. 2006; Novotny et al. 2007; Kwak et al. 2010), with recent findings by Sturm et al. (2013, p.3) that 'a *bona fide* MHC peptide ligand exists in [mouse] urine in an MHC-dependent manner at biologically relevant concentrations' strengthening the case for such a complex peptide/MUP scenario.

## 4. Development of pheromone lures for predator control

It is unlikely that any single ‘magic bullet’ will be found that will act as a super-attractant for all pest mammals, because of the wide variations in olfactory responses outlined above. Indeed, even attracting all individuals of one species is a major challenge. Thus, certain blends of compounds at particular concentrations may need to be formulated that are effective for most individuals. Nielsen et al. (2011) suggested that the dilution-dependent response of male rats to carboxylic acids in female rat faeces might indicate that the ratios between compounds are important. Furthermore, Zhang et al. (2008a) noted that the main sex pheromones of male Norway rats did not produce the same degree of attraction to females as whole-urine samples, indicating that the minor components might also play a role. There may also be synergistic effects among scent components, e.g. the combination of SBT and DEB as a sex attractant from male mouse urine (Jemiolo et al. 1985), as well as concentration-dependent effects (He et al. 2010).

However, Apps (2013, p. 487) noted that ‘There is scant support for the view that mammal semiochemicals code signals as specific ratios between compounds, and no evidence that they depend upon a Gestalt or a chemical image’. Since concentrations of pheromones in urine, for example, can vary with time of day, between individuals, and with diet, stress and gut microbial contents and urine age (Bollard et al. 2001; Kwak et al. 2013), presumably animals have evolved to respond to these chemical signals at various concentrations and will be able to gather information from that variability in the signals. Their responses will also depend on their experience with the odours, with learned behaviour being an important component of semiochemical communication (Jemiolo et al. 1991; Moncho-Bogani et al. 2002). This learned association of volatile pheromones with their non-volatile associates (Martínez-García et al. 2008) may be a limiting factor for the application of some semiochemicals in pest control, as it signifies a very complex chemical and behavioural interplay. Semiochemicals can also condition attractiveness to other odorants (Lanuza et al. 2014).

To complicate things further, semiochemicals tend to have multiple roles in mammals. For example, sex attractants for females may induce fear/aggression in males; and similarly, E,E- $\alpha$ -farnesene and E- $\beta$ -farnesene are attractive to female mice (Jemiolo et al. 1991) but are avoided by male mice (Novotny et al. 1990) and also act as puberty-delaying pheromones (Jemiolo et al. 1992).

There are also cross-species complications, as the farnesenes, squalene and various other compounds are produced not only by rodents, but also by a range of other taxa (Novotny 2003; Novotny & Soini 2008). For instance, 2-heptanone is a sex attractant for mice and rats but acts as a deterrent in honey bee behaviour (Balderrama et al. 2002), and also occurs in ferret urine (Zhang et al. 2005); and alarm pheromones of rodents may make good predator attractants but may deter other rats. Similarly, there may also be issues with using carnivore sex attractants, as they may induce stress/alarm responses in rodents.

### 4.1 Are pheromone-based lures likely to be effective in traps or baits?

Studies to date have had contradictory findings with regard to this question. Female mice are attracted to traps by DEB and SBT (Musso et al. 2017). Shumake et al. (2002) found that neither urine nor preputial gland extracts increased bait preference by laboratory rats, whereas Selvaraj & Archunan (2002b, 2006) found that when a mixture of preputial gland with or without cheek gland extracts was mixed into poison bait there was an increased consumption of zinc-phosphide and a high subsequent mortality of female Norway and ship rats. Urine did not have as marked

an effect as the preputial gland extract, but it was more effective than the cheek gland extract on its own. It is possible that rather than acting as attractants, these extracts actually had a toxin-masking effect, which is another useful role for semiochemicals in pest control (Archunan & Achiraman 2006). By contrast, Murphy et al. (2014) found that urine and scats from female Norway rats were attractive to both male and female Norway rats, and Gsell et al. (2014) and Shapira et al. (2013b,c) demonstrated that the use of live Norway rats or their bedding increased the probability of detecting wild rats. Parsons et al. (2015) used soiled Norway rat bedding material to attract both male and female urban Norway rats to traps.

For pheromones to be effective, they must attract a sufficiently high proportion of the population either to affect abundance directly or to affect breeding success indirectly (Wyatt 2003). A limiting factor here may be that pheromones often only attract one sex, limiting the potential of developing sex lures for rats – for example, Bull (1972) pointed out that it is the male that is attracted to the oestrous female rather than the other way around, but it is the number of reproductive females that determines the future Norway rat population, not the number of sexually active males.

Moreover, some sex pheromones attract females but elicit aggressive responses in males, e.g. SBT, DHB, 3-amino-s-triazole, 4-ethylphenol and 3-ethyl-2,7-dimethyl octane in mice (Novotny et al. 1985; Achiraman & Archunan 2002a). And while E,E- $\alpha$  and E- $\beta$ -farnesene are attractive to female mice, they indicate the dominance status of male mice and so deter investigation by subordinate males (Novotny et al. 1990). This could be a disadvantage if some males initially avoid these scents, but could also be advantageous if it induces sniffing and biting behaviours (Novotny et al. 1985).

Responses to pheromones are also affected by the age and hormonal state of the animals perceiving them. For example, darcin is generally attractive to postpubertal female mice (Mucignat-Caretta et al. 1998), but is not attractive to prepubertal or lactating females (Mucignat-Caretta et al. 1998; Martín-Sánchez et al. 2015). These endocrinological factors may limit the broad application of pheromones as lures for mammals. Different genetic strains of rodents also have different scents (e.g. *Mus musculus domesticus* v. *M. musculus musculus*; Bímová et al. 2009), which may have implications for lure development. So would a lure developed overseas work in New Zealand? The finding that females prefer the scent of genetically different males may work in our favour, but it may be better to look for compounds that do not have a genetic distinction.

