A review of the current knowledge of rodent behaviour in relation to control devices

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CONTENTS

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ABSTRACT

A recent review of techniques used to detect and control the four introduced rodent species found on the New Zealand mainland and islands (house mice *Mus musculus*, ship rats *Rattus rattus*, Norway rats *Rattus norvegicus* and kiore *Rattus exulans*) identified the need for better understanding of rodent behaviour. This report provides a review of the published literature on rodent behaviour in relation to control devices, especially bait stations and baits. The review is based on searches of computer databases and information from key researchers on: taste preferences, meal size, neophobia, feeding behaviour, movements, home ranges and territoriality, bait shyness, aversion, resistance, odours, and colour preference. Other aspects of rodent behaviour, including responses to repellents, sounds and traps, are also briefly summarised.

Keywords: rodent, rat, mouse, *Rattus rattus, Rattus norvegicus, Rattus exulans, Mus musculus*, eradication, control, island, bait, station, behaviour, neophobia, feeding, movement, aversion, resistance

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1. Introduction

1.1 BACKGROUND

This project is a search for current knowledge of rodent behaviour in relation to control devices. The four species of introduced rodents found in New Zealand are the Norway (or brown) rat (*Rattus norvegicus*; Berkenhout, 1769), the ship rat (*Rattus rattus*; Linnaeus, 1758) (commonly also referred to as the roof rat or black rat), kiore (*Rattus exulans*; Peale, 1848) (also known as the Pacific rat or Polynesian rat) and the house mouse (*Mus musculus*; Linnaeus, 1758). All four species cause damage to the native New Zealand flora and/or fauna and are the subject of control programmes by the New Zealand Department of Conservation (DOC). They pose particular threats to island biota (Moors et al. 1992).

Since the late 1970s, rodents have been eradicated from an increasing number of islands around New Zealand and elsewhere (Veitch & Bell 1990; Taylor et al. 2000; Clout & Veitch 2002; Thomas & 2002; Towns & Broome 2003). While New Zealanders are world leaders in rat eradication techniques, particularly on islands, only 61% of mouse eradication attempts in New Zealand from 1980 to the 1990s were successful (Cleghorn & Griffiths 2002, Towns & Broome 2003; Clout & Russell 2005). Rodent control techniques used in New Zealand have been developed primarily with rats as the target species. Successful removal of mice has been limited to islands of 200 ha or less (Hook & Todd 1992; Brown 1993; McKinlay 1999; Veitch 2002b), with the exception of Enderby Island (800 ha) (Amori & Clout 2003), where the main target for eradication was the rabbit (*Oryctolagus cuniculus*) (Torr 2002). The need for mouse-specific control techniques is best summaried by Pursley (1989): 'Establishing controls for either mice or rats is as different as comparing apples and oranges'.

The second aspect of island management that still eludes us is the confidence that we can detect and then eliminate rodents when they first invade (or re-invade) island sanctuaries. These rodents are highly commensal and common around wharves and foreshore areas, and can easily stow away on ships or swim to islands. On reaching rodent-free islands, incoming rodents are often faced with a range of foods and little competition. Because of their particular behavioural traits and ability to rapidly increase their population, the risk of rodents establishing on islands is high. Mice and rats are also good climbers, so have impacts on arboreal as well as ground habitats when they do reach islands. The potential effects of rodents re-establishing on islands from which they have been removed could be catastrophic. Dilks & Towns (2002) list some 'scares' and 'near-misses' that illustrate this concern. Large investments in time and money have been made in clearing islands and the early detection and removal of invading rodents is vital. Most of the baits and delivery systems currently used for controlling rodents have not been comprehensively evaluated to see how attractive they are to those animals that arrive on islands with an abundance of food. The risk of invasion and undetected spread is well illustrated by Frégate Island, Seychelles (Thorsen et al. 2000). Towns & Broome (2003) give some examples of new invasions and re-invasions by rodents of islands in New Zealand. They specify the lack of knowledge of invasion behaviour and lack of tools for effectively intercepting invasions as significant impediments to advances in island conservation (see also Dilks & Towns 2002; McClelland 2002b).

Improved understanding of rodent behaviour is also vital for planning eradication of long-established rat populations on New Zealand islands and for rodent control on the mainland, and on other islands elsewhere in the world (Sowls & Byrd 2002; Amori & Clout 2003; Courchamp et al. 2003; Abdelkrim et al. 2005).

There is a vast literature on the biology and behaviour of rodents (e.g. reviews by Ewer 1971; Rowe 1973; Berry 1981; Mackintosh 1981; Meehan 1984; Barnett 1988; Prakash 1988; Buckle & Smith 1994; Macdonald et al. 1999b; Singleton et al. 1999). This is because mice and laboratory rats (*R. norvegicus*) are used extensively in medical and psychological research, and these commensal rodents are pests world-wide. The ship rat has been studied because it is a widespread pest. While kiore are also considered to be a pest in some places, there is little known about their behaviour, especially in New Zealand. Atkinson & Towns (2001) do not list any information on behaviour in their review of advances in our knowledge of the species between 1990 and 2000.

1.2 INTERPRETATION

When interpreting the information in the literature about rodent behaviour, the history of these species must be considered. The domestication of laboratory rats has had a marked impact on their behaviour (Galef 1970; Shepherd & Inglis 1987; Kotenkova et al. 2003). One of the most studied behavioural differences between domesticated and wild strains of rats is their level of neophobia. While the commensal rat species are thought to have developed their fear of new objects in their familiar environment because of their association with people, 'lab' rats are thought to have lost this neophobia (Barnett & Cowan 1976; Mitchell 1976; Cowan 1977a). Barnett (1956) noted that 'wild' Norway rats have a greater behavioural repertoire than albino rats, and Barnett & Spencer (1953a) noted differences in food preferences between wild and albino rats. We must also differentiate between commensal rats and those living with no contact with people, as is often the case in New Zealand. Little is known about the relative levels of neophobia or other differences in behaviour between truly wild and commensal rats, but it is possible that populations long isolated from human contact will not show the same neophobia as commensal populations (Taylor & Thomas 1989). This is certainly true for rodent species that do not live commensally (Cowan 1977a; Brammer et al. 1988). Therefore, while Macdonald et al. (1999b) give an excellent review of the behavioural ecology of *Rattus norvegicus*, it should be remembered that it is based on the study of commensal populations.

The impact of domestication appears to be less for mice (MacKintosh 1981), but Klimstra (1972) warns that much of the data on behaviour of albino mice has little application in the field. Bronson (1979) suggested that commensal and feral populations of mice differ in many characteristics including social organisation. While mice are generally neophilic (Barnett 1988), Kronenberger & Médioni (1985) argue that wild mice may have rapidly evolved neophobia because of man's fight against rodents.

There can even be differences between different populations of wild rodents (Mitchell et al. 1977). Invasions are often established from one or a few dispersing individuals, so genetic differences between rats could result in substantial phenotypical differences on different islands. Closed populations of mice have been shown to have a deficiency of heterozygotes, while larger populations are genetically variable (Berry 1970). Closed island populations can be expected to show differences in behaviour and population dynamics from populations open to migration, including differences in spatial organisation (Gliwicz 1980). We must also consider the importance of differences in habitat, climate and history of control when drawing generalisations or comparisons amongst the studies referred to in this review.

1.3 OBJECTIVES

The objective of this study was to summarise the current knowledge of rodent behaviour in relation to control devices, by searching recent literature and contacting key researchers on rodent behaviour and control.

To provide a framework for this search, seven key questions were identified:

- Do rodents have different taste preferences? What are they?
- What lures are known to be attractive to the different rodent species?
- Does the degree of neophobia vary between rodent species? Is there any evidence that neophobia can vary throughout the year, with population density or food supply?
- What is the meal size of the different rodents?
- What is known about behaviour of rats in relation to bait stations (e.g. Norway rats like to sit on their haunches when eating bait)? Is anything known about colour preference in rodents?
- How do the movements and home ranges of the species relate to commonly-used bait station spacings?
- What other possible behavioural factors are relevant to rodent control (e.g. poison shyness, resistance)?

2. Methods

To search for current knowledge of rodent behaviour in relation to control devices, I conducted computer-based searches of the published literature and made personal contact with key researchers in New Zealand and other countries. Topics covered included food and bait preferences, bait palatability, spacing systems, investigatory behaviours, feeding behaviour, neophobia, bait size, and bait station designs. I also specifically targeted research on rodents on islands and island eradication programmes. Some incidental information on habitat use on islands is included, but the review does not cover the ecology of the rodent species in depth (nor is the literature on decision analysis regarding when to attempt rodent eradication included (see Harwood 2000; Maguire 2004; Park 2004; Iwatsuki et al. 2005). The computer searches were done through http://STNeasy.cas.org. I specified the Life Sciences category with the following databases: BIOSIS, BIOTECHNO, CABA, Caplus, EMBASE and SCISEARCH. The various combinations of words in the searches are listed in Appendix 1. I also scanned the literature lists of the papers targeted by these searches, and received literature lists and reprints from individual researchers. Potentially useful papers found during the search but not referred to in the text are included in Appendix 2.

