The role of scavenging in the spread of bovine tuberculosis in free-living ferret populations in New Zealand

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Frontispiece

A wild-caught female ferret scavenging a male ferret carcass.

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Ferrets (*Mustela furo*) exhibit high prevalences of bovine tuberculosis (Tb) in some areas of New Zealand. Whether the disease will persist in ferret populations in the absence of external sources of Tb infection is unknown and subject to extensive debate. The pathology of the disease in free-living ferrets suggests that in this species infection arises primarily through ingestion of tuberculous carrion. This thesis investigated the scavenging behaviour of ferrets with a view to determining their importance as a wildlife reservoir for the spread of bovine tuberculosis in New Zealand.

A field trial was undertaken on farmland in North Canterbury, New Zealand, to assess the relative contribution that scavenging of brushtail possum, ferret and hedgehog carcasses is likely to make to the observed tuberculosis prevalence in ferrets. A total of 108 carcasses were laid out in the field for 4-week periods in various seasons. Ferrets visited 35 percent of all the carcasses, with 16 percent of these visits resulting in scavenging. Ferrets were more than twice as likely to visit ferret carcasses as carcasses of other species ($p<0.001$), but did not prefer to scavenge them ($p>0.05$). The number of

visits by ferrets declined in winter, but the scavenging rate per visit did not vary seasonally.

In a second trial, an outdoor enclosure and time-lapse video equipment were used to investigate the feeding behaviour of 10 adult wild-caught ferrets in response to ferret, hedgehog and possum carcasses. Ferrets fed more on possum carcasses than on the other carcass types, whereas there was no significant difference in the number of feeding events on hedgehog and ferret carcasses. On at least 15 of 22 occasions, ferrets ate parts of carcasses that would have put them at high risk of exposure to *Mycobacterium bovis*, had the carcass been infected with Tb. Even when they were not actively feeding, ferrets often had considerable physical contact with ferret carcasses. Few differences in feeding behaviour were observed between sexes, although male ferrets tended to eat more of a carcass than did females. Ferrets fed more frequently during winter but these feeds tended to be shorter in duration.

The implications of the observed scavenging behaviour for Tb transmission are discussed. Scavenging rates in North Canterbury were markedly lower than those observed by other researchers in Otago. It seems unlikely that scavenging alone is capable of maintaining Tb within North Canterbury ferret populations, although in other areas that have higher ferret densities and scavenging rates this remains a possibility.

Keywords: ferret; *Mustela furo*; bovine tuberculosis; *Mycobacterium bovis*; scavenging; maintenance host; reservoir host.

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Chapter 1
INTRODUCTION

1.1 General introduction

Bovine tuberculosis (Tb; *Mycobacterium bovis*) is an exotic disease in New Zealand, most likely brought to this country with domestic cattle (*Bos taurus*) during European colonisation in the 19th century. The natural host of the disease is cattle but it is also highly virulent to humans and the host range in mammals appears unlimited (O'Reilly & Daborn 1995). Bovine tuberculosis is recognised as a serious problem because of the potential health risk it poses to humans through contaminated beef and dairy products, reduced farm productivity, and the potential threat to the country's dairy and meat exports.

Official testing for Tb in New Zealand cattle began in 1945 and had become compulsory in all dairy and beef herds by 1970. These 'test and slaughter' schemes were successful at controlling bovine tuberculosis in many parts of New Zealand but proved less successful in certain areas where the disease continued to reappear in herds from which it had been previously eradicated. Surveys of wildlife in these areas identified the brushtail possum (*Trichosurus vulpecula*) as a potential source of Tb, and by the mid 1970s further epidemiological studies had implicated possums as the major vector for tuberculosis in cattle in those areas (O'Neil & Pharo 1995). Subsequent lethal control of possums in such areas often resulted in a reduction in the number of cattle reactors, providing evidence of a causal link between infected possums and Tb in cattle (Caley *et al.* 1999). The role of possums as a reservoir of Tb is now well-accepted, but numerous other wild animals in New Zealand have also been found infected with the disease and the possibility that some of these may also be reservoirs has remained contentious. In some areas of New Zealand where possum numbers were very low,

there have been ongoing problems of Tb re-infection in stock, and it has been suggested that wild ferrets (*Mustela furo*) may have been responsible for this (Walker *et al.* 1993).

Following their introduction to New Zealand in an attempt to control pest populations of rabbits (*Oryctolagus cuniculus*), ferrets initially had legal protection. By the start of the 20th century they had become regarded as pests themselves and their legal protection was removed (Lavers & Clapperton 1990). There is still a general belief that ferrets are a useful tool in the control of rabbits on agricultural and horticultural farmland, but this benefit is potentially outweighed by the high prevalence of bovine tuberculosis in their populations, their ability to disperse large distances and the damage they cause to native wildlife. The first ferret control operations began in the 1930s primarily due to concerns over predation of native wildlife (Lavers & Clapperton 1990), but are now widely carried out in Tb endemic areas and buffer zones adjacent to these areas by regional councils, research organisations and private pest control agencies.

Ferrets are well known to be highly susceptible to bovine tuberculosis (Dunkin *et al.* 1929), and over the past two decades surveys of ferret populations have revealed prevalences of Tb often exceeding 20% (e.g., Ragg *et al.* 1995b, Caley 1998). It has also been proposed that the prevalence of sub-clinical infections may be substantially higher (Lugton *et al.* 1997a).

Studies of the pathology of Tb in ferrets report fewer lung lesions than are typically seen in possums, suggesting that aerosol transmission of the disease within ferret populations is unlikely (Lugton *et al.* 1997b). The majority of lesions in ferrets are found in lymph nodes associated with the alimentary tract, so it is generally accepted that infections in ferrets most likely arise through the scavenging of tuberculous carrion,

and that intraspecific spread of Tb is uncommon. However, little is known about the scavenging and encounter rates with tuberculous carrion other than the work by Ragg (1997) in an area with high densities of ferrets. It has been suggested that scavenging of other wildlife carrion may not account for the high prevalences of Tb observed in some areas. Den sharing and sequential den usage occurs in areas of high ferret density (Ragg 1998b) and it is possible that these behaviours contribute to the high disease prevalences observed in such areas.

To date, there has been no conclusive evidence to suggest that Tb can persist in a ferret population in complete absence of contact with infected possums. The mechanisms by which ferrets may maintain Tb within their populations are unclear and subject to extensive debate. Thus the status of the ferret as a true reservoir host remains in doubt. Although there is no doubt that the possum is the most significant wildlife vector for Tb nationally, it is possible that, in some localised areas, ferrets may also play a significant role (Morris and Pfeiffer 1995). Consequently, there is an urgent need to clarify whether ferrets might be a reservoir host for Tb in some parts of New Zealand so that sound decisions may be made about ferret management (Caley *et al.* 1997). This is particularly so because ferret control is expensive (Moller *et al.* 1992) and such expenditure may not be justifiable if ferrets prove not to be maintenance hosts of the disease.

1.2 Objectives

This project aimed to gather information on ferret scavenging behaviour relevant to determining the importance of ferrets as a wildlife reservoir for the spread of bovine tuberculosis in New Zealand.

The specific objectives were:

1. To estimate the encounter rates of ferrets with carcasses in the wild.
2. To estimate the frequency of scavenging on carcasses of different types in the wild and, from this, to determine whether ferrets prefer to scavenge on certain carcass types.
3. To investigate sexual differences in feeding behaviour relevant to the spread of Tb.

1.2.1 Structure of the thesis

This thesis begins by discussing historical and ongoing research on wildlife tuberculosis in New Zealand and contrasts the problem in this country with similar problems faced overseas. Chapters three and four deal with a field trial and a pen trial undertaken as part of the research for this thesis, and the last chapter provides a general discussion of findings.

Note that any references to Tb or tuberculosis in this thesis describe infections of bovine tuberculosis caused by *Mycobacterium bovis* bacteria, unless otherwise stated.

Chapter 2
LITERATURE REVIEW

2.1 Introduction

It is now well recognised that New Zealand feral and wild animals are the main source of Tb re-infection of domestic stock. Bovine Tb has been found in at least 13 species of feral or wild animal in New Zealand, including possums, red deer (*Cervus elaphus*, de Lisle & Havill 1985), sika deer (*Cervus nippon*, de Lisle & Havill 1985), cattle, pigs (*Sus scrofa,* McLaughlin 1989), cats (*Felis catus*, de Lisle *et al.* 1990), ferrets, stoats (*Mustela erminea*, Allen 1991), goats (*Capra hircus*, Allen 1987), sheep (*Ovis aries*, Davidson *et al.* 1981), rabbits (*Gill & Jackson, 1993*), hares (*Lepus europaeus occidentalis,* Cooke *et al.* 1993) and hedgehogs (*Erinaceus europaeus,* Lugton *et al.* 1995a). However, few of these species are considered important in the maintenance of Tb or its management (Morris & Pfeiffer 1995).

The importance of any wildlife source of *M. bovis* is related to the prevalence of the disease in that species, the abundance of the species and the degree to which there is transmission of Tb within and from that species. It is important to consider the various kinds of disease host that may occur, depending on the epidemiology of the disease in different wildlife species.

Direct transmission from a pest species to livestock is not necessary for the species to be considered an important source of infection provided there is transmission to another species, which in turn, is capable of transmission to livestock. A species that is capable of transmitting a disease to another species is commonly referred to as a 'vector' of the disease. It should be noted that, although this term is used throughout this thesis and much wildlife Tb literature in New Zealand, the strict usage relates to "invertebrate

animals – usually arthropods – that transmit infectious agents to vertebrates" (Thrusfield, 1997), and so does not correctly describe the role of wildlife Tb hosts in New Zealand. A more correct term would be either a "vertebrate propagative host", or a "link host", which is simply defined as "a host that forms a link between other host species" (Thrusfield, 1997). In addition, the term "prevalence" is widely used both throughout this thesis and wildlife Tb literature in New Zealand. The common usage refers to the degree to which infection occurs within a population (specifically the percentage of infected individuals), and does not necessarily imply that the disease is dominant or widespread.

Host species are categorised according to the way in which the species, or more importantly, a specific population of that species, is involved with the flow of a disease through an ecosystem. The most important category from a Tb management perspective is the "reservoir host". A reservoir host is defined as "one in which an infectious agent normally lives and multiplies, and therefore is a common source of infection to other animals" (Thrusfield, 1997). This requires that there is intraspecific transmission of the disease at a rate that allows it to persist in the host species without any additional interspecific source of infection. A term often used interchangeably with a reservoir host in the literature and this thesis is a "maintenance host", which is defined as "an animal that maintains an infection in the latter's endemic area" (Thrusfield, 1997). This definition also requires that the disease can persist in the absence of additional sources of Tb but does not necessarily imply that the host species is a common source of infection for other animals. It is unlikely, however, that we would find a vertebrate host species in which Tb was present at levels sufficient to maintain the disease, yet these levels not being high enough to provide a common source of infection to other species.