## 4.2 Can we find olfactory lures that will work across all rodent and/or mustelid pests?

Trimethylamine is a major component of the urine of both mouse subspecies, but it is repellent to Norway rats (Li et al. 2013). This may be because it is also a major component of the anal sac secretions of canids (Prete et al. 1976). Mice and rats do share some urinary volatiles, however, which suggests that there is potential for the discovery of a general rodent attractant. For instance, E,E- $\alpha$  and E- $\beta$ -farnesene are attractive to both female mice (Jemiolo et al. 1991) and female Norway rats (Ponmanickam et al. 2010). Farnesenes are also found in hops (Sharpe & Laws 1981), possibly explaining the folk knowledge that beer is a good attractant for mice. However, high concentrations of farnesenes may be needed to attract female mice if used on their own (Jemiolo et al. 1991). Since most of the known rat pheromones are from Norway rats, much more information is needed on the semiochemicals of ship rats before conclusions can be drawn on the generality of using rat scents, particularly since Shapira et al. (2013b) showed that ship rats are not attracted to live Norway rats, indicating differences in the scents of the two species

Mustelids share several anal gland compounds. For example, mustelane is common to stoats, ferrets, European polecats (*M. putorius*), steppe polecats (*M. eversmanni admirata*), mink (*M. vison*) and Siberian weasels (*M. sibirica fortanieri*) (Schildknecht et al. 1976; Crump 1980a;

Brinck et al. 1983; Zhang et al. 2002, p. 734). Likewise, *o*-aminoacetophenone is found in most of these species and has been described as a ‘strong weasel smell compound’ (Zhang et al. 2005). Thus, it may be possible to find a general mustelid odour that is attractive to stoats, ferrets and weasels. Clapperton (1985) found that although ferrets initially chose male ferret odour over male weasel odour in a laboratory bioassay, and the four males tested all spent more time investigating the ferret odour, three of the four females spent more time at the weasel odour; and Harrington et al. (2009) found that mink responded to the odours of European polecats in the same way as to the odours of conspecifics.

Garvey et al. (2016, 2017) found that stoats spent an increased amount of time investigating an area when it was lured with ferret body odour and argued that predators can benefit from such a ‘cautious inspection’ of competitor scents by reducing the energetic costs of foraging, possibly informing them about the time since the other predator was present (Bytheway et al. 2013). Alternatively, it may mean that a general mustelid smell is the source of the attractive bedding scent. Either way, this suggests that a general ‘mustelid’ lure may be feasible. However, Erlinge & Sandell (1988) found that weasels were caught in traps containing stoat odour less frequently than those that smelled of weasel. While 2-propylthietane has shown promise as the basis of a lure for both male and female ferrets, it is less effective as a trap lure for stoats (Clapperton et al. 1994b). Furthermore, natural product lures are more successful than single-compound synthetic lures for both species (Clapperton et al. 1989, 1994b, 1999). More complex combinations of anal gland components may, however, have potential as general mustelid lures, as could the components of stoat and ferret body odours (Garvey et al. 2016; Murphy et al. 2014). Nor might such mustelid lures be repellent to rodents – Garvey et al. (2017) found that observation rates for wild ship rats did not vary between sites with and without ferret body odour lures. This may represent a form of risk assessment, which can be an important driver for a prey species to ‘eavesdrop’ on the scent communication of a predator (Garvey et al. 2016; Jones et al. 2016).

### **4.3 Could more effective lures be produced by combining volatiles with lipocalins/MUPs that are resistant to heating and desiccation?**

The close biochemical association between pheromones and their protein carriers, and the enhanced neurological responses elicited by the combination of these high- and low-molecular-weight components of urine (Yamaguchi et al. 2000; Tirindelli et al. 2009), suggest that it may be worth investigating the development of a lure containing both the volatile scent and its carrier. Scent marks of mammals typically include components with high molecular mass, like the rodent MUPs (Gosling & Roberts 2001). The fact that MUPs extend the life of mouse scent marks also makes them potential components of scent lures. Indeed, Hurst & Beynon (2004: fig. 4) even suggested that in the absence of MUPs, male mouse urinary volatiles stimulate caution and other males will be hesitant to contact the scent. The finding that both male and female mice use MUPs (Stopka et al. 2007) indicates that lures containing MUPs could be attractive to both sexes. Pheromone traps for rodents are under investigation for rodent pest management – Kamalakkannan et al. (2006) suggested that 20-kDa proteins (i.e. MUPs), which bind with pheromonal ligands in rat preputial gland secretions could be used in the development of pheromonal traps, and Rajesh et al. (2016) have suggested that genetic mutation of the oestrus urinary lipocalin protein that occurs at particular high concentrations in female rat urine, could create a long-lasting carrier of the sex attractant farnesol.

#### 4.4 Can rodent pheromones be used to attract predators as well as other rodents?

Prey odours are known attractants for predators (Hughes et al. 2010). It is possible that a general 'rodent' smell would be more effective than specific mouse or rat pheromones in attracting predators rather than conspecifics. The 'mousy' smell feature of the ligand-MUP complex in mice, which demonstrates their species-specificity (Logan et al. 2008), may also be a key feature for attracting predators, and aliphatic aldehydes are prominent in both the body odour and urine, making them potential candidates (Röck et al. 2006).

The use of mouse and rat odour as a stoat lure has been investigated. Clapperton et al. (2006) found that the odour of dead rat induced long periods of interest by some captive stoats. A PVC matrix containing 'ratty' odours (pyrazine, 2-ethyl pyrazine, 2-ethyl-3-methyl pyrazine and m-cresol) was attractive to stoats (Byrom et al. 2003). Burns et al. (2000) had some success with using freeze-dried rats as baits in stoat traps. Freeze-dried mice and rats also elicited responses by captive stoats (Byrom et al. 2003; Clapperton et al. 2006), despite these not containing the key 'ratty' volatile compounds (Byrom et al. 2003). These findings suggest that further work is needed to determine the specific odour components that attract predators to rodents. A promising recent development is the discovery of Zhang et al. (2016) that urine and bedding from Norway rats with elevated amounts of the male pheromones 4-heptanone, 2-heptanone and 9-hydroxy-2-nonanone elicited more investigative behaviour by cats than materials from rats with lower pheromone concentrations.

#### 4.5 Do rodent alarm pheromones have any potential as lures?

Alarm pheromones of Norway rats increase sniffing and investigative behaviours in other rats (Kikusui et al. 2001; Kiyokawa et al. 2004a, 2005), but can also induce escape behaviours (Kiyokawa et al. 2006). Zalaquett & Thiessen (1991) observed that such an apparent dichotomy in response depended upon the behavioural opportunities available to their subject mice. The similarity between mouse alarm pheromones and compounds in mustelid anal sac secretions (Brechtbühl et al. 2013) suggests that stoats and ferrets may well be 'tuned-in' to responding to these odours, indicating that these could be used as carnivore attractants.

Cross-species attraction may not be limited to predator-prey systems. For instance, the insect pheromone Z-7-dodecen-1-yl acetate has also been identified from the Asian elephant (*Elephas maximus*; Rasmussen et al. 1996) and so has received some attention as a potential general semiochemical attractant. However, the results of trials on feral goats (*Capra hircus*) and rats proved disappointing (Veltman et al. 2002; Gould et al. 2007).

#### 4.6 Pheromones and live lures

Pheromones may be the basis for the success of the use of live animals as trap lures. Shapira et al. (2013b,c) demonstrated the potential for using laboratory rats as lures to detect wild Norway rats. Shapira et al. (2013a) recommended the use of laboratory-bred mice as lures for trapping wild mice, as wild mice were equally attracted to familiar and unfamiliar mice, and wild v. laboratory mice. In addition, the diet that was fed to the lure mice also influenced their attractiveness, with mice being more attracted to the urine of individuals that had been fed a high protein diet, implying that this may be involved in the key role of urine MUPs in scent communication in mice.