3. Results

3.1 TASTE PREFERENCES AND LURES

Meehan (1984) cautioned that ‘it is impossible to say which particular foodstuff will be preferred by individual rats or even whole populations—there is no such thing as a universally acceptable bait’. Rowe (1973) made a similar comment about mice. These statements have been confirmed by studies of consumption of foods by wild rats (Clark 1982). Lund (1988b) gave a general summary of the ideal characteristics of rodent baits and additives. No magical additives that made baits irresistible were identified. Marsh (1988) summarised the value of bait additives: ‘Sugars and vegetable oils and animal fats are the most universally effective additives for cereal baits to improve acceptance and palatability. Flavour additives to baits have often decreased rather than increased consumption’. Bait materials and lures that have been shown to be attractive or palatable to the four rodent species are listed in Table 1.

3.1.1 Bait bases

While rodents will eat most seed types, various studies have found preferences for particular seed or grain baits. Whole canary seed is particularly attractive to wild-strain mice, while pinhead oatmeal and wheat were well accepted (Rowe et al. 1974). Pennycuik & Cowan (1990) reported that part wild-strain mice found canary seed, maize and sunflower seeds palatable. Canary seed was again one of the most palatable foods, along with soft wheat and rice in a study of mice in Australia (Robards & Saunders 1998). In Egypt, mice preferred wheat to sorghum, sunflower seeds and bran + 5% molasses (Asran 1993a, b). While canary seed is highly palatable to mice, its small size limits its application in the field. This could be overcome by pelleting the grain with just enough propylene glycol to act as a binder (Robards & Saunders 1998). Pellets are acceptable to mice in the field (Jacobs et al. 2003), but can easily crumble and lose their attractiveness when wet (Twigg & Kay 1992; Robards & Saunders 1998).

Yabe (1979) found that ship rats principally ate fruit and seeds. Among a variety of seeds, millet was highly preferred by commensal ship rats (Khan 1974). Boiled rice has been recommended for *Rattus rattus* and *R. exulans* in Burma (Harrison & Woodville 1950).

Norway rats in a study displayed extreme omnivory (Yabe 1979). Wild Norway rats have been shown to prefer wheat meal to whole wheat, white flour or wheat germ (Barnett & Spencer 1953a), and whole wheat to barley or sausage rusk (Barnett & Spencer 1949). Wild Norway rats caught from refuse dumps and a poultry shed preferred sweet rice, proso millet, peanuts, barley and sunflower seeds to corn (Brooks & Bowerman 1973). They disliked peas, buckwheat, sesame, lentils and raw soybeans. Cooking the soybeans inactivates the bitter protein soyin that causes the dislike. The general preference was for grains of low protein, high carbohydrate and moderate fat or seeds of high protein, low carbohydrate and high fats. The presence of high levels of the starch amylopectin may be the key to the attractiveness of sweet rice to Norway rats (Brooks & Bowerman 1973). Smythe (1976) recommended that composite baits contain 25% protein. Malting (steeping, germinating and drying) the grain can increase carbohydrate content, which has been shown to greatly increase bait acceptance (Nolte 1999).

TABLE 1. SUMMARY OF BAIT MATERIALS AND LURES ATTRACTIVE AND/OR PALATABLE TO MICE AND RATS. PALATABILITY INDICATED BY ×.

BAIT/LURE	MICE	SHIP RATS	NORWAY RATS	KIORE	REFERENCES
Canary seed	×				Rowe et al. 1974; Robards & Saunders 1998; Pennycuik & Cowan 1990
Oats	×			×	Rowe et al. 1974; McFadden 1984
Wheat	×		×		Barnett & Spencer 1949, 1953; Rowe et al. 1974; Asran 1993a, b
Rice		×	×	×	Harrison & Woodville 1950; Brooks & Bowerman 1973; Khan 1974
Millet		×	×		Brooks & Bowerman 1973; Khan 1974
Barley			×	×	Brooks & Bowerman 1973; McFadden 1984
Maize	×			×	McFadden 1984; Pennycuik & Cowan 1990
Sunflower seed	×		×		Brooks & Bowerman 1973; Pennycuik & Cowan 1990
Peanuts			×		Brooks & Bowerman 1973
Cooked soybean			×		Brooks & Bowerman 1973
Sugars	×	×	×		Rowe 1961; Collier & Bolles 1968; Howard et al. 1972; Smythe 1976
Saccharin			×		Wagner 1971
Oils	×	×	×		Rowe et al. 1974; Ahmad et al. 1974; Meehan 1984; Pathak & Saxena 1995
Coconut		×	×	×	McFadden 1984; Bull 1972; Robertson et al. 1998
Agar	×				Moro 2002
Fishmeal	×				Robards & Saunders 1998
Chocolate	×		×		Singh 2003; Weihong et al. 1999
Onion	×				Saxena et al. 1995
Egg (yolk, shell)		×	×		Shafi et al. 1990,1992; Pervez et al. 1999
Yeast		×	×		Shafi et al. 1990, 1992
Cheese			×		Weihong et al. 1999
Soap			×		Weihong et al. 1999
Grape			×		Smythe 1976
Blood & offal			×		Bull 1972
Cinnam-aldehyde			×		Bull 1972
Fish			×		Bull 1972
Raspberry			×		Bull 1972
Aniseed			×		Bull 1972
Banana				×	McFadden 1984
Eucalyptus				×	McFadden 1984
Vanilla				×	McFadden 1984
Clove				×	McFadden 1984

Barley, oats and, to a lesser extent, maize, were readily accepted by kiore (McFadden 1984). Seasonal variation has been reported, with a change to more nutritious food in autumn (Nieder 1986).

3.1.2 Sugars and oils

Using a conditioned food aversion technique (Reidinger et al. 1983; Stewart et al. 1983; Mason et al. 1985), Mason et al. (1991) determined that toxicants cannot be simply classed as bitter, sweet, sour or salty, but have complex flavours to which rodents respond. Bullard et al. (1977) used the responses of Philippine ricefield rats (*Rattus rattus mindanensis*) to show that intensifying the flavour cues of familiar or favoured foods could be a useful way of enhancing bait take. So-called attractants help to keep rodents feeding longer at food sources. They may be effective because they mask the taste of a rodenticide and/or they are palatable in their own right (Meehan 1984).

Sugar is a well-known effective additive for rats and mice, while bitter flavours tend to be rejected (Rowe 1961; Howard et al. 1972; Shimizu et al. 1980; Marsh 1988; Yamaguchi 1995). Norway rats in trials preferred salty and sweet tastes over sour and bitter ones (Karasawa & Muto 1978; Kolody et al. 1993). The most attractive concentrations of sugars have also been assessed in various trials. Howard et al. (1972) recommended 64 g/L in liquid baits for wild-caught and laboratory Norway rats, while Smythe (1976) recommended 1–5% sucrose by weight. Other authors have recommended higher concentrations (Collier & Bolles 1968). When given the choice between sugar on its own and flour, Norway rats consumed only small amounts of the sugar (Barnett 1956). Inverted sugars like maltose, dextrose, fructose and levulose also are acceptable to rodents (Smythe 1976). Of the artificial sweeteners, saccharin was favoured by laboratory rats over cyclamate, while wild Norway and ship rats preferred glucose to saccharin (Wagner 1971). Sugars also help preserve the baits, potentially increasing shelf- and field-life, but also increase bait palatability to invertebrates and reptiles (J. Russell, Auckland University, pers. comm.).

Oils can be effective additives. Meehan (1984) found that the higher the level of oil in bait, the more readily it was taken. Mice have exhibited a preference for high-fat foods (Imiazumi et al. 2001) and rats have an appetite for dietary fats and oil (Elizalde & Sclafani 1990; Ramirez 1993). Glycerin, corn oil, arachis oil and mineral oil were more palatable to mice than olive, linseed or cod-liver oils (Rowe et al. 1974). Groundnut oil probably has a neutral flavour to rodents (neither attractive nor repellent), but may act to mask the flavour of cereals to which rats have developed bait shyness (Bhardwaj & Khan 1979a, b). In conjunction with gur, groundnut oil increased bait consumption by mice more than just the gur alone (Pathak & Saxena 1995). Olive oil enhanced the acceptance of baits to male ship rats in no-choice tests, while soybean oil, sunflower oil, mustard oil, groundnut oil and coconut oils were all preferred over plain bait in choice tests, and groundnut oil was preferred over coconut and mustard oils (Ahmad et al. 1994). However, in the same study, female rats preferred coconut, mustard and, to some extent, sunflower and soybean oil in mixed diets. In a study in the USA, coconut, peanut and corn oils were most prefered by Norway rats, whilst corn oil was preferred over peanut oil by black rats (Meehan 1984). In another study, adhesive oils reduced palatability of oats to all three species of rat tested (Pank 1976).