Therefore, the term "reservoir host" is probably more appropriate than "maintenance host" when classifying the host status of a species.

Species that may be infected with the disease and thereafter contribute intraspecific transmission of the disease, but not at a rate sufficient for it to persist in the absence of additional interspecific sources have been termed "spillover hosts". Infection in a spillover host will disappear progressively if the disease is reduced or eliminated in the species that is the source of infection (Morris and Pfeiffer 1995). Spillover hosts can be a common source of infection to other wildlife, but are symptomatic of infection in other species, and therefore should not be the focus of attempts to manage wildlife Tb.

An "end host", also known as an accidental or incidental host, is described as "one that does not usually transmit an infectious agent to other animals" (Thrusfield, 1997). Populations categorised as such have no value for management because disease in this group is entirely symptomatic of infection in other reservoir species.

When funding is short, the distinction between spillover hosts and reservoir hosts can be critical in the decision whether a host species is a candidate for control. The main difficulty in determining the host status of a species lies in the fact that the disease must be capable of persisting through intraspecific mechanisms alone for the host to be considered a reservoir host, yet it is often difficult to remove all interspecific sources of infection to test whether this is so. Field attempts to classify species, therefore, are usually carried out with a combination of point prevalence studies, DNA fingerprinting and population control measures, with no one of these approaches able to provide a definitive host classification on its own. A variety of such field trials are described in Chapter 2.

Ultimately, long-term population control measures are the only way to obtain compelling evidence from the field that a host status classification is correct but, for this to occur, substantial time, effort and money must be invested. Retrospective confirmation is of little use to a manager trying to establish a set of well-targeted management policies. Shorter-term inferences on the host status of species are therefore made by seeking data from the field in combination with a variety of modelling techniques and a sound knowledge of the ecology of all the species involved. Models can be constructed to predict patterns of disease occurrence and what is likely to occur if various control strategies are adopted, and their predictions are tested against further field data. Most ferret models in New Zealand have primarily investigated the population dynamics of the ferret with emphasis on optimising future control efforts, such as Roberts *et al.* (1999), Barlow & Norbury (2001) and another by Barlow & Kean (1996) who modelled ferret/rabbit interactions.

Caley (2000) used three modelling approaches to directly address the question whether ferrets may be maintenance hosts for Tb; model selection based on age-prevalence data, statistical regression models examining relationships between ferret and possum Tb and abundance, and process-based modelling to estimate the threshold abundance of ferrets required for Tb establishment. The model selection approach identified oral infection as being adequate alone to explain the observed age-specific prevalence of Tb. The regression model revealed a positive association between the prevalence of Tb in ferrets and the abundance of possums, and preliminary results from the process based modelling indicated that the minimum threshold density at which Tb infection can establish in a ferret population is 5.3 ferrets km^{-2}. Caley (2000) suggested that it may therefore be possible in some locations that ferrets maintain Tb, but that in most areas this is unlikely.

Livingstone (1996) proposed a simple model to determine the minimum number of ferrets required to feed on each tuberculous carcass available to maintain observed levels of Tb in a ferret population. In Livingstone's example, 1.2 ferrets were required to feed on each available tuberculous carcass to maintain a 15% prevalence in the ferret population, which he noted appears plausible. Livingstone posed the question whether prevalences as high as 60%, found in some studies, could also be equally explained by this mechanism (See chapter 5).

2.2 Bovine tuberculosis in wildlife

2.2.1 Bovine tuberculosis in overseas wildlife

There are several examples of wildlife Tb reservoirs in other countries that have some relevance to the problems New Zealand faces in trying to determine the host status of its Tb infected wildlife. The following sections outline notable similarities and differences of three of these international species to those in New Zealand, and the current consensus of opinion on their host status.

2.2.1.1 Tuberculosis in badgers in the United Kingdom

Bovine tuberculosis was first identified in badgers (*Meles meles*) in the United Kingdom in 1971 (Muirhead *et al.* 1974). Subsequent studies revealed that *M. bovis* infection was endemic in the badger populations in some areas and that badgers were able to spread the disease to livestock (Nolan & Wilesmith 1994, Eves 1999). Badgers have been implicated in approximately 90% of cases of tuberculosis in cattle in South

West England (Clifton-Hadley & Cheeseman, 1995). The overall prevalence of Tb infection in badgers appears to be partially cyclic, fluctuating from 2 – 12% (Morris *et al.* 1994).

It is thought that badger populations first became infected with *M. bovis* from cattle herds when the disease was more common (O'Conner & O'Malley 1989), or from infected chamois (*Rupicarpa tragus*) or roe deer (*Capreolus capreolus*) (Gallagher & Clifton-Hadley 2000). Once some badgers had become infected, the disease would have spread readily to other badgers because they live in social groups of about 6-10 animals, sharing underground setts (O'Conner & O'Malley 1989).

The favoured habitats for badgers are hilly areas with sandy soil, interspersed with permanent pasture and deciduous woodlands, which may support densities as high as 20 km^{-2}, although 5-8 individuals km^{-2} is considered more typical (Anderson & Trewhella 1985). The density and territory size of badgers is largely determined by the availability of their main food source, earthworms (Anderson & Trewhella 1985).

Badger social groups defend their territories from other groups but usually do not move into other territories. Bite wounds caused during territorial defence are a likely mechanism for the spread of *M. bovis* between social groups (Anderson & Trewhella 1985). Badgers may have highly contaminated mouths resulting from pulmonary infection (Gallagher and Clifton-Hadley, 2000) making their bites highly infective. Gallagher & Nelson (1979) estimated 14% of Tb infection in badgers was due to biting. The frequency of bite wounding is likely to be density dependent with fewer wounds in low-density populations and those populations where home ranges have become stable for long periods of time (Gallagher and Clifton-Hadley, 2000).

The most common site of infection in badgers is the lungs, with 50% of badgers exhibiting pulmonary lesions, although lymph nodes accounted for approximately 40% of lesion sites (Gallagher and Clifton-Hadley, 2000). Tb from pulmonary infection appears to progress relatively slowly. The mean survival time of badgers with Tb resulting from bite wounds was much shorter (117 days) than those with respiratory disease (491 days) (Clifton-Hadley *et al.* 1993). This means the infectious period of badgers with pulmonary infection is likely to be longer than those with infection caused by bite wounds. Badgers infected both mildly and severely with Tb have several potential routes of bacillus excretion (Gavier-Widen *et al.* 2001).

Badgers appear to have a containment phase early in the pathogenesis of Tb in which the primary foci of infection are isolated in scar tissue resulting in a lengthy latency period, possibly measured in years (Gallagher and Clifton-Hadley, 2000). Although the disease may never progress further in some badgers, stress resulting from environmental or social pressures is likely to reactivate the disease in others. This situation is similar to that in humans where most primary infections resolve completely but a small number become active many years later (Gallagher and Clifton-Hadley, 2000).

Several surveys have shown higher infection rates in male badgers than in females (e.g. Gallagher and Nelson 1979, Cheeseman *et al.* 1988), most likely because of behavioural differences in the sexes, territorial defence and home range sizes.

Direct transmission from badgers to cattle is considered unlikely because they usually avoid each other, keeping 10-15 metres apart (Benham and Broom 1989). Cattle generally avoid feeding on areas of pasture soiled with badger faeces and urine, but a

few lower ranked individuals may not avoid them, particularly when overgrazing occurs (Gallagher and Clifton-Hadley, 2000). It is also possible cattle become infected from badger products during investigative behaviour.

Gallagher and Clifton-Hadley (2000) found that on unshaded pasture in winter more than 99% of *M. bovis* bacteria from badger urine died within one week, although small numbers of viable bacteria of "uncertain epidemiological significance" could still be found after 5 weeks. Bronchial pus samples were slightly more resilient, with small numbers still viable after 10 weeks. Faecal bacteria died at a slower rate with only 88% dying in the first 2 weeks and 99.7% by four weeks. In summer, no bacteria were found after 3 days in urine, 1 week in bronchial pus and 2 weeks in faeces.

Wilesmith (1983) demonstrated a direct association between sett density and occurrences of Tb in cattle. Cheeseman *et al.* (1989) confirmed that areas known to have high sett densities also had the highest prevalences of Tb in badgers, although, at the individual group level, there was no such relationship. These factors suggest Tb maintenance in the badger populations.

High rates of pulmonary disease and bite wounding suggest that horizontal infection is the main pathway of infection in badgers. Respiratory infections are thought to indicate intraspecific transmission and are a common feature of maintenance hosts (Morris & Pfeiffer 1994). Badgers are thus considered maintenance hosts for *M. bovis* (Gallagher and Clifton-Hadley 2000) and the main wildlife vector of Tb both in the United Kingdom (Dunnet *et al.* 1986) and in Ireland (O'Connor & O'Maley, 1989).

2.2.1.2 Tuberculosis in buffalo in the Kruger National Park, South Africa

Bovine tuberculosis was first introduced to southern Africa with English and Dutch cattle herds in the 19th century (Tanner & Michel 1999). The first case of Tb in cattle was reported in 1880 but it was not found in wildlife until 1928 when it was discovered in greater kudu (*Tragelaphus strepsiceros*) (Paine & Martinaglia 1928).

An extensive survey of buffalo (*Syncerus caffer*) by Basson *et al.* (1970) and routine meat inspection of over 8000 buffalo carcasses between 1970 and 1980 failed to detect tuberculosis but, in 1990, a cull of 57 buffalo revealed a prevalence of 15% (Bengis *et al.* 1996) suggesting a rapid increase in the prevalence of the disease since the earlier surveys. By 1996 prevalences as high as 70% were reported in some buffalo herds (Bengis *et al.* 1996), and by 1999 prevalences as high as 90% had been recorded (Tanner & Michel 1999).

Tuberculosis has now become widespread through the southern region of the park and is rapidly spreading northwards (Tanner & Michel 1999). Since 1995, Tb has been identified in at least five other local species of wildlife, mostly carnivores. Concern has been noted that spillover of the disease into other species may result in maintenance of the disease in these populations, especially lions (*Panthera leo*), which are capable of being maintenance hosts in zoo situations (Keet *et al.* 1996). However, there is no evidence to suggest free-living lions are necessarily able to become maintenance hosts for bovine tuberculosis.