However, although this could be a useful technique in some situations, the restrictions on using captive live animals (e.g. visiting the captive animals daily) makes this impractical over large areas or for long-term deployment. For instance, when this technique was suggested in response to a rat incursion on Mana Island, there was a delay before the animals could be deployed, as iwi

consultation was needed (Brown et al. 2012). In addition, biosecurity concerns were also raised, as was the difficulty of caring for the captive rats on the island by field staff. Shapira (2014) summarised these issues and provided guidelines for the use of live rodent lures.

## 4.7 Commercialisation

Despite the potential for developing pheromone lures, few commercial products appear to have been brought to market, even for worldwide pest species. While CS<sub>2</sub> is both attractive and capable of increasing bait acceptance to Norway rats (Shumake & Hakim 2000; Shumake et al. 2002) and to ship rats (Parshad 2002; Veer et al. 2002), CS<sub>2</sub> rated behind a range of food-based attractants in pen trials on wild Norway rats (Witmer et al. 2008), and Koehler et al. (1994) found that CS<sub>2</sub> in a stable starch xanthate matrix had limited success as an attractant to Norway rats, ship rats and Polynesian rats (*R. exulans*, kiore).

Farnesol from the preputial glands of ship rats is currently under investigation as a rat attractant for use in pest control in India, with Archunan (2013) noting that it was ‘a promising candidate to develop “Biotrap” for rat pest’. The Norway rat pheromone blend reported by Takács et al. (2016) has also been combined with food odours and rat-pup sounds in a ‘Stimulating new formula’ ([www.cbc.ca/news/technology/brown-rat-sexy-bait-1.3530170](http://www.cbc.ca/news/technology/brown-rat-sexy-bait-1.3530170)). However, one proprietary rodent-scented lure that included MUPs proved to be less attractive to stoats than minced rabbit meat (Montague 2002).

Robinson & Copson (2014) reported on use of the commercial cat pheromone Feliway® (Virbac, Peakhurst, NSW, Australia) for trapping cats on Macquarie Island. However, they did not provide any information on its relative success compared with other attractants. This product is a synthesised FFP that helps to reduce stress (<http://www.feliway.com/nz/FELIWAY/The-Science-Behind-Feliway>) ([www.virbac.co.nz/](http://www.virbac.co.nz/); accessed 26 March 2017). Felinine would also appear to be a promising cat lure because of its stability except at very high temperatures (Rutherford et al. 2004); however, it is the breakdown products of felinine that produce the strong tom cat odour rather than felinine itself (Joulain & Laurent 1989) – although Rutherford et al. (2004) did find that synthetic felinine solution had a strong catty odour. Pen and field trials are yet to confirm that scent-based lures are more effective at luring cats than food-based lures (Edwards et al. 1997; Short et al. 2002). Furthermore, the potential for cat pheromone lures may be limited to certain times of the year and periods when prey species are abundant so food-based lures are less attractive.

Mustelid lures consisting of compounds in the anal sac secretions encased in a long-life, slow-release matrix have shown promise in the field (Clapperton et al. 1989, 1994b, 1999; Spurr et al. 2004), but there has been no reported progress in commercialising these lures. Initial trials used high concentrations of semiochemicals and simple choice-style bioassay techniques. However, direct observations of mustelid investigation of scent marks suggest that they, like other mammals, investigate scents that are imperceptible to the human nose (BKC, pers. obs.). Jackson et al. (2016b) found that there was an inverse relationship between food-based lure concentrations and attractiveness to rats in a concentration range of 0.01 to 10,000 ppm, suggesting that some of the earlier lure candidates should be re-assessed using lower concentrations. However, trials by Spurr et al. (2004) indicated that both male and female ferrets responded in a positive dose-dependent manner to increasing concentrations of female anal sac scents within the range of 0.1% to 2%. An expanded range of identified anal sac compounds and urine volatiles is now available for testing.

Another limitation in producing effective commercial lures could be the availability of suitable long-life matrices. The practical use of pheromones will require the development of slow-release systems. The original plastic rope (PheroTech Inc., Canada) used by Clapperton et al. (1994b) was unavailable in New Zealand, so later trials (Clapperton et al. 1999; Spurr et al. 2004) used the casein-based material Albert® (University of Otago, Dunedin). However, polyethylene ‘twist ties’, sachets

and vials are now widely available. Pheromones have been used in insect pest control for decades, and matrices and encapsulation techniques have been developed for insect pheromone applications e.g., natural rubber septa (West Pharmaceuticals Services Inc., PA, USA), styrene-butadiene rubber (Skellerup Industries Ltd, New Zealand), and the wax-based SPLAT® (ISCA Technologies, California, USA). Such rubber matrices can be matched to the chemical structure of the pheromones to achieve the necessary binding of the lure into the carrier (A. Twidle, PFR, Lincoln, New Zealand, pers. comm.). Aerosol sprays can be used to release bursts of fresh lure at timed intervals. Although these can be expensive (Suckling et al. 2007), suitable programming can maximise efficiency (McGhee et al. 2016). Solid plastics such as those used in 'Nara® Bloc' (Futura, Germany) may be suitable for the deployment of carnivore and rodent semiochemicals, and Connovation Ltd also produce a 'Solid State' lure block. A recent review by Heuskin et al. (2011) covered many of the practical issues associated with dispensing semiochemicals into the environment.

As discussed above (Section 4), there is debate over to what extent it is necessary to ensure that the released lure maintains a consistent chemical signature. For instance, can MUPs with a naturally slow volatile pheromone release be utilised, or will the varying responses of mammals to the relative concentrations of MUPs and volatiles affect their responses to lures of different ages? They may avoid close contact with a 'fresh' lure if it indicates the odour of a dominant territory holder, approach more closely an aging odour source to determine its chemical message, and to determine when the scent was laid and thus the risk of an encounter with the presumed scent marker (Gosling & Roberts 2001). They may ignore a scent that is so old that it holds little communication value.

Finally, combining scent with other stimuli should be investigated to create multisensory baits (Robbins et al. 2007). The new technology of 3D printing may prove useful in producing realistic prey-shaped baits that could act as visual lures combined with pheromonal lures. Acoustic lures and mechanisms to create moving baits should also be investigated, as mustelids and cats rely on prey sounds and movement as triggers for prey location and attack behaviour (Fitzgerald & Turner 2000; King 2005).

Lure cost may be another limitation to the use of mammalian pheromones. While some of the rodent pheromones can be synthesised (Tashiro et al. 2008), Wyatt (2003, p. 268) noted that 'The specificity of pheromones, which is their strength for minimal impact, is a commercial disadvantage', indicating that there are economic barriers for the widespread use of pheromones in pest control. Thus, although there may be a worldwide market for rat and mouse lures (Gilbert & Firestein 2002), the development of lures for ferrets, stoats and possums, which are New Zealand-specific pests, may be less cost-effective.