3.1.3 Other additives and lures

Mice in a study exhibited a preference for monosodium glutamate (MSG) and NaCl (salt), but more so for sugars (Yamaguchi 1995). On Thevenard Island (Australia), mice selected parrot seed coated with agar more often than either the seed alone or seed coated with wax (Moro 2002). The addition of salt to these baits increased bait consumption. Also in Australia, fishmeal was a successful additive to bait for mice (Robards & Saunders 1998; Jacobs et al. 2003). These authors listed a range of other additives that made no difference to consumption, including chocolate, cheese, aniseed, peanut oil and honey. By contrast, chocolate is used elsewhere as an effective trap attractant for mice (author, pers. obs.), to such an extent that UK researchers have developed a chocolate mousetrap (Singh 2003). The addition of 2% onion pulp (but not garlic, ginger or tulsi) improved consumption of bajra flour by by mice in India (Saxena et al. 1995).

Egg yolk and yeast were successful additives to poison baits for wild-caught ship rats in Pakistan, more so than minced meat, egg shell, sheep blood or chicken blood (Shafi et al. 1990). Conversely, egg shell ranked the highest, then egg yolk, yeast and minced meat in field trials in Pakistan (Pervez et al. 1999). Toasted coconut has been used successfully as bait in traps in Rarotonga (Robertson et al. 1998).

A bait type often used for rats in New Zealand is peanut butter and rolled oats, while the hazelnut spread 'Nutella' has been successful with Norway rats (J. Russell, pers. comm.). On Browns Island, Hauraki Gulf, Auckland, cheese, chocolate and soap were preferred (in that order) over wax and oiled wood by Norway rats (Weihong et al. 1999). Tabuchi et al. (1991) listed black pepper, milk and coffee as highly preferrred food-related odours; while nut, peppermint, plum, orange and cheese also elicited a bar-pressing response from rats. Smythe (1976) suggested that some additives act as 'curiosity enhancers' to rodents and mentioned, in particular, a 'powerful, persistent synthetic grape flavour'. This was effective when used as a coating for plastic bags containing the baits, but not when added into the bait. Raw fish and beef, dried dog food, coconut oil, fresh or dried blood, chicken offal, cinnamaldehyde, raspberry, aniseed and other commercial products have all been attributed with attractive properties for Norway rats (Bull 1972). Shafi et al. (1992) found that yeast was the most palatable additive to flour/rice baits, followed by egg shell, with egg yolk, sheep and chicken blood and minced meat being less preferred. Schisla et al. (1970) described the success of 'Dexide'—a carbohydrate with flavour material—that increased the consumption and efficacy of warfarin to mice, ship rats and Norway rats. Salt and MSG are variable in their effect, and were disliked at concentrations above 0.5% (Ohara & Naim 1977; Marsh 1986, 1988; Kolodiy et al. 1993). Female rats consumed more salt than male rats (Flynn et al. 1993).

McFadden (1984) listed aniseed, banana, coconut, clove, eucalyptus and vanilla as acceptable lures for kiore. Veitch (1995) found that kiore preferred Rentokil Rid Rat baits that contained 7.5 ml/L of sucaryl over the standard baits that contained vanilla and carbon disulphide, and those with chocolate and oil, or coconut or vegetable oil.

3.1.4 Formulations

In preliminary bait trials with wild-caught mice, O'Connor & Booth (2001) found that PESTOFF® and Talon®50WB were more palatable and effective than Racumin® or Talon®20P. PESTOFF®20R was, however, less palatable to mice from Mokoia Island than standard Challenge diet (Cleghorn & Griffiths 2002). Wild-caught mice found both non-toxic and toxic Talon®20P cereal pellets more palatable than the RS5 cereal pellets or fishmeal pelleted 'cat baits' tested by Morgan et al. (1996), presented either in a simulated aerial drop or in bait stations. Talon wax blocks were preferred over kibbled wheat, poultry pellets and Mapua pellets by mice on Mana Island, Wellington (Todd & Miskelly unpubl. report cited in Cleghorn & Griffiths 2002). Talon wax blocks controlled mice on Varanus Island, Australia (J. Angus, pers. comm. in Moro 2002).

Ship rats wild-caught from poultry sheds in India preferred freshly-prepared formulations of Quintox® in a white flour/sugar/groundnut oil mix over commercially available Quintox® cake and pellets (Saini & Parshad 1992).

Airey & O'Connor (2003) found Talon® 50WB and Storm® wax blocks had low palatability when presented to wild-caught Norway rats, and resulted in low mortality. RS5 pellets and Talon®20P pellets were both preferred over fishmeal cat pellets by wild-caught ship rats (Morgan et al. 1996). Storm was effective against kiore on Double Island (McFadden 1992), as was Talon®20P on Burgess Island (McFadden & Greene 1994).

Bait formulations often contain wax to enhance bait longevity and water-resistance (O'Connor & Eason 2000). Symthe (1976) cautioned that rats in Hawaii were averse to wax, and that waxes can vary in hardness. Norway rats on the Noises Islands found 'too much' wax unattractive (Moors 1985a). Ross et al. (2000) tested Pestoff baits with and without an unspecified additive and found that the additive had no effect on palatability. The pelleted Pestoff formulation was more palatable than the block formulation, and also more palatable than Ditrac Blox.

Adhesives may be needed to hold the poison onto the bait, especially in aerial operations. Pank (1976) found that zinc phosphide baits containing Alcolec S were more effective than those containing corn oil.

3.1.5 Hardness

Hardness affects bait preference of rodents. Smythe (1976) suggested that rodents will gnaw on anything, but baits with a hardness between that of soft wheat and water-soaked corn appeared to be optimum. Ford (1977) found that increasing hardness of diet reduced food wastage by mice and rats, that less wastage occurred when they were fed pellets made from finely ground materials (an effect that was not related to hardness), and that apparent food consumption increased with the softness of the diet. Robards & Saunders (1998) found that mice preferred soft wheat varieties. Dehusking of whole grains by rodents can lead to the removal of the poison and thus lower efficacy (Smythe 1976). McFadden (1984) commented that kibbled grains are more practical than whole grains, as they allowed the poison to be absorbed into the kernel. Similarly, both laboratory Norway rats and wild-caught ship rats have been observed to leave the skin of carrots (author, pers. obs.).

3.1.6 Wrappings

Wrapped bait is often left on islands after eradication programmes as a security against possible rodent survivors (Towns et al. 1994). Rodents can easily chew through paper, plastic and 'fiber' (e.g. Shumake et al. 2000). However, wrapping bait in tinfoil or in ziplock plastic bags reduced its palatability and efficacy to mice (Brown 1993) and to Norway rats in trials (Airey & O'Connor 2003).

3.1.7 Colour

The addition of green dye had no effect on the consumption of wheat by mice (Robards & Saunders 1998). McFadden (1984) mentioned a trial in which green dye appeared to reduce the palatability of baits for kiore. Meehan (1984) stated that 'rats and mice are almost certainly colour blind, but yellow and green are more "attractive" as they are seen as a very light grey'. Mice can discriminate amongst colours, and laboratory mice preferred white cages over black, green and, particularly, red ones (Walton 1933a, b; Sherwin & Glen 2003).

3.1.8 Gnaw sticks

Gnaw sticks are often used to determine the presence of rodents (e.g. Hook & Todd 1992; Jansen 1993; Adams 1997; Shaw 1997; Garcia et al. 2002). Typically, they are made of wood soaked in vegetable oil. Wax or cereal/wax blocks, candles, chocolate and soap are also sometimes used (Towns et al. 1994, 1995; Brown 1997; Nelson et al. 2002; Veitch 2002d). There have been no specific studies comparing the attractiveness or 'gnaw-ability' of different sorts of gnaw sticks.

3.2 MEAL SIZE

The study by Mutze (1991) on turnover rates in wild mice indicated that mice need to eat 17% of their body mass each day to maintain that mass. Mice are considered to be light and intermittent feeders compared with rats (Crowcroft & Jeffers 1961).

Clark (1982) observed that meals of ship rats tend to be dominated by one food. Wild-caught ship rats in captivity consumed an average 14–18 g of pellets per day (plus a slice of apple) (B.K. Clapperton et al., unpubl. data).