Veterinary reports show that outbreaks of tuberculosis in farmed cattle in the area occurred in the early 1960s, in 1982, 1983 and 1984. Bengis *et al.* (1996) reported that close contact between cattle and buffalo is likely to have occurred because there were

also outbreaks of Corridor disease (buffalo-associated theileriosis) in cattle during these periods. It is likely that transmission of Tb to cattle occurred during one or more of these periods. This suggests Tb may have been present at low levels in the buffalo populations for between 6 and 40 years before it was detected in 1990. DNA fingerprinting has subsequently indicated that the source of *M. bovis* infection in buffalo is likely to have come from the cattle outbreak during the 1960s (Tanner & Michel 1999). It is therefore likely that the disease has been maintained in the buffalo for many years at low levels and has only recently reached epidemic levels.

2.2.1.3 Tuberculosis in white-tailed deer in Michigan, USA

Approximately 50 years ago, Michigan State had the highest cattle Tb reactor rates in the United States and accounted for 30% of the national reactor total (Frye 1995). Following the initiation of a bovine tuberculosis eradication programme in 1979, Michigan became classified as Tb free. However, in 1994 a free-ranging male white-tailed deer (*Odocoileus virginianus*) on the North Eastern Michigan Peninsula was found infected with *M. bovis* (Schmitt *et al.* 1997). Shortly thereafter, the US Department of Agriculture tested all livestock within a 16 km radius of the infected individual and 14 deer within an 8 km radius but found no additional infection. However, a more comprehensive survey of wild white-tailed deer by Schmitt *et al.* (1997) revealed an overall prevalence of 3.5% in the local population, 18 years after bovine Tb had officially been eradicated from the state. The presence of *M. bovis* infected wild deer suggests that Tb was either maintained unnoticed within the wild deer population for at least 18 years in the absence of infected livestock, or that a relatively recent re-infection occurred from another wildlife species. In the absence of any other known wildlife sources of infection, it has generally been assumed that wild

deer are maintaining Tb at low levels. A state-wide survey of free-ranging deer has shown that deer elsewhere in Michigan are free of Tb (Schmitt *et al.* 1997). McCarthy & Miller (1998) estimated Tb was introduced into the white-tailed deer population about 1955 and that, if the initial introduction were more recent, transmission rates necessary to achieve the observed prevalence seen in 1995 would be required to be substantially higher than their estimates suggested. However, it is not known how long the measured 3.5% prevalence has been present and undetected in the deer population and no data are available on transmission rates between the free-living white-tailed deer in this region.

Supplemental feeding of deer by Michigan hunters is common for periods of around 4-5 months during winter (USDA 1999). The natural density of white-tailed deer is estimated to be approximately 9-10 km^{-2} in Michigan, but densities of 19-23 km^{-2} have been maintained for many years through supplemental feeding and baiting by hunters and the general public (Schmitt *et al.* 1997). At some supplemental feeding areas several hundred deer have been observed feeding. It is therefore considered that supplemental feeding, and the consequent congregation of unnaturally high numbers of deer, are likely to be responsible for the spread of *M. bovis* in the state (Schmitt *et al.* 1997). A voluntary ban on supplemental feeding was put in place in 1996 with the aim of reducing the numbers of deer congregating at feeding sites, and therefore the chances of disease transmission.

Radio-tracking of 95 white-tailed deer by Van Deelen *et al.* (1997) showed that natural mortality due to food pressure accounted for approximately 10% of annual deaths, predation accounted for approximately 20% and hunting for approximately 45%, with 25% of mortality due to other or unknown causes. Stress caused by food shortage may

activate latent Tb or suppress the immune system of an individual making it more prone to infection by *M. bovis*, so it is possible that supplemental feeding reduces the natural prevalence of Tb in white-tailed deer to a certain extent. However, the effect of increasing transmission rates between deer due to congregation probably outweighs the beneficial effects of supplemental feeding. It is possible that supplemental feeding may have helped conceal a long-term, low-level maintenance of Tb by reducing stress-induced gross infection.

The field surveys by Schmitt *et al.* (1997) suggested that generalised infection was rare. Lesions were most common in the medial retropharyngeal lymph nodes (86% of primary foci) suggesting uptake of *M. bovis* is primarily via the oral cavity. Pulmonary infection was found in 6 of 15 (40%) infected deer, which suggests aerosol infection might be an important mechanism for bacterial excretion and transmission.

Male deer exhibit non-significantly higher rates of infection (9 of 198 males infected versus 3 of 132 females infected). No infected animals were found under 1.5 years of age, although only 12 infected animals were in this sample. The average and median ages tended to be lower for males infected with Tb than for females, which suggests that males experience a higher force of infection.

A management strategy proposed by Schmitt *et al.* (1997) involved surveying wildlife populations, testing livestock, reducing supplemental feeding of deer, reducing deer density and educating the public. To date, surveys of wildlife by Bruning-Fann *et al.* (2000) have isolated *M. bovis* from several carnivore species from the area including six coyotes (*Canis latrans*), two raccoons (*Procyon lotor*), one red fox (*Vulpes vulpes*), one black bear (*Ursus americanus*) and one bobcat (*Felis rufus*). Infections in these species

are thought to result from feeding on *M. bovis* infected deer. There is no known mechanism by which Tb may spread from carnivores back to deer, so infection in these carnivore species is assumed to be spillover in nature.

McCarthy & Miller (1998) estimated an incubation period of 2 years in their model based on the lesion size and distribution described by Schmitt *et al.* (1997), and noted that the effects of any management on the prevalence of Tb would therefore take several years to become apparent. The McCarthy & Miller model predicted runaway Tb infection rising from current levels to between approximately 15 and 24% over the next 25 years and that neither lowered deer survival nor reduced transmission rates would completely eliminate disease from deer populations. However, if Tb has been present in the deer populations for longer than the 40 years estimated, the rate of increase predicted by the model will be slower and the runaway effect less evident. Field data gathered since the model was constructed have not shown the increase in prevalence predicted by the model, but data are so far limited to only 4 years. A recent increase in the Tb reactor rates of cattle herds may suggest an increasing prevalence of Tb in wild deer in the area (USDA 1999).

2.2.2 Bovine tuberculosis in wildlife on New Zealand farmland

Most species of land mammal are susceptible to infection by *M. bovis*, but primary concern is over those wildlife species that are likely to cause infection of livestock. Species such as possums, ferrets and hedgehogs, which live on or near farmland, are most likely to be problematic in this respect. Other species such as deer and pigs may also play a role, but to a lesser extent.

2.2.2.1 Brushtail possums

Brushtail possums are considered the major wildlife reservoir of tuberculosis infecting stock in New Zealand (O'Neil and Pharo 1995, Morris & Pfeiffer 1995, Caley *et al.* 1998a). Various lines of evidence lead researchers to this conclusion, although none alone is conclusive. DNA fingerprinting of *M. bovis* infections shows that cattle and possum populations are often infected by the same strain of the disease (de Lisle *et al.* 1995). Infections in possums and cattle also tend to be spatially and temporally associated (Davidson, 1976), and control of possum populations often leads to reductions in Tb prevalence in both possums and nearby cattle herds (Caley *et al.* 1999). Biologically plausible mechanisms for the transfer of the disease from possums to stock, such as behavioural interactions, have also been documented (Sauter & Morris 1995).

How possums came to be infected with tuberculosis is unknown because they are not infected in Australia, but it has been speculated that undiscovered long-term infection in wild deer several decades ago could have been responsible for the initial establishment of the disease in wild possums (Morris & Pfeiffer 1995). Possums eat meat occasionally (Nugent *et al.* 2000), so initial infection may have resulted from scavenging an infected deer carcass.

The prevalence of gross tuberculous lesions in possums is generally low, around 2% (Pfeiffer *et al.* 1995), however, combined with their high population densities possum populations are a major source of infection. Densities of possums in the range of 7-24 per ha are typical in good possum habitat such as the West Coast of the South Island, whereas populations can be very sparse or absent in semi-arid high-country areas (Cowan 1990). Hickling & Thomas (1990) estimated that possum densities in semi-arid areas of South Canterbury were between 0.37-0.63 per ha. The distribution of

tuberculous possums tends to be patchy, with small subpopulations having high rates of infection while most possums remain free of the disease (Hickling, 1995).

Morris & Pfeiffer (1995) identified three main pathways by which tuberculosis is transmitted between possums. First, possums may encounter *M. bovis* early in their life by way of pseudo-vertical transmission from their mother during rearing. Transmission of *M. bovis* to joeys can occur through infected maternal milk, since at least 12% of lactating females have been found with infected mammary glands (Morris & Pfeiffer 1995). Possums exhibit a high rate of pulmonary infection, so aerial transmission is likely to be the main mechanism for spread from mother to offspring (Jackson *et al.* 1995b). Morris (1995) estimated that 40% of infections in possums arise from psuedo-vertical transmission.

Second, horizontal transmission of *M. bovis* can occur during mating, territorial defence, den sharing and mutual grooming. Male possums often actively compete for oestrous females, territories and dens. High rates of infection of the superficial lymph nodes are common which, while consistent with infection expected from fighting, is considered unlikely because no tuberculous bite wounds have been found in possums (Coleman & Caley, 2000). In addition, female possums and young possums show similar infection levels even though fighting is typically an adult male behaviour (Jackson *et al.* 1995c). Respiratory tract infections have been found at rates as high as 59% (Pfeiffer *et al.* 1995) and 75% (Jackson *et al.* 1995b) of infected possums and it is widely considered that this is the principal route for transmission to other possums (Jackson *et al.* 1995c). The generation of aerosols from loud aggressive vocalisations is likely to be an important mechanism for the transmission of Tb. Excretion of *M. bovis* into the environment also occurs through urine, faeces, saliva and discharging sinuses

and lesions, but the importance of these routes of infection is unclear. Morris (1995) estimated that 50% of infections in possums might be due to a combination of these horizontal transmission routes.

The third pathway identified was the indirect transmission among mature possums such as through sequential den sharing, sequential territory marking of a common marking site or contamination of other commonly used areas such as tracks. However, this is considered the least important of the three routes for Tb infection in possums, accounting for an estimated 10% of infections (Morris, 1995).

Captive possums experimentally infected with *M. bovis* develop progressive symptoms and may die within 25 to 100 days (O'Hara *et al.* 1976). The speed of disease progression depends, in part, on the size of the infective dose (Jackson *et al.* 1995c). In the field, however, disease progression is not usually as rapid as in captive trials with some possums living well over a year after infection (Jackson *et al.* 1995b).