## 5. Additional applications

### 5.1 Behaviour modifiers

Some pheromones induce touching, licking and chewing responses. Therefore, these could be utilised to increase the sampling of toxic baits, or immunocontraception or chemosterilisation delivery systems, which require licking and/or chewing and absorption in the buccal cavity or gut – delivery is one of the major hurdles in implementing these control strategies (Hygnstrom et al. 1994; Barlow 2000; Fagerstone et al. 2002).

The mouse urine pheromone 1I2MU can elicit licking and grooming responses, as well as approach and sniffing behaviours (Achiraman et al. 2010a), and so may enhance bait take. Similarly, the licking response of mother rats in the presence of dodecyl propionate, which is secreted by pups, has been well established (Brouette-Lahlou et al. 1991a,b; Lévy et al. 2004), but there has been no application of this compound in bait formulations. Recent findings that lipocalin  $\alpha_{2u}$ -globulin may be involved in carrying this pheromone or even eliciting the response (Ponmanickam et al. 2009) indicates once again that the MUP may be an important part of a behaviour-modifying pheromonal biocontrol agent. One limitation appears to be that while pup odours elicit positive responses from female rats during parturition and lactation, they find the odour of young rats aversive outside these periods. However, this could be overcome by infusing the accessory olfactory bulb with the gamma-aminobutyric acid type A antagonist bicuculline (Carretero et al. 2003) – although other work attempting to utilise gamma-aminobutyric acid as a pest attractant has not met with much success to date (Veltman et al. 2002).

Volatiles can be detected and responded to at a distance, avoiding the need for close contact (Hurst & Beynon 2004). Therefore, the incorporation of MUPs into bait formulations as well as volatiles may be a useful strategy to increase physical contact with baits, as these elicit close investigation. For example, a combination of farnesol and  $\alpha_{2u}$ -globulin may produce a long-lasting attractant for rats that also induces bait contact.

It is also possible that calming pheromones could be used to modify behaviour to increase trap entrance rates. Not only does FFP make cats calmer, but it may also increase their interest in food and grooming (Griffith et al. 2000, cited in Frank et al. 2010), suggesting its potential as a bait additive for toxins that must be either consumed or licked. Grooming by pests is currently being investigated as a behavioural strategy for increasing poison consumption (Read 2010; Blackie et al. 2014; Murphy et al. 2014; Read et al. 2014, 2015), and so FFP, which is available in a synthetic form, may be worth assessing as a lure to be used in combination with para-aminopropiophenone gel in grooming traps for cats. Nouvel et al. (2013) also described a pheromone mix that is designed to reduce stress and anxiety in domestic, farm and zoo animals, including cats. This mix has a basic pheromone composition of  $\geq 30\%$  squalene,  $\geq 10\%$  linoleic acid and  $\geq 1\%$  1-docosanol (behenyl alcohol or docosyl alcohol), and can also include cholesterol or a mixture of additional fatty acids.

The stress-reducing cat facial F3 pheromone is marketed as Feliway® (Beck 2013), while F4, which is used to reduce aggression, is available as Felifriend® (Pageat & Cozzi 2011). The scratching-inducing pheromone FIS is also available as a commercial, synthetic product known as ScratchyLicious® (Pageat et al. 2009). This could potentially be used to encourage cats to access poison bait packages that are designed to be safe for non-target species.

## 5.2 Monitoring of populations and incursions

Pest control often involves monitoring the target populations or detecting island invaders, which can be done by detecting scent marks. For instance, the relative abundance of otter (*Lutra lutra*) populations is monitored by counting faecal spraints (Hutchings & White 2000), and conspicuous beaver (*Castor canadensis*) spraints and urine marks in snow can also be counted (Müller-Schwarze 1990, cited in Wyatt 2003). However, these systems require visual rather than olfactory signals to be detected. If we could develop smarter technologies for detecting odorous materials in the environment, it may be possible to detect the presence of pest mammals by the scents they leave on surfaces. Such systems are already in place for assessing pollution (Lin et al. 2000; Yuwono & Schulze Lammers 2004) and in forensics (Baldisserra et al. 2005), through the use of electronic noses or detection dogs (Williams & Johnston 2002; Wasilewski et al. 2017). It is also possible that the longer-lasting non-volatile odour-binding proteins that carry the pheromones (Hurst et al. 1998) might be more detectable and useful for an environmental chemical detection system (Tuccori 2014). A better understanding of how pheromones and their carriers are detected by the vomeronasal organ (Leinders-Zufall et al. 2000; Luo & Katz 2004; Kannan et al. 2011) may help to inform designers of such odour detection systems. Kralicek et al. (2017) have suggested a system by which volatile or water-borne chemicals released by predators could be detected in the environment by biosensors and relayed by wireless devices to inform wildlife managers of pest incursions.

## 5.3 Mating disruption

The widespread distribution of pheromones is used to control insect pests by making it difficult for males to locate females because they cannot follow a single pheromonal plume (Cardé & Minks 1995). This approach is unlikely to be as successful in the control of pest mammals because of the complexity of mammalian behaviour, including the responses to odours. However, there may be more subtle ways of using pheromones to interfere with the breeding success of mammals (Archunan & Achiraman 2006).

It may be possible to manipulate female reproductive abilities via interference with pheromone communications, e.g. by utilising the pregnancy-blocking, or Bruce effect, of compounds in mouse urine (Bruce 1959) or other primer pheromones (Koyama 2004). Male pheromones can affect implantation rates in female mice (Marchlewska-Koj et al. 1980), with females learning the profile of the scent of the stud male mouse and prolonged overriding of this scent with that of another male preventing implantation of the embryo (Thomas & Dominic 1987). Low-molecular-weight volatiles (but not high-molecular-weight MUPs) appear to play an important role in this pheromonal effect (Peele et al. 2003). Thompson et al. (2013) also demonstrated the pregnancy-blocking power of extracts of unfamiliar male urine and saliva with or without the MHC class I (H2d haplotype) peptide in laboratory mice. However, pregnancy blocking has not been demonstrated in wild mice and this effect requires high concentrations of pheromones if they are not bound to proteins (Peele et al. 2003; Thom & Hurst 2004), indicating that it would have limited field application. Moreover, no such pregnancy-blocking pheromone has been described from rat urine.

In mice, SBT, DHB and 2-heptanone are involved in control of the oestrous cycle, all of which can be synthetically produced (Leinders-Zufall et al. 2000; Novotny 2003). However, whether these could be used, for example, to induce ovulation out of season to interfere with the normal timing of reproduction, has not yet been explored. SBT and DHB also potentiate aggression in male mice (Novotny et al. 1985, 2003), so the use of these compounds as biocontrol agents could have multiple effects. In addition, MUPs from male mice influence ovulation in female mice (Morè 2006), but no one has looked at how we could use this knowledge to block ovulation.