Adult Norway rats have exhibited a preference for food particles 0.4 to 0.7 cm in diameter (Smythe 1976; Lund 1988b—diameter given in mm, presumably in error). This appears to be the size of particle most suitable for a rat to hold in its forepaws while eating. Larger-sized pieces may be hoarded by some rats. Daily intake of different foods can vary greatly (Barnett 1956). A medium-sized Norway rat can take six to eight grains of wheat in its mouth at one time, making a mouthful weighing about 2.1 g. In one study, adult laboratory rats ate, on average, about 19 g of pellets per day (B.K. Clapperton et al., unpubl. data). Laboratory rats in one study had three or four distinct feeding bouts, eating an estimated 2.5–6 g during each bout (Roger Quy, Central Science Laboratory, MAFF, UK, pers. comm.); while in another study they averaged nine or ten meals per night, eating an average of 2.3 g per meal (Zorrilla et al. 2005). Wild rats tend to have shorter meals than laboratory rats, visiting food sites more frequently but for shorter periods of time (Barnett et al. 1978). In Norway rats, differences in meal size are attributable to differences in sex, size and reproductive status. Females forage in many short visits, while males use fewer, longer visits (Inglis et al. 1996). Shepherd & Inglis (1987) found that a pregnant or lactating female ate the most and her meals were longer and larger than those of the males; but her feeding rate was no greater. The mean amounts eaten by rats in that study varied between 16.3 and 84.6 g/day. The number of meals varied from 5 to 11 per day. Food intake is thus adjusted to calorific expenditure (Macdonald et al. 1999b).

Differences in the rate of feeding or the number and size of meals amongst individual Norway rats imply that there are likely to be differences between individuals in susceptibility to poison shyness resulting from ingestion of sub-lethal doses (Shepherd & Inglis 1987).

3.3 NEOPHOBIA

The neophobic response can be one of the most pertinent obstacles to efficient rat control (Lund 1988a). Barnett (1958) defined neophobia as the avoidance of an unfamiliar object in a familiar place. It causes problems in poisoning programmes because neophobic animals will avoid new foods and even foods previously eaten if they are placed on or in a novel object (Barnett 1988). The response varies not only between species (see below) but also between populations of the same species (Mitchell et al. 1977) and between individual animals (Cowan & Barnett 1975; Cowan 1977a). The phenomenon of neophobia is reviewed by Brigham & Sibley (1999).

Some researchers have classed mice as neophilic, i.e. that they have a tendency to approach unfamiliar places or objects (Chitty 1954; Barnett 1988), but other researchers dissagree. Misslin & Ropartz (1981) found that a novel object placed in a familiar environment did, in fact, release avoidance and burying responses in laboratory mice. Kronenberger & Médioni (1985) demonstrated a greater level of neophobia in wild mice than in laboratory mice. Wolfe (1969) and Connor (1975) also found that captive wild mice developed a weak neophobic response. However, the same authors pointed out that the very pronounced, long-lasting avoidance behaviour of wild *Rattus* species is essentially absent in wild *Mus.* Mice can be quite cautious about taking new baits, and use sampling to test new foods (Chitty 1954; Brown 1993). But one study found that in cereal crops baiting success was not improved by pre-baiting (Mutze 1989). These studies also recommended that baiting success would be improved if bait stations were moved around (see also Berry 1981); although Ajao & Hurst (1992) found that mice preferred to feed from the same station over consecutive nights. Mice are drawn to new feeding sites (Crowcroft 1959; Berry 1981; Rowe 1981). Niemeyer (2002) recommended that clearing of vegetation in front of mouse traps attracts mice to investigate the area. In Australia, mice readily enter live-capture traps on the first night traps are placed in fields. However, there was significant heterogeneity in trappability over seven consecutive nights (Davis et al. 2003).

Ship rats living in close association with people show neophobia, although there is also some conflicting evidence (Meehan 1984). Cowan (1976) demonstrated how changing from a familiar food basket to a novel one or moving the familiar basket to an unfamiliar position, evoked 'new object reaction' in ship rats. Altering the smell of the basket or presenting a new food in it did not evoke avoidance. It may take several weeks for ship rats to enter bait stations (Howard 1987), or only 1–2 days (Watson 1954; Advani & Idris 1982). It is not known whether or not truly wild populations are less neophobic because of their long period of time with no association with people.

Commensal Norway rats are considered to be particularly neophobic (Barnett & Cowan 1976; Cowan 1977a; Meehan 1984; Moors et al. 1992). This makes them difficult to trap or to attract into bait stations. Adult females can be particularly difficult (Thorsen et al. 2000). Lund (1988a) discussed the issue of neophobia in relation to baiting techniques for rats, and recommended that bait stations be placed close to a runway, not directly on it (citing Howard 1986a, b), and should never be moved during a control period. Inglis et al. (1996) recommended that baits should be covered by materials already present at the site, and that use of natural holes or other natural sources of protection for baits, rather than man-made bait stations, can reduce the problem of neophobia. Establishing permanent bait stations and/or pre-feeding the target rats with familiar highly palatable foods are suggested ways of mitigating the effects of neophobia (Inglis et al. 1996). Even small differences in the appearance or construction of bait stations, or in their odour, may be detected by rats. Shepherd & Inglis (1987) demonstrated the importance of addressing the problem of neophobia. In that study, captured commensal Norway rats ate more difenacoum bait in a familiar container than their standard diet in a novel feeder. This result indicates that neophobia towards a palatable food, even one containing poison, is likely to be transient compared with the neophobia towards a new object such as a bait station (see also Inglis et al. 1996). Feeding from novel food containers can be delayed by several days, while feeding on novel foods normally occurs towards the end of the first night (Brunton 1995). Inglis et al (1996) calculated that the introduction of novel bait containers doubled the number of days needed to accumulate a lethal dose for brodifacoum (1 day to 2 days), and increased it 14-fold for difenacoum (1 day to 14 days). Norway rat populations isolated from human contact for many generations on Breaksea and Hawea Islands did not appear to be neophobic (Taylor & Thomas 1989, 1993). Neophobia may also be reduced in individuals infected with the parasite *Toxoplasma gondii* (Macdonald et al. 1999a, b). Inglis et al. (1996) found no sex differences in the degress of neophobia to novel foods.

There is little information available about neophobia in kiore. Moors et al. (1992) stated that kiore may even be attracted to new objects, but Harrison & Woodville (1950) mentioned avoidance of a new food container by *R. exulans* living as house-rats in Burma. Nelson et al. (2002) suggested neophobia as a possible reason for the failure of Polynesian rats in Hawaii to use bait stations.

3.4 FEEDING BEHAVIOUR

Mice may visit many feeding locations during a single foray (Crowcroft & Jeffers 1961). They appear to feed quite randomly. Although a few feeding areas may be heavily exploited during the course of one night, these sites vary from night to night (Meehan 1984). Mice have been described as light and erratic feeders, making it difficult to ensure that each individual receives a lethal dose of poison (Rowe 1973). For example, a high degree of variability in Pestoff 20R bait consumption was recorded between individual mice from Mokoia Island (Cleghorn & Griffiths 2002).

Ewer (1971) describes the eating, prey killing and drinking behaviour of ship rats. Notably, they are very adept at manipulating food particles, and perching on their haunches or clinging to branches. There are photographs of a rat sitting on a 1.6-mm diameter wire, 'fishing' up a nut on a string and eating it while still perched on the wire.

Both wild and laboratory Norway rats show marked exploratory and sampling behaviour (Barnett 1956). When unfamiliar foods are provided to Norway rats in familiar conditions, they are sampled during the first feeding period (Barnett 1956). The amount eaten then is not a good indicator of preference when feeding has stabilised. This stabilising usually takes 1 or 2 days. Both adult and juvenile rats exhibit sampling behaviour, the only difference being that adult rats spill less food (Barnett 1956). Young rats do a lot of sampling and exploration that could lead them to food sources (Barnett 1956). Sampling can result in the change from feeding on one food to another or from one feeding site to another (Barnett 1956). Such changes take several days in wild Norway rats (Barnett & Spencer 1953a). When provided with a range of unfamiliar foods, wild Norway rats do not sample among them in a manner that would facilitate identification of any toxin present (Beck et al. 1988).

Barnett (1956) observed Norway rats licking their food-covered forepaws and even the mouths of other rats. Young that were still suckling licked the paws and mouth of the mother. Norway rats will sit back on their haunches and hold grain in their front paws (Meehan 1984). Mice will pick up a grain in their front paws and dehusk and eat it rather like they were peeling and eating a banana (Meehan 1984).