Male possums have higher prevalences of Tb than females both in mature and immature individuals (Jackson *et al.* 1995b), probably because males are more mobile than females (Coleman & Green 1984) and aggressive interaction is more common. Female possums with pouch young tend to have higher prevalences of Tb than those without young, perhaps as a consequence of immunosuppression during pregnancy (Pfeiffer *et al.* 1995). Adult females also had more infections in the intestinal tract than did adult males (Pfeiffer *et al.* 1995).

Barlow (1991) found there was no relationship between the prevalence of gross lesions in possums and relative possum density, but Hickling (1995) and Caley *et al.* (2001)

found there was a density disease relationship within local patches of Tb infection. These "hot spots" of infection are common in possum populations (Coleman 1988, Pfeiffer *et al.* 1995) and strongly suggest possum to possum disease transmission.

Jackson *et al.* (1995b) found no significant association between infection and age of possums or body condition, although weight loss was apparent in the later stages of the disease before death.

Historical data indicate that the prevalence of *M. bovis* infection in possums is highest on forest-pasture margins (Coleman 1988). Behavioural factors, such as interaction with cattle, may be responsible. However, recent analysis by Caley *et al.* (2001) suggested a plausible alternative explanation for this forest-pasture-margin effect in that pasture is found on the productive lowlands, which by their nature support more productive neighbouring forest, and therefore higher densities of possums.

The ecology of possums is strongly influenced by season and therefore the epidemiology of Tb in possum populations is also seasonal. Possums have a seasonal breeding pattern with most births between March and June and, in some populations, an additional season between September and November (Pfeiffer *et al.* 1995). Infection rates in possums were higher at the end of summer, when mating occurs and environmental stress is likely to depress their immune systems (Pfeiffer *et al.* 1995).

Immature possums disperse at approximately 9 months of age. Dispersal distances up to 40 km have been recorded, with males dispersing earlier and further than females (Cowan *et al.* 1996, Efford 1998). During dispersal, an immature possum may pass through Tb infected populations, use a relatively high number of den sites and have

numerous encounters with resident possums. This may be why juvenile males often show higher prevalences of Tb than females (Pfeiffer *et al.* 1995).

Home ranges of possums of all ages and sexes overlap extensively although co-dominant individuals tend to avoid each other, only defending the immediate area around dens or den trees (Cowan 1990) and seasonal food sources (Jolly 1976). Possums often use five to ten different den sites that are also used by other possums, although not usually simultaneously (Cowan 1990). Usually, dens are defended from other possums but, in areas where den availability is low, such as on farmland, multiple possums may share dens (e.g., Fairweather *et al.* 1987). Caley *et al.* (1998a) found that the probability of den sharing was density dependent, with den sharing less common after population reduction. Female-female sharing of dens is most common but both female-male and male-male den sharing also occurs (Cowan 1989). The probability of transmission of *M. bovis* is considered to increase when den sharing occurs, as it would favour aerosol infection.

Coleman *et al.* (1999) suggested that upsurges in Tb prevalence may occasionally occur due to adverse environmental conditions, followed by crashes in possum numbers due to the disease. High prevalences of Tb such as 60% are therefore likely to be only short-term effects.

Overall, possums have a high rate of pulmonary tuberculosis, a moderate level of social interaction, and a high sensitivity to infection but possibly a short infectious period. These factors coupled with their high population density give them a high propensity to be important vectors of Tb. Possums have long been considered reservoir hosts of *M.*

bovis and there has been no evidence to the contrary in areas with high possum numbers. There is now little doubt that possums are a reservoir host for *M. bovis*.

2.2.2.2 Red deer

Red deer were first introduced into New Zealand in 1851, mostly from Australia and the United Kingdom and by the late 1940s they were widespread throughout most suitable ranges in New Zealand (Challies 1990) at a density of 2-12 km^{-2} (Nugent & Mackereth 1996). Bovine tuberculosis was first identified in wild red deer in 1956 (Lugton *et al.* 1997c). The disease was not found in farmed deer until 1978, eight years after deer farming was first licensed in New Zealand (Beatson & Hutton 1981). A voluntary testing scheme was introduced in 1985, after which deer herd reactor rates began to drop significantly (Carter & Livingstone 2000). In 1990, this scheme was replaced with a compulsory scheme, which has since been incorporated into the Animal Health Board's Tb Pest Management Strategies (Carter & Livingstone 2000).

In wild red deer, the disease can become well-established in subpopulations where Tb prevalence can be high (typically in the range of 14 to 30%) (Nugent & Mackereth 1996, Lugton *et al.* 1998). Based on slaughterhouse data, Hathaway *et al.* (1994) found that more than half of the farmed deer that exhibited Tb lesions did so in the retropharyngeal lymph nodes. Peripheral tissue infection was rare, which suggests that, on farms, most uptake of *M. bovis* by deer is via the oral cavity. The progression of Tb infection in deer experimentally infected via the tonsils appears to follow that of naturally infected deer (Mackintosh *et al.* 1998) further implicating oral infection (Hathaway *et al.* 1994).

Lugton *et al.* (1997c) found that wild red deer less than 13 months old had a low prevalence of Tb infection despite prevalences high as 40% in their mothers. This implies that there is little vertical or pseudo-vertical transmission of Tb in deer and that deer calves exhibit behavioural characteristics that reduce their risk of infection. Lugton *et al.* (1997c) suggested that young deer may be more timid and therefore tend to avoid possums or other potential sources of infection, whereas older bold individuals, that closely investigate infected possums, are more likely to become infected.

Sex does not appear to significantly affect the chance of *M.* bovis infection in deer, but infection increases with age (Lugton *et al.* 1998). Age dependent infection is typical of animals that encounter *M. bovis* at a relatively steady rate throughout their lives.

The high prevalences of Tb found in deer may reflect interspecific transmission of disease to deer from another species, usually possums (Lugton *et al.* 1998). Coughing and generation of aerosols seem unlikely to be a major route for the transmission of *M. bovis* between deer because coughing is not a common sign of infection in deer as it is in cattle. In addition, helicopter shooters have reported that deer severely afflicted with Tb tend to isolate themselves from other deer (Lugton *et al.* 1998), which would make intraspecific transfer less likely.

It is known that possum control alone can reduce Tb levels in deer even if the deer themselves have not been controlled (G. Nugent, unpublished data). Nevertheless, complete eradication of Tb in deer would probably also require control of deer populations in habitats that favour the long-term persistence of infection (Lugton *et al.* 1998).

The low prevalences of *M. bovis* infection in deer in the absence of other tuberculous animals, and the apparent lack of effective intraspecific transfer, suggest that if deer are reservoir hosts they are poor ones. Although farmed deer are capable of maintaining Tb within a sub population (e.g. Griffin *et al.* 1998) they live at much higher densities than do wild deer. Tb does not appear to transmit easily between wild deer but they may still be able to maintain a low prevalence of Tb (Lugton *et al.* 1998; Nugent & Mackereth 1996). The maintenance status of deer is likely to be density dependent and spatially patchy.

2.2.2.3 Pigs

M. bovis infection in feral pigs was first reported in 1964 (Ekdahl *et al.* 1970). Feral pigs exhibit high prevalences of infection (e.g., 33% in Central Otago; Wakelin & Churchman 1991) with some localised populations reaching prevalences as high as 96% (Lugton 1997). Relatively little is known about the epidemiology of Tb in pigs in New Zealand, and inferences are often made from the more extensive studies of pig tuberculosis in the Northern Territory, Australia. Control of water buffalo (*Bubalus bubalis*) and domestic cattle infected with Tb in the Northern Territory led to significant reductions of Tb in pigs even though pigs were not actively controlled (McInerney *et al.* 1995). It is generally assumed that because pigs in Australia were dead-end hosts of *M. bovis* that this is also true in New Zealand.

M. bovis is found in feral pig populations in most areas that Tb is considered endemic. Wakelin & Churchman (1991) found a 32% prevalence of Tb in pigs in Central Otago, with 29% of these cases being generalised. The area of infection was confined to two catchments despite the ease of movement for pigs around the area. De Lisle *et al.* (1994)

suggested the high level of generalised infection found in this study indicates horizontal transmission, but the disease status of the possums in the immediate area at that time is unknown and it is not, therefore, possible to determine whether the infection was caused by horizontal mechanisms or from the scavenging of possum carcasses in a Tb "hot spot". The lymph nodes in the head were the main site of infection in this and other studies (Nuttal 1986, McLaughlan 1989), indicating the primary source of infection was probably infected carrion (de Lisle *et al.* 1994). However, 33% of infected pigs had either lung or bronchial lymph node lesions suggesting aerosol transmission between animals may also occur.

Wakelin & Churchman (1991) found there was no significant difference in the infection rates of female and male pigs, but that prevalence of infection increased with age. Despite this, there is evidence that older pigs are more resistant to infection from *M. bovis* than young pigs (Corner *et al.* 1981).

Corner *et al.* (1981) suggested that transmission from pigs back to cattle or buffalo is unlikely in Australia because of the low prevalence of generalised disease, a lack of pulmonary lesions, lack of obvious routes of excretion from infected pigs, and the lack of contact between the various species. A similar situation appears to exist in New Zealand.

There is no evidence to suggest that pigs in New Zealand maintain Tb in the absence of other sources of infection. Most authors agree that infection in pigs arises from scavenging on infected possum carcasses and other carrion (de Lisle 1994, Nugent *et al. in press*) and that transmission of *M. bovis* infection between pigs or from pigs to other animals is not epidemiologically significant (O'Reilly & Daborn 1995). However, pigs

may make an excellent indicator species for detecting low levels of Tb in other wildlife because they are highly susceptible to infection and cover large distances (G. Nugent *et al. in press*).

2.2.2.4 Hedgehogs

Of the mammals that may play an important role in the spread and maintenance of Tb in New Zealand, least is known about the hedgehog. Several authors have studied the ecology of the hedgehog in New Zealand, but little is known about the epidemiology of Tb in hedgehogs other than work by Lugton *et al.* (1995a) and Lugton *et al.* (1995c).

Hedgehogs were first introduced to New Zealand in 1870, and are now abundant throughout lowland areas of New Zealand, particularly in coastal areas (Brockie, 1990). They are predominantly insectivorous, feeding on slugs, beetles, millipedes, garden snails, insect larvae, earwigs and spiders. However, they are opportunist feeders and will feed on any animal material available. Fly maggots make up a small portion of the diet (Brockie, 1958), and Lugton *et al.* (1995a) found 13% of hedgehogs had mammalian tissue in their gut.