It may also be possible to manipulate the sexual behaviour of male rodents. For instance, a broadcast odour of a mixture of common carboxyl acids (Nielsen et al. 2011) or faeces from various mammals (Rampin et al. 2006) or oestrous female scent (Sachs 1997) could be used to alter the penile-erection response of rats – although a pheromone that inhibits such behaviour may be more useful! Ferrero et al. (2013, p. 368) described an exocrine-gland secreting peptide 22 (ESP22) from juvenile mice that has a ‘powerful inhibiting effect on adult male mating behaviour’ and Kobayashi et al. (2011) showed that rat alarm pheromone collected from the perianal region of male rats can interfere with male mating behaviour, extending the time to successful ejaculation.

## 5.4 Pheromones and biological control

The interplay between the use of odours for social recognition and the disease status of individuals could be explored from the perspective of pest control. Mice not only detect conspecifics suffering from infectious diseases based on their social odours, but also use this information in mate choice (Penn & Potts 1998b; Penn et al. 1998; Beauchamp & Yamazaki 2003; Lopes & König 2016). Similarly, rodents select mates that are not infected by parasites (Kavaliers et al. 2003a,b, 2005; Zala et al. 2004; Gerlinskaya et al. 2012). Lanuza et al. (2014) reported that the attractiveness of the mouse pheromone darcin is lost from the urine of male mice infected with the nematode *Aspiculuris tetraptera*. It is not known whether this is due to other scents overriding the scent of the pheromone or some other mechanism causing the darcin to become undetectable.

It may also be possible that non-toxic, environmentally friendly biocontrol systems could be developed to allow baits including pheromonal precursors or blocking compounds that code for ‘infected’ or ‘uninfected’ to be distributed. The aim here could be either to reduce breeding success or, conversely, to enhance the use of parasites or diseases as biocontrol agents.

## 6. Conclusions

A literature search on the pheromones of rodents, carnivores and marsupials revealed that we know a great deal about mice and a reasonable amount about Norway rats, but relatively little about the other key mammalian predator species in New Zealand. It is not by chance that most available information is on laboratory-bred strains of animals used in model systems for human health and fundamental biochemical research.

While insect pheromone systems exhibit simple chemical-response interfaces, the semiochemicals utilised by mammals tend to have multiple roles. Furthermore, different species can respond differently to the same compounds, with semiochemicals that attract one species potentially deterring another, limiting their usefulness in a multispecies approach to pest management. However, closely related species may be attracted to a 'common' scent. The responses of predators to each other's odours suggest that a general synthetic 'mustelid' lure could be developed with increased knowledge of the composition and responses to mustelid urine, body and anal sac odours. Therefore, determining what role these pheromones will play when employed as biocontrol agents will be a challenging task. Moreover, mammalian pheromones often appear to be most attractive in combination rather than as single compound lures, with potential changes in responses resulting from aging of lures in the environment. Determining the effect of concentration of compounds will also be necessary to ensure that lures attract animals from afar but do not deter them when close to a control device. While live lure animals may be the ultimate source of pheromone attractants, there are limitations for their use.

It is also clear that MUPs could be key components of long-life lures for rodents and possibly other species, enticing animals to make direct contact with control devices. However, this would require a better understanding of the potential different roles of MUPs in rats and cats compared with the more thoroughly studied mice. The learned component of responses to pheromones and the role of MUPs in that learning suggest a complex system of responses to pheromones.

While research to date has allowed the development of new models of scent communication that integrate airborne and involatile compounds (Hurst 2009), there remains much to explore, even in terms of our understanding of the chemistry of scent communication. As Meinwald (2003) plaintively stated, 'Are we there yet?' - we think not. But at least the major challenge of progressing the research front from a fundamental knowledge of pheromone structure, neurobiology and behaviour to application in pest management has begun. Emerging technologies may help to solve the issues of creating cost-effective, long-life commercially feasible attractants and behavioural or physiological modifiers. To achieve New Zealand's vision to become predator free by 2050, new technologies will be needed and the development of long-lasting pheromone lures could be instrumental in helping to make this a reality.

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## 8. Glossary

### Pheromones

DEB	3,4-dehydro-exo-brevicommin
DHB	2,3-dehydro-exo-brevicommin
ESP	exocrine-gland secreting peptide
FFP	feline facial pheromone
1I2MU	1-iodo-2-methyl undecane
MUP	major urinary protein
SBT	2-sec-butyl-4,5-dihydrothiazole

### Neurological terms

MHC	major histocompatibility complex
OR	odorant receptor
TAAR	trace amine-associated receptor

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# Appendix 1

## Rodent pheromones

Summary of the known or potential mouse and rat pheromones with relevant post-2000 references

### A. Mice

PHEROMONE	SEX	SOURCE	FUNCTION	REFERENCES
Acrylanilide	F	Urine		Achiraman & Archunan 2006
Auzulene	F	Urine		Achiraman & Archunan 2006
3-Amino-s-triazole	M	Urine	Female attractant, male aggression	Achiraman & Archunan 2002a
Benzaldehyde	M	Urine, body		Röck et al. 2006
Benzylmethylketone	M	Urine		Röck et al. 2006
Butanoic acid	M	Body		Röck et al. 2006
(S)-2-(sec-Butyl)-4,5-dihydrothiazole (SBT)	M/F	Urine	Oestrus synchronisation, puberty acceleration, sex attractant male age, male aggression, alarm, scent age	Leinders-Zufall et al. 2000; Cavaggioni et al. 2003; Novotny 2003, 2007; Hurst & Beynon 2004; Willse et al. 2005; Cavaggioni et al. 2006; Röck et al. 2006; Novotny et al. 2007; Brechbühl et al. 2013; Musso 2016; Musso et al. 2017
2-Butyl-1-octanol	M/F	Urine	Scent age; indicator of oestrus	Achiraman & Archunan 2006; Cavaggioni et al. 2006
Caryophyllene	F	Urine	Indicate oestrus	Achiraman & Archunan 2006
1-Chloro hexadecane	F	Urine		Achiraman & Archunan 2006
Cinnamoyl chloride	F	Urine		Achiraman & Archunan 2006
Copanene	F	Urine	Indicate oestrus	Achiraman & Archunan 2006
Corticosterone-21-sulphate	F	Urine	Physiological state	Nodari et al. 2008
3-Cyclohexene-1-methanol	M	Urine	Male attractant	Achiraman & Archunan 2002a, 2005
1-H-Cyclopop-e.auzulene	F	Urine	Indicate oestrus	Achiraman & Archunan 2006
Darcin	M	Urine	Female attractant	Phelan et al. 2010; Roberts et al. 2010, 2014; Lanuza et al. 2014; Martín-Sánchez et al. 2015
Decanal	M	Urine, body	Conspecific recognition	Röck et al. 2006
Decanoic acid	F	Urine		Achiraman & Archunan 2006
o-Decyl hydroxyl amine	F	Urine		Achiraman & Archunan 2006
2,3-Dehydro-exo-brevicommin (DHB)	M/F	Urine, body	Oestrus synchronisation, puberty acceleration	Leinders-Zufall et al. 2000; Novotny 2003, 2007; Hurst & Beynon 2004; Cavaggioni et al. 2006; Röck et al. 2006
3,4-Dehydro-exo-brevicommin* (DEB)	M	Urine	Male age	Musso 2016; Musso et al. 2017
Dihydrofurans	M	Urine		Novotny et al. 2007
2,3-Dimethyl heptane	F	Urine		Achiraman & Archunan 2006
4,5-Dimethyl nonane	F	Urine		Achiraman & Archunan 2006
2,4-Dimethyl-phenol	M	Urine	Scent age	Cavaggioni et al. 2006
2,5-Dimethylpyrazine	F	Urine	Puberty delay, male aggression, sex attractant, shortening of oestrous cycle (Lee-Boot effect), reduced testis weight, high offspring mortality	Novotny 2003; Leinders-Zufall et al. 2000; Koyama 2004, 2016; Willse et al. 2005; Röck et al. 2006; Thompson et al. 2013
Dimethyl disulphide	M	Body, urine		Lin et al. 2005; Röck et al. 2006
6,10-dimethyl-5,9-undecaden-2-one	M	Urine	Scent age	Cavaggioni et al. 2006
3,7-Dimethyl undecane	F	Urine		Achiraman & Archunan 2006
Dodecane	F	Urine		Achiraman & Archunan 2006
Eicosane	F	Urine		Achiraman & Archunan 2006
3-Ethyl-2,7-dimethyl octane	M	Urine	Female attractant, male aggression, releaser	Achiraman & Archunan 2002a, 2005