There have been many studies of social facilitation of feeding in rats. Norway rats follow trails left by other rats to find food (Galef & Buckley 1996). Cues transmitted from a mother to her pups during the nursing period are sufficient to determine the dietary preference of the young at weaning (Galef & Clark 1972; Valsecchi et al. 1993). Barnett (1956) noted that young Norway rats tend to orientate themselves towards their mother, thus being led indirectly to food sources. No evidence was found of deliberate guidance by mothers. Young rats stay close to the adults so they tend to eat what the adults eat, and this becomes their familiar diet (Galef & Clark 1971; Galef 1977). Naive rats will choose an unfamiliar food after observing another rat feeding on that food (Posadas-Andrews & Roper 1983; Galef et al. 1984; Strupp & Levitsky 1984; Galef & Whiskin 2000, 2001). Mice also learn food preferences from observing other mice feeding (Valsecchi et al. 1996). Food preferences in Norway rats can also be mediated by odour cues left at feeding sites by conspecifics (Galef & Heiber

1976; Laland & Plotkin 1991), but the effect is not so pronounced in wild mice (Valsecchi et al. 1966). Lavin et al. (1980) and Bond (1984) presented data that support the idea that a non-poisoned rat can learn to avoid a novel flavour by perceiving the sick state of a poisoned conspecific rat and using that cue to avoid potentially dangerous foods. However, Galef et al. (1990) failed to provide any evidence that naive observer rats will learn to avoid a food as a result of interacting with demonstrator rats that had eaten the food and exhibited symptoms of toxicosis. There is evidence that rat foetuses are able to learn odour aversions (Smotherman 1982).

Mice (Ylonen et al. 2002) and Norway rats (Barnett & Spencer 1953a) prefer to feed at sites close to cover. Norway rats will drag food items to cover unless the food is too heavy, or they can feed undisturbed (Barnett & Spencer 1953a). Enderpols et al. (2003) found that farmers who complied with a prescribed bait station placement plan were most likely to achieve complete eradication of rats. Bait acceptance levels in Norway rats on farms were highest in bait stations located at specific structural elements on a farm which were the sites of highest rat activity (Endepols & Klemann 2004), and social interactions also affected choice of bait stations (Klemann & Pelz 2005). Macdonald et al. (1999b) discussed the role of predators in the feeding behaviour of rats. Hoarding is another aspect of feeding behaviour that can influence bait take. Sheikher & Malhi (1983) found no evidence of hoarding by mice, but Naumov (1940) described how mice in the Ukraine store food for the winter. Norway rats will hoard food after initial bouts of feeding if they are hungry (Barnett & Spencer 1951; Fantino & Cabanac 1980; Wallace 2003). Some types of food are more likely to be hoarded than others (Barnett & Spencer 1951). Food size, number of feeding sites, distance to the burrow and group size all influence food-carrying behaviour (Whishaw & Tomie 1989; Whishaw et al. 1989; Whishaw & Dringenberg 1991; Thullier et al. 1992; Nakatsuyama & Fujita 1995). Females, especially while lactating, are more likely to hoard than males (Boice 1977; Meehan 1984). Ship rats do not like to feed far from shelter and will hoard food more frequently than kiore (McCartney 1972). Not all stored food is eaten—food caches have been found full of fungus (Meehan 1984). Veitch (2002a) suggested that food hoarded by Norway rats on Browns Island was then available to mice after the rats had died. Kiore will also hoard poison pellets (Cash & Gaze 2000). McKenzie (1993) noted kiore on Motuopao Island nesting in grass close to bait stations and feeding at regular intervals on the bait.

3.5 SOCIAL BEHAVIOUR

Wolff (2003) described rodent behaviour systems as complex, variable and adapted to high reproductive rates and marked changes in density (see also Berry 1981).

Social behaviour can influence which animals have access to bait stations. In commensal situations, large numbers of rats may use a single bait station (Shorten 1954). But in a captive Norway rat colony, it was observed that there was usually a 'pioneer' rat that regularly appeared first in a feeding period (Barnett & Spencer 1951). Subordinate mice (Rowe 1973) and Norway rats (Berdoy 1991) fed when dominant animals were inactive. Similarly, Drickamer

& Springer (1998) found that while there were no significant differences in nocturnal activity patterns by age or sex, subordinate male mice were active early in the night and dominant males were active later. Dubock (1982) suggested that socially inferior rats might only be allowed to feed from a bait station during the later stage of a poison operation, as they are excluded by dominant individuals. Shepherd & Inglis (1987) also found that a dominant female Norway rat could deter even the males from using the same food source. Taylor & Thomas (1993) advocated the use of permanent bait stations so that less-dominant individual Norway rats could learn from others to access the bait. Norway rats will sometimes feed together at bait stations (J. Russell, pers. comm.). This group feeding gives individuals a degree of protection from predators (Roger Quy, pers. comm.). Ship rats are more gregarious and less aggressive than kiore, relying more on grooming and stereotyped agonistic postures (McCartney 1972).

3.6 MOVEMENTS AND HOME RANGE

Meehan (1984) summarised the pre-1980s literature on movements of rats and mice. Movements and home ranges of rodents in New Zealand have been summarised by Atkinson & Moller (1990), Innes (1990), Moors (1990) and Murphy & Pickard (1990). Gliwicz (1980) characterised island populations of rodents (bank voles and deer mice) as having smaller home ranges than in open systems. Norway rats can climb trees and ship rats and mice will jump and climb to get to food (Timm & Salmon 1988).

There are numerous references from around the world to movements of mice (Young et al. 1952; Brown 1953; Pearson 1963; DeLong 1967; Tomich 1970; Berry & Jakobson 1974; Nikitina et al. 1976; Twigg et al. 1991, 2002). The most notable findings are reported in the following text. Mice tend not to move great distances. In an agricultural setting in Australia, one third of the mice were caught in the same trap location, and the maximum recorded movement was 60 m (Twigg et al. 2002). Most estimates of average home range size for free-ranging wild mice vary between 0.0035 and 8.024 ha (Lidicker 1966; Fitzgerald et al. 1981; Sage 1981; Krebs et al. 1995; Chambers et al. 2000). In the Orongorongo Valley, New Zealand, mice would visit many parts of their ranges in one night (Fitzgerald et al. 1981). Males tend to travel further than females (Lidicker 1966; Quadagno 1968; Tomich 1970; Hackmann et al. 1980; Mikesic & Drickamer 1992), but Fitzgerald et al. (1981) found that female home ranges sometimes matched those of males. Female home range size can increase in winter (Lidicker 1966). In feral mice in San Francisco, movement peaks occurred in the coldest part of winter, during the breeding season and when the population was nearly extinct (Lidicker 1966). In Australian wheatfields, ranges of mice could be ten times larger outside of the breeding season than during it (Krebs et al. 1995). Home range size may also be affected by competition from other rodents (Quadagno 1968). Mice seldom cross roads (Kozel & Fleharty 1979; Wilkins 1982), and they prefer to stay close to cover (Gray et al. 2000). Female mice stay near the nest around parturition and thereafter spend more and more time away from it (Barnett & McEwan 1973). Usually juveniles disperse, setting up territories in unoccupied space (DeLong 1967; Mackintosh

1981), but older mice will move if habitat conditions deteriorate (Newsome 1969a, b). Mice living in refuge habitat (along fencelines) in Australian wheatfields would make foraging movements extending to about 20–30 m into the crop (Jacob et al. 2004). Successful island eradications of mice have used bait station spacings of 25 or 50 m (Hook & Todd 1992; Brown 1993). Twigg et al. (1991) recommended bait station spacings of no more than 20 m in Australian soybean crops. Moro (2001) found that mouse densities declined more on grids with bait stations spaced every 10 m than on grids baited every 20 m; and according to Moro (2001), manufacturer recommendations for the use of Talon for mouse control is for baits to be no more than 3 m apart.

Ship rat movements are, typically, also small. Estimates of average movements between captures vary from 18 to 174 m (Spencer & Davis 1950; Watson 1951; LaVoie et al. 1970; Daniel 1972; Temme 1973; Innes & Skipworth 1983; Dowding & Murphy 1994). In New Zealand forests, ship rats have been recorded as evenly (Innes & Skipworth 1983) or patchily distributed (Dowding & Murphy 1994) in home ranges averaging about 1 ha for males and smaller for females (Tomich 1970; Innes & Skipworth 1983; Hickson et al. 1986; Dowding & Murphy 1994). In Fiordland, in March 2000, three male ship rats had home ranges of 7.5, 9.1 and 11.4 ha, while two females had home ranges of 0.89 and 0.27 ha (Pryde et al. 2005). Home range sizes in the Orongorongo Valley estimated by Daniel (1972) were much smaller (0.17 ha for males and 0.08 ha for females). Ranges are sometimes exclusive, but Dowding & Murphy (1994) found substantial overlap in ranges, both between and within sexes, and den sharing. Male ranges may increase during the breeding season. In Tenerife, Canary Islands, ship rats were more active along roads than in other parts of forests (Delgado et al. 2001). Roads that ran on forest ridges and slopes were used more than those in ravine beds in laurel forest, but there was no topographical difference in road use in pine forest. At North Head, New South Wales, ship rats favoured habitat with dense understorey, especially with enhanced leaf litter (Cox et al. 2000). On Macquarie Island, ship rats were found in areas with extensive stands of tussock, including beaches, raised coastal terraces, coastal hill slopes, coastal ridge tops, coastal rock stands, and stream courses (Pye et al. 1999). The tussock fringes of stream courses were important dispersal corridors into the inner areas of the island. A bait station spacing of 100 m is considered suitable for ship rats (Innes 1995); although, if home ranges are less than 1 ha (as is the case for most females), not all rats will have access to a bait station in their home range at this spacing. However, as neighbouring rats are removed by the poisoning, the remaining rats are likely to move into the unoccupied space (Innes 1990).