On improved pasture, hedgehogs have small home ranges (between 0.8 ha and 4.6 ha in size; Campbell 1973, Reeves 1994) that overlap extensively. In drier country hedgehogs range more widely (e.g. up to 100 ha; Moss 1999). The home range of males tends to be smaller than that of females (Parkes 1975). Hedgehogs are usually relatively solitary but may crowd together to exploit rich food sources (Brockie 1990). Parkes (1975) estimated hedgehog density to be between 1.1–2.5 per ha in lowland farm habitats.

Brockie (1956) found pulmonary lesions containing acid-fast organisms in one hedgehog of 155 examined, possibly the earliest record of wildlife tuberculosis in New Zealand. Brockie (1990) noted that the prevalence of Tb in hedgehogs would be well below 1% and of little importance compared with possums. However, a 1994 survey of hedgehogs in the Wairarapa confirmed *M.* bovis infection in hedgehogs at a prevalence of 5% (4 of 79; Lugton *et al.* 1995a). Further data collected from the same area in 1995 revealed the prevalence was lower than the previous study at 3.9% (6 of 157; Lugton *et al.* 1995c), although Lugton *et al.* (1995a) suggested that the true prevalence may be higher than that reported. As part of a study of ferret tuberculosis in North Canterbury, New Zealand, approximately 50 hedgehogs were necropsied and no gross lesions indicating Tb were found (P. Caley *pers. comm.*) despite a prevalence of around 10-12% in the local ferret population at the time (Caley *et al.* 1998b).

In the study by Lugton *et al.* (1995c), single site pulmonary lesions were found in three of the six infected hedgehogs and were also present in two of the other three generalised cases of Tb. The occurrence of five cases of pulmonary infection from six infected hedgehogs suggest that horizontal transmission may be a factor although Lugton *et al.* (1995c) noted that tuberculous possums were in the area and they suspected that these were the source of infection.

Because the home ranges of hedgehogs on improved pasture are small, it is likely that Tb in hedgehogs indicates that a tuberculous animal has died in the area (Lugton *et al.* 1995a). In addition to the small home ranges of hedgehogs, their ease of capture and moderate prevalence of Tb may make them a useful small-scale indicator species (Lugton *et al.* 1995b). Although horizontal transmission of Tb may occur in some

situations, it is generally thought that hedgehogs in New Zealand are another spillover host for tuberculosis (Lugton *et al.* 1995b).

2.2.2.5 Ferrets

Ferrets were first introduced to New Zealand around 1880 in an attempt at biological control of rabbits that had by then become a serious agricultural pest. Thousands of ferrets were imported from England between 1882 and 1884 and thousands more were bred locally (Lavers & Clapperton 1990). By 1900 they were well established in the wild and quickly spread throughout the country. A survey conducted in 1948 showed they were common throughout most of both main islands, except for areas with particularly high rainfall and correspondingly low rabbit numbers. Ferrets have not been reported on any offshore islands or on Stewart Island (Fitzgerald *et al.* 1984). They are most commonly found in pastoral habitats usually where herbs, scrub or woody cover is present (Ragg & Moller 2000) and occasionally in the fringes of forests (King and Moody 1982).

Rabbit is the main component of the diet of ferrets, so their distribution closely follows that of the rabbit (Pierce 1987, Smith *et al.* 1995). The highest abundances of ferrets are in Central Otago, MacKenzie Basin and Marlborough (Lavers & Clapperton 1990). In addition to rabbit as their main food, ferrets opportunistically feed on small mammals such as mice, hedgehogs and a variety of birds, fish, reptiles and invertebrates. Smith *et al.* (1995) found possum and hedgehog each made up 5% of ferret diet. These provide a small supplement to rabbit during summer but, in many areas, become a more substantial component of the ferret diet in autumn and winter when young rabbit is less easily obtained (Roser & Lavers 1976, Gibb *et al.* 1978). Female ferrets tend to eat

smaller animals such as mice, birds and invertebrates, while males feed more often on larger prey such as lagomorphs, possums, and hedgehogs (Roser & Lavers 1976, Smith *et al.* 1995, Ragg 1998a).

Ferrets breed from the beginning of August until around March and could potentially have two litters in one season (Mills 1994, Lavers & Clapperton 1990), but this appears to occur rarely, if at all, in the wild (Caley *et al.* 1998b). Mating can last for an hour or more during which biting of females by males is common (Lavers & Clapperton 1990, Moors & Lavers 1981). Usually 4-8 kittens are born around October or November. Young ferrets are able to eat meat within 30 days, are weaned within 6-8 weeks and disperse from their natal territory at about 3 months of age. Young male ferrets tend to disperse before females and also tend to disperse further, with females often taking up residence near their natal territory (Moors & Lavers 1981). Dispersal distances of nearly 50 km over several months have been reported, and such movements have included crossing large rivers and other geographic barriers (Mills 1994). Caley and Morris (2001) suggested that dispersal pressure may be density dependent, because low post-control populations of ferrets exhibited little or no dispersal whereas dispersal increased as the population recovered.

After dispersal, most ferrets establish a home range although some males remain transient. Home range sizes vary from 2-372 ha depending on sex, food density and ferret density (Moller *et al.* 1996). Males tend to have larger home ranges than females, possibly due to their larger size and corresponding higher energy requirements (Mills 1994). Ferrets have been reported to exhibit intrasexual territoriality, particularly in males (Moors & Lavers 1981; Medina-Vogel 1998) however, in areas with high prey abundance this seems to be less evident (Ragg 1997, Norbury *et al.* 1998, Young 1998).

Several authors have estimated densities of ferrets in the Otago area. Ragg (1997) estimated 2.8 - 8.4 ferrets km^{-2}, Cross *et al.* (1998) estimated a density of 5.3-8.4 ferrets km^{-2} and Middlemiss (1995) estimated 4.4 ferrets km^{-2}. In North Canterbury, Caley & Morriss (2001) estimated densities in the range of 1.7 to 2.5 ferrets km^{-2}, and for the North Island the only published estimate of ferret density was 4-5.2 ferrets km^{-2} at Pukepuke Lagoon in the Manawatu (Lavers & Clapperton 1990).

Although ferrets usually give birth to 4-8 kittens each year (Lavers and Clapperton, 1990), winter mortality is very high with many dying before reaching 12 months of age (Mills 1994, Caley & Morriss 2001). Ferrets in North Canterbury are estimated to have an average life expectancy of 1.3 years and a yearly survival probability of 0.55, with survival rates improving when ferret densities are low (Caley & Morriss 2001).

The high mobility, dynamic nature of their home ranges and high birth rate enable ferrets to very quickly repopulate areas after control operations. Reinvasion times of several days for ferret home ranges have been recorded (Young 1998). Caley *et al.* (1998b) found that, during February, 90% of trapped ferrets were juveniles, indicating the potential for quick population recovery at certain times of year, although juvenile trappability may have affected this result. Ferret control operations coinciding with periods of high juvenile dispersal are therefore likely to be ineffective because cleared home ranges will quickly be reoccupied (Young 1998, Ragg 2000). The possibility of density dependent mortality (Caley & Morriss 2001) further reinforces the problem of rapid reinvasion after control operations.

Tb is widespread in ferrets throughout Tb endemic areas, and is thought to be highest in areas with high rabbit abundance (Ragg *et al.* 1995b). Tb infection in ferrets generally follows the distribution of possums, although exceptions have been noted. Lugton *et al.* (1997b) found a prevalence of 26% from areas with minimal or no recognised possum Tb, although Tb had been historically present in the area. Caley (1998) found that the prevalence of Tb in ferrets was positively correlated with possum abundance and unrelated to ferret abundance, which suggests that possums were the main source of ferret infection. Using DNA restriction techniques, Ragg *et al.* (1995a) found different strains of *M. bovis* in ferrets from those in farmed deer and possums, suggesting ferrets were becoming infected from an alternative source, and that there was a possibility of ferret-ferret spread of the disease. However the sample size of infected possums from the immediate area may have been insufficient to detect duplicate strains.

Ferrets are mustelids, of which the badger is already considered a maintenance host. Ferrets are highly prone to infection by *M. bovis* and prevalences of infection typically in the range 15-60%, although a prevalence of 96% was recorded by Lugton *et al.* (1997b) from a sample of 24 ferrets. Ragg (1997) found that male ferrets had a significantly higher prevalence than females and that adults had significantly more than juveniles. Ferrets could well be a maintenance host in certain circumstances.

Typically, ferret Tb lesions have large numbers of acid-fast organisms indicating, like possums, that ferrets are very susceptible to infection with *M. bovis* (de Lisle *et al.*, 1993). However, the progression of Tb in ferrets is less aggressive and less destructive than in many other mammals (Lugton *et al.* 1997a). Lugton *et al.* (1997a) also noted that ferrets, once infected, appear to keep the disease under control for an extended time during which the lesions progress slowly. Tuberculosis does not affect the general

health or body reserves of the ferret until the later stages of the disease when sufficient *M. bovis* and asociated antigens have built up.

Experimentally infected ferrets died within 6 months in one experiment (Symmers *et al.* in Lugton *et al.* 1997b) and from 7 weeks to 5 months in another (Dunkin *et al.* 1929). However, experimentally infected animals typically exhibit more rapid disease progression than do wild ferrets, and Lugton *et al.* (1997b) estimated that while a few infected wild ferrets live only a few months, most live for over a year.

The majority of lesions found in infected wild ferrets are associated with the alimentary tract, suggesting that infection is acquired by ingesting material from infected prey or carrion rather by aerial infection (Ragg *et al.* 1995a, Lugton *et al.* 1997a). Ragg *et al.* (1995a) found 60% of single site lesions were in the mesenteric lymph nodes and Lugton *et al.* (1997a) similarly found 45% of gross lesions in the jejunal lymph nodes, both of which indicate initial infection in the gut.

Ferrets exhibit an almost universal infection of the liver, regardless of what other sites are infected, demonstrating that bacilli readily escape from nodal lesions, are distributed by the blood stream early in the course of infection, and are trapped in the liver (Lugton *et al.* 1997a). Pulmonary infection is rare in ferrets compared with possums. Ragg *et al.* (1995a) found only 2.9% of lesions in the lungs although Lugton *et al.* (1997a) found 17% of infected ferrets had gross lesions in the lungs containing acid-fast organisms. Lugton *et al.* (1997a) and Caley *et al.* (1998b) found that one third of infected ferrets showed no gross lesions, so studies that estimate Tb prevalence using only gross lesions would typically underestimate true prevalence.