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PHEROMONE	SEX	SOURCE	FUNCTION	REFERENCES
1-Ethoxy octadecane	F	Urine		Achiraman & Archunan 2006
4-Ethylphenol	M	Urine	Female attractant, male aggression, scent age	Achiraman & Archunan 2002a; Cavaggioni et al. 2006; Röck et al. 2006
EE- $\alpha$ - and E- $\beta$ -farnesenes <sup>†</sup>	M	Preputial, body	Puberty delay, oestrus induction, sex attractant, male aggression	Leinders-Zufall et al. 2000; Novotny 2003; Röck et al. 2006
Exocrine-gland secreting peptides (ESPs)	M	Lachrymal, submaxillary	Induce lordosis, individual identity	Luo et al. 2003; Hurst 2009; Haga et al. 2010; Ferrero et al. 2013; Yoshinaga et al. 2013; Abe & Touhara 2014; Cavalier et al. 2014
Heptadecane	F	Urine		Achiraman & Archunan 2006
Heptanal	M	Body, urine		Röck et al. 2006
2-Heptanone (Heptan-2-one)	M/F	Urine	Oestrus extension	Leinders-Zufall et al. 2000; Novotny 2003, 2007; Xu et al. 2005; Röck et al. 2006
3-Hepten-2-one	M	Urine		Röck et al. 2006; Novotny et al. 2007
4-Hepten-2-one	F	Urine	Puberty delay	Koyama 2004
5-Hepten-2-one	M	Urine	Genetic strain, Puberty delay	Koyama 2004; Novotny 2007
Hexadecane	F	Urine		Achiraman & Archunan 2006
Hexadecanol	M	Preputial	Female (and male) attractant	Zhang et al. 2007, 2008a
1-Hexadecanol acetate	M	Preputial	Female attractant	Zhang et al. 2007
Hexadecyl acetate		Preputial	Female (and male) attractant	Zhang et al. 2008a
Hexanal	M	Urine, body		Röck et al. 2006
Hexanoic acid	M	Body		Röck et al. 2006
1-Hexanol	M	Body		Röck et al. 2006
3-Hydroxy-2-butanone	M	Urine, body		Röck et al. 2006
6-Hydroxy-6-methyl-3-heptanone	M	Urine, body	Puberty acceleration	Leinders-Zufall et al. 2000; Novotny 2003; Röck et al. 2006
Indole	M	Body, urine	Scent age	Cavaggioni et al. 2006; Röck et al. 2006
1-Iodo-2-methylundecane (112MU)	F	Urine	Male attractant, induction of licking and grooming, indicate oestrus	Achiraman & Archunan 2002a, 2006; Achiraman et al. 2010a
Isoamylamine	M	Urine	Puberty acceleration	Archunan & Achiraman 2006
Isobutylamine	M	Urine	Puberty acceleration; vomeronasal agonist	Archunan & Achiraman 2006; Rodriguez & Boehm 2009
Isocroctyl hydrazine	F	Urine		Achiraman & Archunan 2006
Iso octanol	F	Urine	Indicate oestrus	Achiraman & Archunan 2006
2-Isopropyl-4,5-dihydrothiazole	M	Urine	Male age	Osada et al. 2008
Linalool	M	Urine	Scent age	Cavaggioni et al. 2006
1-Methoxy-2-propanol	M	Urine, body		Röck et al. 2006
3-Methyl-2-butanone	M	Urine		Röck et al. 2006
2-Methyl-butanoic acid	M	Urine, body		Röck et al. 2006
3-Methyl-butanoic acid	M	Urine, body		Röck et al. 2006
2-Methyl-3-buten-2-ol	M	Urine		Röck et al. 2006
3-Methyl-2-buten-1-ol	M	Urine		Röck et al. 2006
3-Methyl-3-buten-1-ol	M	Urine, body		Röck et al. 2006
3-Methyl-cyclopentanone	M	Urine		Röck et al. 2006
4-Nethyl-2-heptanone	F	Urine		Achiraman & Archunan 2006
6-Methyl-5-hepten-2-one	M	Urine, body		Röck et al. 2006; Novotny et al. 2007
4-Methyl-phenol	M/F	Urine, body		Achiraman & Archunan 2006; Röck et al. 2006
N-Methyl-3-piperidine carboamide	F	Urine		Achiraman & Archunan 2006
Methylbutyric acid	M	Urine	Age	Osada et al. 2003; Nielsen et al. 2011
4-Methyl-2-propyl-1-heptanol	F	Urine		Achiraman & Archunan 2006
(Methylthio)methanethiol	M	Urine	Female attractant	Lin et al. 2005
6-Methyl octadecane	F	Urine		Achiraman & Archunan 2006
o-Nitrobenzaldehyde	F	Urine		Achiraman & Archunan 2006