Norway rats can move many kilometres, but average movements of radio-tracked rats in arable land were 340 m for females and 660 m for males (Taylor & Quy 1978). The tracked rats usually kept to hedgerows, but some crossed open areas for up to 500 m. These movements were considered to be changes in home sites, and males made them every 7 days and females every 14 days (Taylor 1978). Captive rats systematically patrolled their home ranges (Cowan 1977b). Norway rats living near human food depots moved shorter distances than the above stated (Davis et al. 1948; Hardy & Taylor 1979; Hartley & Bishop 1979). Norway rats studied by Davis et al. (1948) and Kemper (1960, cited in Davis 1953) moved up to about 45 m between places of shelter and food. Kunkel (1989) noted that home range size in urban parks was dependent on the proximity of burrows to food sources. On the Noises Islands, Norway rats travelled widely (average distance 113 m) between successive captures, with males moving further than females (Moors 1985b). Over 2–5 nights, Norway rats on Whale Island moved on average 72 m (Bettesworth 1972). Distances travelled and home ranges of Norway rats increased as food became more dispersed (Hardy & Taylor 1979). Gibson (1973) studied a Norway rat burrow system near Christchurch. The removal of two lactating females from the colony resulted in the nestlings moving beyond their burrows and subsequently being captured. Norway rats on the islands of South Georgia were found mostly in dense stands of coastal tussock grasslands, with burrows excavated out of the peat (Pye & Bonner 1980). Hartley & Bishop (1979) made the observation that Norway rat infestations in hedges were always associated with streams. Norway rat home ranges on Kapiti Island averaged 5.78 ha for males and 5.13 ha for one female (Bramley 1999). Home range lengths averaged 438.7 m (males) and 459 m (females). Successful island eradications of Norway rats have used bait station spacings of 50 or 100 m (Moors 1985a; Taylor & Thomas 1993; Kaiser et al. 1997; Taylor et al. 2000). Newly arrived on Frégate Island, a Norway rat settled in one area, around which its offspring also settled (Thorsen et al. 2000). Most captures of rats on this island were in a 75 × 60 m area until 8 months after the invasion.

Kiore nest and feed in trees (Daniel 1969; McCartney 1970; Williams 1973; Moors et al. 1992), and make arboreal runways through coconut fronds (McCartney 1970). However, they are only occasionally captured in the forest canopy (Stone 1985; Sugihara 1997). Average kiore home ranges on Kapiti Island were much smaller than those of Norway rats (0.14 ha for males and 0.18 ha for females). Range lengths were 51.8 m (males) and 67.2 m (females) (Bramley 1999). The kiore were in the areas of denser vegetation, where they may not easily come in contact with poison baits (Bramley 1999). Kiore on Stewart Island were most abundant in manuka and riparian shrubland, habitats with dense ground cover (Harper et al. 2005). Home ranges of kiore on Tiritiri Matangi Island averaged 37–60 m but were very variable in size (Nicholas 1982). Size and shape of kiore home ranges varied with habitat and population density in Hawaii (Jackson & Strecker 1962; Nass 1977, but see Wirtz 1972). Dwyer (1978) found segregation of males and females, and amongst age classes. Male kiore in New Zealand tend to move further than females and adults further than juveniles (Moller 1977; Nicholas 1982). This has also been shown to be the case in the Pacific and Asia (Jackson & Strecker 1962; Tomich 1970; Tamarin & Malecha 1971; Wirtz 1972; Lindsey et al. 1973; Williams 1974; Nass 1977; Dwyer 1978). In sugarcane, average distances kiore moved between successive captures was about 35 m (Lindsey et al. 1973). Successful island eradications of kiore have used bait station spacings of 50 m (McFadden & Towns 1991; McKenzie 1993; McFadden 1997; Cash & Gaze 2000). The 100-m spacing of bait stations on Coppermine Island may have contributed to the failure of the kiore eradication there (McFadden 1997). Bait stations 20–25 m apart may be necessary for kiore (Bramley 1999).

3.7 TERRITORIALITY

Mice have a flexible form of territoriality, dependent on the distribution of resources and population dynamics (Myers 1974; Lloyd 1975; Hackmann et al. 1980; Maly et al. 1985; Hurst 1987a; Krebs et al. 1995b; Chambers et al. 2000; Gray et al. 2000, 2002). The apparent difference in social organisation between field and commensal rodents seems to be due primarily to the fact that food is much more evenly distributed in most field situations. In commensal situations, mice form cohesive social groups, or demes, that defend a communal territory (Crowcroft 1955; Crowcroft & Rowe 1963; Lidicker 1976; Mackintosh 1981; Singleton 1983). Territory boundaries tend to form where there are distinctive physical features (Mackintosh 1981; Singleton & Hay 1983). When mice are at high densities in agricultural landscapes, home ranges overlap, and at the end of the breeding season the mice become nomadic (Krebs et al. 1995a, b; Chambers et al. 2000). In evergreen New Zealand forests, where mouse densities are low, there is exclusive use of space by both sexes, and territorial defence (Fitzgerald et al. 1981), although mice did maintain group territories in the Marlborough Sounds (Murphy & Pickard 1990).

Ship rats in New Zealand forest generally do not live in colonies like commensal rats (Hooker & Innes 1995), although Dowding & Murphy (1994) recorded them denning together. Adult females tend to occupy exclusive areas in the breeding season (Innes & Skipworth 1983; Hickson et al. 1986), but not always, and rats have been observed together, usually one following another. There has been no published study of territoriality of Norway rats or kiore in New Zealand. Macdonald et al. (1999b) summarised the social system of commensal Norway rats in Britain. Where resources were scarce or scattered, males appeared to maintain exclusive ranges, with access to numerous females. Groups developed around reliable food supplies. Social organisation in a captive colony of kiore was described as hierarchical, with females dominant over males (Davis 1979).

Rodents, particularly kiore, probably avoid other rodent species, but habitat structure is more important than direct competition in determining their distribution (Dick 1985; Bramley 1999). Norway rats may, however, prey on kiore (Bramley 1999). It has been suggested that interference from Norway rats may cause kiore to feed more up in trees (Atkinson & Moller 1990). Ship rats may dominate kiore (Russell & Clout 2004), and the two species compete for nest sites (McCartney 1970). Ship rats have been observed killing mice (Ewer 1971).

3.8 RESPONSES TO BAIT STATIONS

A lot of the thrust of rodent bait station development has been not for the improvement of efficacy but, rather, for the reduction of pesticide hazards (Kaukeinen 1989; Jacobs 1990). Some issues of concern elsewhere are not necessarily relevant to rodent control on New Zealand islands. Obviously, an assessment of non-target risks will affect bait station design. The entrance hole should be just large enough for the largest target rodent to enter (Lund 1988b). Howard (1987) noted that a station should be large enough for the target rodents to be comfortable while feeding in the box. This is important, not just to ensure that a visiting rodent eats plenty of bait, but also that it eats it in the box, not removing it. It is important that the interiors of bait stations are large enough for Norway rats to sit in their preferred position on their haunches to eat the bait (Roger Quy, pers. comm.).

Bohills et al. (1982) found that mice were more likely to consume baits inside small bait boxes than from large boxes or open trays. Eight bait station designs tested by Kaukeinen (1989) did not differ in mouse utilisation. In contrast, rats varied in their use of these stations. Volfova & Stejskal (2003) found that mice preferred the largest plastic box they tested. They suggested that the mice were opting for a 'bed and breakfast' strategy. Given a choice between two stations of the same size and shape, the mice chose one made of metal over one made of paper.

Bait stations can be made of wood, plastic or bamboo. If made of metal, Howard (1987) recommended that they have a plastic or some other liner. Lund (1988b) stated that wooden boxes are generally better accepted by rodents than metal ones (see section 3.3 of this report). Bohills et al. (1982) found that mice preferred cardboard boxes over those made of plastic. Cylinders were preferred over triangular, but not rectangular, boxes. A study by Ajao & Hurst (1992) found that mice took more food from cardboard stations than plastic stations of identical design. The baffles placed inside commercial bait stations to prevent children from reaching in may prevent group feeding by Norway rats (Roger Quy, pers. comm.).