There are several differences between ferrets and possums with regard to the three main Tb maintenance pathways of infection identified by Morris & Pfeiffer (1995). First, pseudo-vertical transmission appears to occur less frequently in ferrets, with few infected immature ferrets being found and a low prevalence of infection in the female's mammary glands. Lugton *et al.* (1997b) found one of eight ferrets with mammary gland infection and none of 54 in a later study (Lugton *et al.* 1997a). Lugton *et al.* (1997b) found two juvenile ferrets infected with Tb, but these were in areas with a high prevalence in possums. Ragg (1997) found 5% of ferrets aged between 2 and 4 months were clinically infected, which suggests that some ferrets became infected before weaning. Again, it is not clear whether this indicates pseudo-vertical transmission because it is possible that infection occurred due to feeding on infected carrion brought back to the den by the mother. Ragg (1997) suggested that, if risk of infection is constant throughout the life of a ferret due to scavenging on infected carrion, then the prevalence of Tb in ferrets would be expected to rise as they age, but Tb prevalence in adults was stable, indicating that disease may have been acquired early in life and that the incubation period was long, the disease was latent or lesions had resolved. However, Lugton *et al.* (1997b) found that the prevalence of infection did rise with age, being 2.8 times higher for every 6 months of life. Caley *et al.* (1998b) also found the prevalence of Tb in ferrets was highly age specific.

Secondly, horizontal transmission appears more likely in ferrets than in possums due to bite wounds, but less likely than in possums due to aerial transmission. Bite wounds are commonly found in trapped feral ferrets (e.g., 40% of individuals; Lugton *et al.* 1997b) mainly during the breeding season (Ragg 1997). Ragg *et al.* (1995a) found 40% of infections occurred in the peripheral lymph nodes (22% were single site infections), and suggested that these infections may have arisen from interactions such as fighting

during the mating season. However, Lugton *et al.* (1997a) noted that possums are also commonly infected in the peripheral nodes early in the progression of the disease and that skin infection is apparently not involved in these cases. Lugton *et al.* (1997b) found that about one quarter of infected ferrets had evidence of oral excretion of bacilli, apparently unrelated to the stage of disease. Lugton *et al.* (1997b) suggested that only oral shedding, mammary involvement and draining fistulae would seem likely to play a significant role in the intraspecific transfer of infection among ferrets. Ferrets use latrines near their dens sites to deposit faeces and also to mark their territory with anal gland secretions and urine, so it is possible that transmission could occur through sniffing of faeces (Qureshi *et al.* 2000).

Horizontal transmission may also occur through simultaneous den sharing and communal feeding. Ferrets use multiple den sites within their home ranges (Norbury *et al.* 1998) and are known to share dens with other ferrets, at least under some circumstances (Ragg 1998b, Norbury *et al.* 1998). Ragg (1998b) found that, in 7.4% of observations, simultaneous den sharing took place and Norbury *et al.* (1998) found two of 41 dens to be shared, both by adult males. Qureshi *et al.* (2000) found that even when presented with alternate den sites, captive ferrets opted to share dens, with up to five ferrets sharing a den in some instances. Anal and genital sniffing, fighting, mating and playing have all been observed in captive ferrets. Given that anal excretion of *M. bovis* has been found in 16% of faecal swabs taken from infected ferrets by Lugton *et al.* (1997b), it is plausible that infection may occur due to this behaviour. Ragg (1997) found that in 8 of 12 observations of ferret scavenging, communal feeding occurred and, in one case, four ferrets were observed feeding at one carcass. Playing and fighting may also cause direct transfer of *M. bovis* bacilli, since ferrets can exhibit open lesions (e.g., 11.7% of individuals; Ragg *et al.* 1995a).

Maintenance hosts typically have a high rate of respiratory tract infections (Morris & Pfeiffer 1994). Single site infections in possums are most commonly found in the respiratory tract but respiratory infection is rare in ferrets (Ragg *et al.* 1995a). The low rates of pulmonary infection and excretion in the studies by Ragg *et al.* (1995a) and Lugton *et al.* (1997b) do not favour the excretion of bacilli from the respiratory tract, and respiratory shedding was limited to animals with advanced disease. This suggests the infectious period for respiratory transmission is brief.

Intraspecific transmission of tuberculosis between ferrets may also occur through scavenging of ferret carcasses. Ragg (1997) found that cannibalism occurred in 45% of encounters with ferret carcasses and that ferrets spent more time near ferret carcasses than carcasses of other species of animal.

Thirdly, the potential for indirect transmission appears similarly lower than in possums. Ragg (1998b) found that 80% of the sequential den sharing occurred within 14 days of previous occupation, well within the survival period of *M. bovis* bacilli in a den (Jackson *et al.* 1995a). However, although den sharing occurs, Ragg (1995a) found that 11.7% of tuberculous ferrets had open lesions providing a mechanism for contamination on dens, but at a lower rate than possums.

Transmission of *M. bovis* from ferrets to livestock is thought to be substantially less important than from possums. Sauter & Morris (1995) found that possums were closely investigated 7.7 times as often as ferrets by cattle and 5.7 times as often by deer. They suggested that the pungent, characteristically predatory scent of ferrets was likely to reduce the interest cattle and deer showed in them. However, Caley *et al.* (1998b)

demonstrated that reducing ferret numbers also caused a reduction in cattle reactors, providing considerable evidence that ferrets were transmitting Tb to cattle.

Most of the species examined in this chapter that are regarded as true maintenance hosts have high rates of pulmonary infection (e.g., badgers, white-tailed deer and possums). However, the epidemiology of infection in feral ferrets most closely resembles that of feral pigs (Caley, 2000), which are considered to be spillover hosts for the disease (McInerney *et al.* 1995). It is unlikely that pseudo-vertical transmission and horizontal infection resulting from biting and aerosols could account for the prevalences of 60% and higher observed in some ferret populations. If the inference that most infection in ferrets arises from the ingestion of infected material is correct, then, for ferrets to be maintenance hosts, extremely high rates of cannibalism would be required.

2.3 Management of tuberculous wildlife in New Zealand

The New Zealand Animal Health Board (AHB) has the stated long-term goal of the "eradication of tuberculosis from domestic animals in New Zealand" (Animal Health Board 1995). The primary motives behind this goal are the protection of human and animal health, the reduction of production wastage and the safeguarding of access to the country's main overseas markets. A National Pest Management Strategy (NPMS) was proposed by the AHB in 1995 and implemented on 1 November 1996. The objectives of this strategy and their results are summarised in Table 2.1. The success of this first NPMS exceeded expectations in reducing the number of infected herds, but did not meet the objective of preventing the expansion of vector risk areas. It is estimated that more than 90% of new infections and persistent infections are attributable to a wildlife vector source and that the level of funding of vector control will be the principal

determinant of success of the next NPMS (AHB 1999). The second NPMS is currently in the final stages of the consultation process and is due to be implemented after July 2001. It is expected that there will be an increase in funding, with the aim of halting the extension of vector risk areas in the coming decade.

Table 2.1: Objectives of the 1995 National Pest Management Strategy and their outcomes as of June 1999 (AHB 1999).

Objective	**Result**
Reduce infected herds in vector free areas from 0.7 to 0.2%	Dairy cattle reduced to: 0.19% Beef cattle: 0.14% Deer: 0.5%
Prevent establishment of new vector risk areas and/or the expansion of existing vector risk areas into vector free farmland.	Four new vector risk areas defined. Extensions to existing vector risk areas have occurred at 22 locations.
Reduce infected herds in vector risk areas from 17 to 11%	Dairy cattle reduced to: 5.86% Beef cattle: 5.15% Deer: 5.59%

By the end of the first NPMS, vector control was funded at $29m. Most of the effort and cost of this control was spent on lethal control of tuberculous possums. There would be major implications for the effectiveness of existing possum control if this control was expanded to include another widespread species such as the ferret.

In certain problem areas, ferrets are already a recognised control target. Nevertheless, ferrets are much more costly to control than possums so compelling evidence of ferrets' role in the intraspecific maintenance of Tb should be required before such inclusions be made to the existing NPMS.

Therefore, the two experimental studies described in the following chapters aim to help clarify the likely host status of ferrets by gaining a better understanding of their scavenging behaviour, which is the main proposed route of Tb infection in this species.

Chapter 3
SCAVENGING BY FREE RANGING FERRETS IN NORTH CANTERBURY, NEW ZEALAND

3.1 Introduction

In the dry farmland habitats where ferrets are abundant, possums, hedgehogs and other ferrets are likely to be the most abundant sources of potentially infected carrion. This study investigated the scavenging behaviour of free-ranging ferrets to estimate their encounter and scavenging rates on these three carcass types. Estimates of the encounter and scavenging rates will help determine the relative contribution of each carcass type to the observed tuberculosis prevalence in ferrets, and thus the likelihood that Tb can be maintained within ferret populations with and without the presence of other sources of wildlife infection.

Studies of the pathology of Tb in ferrets showed that infection is predominantly by the alimentary route (Lugton *et al.* 1997a). Up to 11% of infected ferrets have been shown to have open lesions (Ragg *et al.* 1995a) but ferrets are not generally regarded as particularly sociable animals and therefore scavenging of tuberculous material is considered the most important source of infection.

3.2 Methods

The scavenging behaviour of wild ferrets was studied on farms in an area of North Canterbury, New Zealand, ranging from 42°51'S - 42°04'S, and 172°30'E - 172°56'E. Within this area, ferret behaviour was investigated by laying out carcasses in large wire cages along c. 90 km of access roads in areas of moderate to high ferret abundance.

Cages were 600x400x400 mm with a tracking tunnel attached at one end. The tracking tunnels were made from a 150x800 mm section of plastic drain pipe cut down its length with a 70 mm wide wooden tracking plate inserted in the base (Fig. 3.1). The tracking plate consisted of a central 160 mm long 'ink pad' with a 270 mm long sheet of tracking paper at either end. The inkpad was produced by painting the wooden surface of the plate to prevent ink absorption then covering it with a double layer of flannelette fabric. The ink consisted of 30% ferric nitrate, 44% polyethylene glycol, 15% detergent and 11% water by weight (King & Edgar 1977), which was sprayed on the inkpad. Tracking paper was cut to size, stapled to the plate and sprayed with a mixture of 5% tannic acid, 75% ethanol and 20% water by weight. The ink was replenished whenever it began to dry out, which was typically weekly during autumn and every two to three weeks in winter. Tracking paper was replaced weekly.