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PHEROMONE	SEX	SOURCE	FUNCTION	REFERENCES
Nitromethane	M	Body		Röck et al. 2006
Nonadecanol	F	Urine		Achiraman & Archunan 2006
Nonanal	M/F	Urine, body		Achiraman & Archunan 2006; Röck et al. 2006
Octacosane	F	Urine		Achiraman & Archunan 2006
Octadecane	F	Urine		Achiraman & Archunan 2006
Octanal	M	Urine, body		Röck et al. 2006
1-Octene	M	Body		Röck et al. 2006
Pentadecane	F	Urine		Achiraman & Archunan 2006
Pentanal	M	Urine, body		Röck et al. 2006
Pentanol	M	Body		Röck et al. 2006
2-Pentanone	M	Urine, body		Röck et al. 2006
3-Penten-2-one	M	Urine		Röck et al. 2006
cis-2-Penten-1-yl-acetate	F	Urine	Puberty delay	Dulac & Torello 2003; Koyama 2004
n-Pentyl acetate	F	Urine	Suppression of oestrous cycle, puberty delay	Dulac & Torello 2003
Phenol	M	Urine, body		Röck et al. 2006
2-Phenylacetamide	M	Urine	Age	Osada et al. 2003
4-pregnene-11 $\beta$ ,21-diol-3,20-dione-21-sulphate	F	Urine	Physiological state	Nodari et al. 2008
4-Pregnene-11 $\beta$ ,20,21-triol-3-one-21-sulphate	F	Urine	Physiological state	Nodari et al. 2008
Propanoic acid	M	Body		Röck et al. 2006
2-Propyl-1-heptanol	F	Urine		Achiraman & Archunan 2006
Tetradecane	F	Urine		Achiraman & Archunan 2006
Tridecane	F	Urine		Achiraman & Archunan 2006
Trimethylamine	M	Urine, body	General attractant	Röck et al. 2006; Li et al. 2013; Stensmyr & Maderspacher 2013
Undecane	F	Urine		Achiraman & Archunan 2006

\* (1R,5S,7R)-Ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]oct-3-ene.

† (E,E)-3,7,11-Trimethyl-1,3,6,10-dodecatetraene and (E)-7,11-dimethyl-3-methylene-1,6,10-dodecatriene.

## B. Rats

PHEROMONE	SPECIES	SEX	SOURCE	FUNCTION	REFERENCES
4-Azidoheptane	Ship	M/F	Urine	Sex attractant	Selvaraj & Archunan 2002a
1,2-Benzenedicarboxylic acid butyl (2-ethylhexyl) ester	Norway	M	Cheek	General attractant	Kannan & Archunan 2001b
1,2-Benzene dicarboxylic acid butyl (2-methylpropyl) ester	Norway	M/F	Preputial, cheek	General attractant	Kannan & Archunan 2001b
1,2-Benzenedicarboxylic acid diisooctyl ester	Norway		Preputial	Same sex attractant	van der Hurk 2011
Beta-bisabolene	Ship	M	Preputial		Rajkumar et al. 2010a
Butanoic acid	Norway	F	Faeces	Male penile response	Nielsen et al. 2011
1-Chlorodecane	Ship	M	Urine	Sex attractant	Selvaraj & Archunan 2002a; Rajkumar et al. 2009, 2010a
m- or -p-Cresol	Ship		Body		Byrom et al. 2003
Cyclohexene	Ship	M	Preputial		Rajkumar et al. 2010a
3-Cyclohexene	Ship	M	Preputial		Rajkumar et al. 2010a
2,6,10 dedecatrien-1-ol,3,7,11-trimethyl-(Z,E)	Norway	F	Cheek	General attractant	Kannan & Archunan 2001b
6,11-Dihydro-dibenz-b,e-oxepin-11-one	Norway	F	Preputial	Sex attractant	Kannan & Archunan 2001a
Dimethyl sulphone	Norway	M	Urine	Female non-kin choice	Zhang & Zhang 2011

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PHEROMONE	SPECIES	SEX	SOURCE	FUNCTION	REFERENCES
2,6,10-Dodecatrien-1-ol-3,7,11-trimethyl(Z)	Norway	M/F	Preputial	Sex attractant	Kannan & Archunan 2001a
Dodecyl propionate	Norway		Preputial	Ano-genital licking	Lévy et al. 2004
Ethanol,2-(octylthio)	Ship	M	Urine	Sex attractant	Selvaraj & Archunan 2002a
3-ethyl-2-heptanone	Norway	M	Urine, faeces	Sex attractant	Takács et al. 2016
4-Ethylphenol	Norway	M/F	Urine	Female attractant	Zhang et al. 2008b; Osada et a. 2009; Zhang & Zhang 2011
2 ethyl-5 methyl pyrazine	Ship		Body		Byrom et al. 2003
2-Ethyl pyrazine	Ship		Body		Byrom et al. 2003
EE- $\alpha$ - and E- $\beta$ -farnesenes <sup>†</sup>	Norway	M/F	Preputial	Sex attractant, male dominance	Pohorecky et al. 2008; Zhang et al. 2008b
Farnesol 1, 2	Norway Ship		Preputial	Sex attractant	Ponmanickam et al. 2010; Rajkumar et al. 2010a; Archunan 2013
Geranyl linalool isomer	Norway		Preputial	Sex attractant	Ponmanickam et al. 2010
2-Heptanone (Heptan-2-one)	Norway	M/F	Urine	Sex attractant	Zhang et al. 2008b, 2016; Osada et al. 2009; Zhang & Zhang 2011; Takács et al. 2016
4-Heptanone (Heptan-4-one)	Norway	M	Urine	Sex attractant	Zhang et al. 2008b, 2016; Zhang & Zhang 2011
Hexadecane	Ship	M	Urine		Rajkumar et al. 2009, 2010a
Hexadecatetraene	Ship	M	Preputial		Rajkumar et al. 2010a
Hexanal	Norway	M	Peri-anal	Stress induction	Inagaki et al. 2014; Kiyokawa 2015
Hydroperoxide	Ship	M/F	Urine	Sex attractant	Selvaraj & Archunan 2002a
Lanosterol	Norway	M	Preputial	Sex attractant	Ponmanickam et al. 2010
3-Methylbutyric acid	Norway	F	Faeces	Male penile response	Nielsen et al. 2011
6-Methyl-5-hepten-2-one	Norway	F	Faeces	Male penile response	Nielsen et al. 2013
2-Methyl-N-phenyl-2-propenamide	Ship	M	Urine		Rajkumar et al. 2009, 2010a
4-Methylphenol	Norway	M	Urine	Sex attractant	Osada et al. 2009
4-Methylpentanal	Norway	M	Peri-anal	Stress induction	Inagaki et al. 2014; Kiyokawa 2015
2-Methylpropanoic acid	Norway	F	Faeces	Male penile response	Nielsen et al. 2011
1-Nitropentane	Ship	F	Urine	Sex/general attractant	Selvaraj & Archunan 2002a
2-Nonanone	Norway	M	Urine, faeces	Sex attractant	Takács et al. 2016
4-Nonanone	Norway	M	Urine, faeces	Sex attractant	Takács et al. 2016
2-octanone	Norway	M	Urine, faeces	Sex attractant	Takács et al. 2016
di-n-Octyl phthalate	Norway	M	Preputial, cheek	Sex attractant	Kannan & Archunan 2001b
Oxirane	Norway		Preputial	Sex attractant	Ponmanickam et al. 2010
1-Pentene	Ship	M	Preputial		Rajkumar et al. 2010a
Pentanoic acid	Norway	F	Faeces	Male penile response	Nielsen et al. 2011
Phenol	Norway	M	Urine	Sex attractant	Zhang et al. 2008b
Propanoic acid	Norway	F	Faeces	Male penile response	Nielsen et al. 2011
Pyrazine	Ship		Body		Byrom et al. 2003
Squalene	Norway	M	Preputial/ clitoral/urine	Sex attractant	Zhang et al. 2008b; Achiraman et al. 2011a
1,3,5-Triazone-2,4-diamine	Ship	M	Urine	Same sex attractant	Selvaraj & Archunan 2002a
2,6,11-Trimethyl decane	Ship	M	Urine		Rajkumar et al. 2009, 2010a