Corrigan & Williams (1986) descibed a PVC piping T-station designed for the control of mice in poultry operations. Kaukeinen (1987) noted that simpler designs were, in general, used sooner and to a greater extent by Norway rats than more complex designs. Weihong et al. (1999) found that wire-mesh trap covers were more often entered by Norway rats than those made of clear plastic or galvanised iron. Erickson et al. (1990) devised an ingenious station design for ship rats that excludes deer mice and house mice. The station is set on a central pole that is easily climbed by the rats, but not the smaller rodents. This design could have potential for the exclusion of other ground-dwelling non-target species. A 20-L plastic bucket design with wooden ramps also makes use of the climbing behaviour of ship rats for bait access (Morris 2002). Innes (1995) commented that less bait would be wasted if bait stations for ship rats were off the ground away from dampness on Norfolk Island. In a macadamia nut orchard in Hawaii, baits placed in the trees were more often taken than those placed on the ground (Tobin et al. 1997). Ship rats appeared to enter yellow 'Nova Pipe' stations freely (Taylor 1984). McFadden (1984) used large plastic containers with 70-mm-diameter holes at either end. He found that kiore on Lady Alice Island entered these containers and fed on the bait, but Norway rats on the Noises Islands were reluctant to enter them (Moors 1985a). Spurr et al. (2005) found that captive Norway rats preferred to enter and eat bait from wooden boxes, yellow 'Nova Pipe' or black plastic boxes than larger white plastic containers.

3.9 OTHER FACTORS

3.9.1 Behavioural resistance

This concept covers the various behavioural characteristics that make it hard to control a rodent population that has had previous experience with poisoning. It was defined by Brunton et al. (1993) as 'behavioural traits which diminish a rat's tendency to eat palatable poison to which it otherwise has access to consume a lethal dose'. It includes learned behaviours like the development of bait shyness and poison avoidance through conditioned food aversion learning, and enhanced neophobia (Brunton et al. 1993). Beyond this, Humphries et al. (1992, 2000) have provided evidence that some populations of house mice in Birmingham show **inherited** behavioural cereal bait aversion. Such innate behaviours include neophobia and the ability to detect and recognise poison. Bait shyness can lead to enhanced neophobia. Rats that have survived poisoning operations are more neophobic than those never exposed to poison (Macdonald et al. 1999b). Greaves (1994) noted that 'avoidance behaviour, which could be heritable, can and does reduce the efficacy of rodenticides and may also enhance the effects of physiological resistance' (see below). Behavioural resistance can be exacerbated by the presence of ample alternative foods so that the rodents are not pressured to eat the poison baits, and by other ecological factors (Greaves et al. 1982b; Berdoy & Macdonald 1991; Quy et al. 1992; Macdonald et al. 1999b).

3.9.2 Bait shyness and poison aversion

There is a vast literature on the development of bait shyness and poison aversion in rodents. I do not attempt a comprehensive review of the knowledge here, but draw attention to some of the relevant literature. Early studies include that of Richter (1953) and Rozin (1968). Some of the key papers on the mechanisms of aversion learning include Nachman & Ashe (1973), Nachman & Jones (1974), Nachman & Hartley (1975) and Best & Batson (1977). A number of researchers, especially in India, have looked at the role of various food characteristics in the development of conditioned food aversions, and aversions to different poisons (e.g. Howard et al. 1968; Bhardwaj & Khan 1978; 1979a, b; 1980; Rao et al. 1980; Bhardwaj et al. 1984; Jain & Sarkar 1984; Naheed & Khan 1989, 1990; Singh & Saxena 1991; Zeinelabdin & Marsh 1991; Saxena & Mathur 1995; Saxena et al. 1995). Mice did not develop bait shyness to Quintox® (Twigg & Kay 1992). Thomas & Taylor (2002) noted that either bait shyness or poison resistance was apparent in the rat population on Ulva Island. Reviews of aversion learning are found in Domjan et al. (1977), Domjan (1980), Garcia et al. (1985), Lund (1988a), and Prakash (1988). Riley & Clark (1977) provide a bibliography on conditioned taste aversion literature. Cowan et al. (1994) recommended micro-encapsulation of poisons as a way of reducing the formation of learned aversions, by delaying the symptoms of poisoning.

3.9.3 Resistance

Rats can also be physiologically resistant to poisons (Thijssen 1995; Taylor et al. 1996). This is a genetic trait that has been selected for over generations of exposure to certain rodenticides (Greaves 1994; Kohn & Pelz 1999; Kohn et al. 2003). Warfarin-resistant mice, Norway rats and ship rats have been found in England and Europe (Boyle 1960; Greaves et al. 1976; Greaves 1994). Warfarin-resistant rats can be also resistant to difenacoum (Greaves et al. 1982a, b). The issues of bait avoidance and the efficacy of poisons against warfarin- and difenacoum-resistant rats were discussed by Quy et al. (1992). Cleghorn & Griffiths (2002) found no evidence of resistance to brodifacoum in mice from Mokoia Island.

3.9.4 Odours

Odours play an important role in feeding, social and reproductive behaviour of rodents (Bronson 1976; Hurst 1990a, b, c, 1993). They can affect rodent responses to traps, baits and bait stations (Becker 1977; Stoddart 1983). The odour of preferred foods and male mouse urine increased mouse investigatory behaviour (Pennycuik & Cowan 1990), while consumption of high-fat foods by mice was mediated by odour cues (Kinney & Antil 1996). Hurst (1987b) proposed that urine marks may provide cues or orientation and may enhance the rapid detection of novel objects. The odour left in traps by recent occupants affect mice in different ways, dependent on sex, age and reproductive status (Rowe 1970; Wuensch 1982; Drickamer 1995, 1997; Drickamer et al. 1992). In general, though, traps scented with the odour of mouse have achieved higher catch rates than clean traps (Temme 1980). Bait stations scented with the odour of sexually mature mice were visited more often by male mice than clean stations (Volfova & Stejskal 2003). As mentioned earlier, scent trails left by conspecifics lead rats to food sites (Galef & Buckley 1996), and urinal and faecal deposits at food sites can transmit food preferences amongst rats (Galef & Heiber 1976; Laland & Plotkin 1991; Valsecchi et al. 1993; Selvaraj & Archunan 2002b). The bioactivity of some of the components of rat urine has been described by Selvaraj & Archunan (2002a). Bull (1972) found that odours failed to influence feeding activity at preferred or non-preferred sites.

Sulphur-containing compounds found in rat gland extracts can attract ship rats, Norway rats and mice to baits. This response is concentration-dependant. Carbon disulphide is attractive at concentrations between 0.0001% and 0.005% but can be repellent to ship rats at 0.01% (Bean et al. 1988; Shumake & Hakim 2001; Shumake et al. 2002; Veer et al. 2002). However, Parshad (2002) reported improved zinc phosphide bait acceptance and trapping of ship rats with the addition of 1%. Dimethyl sulphide and dimethyl disulphide are similarly attractive to ship rats (Veer et al. 2002). Carbon disulphide can, however, evaporate rapidly off baits (Veitch 1995).

Mice in trials avoided human odours (Drickamer et al. 1992). Norway rats have also been found to be responsive to human odour (Taylor et al. 1974a). Naive rats avoided the odours of predators, but predator-experienced ship rats and Norway rats did not (Bramley 1999), and rats in this study did not avoid feeding stations tainted with synthetic predator odours.

3.9.5 Repellents

While a full search of the literature on repellents is outside the scope of this review, the following information is relevant. Aniseed is thought to be repellent to Norway rats (Barnett & Spencer 1953b). Capsacin and, to a lesser extent, denatonium, have deterred rats from gnawing (Shumake et al. 2000). Bitrex® has been commonly added to baits to produce a bitter taste to humans. Kaukeinen & Buckle (1992) found that wild commensal Norway rats and mice accepted Bitrex® at 10 ppm in Talon® and Klerat®. However, kiore on Little Barrier Island chose Bitrex-free baits over those containing Bitrex (Veitch 2002c), and at least two eradication attempts using Bitrex have failed (I. McFadden, pers. comm. in McClelland 2002a). Compounds added to baits as bird repellents can reduce palatability, although cinnanamide and tannic acid were acceptable to laboratory-bred Norway rats (Spurr et al. 2001), as were combinations of cinnamon/Avex® (B.K. Clapperton et al. unpubl. data). Combinations of d-pulegone/Avex® were less palatable to both rat species (B.K. Clapperton et al., unpubl. data). Fungicides can reduce bait palatability, but Smythe (1976) found that para-nitrophenol can be acceptable (to unspecified rodents) at an appropriate level.

Ultrasonic sound was once heralded as a promising rat repellent system (Pinel 1972, 1974). High-intensity ultrasonic sound elicits a flight response, and rats rapidly learn to avoid sources of noxious sound. However, while there are ultrasonic products available for domestic use, this system is not used in large-scale rodent control. There is no scientific evidence that ultrasonic devices are effective, presumably because of problems with habituation and practicalities of field application.