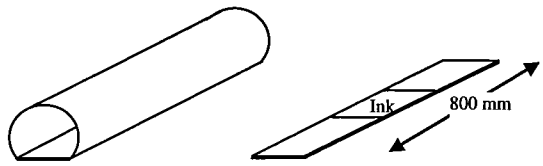

Figure 3.1: Tracking tunnel and plate design.

Carcasses of ferrets, possums and hedgehogs were collected from the study area by trapping with cage traps and Size 1 Victor™ leg hold traps. Traps were mostly set in shelter-belts or near barns, particularly those near waterways, in locations that were inaccessible to stock. Trapped animals were killed by a blow to the head with a hammer or headshot with a .22 calibre rifle. Carcasses were stored frozen and thawed when required.

Caged carcasses were placed at approximately 1 km intervals along the margins of access roads throughout the study area. A 1 km spacing was chosen to minimise the chance of a single ferret feeding at multiple cages, and was measured using a car odometer. If the location fell within 50-100 m of a house, the cage was moved further along the road if requested by the landowner. After the removal of some carcasses by scavengers, hedgehog and ferret carcasses were secured with bailing twine to prevent their removal. The bailing twine was of a sufficient length to allow scavengers to freely move the carcass around the cage but not out through the tunnel. Possums were not secured, as they were too large to be pulled through the tunnels.

The cages were placed 5-10 m away from the roadside verge in habitats similar to those where the carcass animals had been trapped. The number of cages baited at any time was determined by the availability of carcasses, but totalled 108 during the study period from March to early August 1997. Approximately equal numbers of carcasses were monitored in the first and second half of the study period.

Carcass decay was scored from 1 to 4 at weekly intervals. A score of 1 was given to a carcass that was either fresh or "fly blown" but without maggots. Level 2 was a partly desiccated carcass with few to moderate numbers of maggots of medium size. Level 3 was a carcass with a mass of usually large maggots, through to a carcass on which maggot numbers were beginning to decline. Level 4 was a completely desiccated carcass with few or no remaining maggots and most or all flesh removed.

Cages were checked weekly, with visits and/or scavenging by ferrets and other species assessed by examination of the tracking paper. Each cage was checked for 4 weeks, after which time it was relocated and baited with a fresh carcass. The one-month monitoring period was chosen to enable estimation of the probability of a carcass being scavenged within the likely maximum survival time of *M. bovis* within the carcass (Jackson *et al.* 1995a).

When more than two sets of tracks (i.e., one in and one out) were recorded on the tracking paper, it was not possible to distinguish tracks made by multiple ferrets visiting and single ferrets visiting multiple times. These visits were treated conservatively and recorded as being by a single ferret.

Data were analysed using a chi square test of association to test for differences between scavenging species and carcass type. Decay rates of carcasses in autumn and winter were compared using a paired t-test.

3.3 Results

3.3.1 Seasonal patterns in carcass visits and scavenging

Of the 108 caged carcasses set out, 102 completed the 4-week test period. Two were removed by human interference, and four cages had the carcass removed or completely eaten by a scavenger before the 4-week period ended. On average, each cage was visited by 1.45 animals during the study period, with 35% of cages being visited by at least one ferret, 6% by at least one cat, 24% by at least one hedgehog, and 30% by other species such as mice, rats and stoats. There were no occasions on which two different species visited a carcass within the same week, so it was possible to identify the scavenging species for all visits. A total of 62 distinct ferret visits were recorded. In 55% of these visits, the tunnels were visited more than once by a ferret.

The proportion of cages visited per week declined significantly from autumn (March-May) to winter (June to August) for ferrets and also for other species (χ^2=13.5, d.f.=5, p=0.019 for ferrets, χ^2=37.2, d.f.=5, p<0.001 for other species). Visitation rates were lowest in July for ferrets and in June for other species (Fig. 3.2). The decline tended to be more pronounced for species other than ferrets, but the difference was not statistically significant ($p > 0.05$).

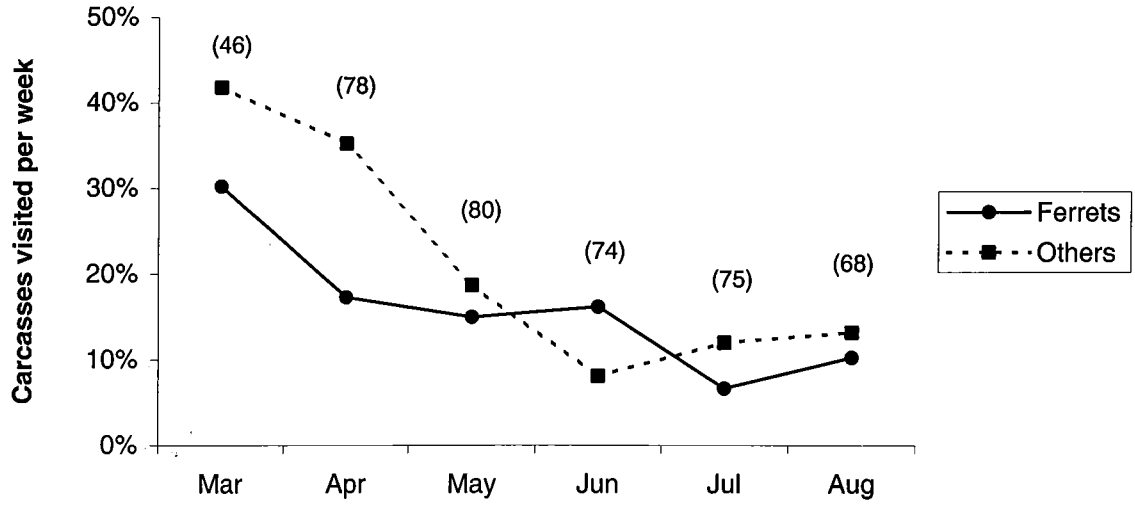

Figure 3.2: Monthly changes in carcass visitation rates by ferrets and other scavenging species (values in parentheses are no. of cage-weeks in each month).

Rates of ferrets visiting ferret carcasses were higher in autumn (29%) than winter (10%; χ^2=9.89, d.f.=1, p<0.01) but not significantly different for other carcass types or for scavenging rates between the two seasons.

In autumn, 17% of cage visits involved scavenging (16% of visits by ferrets, 12% by cats and 29% by hedgehogs); there was no significant difference between these scavenging rates (χ^2=0.08, p=0.77). Ferret scavenging rates per visit in winter (13%) were similar to those in autumn (p=0.34). In winter, there was negligible scavenging by species other than ferrets, although the difference between ferrets and other species was not statistically significant (χ^2=1.98, p=0.23).

Overall, ferrets scavenged 8% of all carcasses in autumn but only 2% in winter. However, this difference was not statistically significant (χ^2=1.42, p=0.23).

3.3.2 Carcass preferences

Ferrets were more than twice as likely to visit ferret carcasses than to visit carcasses of other species (χ^2=30.4, p<0.001) (Fig. 3.3). However, ferret-ferret visits tended to be less likely to result in scavenging than were ferret visits to other species (χ^2=1.2, p=0.27) (Fig. 3.4). The higher rate of ferret-ferret visits, combined with a lower rate of ferret-ferret scavenging during such visits, produced a roughly equal consumption of each carcass type by ferrets. That is, ferrets fed on 10% of total available ferret carcasses, 6% of hedgehog carcasses, and 8% of possum carcasses. These differences were not significant (χ^2=0.24, p=0.62).

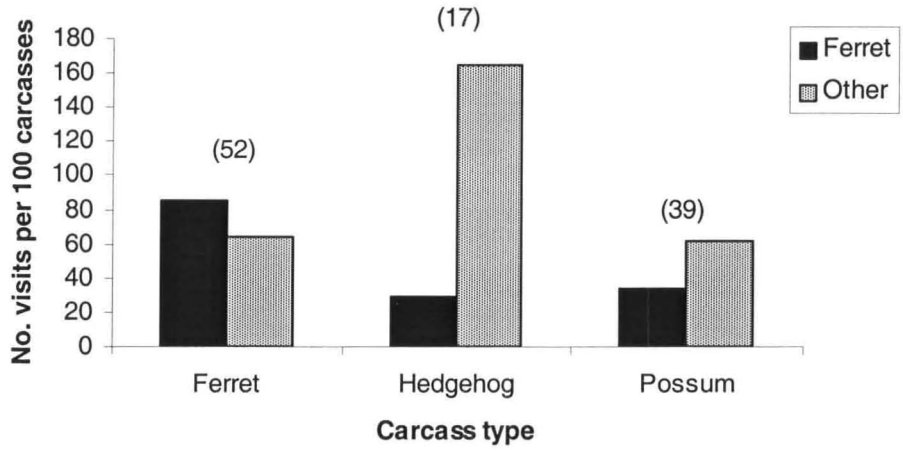

Figure 3.3: Rate of visits by ferrets and other species to three carcass types (values in parentheses are no. of carcasses).

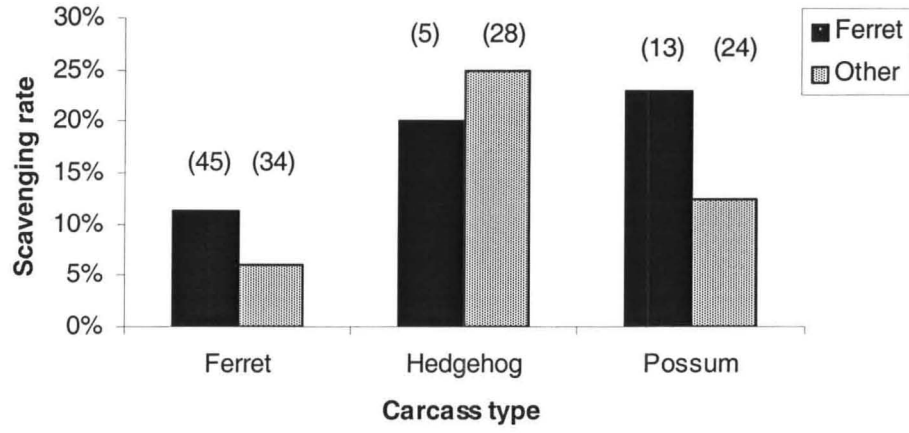

Figure 3.4: Proportion of visits to three carcass types that resulted in scavenging by ferrets, and other species (values in parentheses are no. of visits).