# Appendix 2

## Cat pheromones

Summary of the known or potential domestic cat pheromones with relevant post-2000 references

PHEROMONE	SEX	SOURCE	FUNCTION	REFERENCES
2-Amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid (felinine)	M/F	Urine	Territorial marking, sex attractant	Hendriks et al. 2001; Rutherford et al. 2002, 2004; Miyazaki et al. 2008
Cauxin	M/F	Urine	Sniffing, licking lips	Miyazaki et al. 2006a,b, 2008
3-Methyl-3-methylthio-1-butanol		Urine	Recognition	Miyazaki et al. 2008
3-Mercapto-3-methyl-1-butanol		Urine	Recognition	Miyazaki et al. 2008; Apps et al. 2014
3-Mercapto-3-methylbutyl formate		Urine	Recognition	Miyazaki et al. 2008
3-Methyl-3-(2-methyl-disulphanyl)-1-butanol		Urine	Recognition	Miyazaki et al. 2008
Feline facial pheromone (FFP) F3	M/F	Facial glands	Familiarisation & calming, territorial marking,	Kronen et al. 2006
Fel d 1, 3, 4, 7 & 8		Submandibular	Unknown	Ichikawa et al. 2001a,b; Smith et al. 2004, 2011
Valeric acid	F	Vagina of oestrous females	Restlessness in males, induction/facilitation of oestrous in females	Van der Hurk 2011

# Appendix 3

## Mustelid pheromones

Summary of the known or potential ferret, stoat and weasel pheromones with relevant post-2000 references

No specific functions of individual components of mustelid odours have been determined.

PHEROMONE	SPECIES	SEX*	SOURCE	REFERENCE
Acetic acid	Ferret	M/F	Urine	Zhang et al. 2005
Acetophenone	Ferret	M/F	Anal/urine	Zhang et al. 2005
Benzaldehyde	Ferret	M/F	Anal/urine	Zhang et al. 2005
Benzothiazole	Ferret	M/F	Anal/urine	Zhang et al. 2005
Decanal	Ferret	M/F	Urine	Zhang et al. 2005
2-Decanone	Ferret	M/F	Urine	Zhang et al. 2005
3,3-Dimethyl-1,2-dithiolane	Ferret, weasel	M/F	Anal	Zhang et al. 2005
2,2-Dimethylthietane (Mustelane)	Ferret, stoat	M/F	Anal	Zhang et al. 2005
2,3-Dimethylthietane	Ferret, stoat, weasel	F	Anal	Zhang et al. 2005
2,4-Dimethylthietane	Ferret	M/F	Anal	Zhang et al. 2005
3,3-Dimethyl-1,2-dithiolane	Ferret	M/F	Anal	Zhang et al. 2005
3,4-Dimethyl-1,2-dithiolane	Ferret	F	Anal	Zhang et al. 2005
2,5-Dimethylpyrazine	Ferret	M/F	Urine	Zhang et al. 2005
Dimethoxyacetophenone	Ferret	M/F	Urine	Zhang et al. 2005
2,2-Dimethoxy-1-phenylethanone	Ferret		Urine	
3-Ethylcyclopentanone	Ferret	M/F	Urine	Zhang et al. 2005
3-Ethyl-1,2-dimethyl-1,2-dithiolane	Ferret, stoat	F	Anal	Zhang et al. 2005; van der Hurk 2011
2-Ethyl-3-methylthietane	Ferret	M/F	Anal	Zhang et al. 2005

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PHEROMONE	SPECIES	SEX*	SOURCE	REFERENCE
2-Ethylthietane	Ferret, Stoat	M/F F	Anal	Zhang et al. 2005 van der Hurk 2011
Geranyl acetone <sup>‡</sup>	Ferret		Anal/urine	Zhang et al. 2005
Heptanal	Ferret	M/F	Urine	Zhang et al. 2005
2-Heptanone (Heptan-2-one)	Ferret	<b>M/F</b>	Urine	Zhang et al. 2005
4-Heptanone (Heptan-4-one)	Ferret	<b>M/F</b>	Urine	Zhang et al. 2005
Hexanal	Ferret	M/F	Urine	Zhang et al. 2005
Indole <sup>§</sup>	Ferret, Stoat, Weasel	M/F	Anal	Zhang et al. 2005
2-Isopropylthietane	Ferret	M/F	Anal	Zhang et al. 2005
6-Methyl-5-hepten-2-one	Ferret	M/F	Anal/urine	Zhang et al. 2005
6-Methyl-6-hepten-2-one	Ferret	M/F	Urine	No relevant references
2-Methylquinoline	Ferret	M/F	Anal/urine	Zhang et al. 2005
4-Methylquinazoline	Ferret	<b>M/F</b>	Anal/urine	Zhang et al. 2005
Nonanal	Ferret	M/F	Anal/urine	Zhang et al. 2005
Octanal	Ferret	M/F	Urine	Zhang et al. 2005
2-Octanone	Ferret	M/F	Anal	Zhang et al. 2005
Ortho-aminoacetophenone	Ferret Stoat Weasel	<b>M/F</b> M	Anal/urine	Zhang et al. 2005 van der Hurk 2011 Zhang et al. 2003
2-Pentylthietane	Ferret, stoat	M/F	Anal	Zhang et al. 2005
2-Propylthietane	Ferret Stoat	M/F M/F	Anal	Zhang et al. 2005
3-Propyl-1,2-dithiolane	Ferret Stoat	M/F	Anal	Zhang et al. 2005
Quinoline	Ferret	M/F	Anal/urine	Zhang et al. 2005
IS (7-tridecanone)	Ferret	M/F	Urine	Zhang et al. 2005
1-Undecanol	Ferret	M/F	Urine	Zhang et al. 2005

\* Bold indicates the compound is at a significantly higher concentration in that sex (following Zhang et al. 2005).

‡ (E)-6,10-Dimethyl-5,9-undecadien-2-one.

§ 2,3-Benzopyrrole.