3.9.6 Grooming

One behavioural trait of mice that has been taken advantage of in pest control is grooming. Poisonous dust laid on mouse runways or in holes collects on the animals and is ingested during grooming (Rowe 1973).

3.9.7 Responses to traps

The role of residual odours on trap efficacy has been covered above (see section 3.9.4). Different species of rodents are not equally trappable—Norway rats are comparatively difficult to trap (Taylor et al. 1974b). Individual rodents are also not equally trappable, because of a combination of intrinsic factors and experience (Crowcroft & Jeffers 1961; Hurst & Berreen 1985; Khan 1992). Individual mice, especially females, can be either trap-prone or trap-shy. Males and females can show different levels of trappability, as can adults and subadults (Drickamer et al. 1999). Extrinsic factors (e.g. humidity, temperature and vegetation cover) can change the relative trappability of mice (Drickamer 1999; Davis et al 2003).

3.9.8 Practical matters

Smythe (1976) and Timm & Salmon (1988) noted that baits and bait materials are often stored with other chemicals. They can thus become tainted and possibly unattractive to rodents. Morgan et al. (1996) showed that mixed storage of Talon, RS5 and fishmeal baits reduced consumption of the Talon baits by mice, but did not affect ship rat consumption of any of the baits. Smythe (1976) also commented that baiting programmes are often ineffective because of poor-quality bait materials, stating that rodents do not like grain that is rodent-contaminated, dirty, old, stale or musty. Asran (1993a) found that mice preferred fresh baits to old baits that had been infested with insects. However, Roger Quy (pers. comm.) was surprised at the wide variety of foods eaten by wild rodents, including some disgusting-looking or smelling foods; and Twigg et al. (2002) found that ZP wheat bait that had been in dry storage for 3.5 years was more effective at killing mice than fresh bait. This was attributed to the lack of the typical strong zinc phosphide smell in the aged bait. Likewise, Reserpine baits that had been in storage for 1–9 months were as palatable as fresh baits to mice (Meehan 1980).

Feeding by non-target species can also influence bait take. Jacob et al. (2002) found that in bait stations designed for mice in Australia, pellet baits were removed more by ants than by mice.

4. Discussion and conclusions

There have been few comparative studies of behavioural responses of pest rodents to control devices. There is ample literature on rodent behaviour in regards to medical research and psychology. Research related to pest rodents was focused on specific pest species.

There is much information available on attractants, but there are no magical attractants for all rodents. There is wide variability between species, between populations and between individuals in taste preferences. As a general rule, familiar foods with enhanced levels of sugar, fat or oil and/or salt are likely to make acceptable baits. Various formulations are available, often containing wax to improve environmental longevity. Soft baits are, in general, more preferred, but can lead to more wastage. Bait size should be suitable for the feeding habits of the target rodent.

Levels of neophobia vary amongst the four rodent species present in New Zealand. Little is known about variation in neophobia over time, or with population density or food supplies. Cowan (1977a) made the important point that neophobia may have arisen as a result of selection during the development of the commensal habitat. He proposed that isolated populations of rats, living now in the absence of such selection, as on islands, might show little new-object reaction. The significance of this for island re-invasion is that while rat populations long established on islands may not show neophobia and thus may be easy to eradicate, new invaders from commensal populations may be a lot more wary of baits and bait stations. Alternatively, the difficulties eradicating rats recently arrived on islands may be more due to low density reducing competition and therefore less pressure for rats to feed on less-preferred foods (i.e. baits).

The implication from the different feeding behaviours and neophobic responses between rats and mice is that while rat bait stations need to be kept in one place for many nights to overcome neophobia; for mice, a better strategy is to move the bait stations to encourage exploration. Movement patterns of the different species indicate that different bait station spacings may be needed, depending upon the target species. The effectiveness of bait stations above ground level should be assessed.

The movements of wild rats are largely the result of the two inherent (but opposing) tendencies to explore and to avoid (Barnett 1956). The complex interaction between different behavioural responses to food and bait stations by various rats was well summed up by Shepherd & Inglis (1987), discussing commensal Norway rats: 'We have two possible answers to the question of "Which rats do not eat the poison when a treatment fails?" The first is that it is the subordinates, who have been excluded from the “delicious” rat bait by the dominant animals. In this case a little perseverance should do the trick; once the dominants have been eliminated, the subordinates will eat the bait in their turn. The second answer is that the survivors are the dominant animals who are most neophobic and have not been tempted away from their familiar diet. In this case simple perseverance with the treatment is unlikely to succeed’.

Territoriality of rodents varies from species to species and with ecological conditions. The ability of individuals in a population to access baits or bait stations could vary with population density, or food supply. Placing of control devices should thus be determined with reference to the socio-ecological characteristics of the population in question.

Issues such as bait shyness and other forms of behavioural resistance obviously play a major role in the success of ongoing rodent control operations, and there is substantial literature on these subjects. Their application to one-off operations on islands, however, is limited. They have application to re-invasion by rodents. Knowledge of the history of control of populations from which re-invaders come would allow an assessment of the significance of these behavioural traits to eradication efforts.

The interactions between behaviour of the rodents and ecological factors will determine the success of poison baiting. Rowe et al. (1974) concisely stated a common theme in the literature: ‘House-mice are most difficult to control in places where food and cover coincide and are extensive’. This message is being heeded. Miller & Miller (1995) noted that successful island rodent eradication programmes have been timed to coincide with low population numbers and the cessation of breeding, and a limited food supply. According to Roger Quy (pers. comm.): ‘The key feature determining the degree of success during control operations is the stability of the habitat and thus the likelihood that individuals will actively or inadvertently avoid traps, baits or bait containers’. Gray & Hurst (1997) also stress the impact of environmental factors on the social behaviour and, thus, spatial dispersion of mice.

No matter what behavioural challenges rodents provide, with adequate resources, it is possible to eradicate them, at least from restricted areas. As Elton (1940) remarked: ‘One reason why even very efficiently organised destruction of rodents does not extinguish them is really the same reason why a predatory animal does not wipe out its prey: when rodents become scarce pursuit is no longer worth the expenditure of energy needed to make a kill’. But as Rowe (1973) concluded: ‘With the mouse just such pursuit is essential if populations are to be eradicated’.

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Appendix 1

COMBINATIONS OF WORDS USED IN THE STNEASY SEARCHES

In some cases the words were searched for only in the title. The words were spelt using both English and American spellings.

SEARCH	FIRST TERMS	AND SECOND TERMS	AND THIRD TERMS
1	mouse OR mice OR Mus	bait OR food	preference
2	mouse OR mice OR Mus	bait OR lure	palatability OR attractiveness
3	mouse OR mice OR Mus OR rat OR rattus OR rodent	bait OR food OR lure	neophobia OR investigatory
4	rat OR Rattus OR rodent OR attractiveness	preference OR palatability	bait OR lure
5	mouse OR mice OR Mus rat OR rattus OR rodent	bait station OR bait container	
6	mouse OR Mus	home range OR territory OR territorial	
7	mouse OR Mus OR rat OR Rattus	poison OR toxin OR bait OR rodenticide	aversion OR shyness
8	mouse OR rodent OR Mus	eradication	
9	mouse OR Mus	social organisation OR spacing behaviour	
10	mouse OR mice OR Mus OR rat OR Rattus	taste OR flavour OR food	preference OR choice
11	mouse OR mice OR Mus OR rat OR Rattus	meal OR bait OR food	size OR quantity OR amount
12	mouse OR mice OR Mus OR rat OR Rattus OR rodent	eat OR eating OR feeding OR foraging	behaviour
13	rat OR Rattus OR home range OR territorial	social organisation OR spacing behaviour	
14	mouse OR Mus OR rat OR Rattus OR rodent	invasion OR invasive	behaviour
15	mouse OR Mus OR rat OR Rattus OR rodent	invasion OR invasive AND island	behaviour
16	mouse OR Mus OR rat OR Rattus OR mice	response OR bait OR baiting OR behaviour	trap OR trapping
17	mouse OR Mus OR rat OR Rattus OR mice	preference OR behaviour OR sight OR vision OR choice	colour
18	mouse OR Mus OR rat OR Rattus OR mice OR rodent	detect OR detection NOT cell OR gene	habitat OR island OR environment
19	mouse OR Mus OR rat OR Rattus OR mice OR rodent	pest OR control OR repel OR averse OR avoid	sound OR sonic OR ultra OR noise
20	mouse OR Mus OR rat OR Rattus OR mice OR rodent	gnaw	

Appendix 2

FURTHER BIBLIOGRAPHY

The following references are to papers that were found during the preparation of this review. They are not referred to in the text because either they do not have specific information on rodent behaviour, or it was not possible to obtain copies in time to assess their information value. They may contain useful information on such matters as responses of rodents to various poison formulations, and the success of rodent control operations.

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