Ferrets preferred fresh or moderately fresh carcasses and did not scavenge on any carcasses with a decay index higher than 2 (Fig. 3.5).

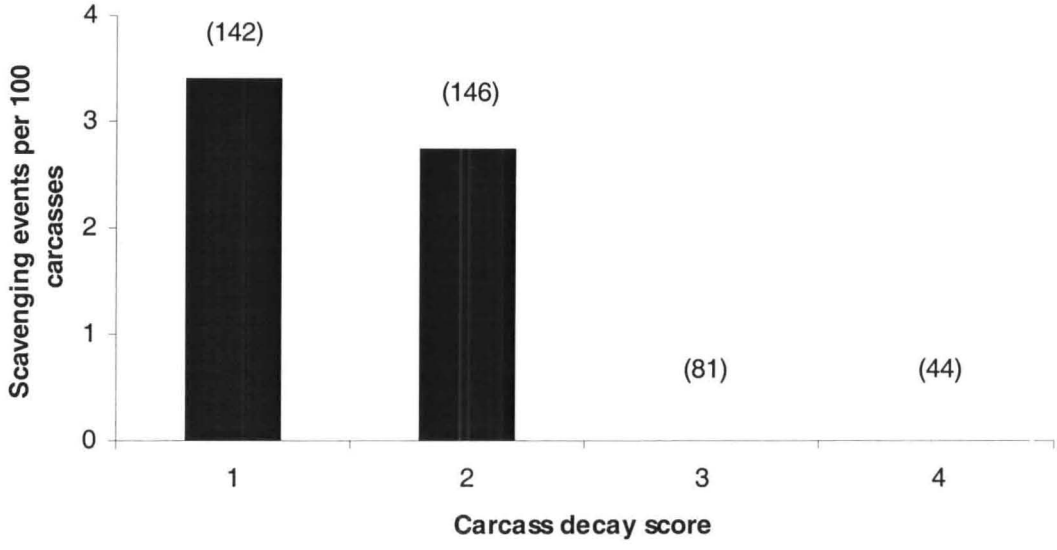

Figure 3.5: Rate of scavenging by ferrets on different levels of carcass quality by visiting ferrets (values in parentheses are number of carcass-weeks; all carcass types pooled).

In autumn, 95% of carcasses reached a decay level of 3 or 4 during the 4-week trial period but in winter, 80% of carcasses reached only level 2, and none reached level 4 (Fig. 3.6). This seasonal difference in decay was highly significant ($p<0.001$, d.f.=98). During autumn, carcasses became desiccated quickly and were often dry by the end of the 4-week period. Wet and cold conditions in winter prevented carcasses from drying out and substantial amounts of flesh remained after 4 weeks. Some carcasses were found partially frozen by frost and once, for a period of 2 – 3 days, some carcasses were partially covered by snow. During these cold periods, maggot abundance and growth was noticeably reduced.

There were no differences in the rates at which the different carcass types decayed. Mean decay scores after 4 weeks were 3.4, 3.4 and 3.6 in the first period, and 2.1, 2.0 and 2.2 in the second period, for ferret, hedgehog and possum carcasses respectively ($p>0.05$ for both seasons).

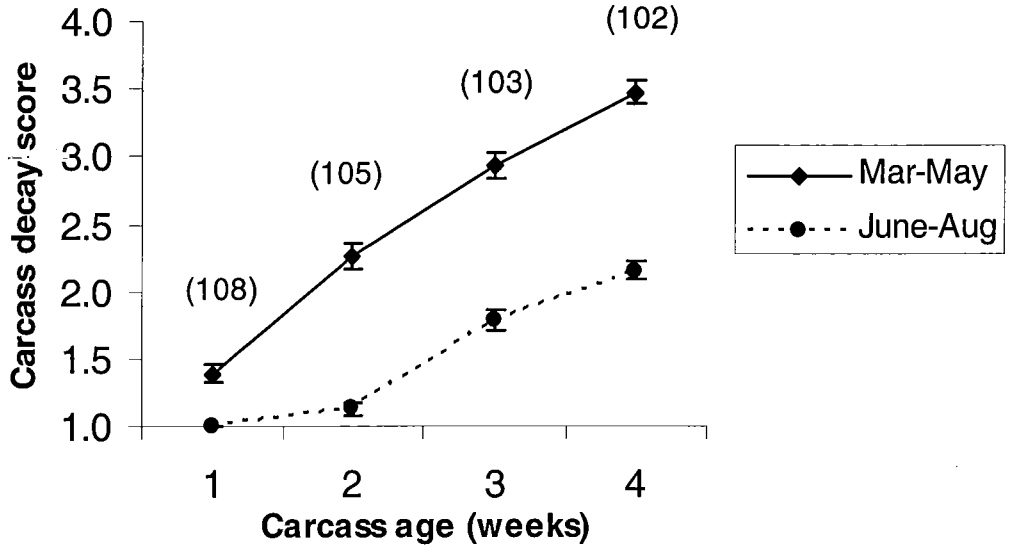

Figure 3.6: Change in average decay score of carcasses during 4 weeks of exposure in autumn (March-May) and winter (June-August). Means are presented ± SE. (values in parentheses are number of carcasses; all carcass types pooled).

3.4 Discussion

The frequency of visits, and particularly of scavenging, was lower than expected for all species. It is possible the cages deterred some animals from feeding as freely as they would have otherwise, though tunnels are generally regarded as being attractive to ferrets (e.g., Hammond 1996; Rutherford 1996). Ferrets have recently been found to exhibit neophobia of traps, but only for 3-4 days (A. Byrom *pers. comm.*). No interpretation can be made about the relative encounter rates of hedgehogs and ferrets as their responses to the presence of tunnels and cages are likely to be different.

Ragg (1997) studied the scavenging behaviour of a variety of species on possum, ferret, rabbit and hedgehog carcasses using time-lapse cameras and infrared lights in pastoral farmland. The encounter and scavenging rates by ferrets in the present study were consistently lower than those recorded by Ragg (1997) (Table 3.1). Ferret density in the area studied by Ragg was higher than the likely density in North Canterbury, so it is not clear whether ferret density, the presence of cages, or some other factor is responsible for the differences. (For example, Ragg's infrared lights could have enticed ferrets towards the carcasses, although this seems unlikely). The true encounter and scavenging rates on natural carcasses in North Canterbury probably lie somewhere between the values estimated in the current study and those of Ragg, so results from the present study should be considered conservative values of the nature of scavenging in North Canterbury.

More than half the tunnels that were visited by a ferret were later re-visited. Given the sparse and scattered nature of visits to tunnels in this study, these multiple visits are most likely a single ferret returning to the carcass and/or a clustered population of

ferrets. The former appears more likely, because the visits were temporally clustered. Nevertheless, ferret home ranges overlap extensively between sexes and transient ferrets are common (Moors and Lavers 1981, Young 1998). Again, the estimates of scavenging will be conservative because these re-visits have been omitted from the analysis.

Table 3.1 Comparison of the seasonal encounter and scavenging rates of encountered carcasses by ferrets in the present study with those of Ragg (1997); total no. of carcasses in parentheses.

Carcass Type	Activity	Overall	Autumn	Winter	Ragg (1997)[1]
Ferret	Encounter	44% (52)	64% (28)	20% (24)	80% (10)
	Scavenge	13% (23)	27% (18)	0% (5)	62% (8)
Possum	Encounter	23% (39)	12% (17)	31% (22)	75% (12)
	Scavenge	33% (9)	50% (2)	28% (7)	88% (9)
Hedgehog	Encounter	24% (17)	25% (16)	0% (1)	0% (2)
	Scavenge	25% (4)	25% (4)	0% (0)	0% (0)

[1] Conducted from April to July

Ferrets were more than twice as likely to visit ferret carcasses than carcasses of possums or hedgehogs. This suggests that ferrets either did not enter all the cages they encountered (and thus that they considered some carcasses of more interest than others) or that there was a bias toward encountering ferret carcasses. The scent of ferrets is noticeably stronger than that of possums and hedgehogs, which may allow scavengers to detect a ferret carcass from further away than other carcass types. Hedgehogs may also tend to avoid the scent of ferrets, which are a potential hedgehog predator.

During ferret visits to ferret carcasses, fewer carcasses were actually scavenged compared with visits to other carcass types. This may indicate that ferret visits to ferret carcasses are influenced by social factors such as territorial defence or sexual stimuli. Ragg (1997) found a similar response in ferrets in Otago; that is, when ferrets encountered a ferret carcass they spent longer close to it than they did when encountering possum or hedgehog carcasses, yet ate fewer ferret carcasses than hedgehogs or possums. The exact behaviour of ferrets while close to a ferret carcass

may warrant further research, since such behaviour could be a significant route for the spread of Tb within a ferret population (See also Chapter 4).

Ferrets tended to prefer feeding on possum and hedgehog carcasses over ferret carcasses, although the differences were not significant and the number of scavenging events was too low to make any inferences about carcass preference. However, Ragg (1997) also found a significant preference for possum carcasses over ferret carcasses. This apparent preference for possum carcasses over ferret carcasses lends weight to the argument that tuberculous possums are the major source of Tb for ferrets, and that ferrets may not be maintenance hosts for Tb.

The proportion of cages visited declined in winter for ferrets and also for the other species. This decline in visitation rates for other species was likely to be due to hedgehogs beginning to hibernate and cats growing too large to fit into the tunnels. The last recorded hedgehog visit was at the beginning of June, which is consistent with the typical hibernation period of hedgehogs (Brockie 1974). Cat visits were recorded for only the first 3 months of the experiment and these were most likely juveniles (personal observations suggest that even a medium-sized domestic cat could not fit through the tunnel, even when coaxed with food).

The reason that ferret visits also declined from autumn to winter is less clear, but may reflect a decline in ferret abundance and/or activity during winter. Ferret annual mortality is very high, with typical survival being approximately 55% (Caley & Morriss 2001). The reduction in visits during winter is possibly due to a combination of this mortality and the remaining ferrets being less active during winter. Seasonal differences in scavenging may affect the time of year that ferrets begin exhibiting symptoms of

tuberculosis, and ultimately the availability of Tb infected ferret carcasses to other ferrets. However, seasonally influenced environmental stress may play a more important role in this respect. The seasonal change in availability of tuberculous ferret carcasses may be an important factor in determining ferrets' ability to be maintenance hosts for the disease.

The number of ferret visits declined from autumn to winter, yet the proportion of visits involving scavenging did not vary dramatically (17% and 13% respectively). It was expected that, during winter, when food availability is low, ferrets would be more likely to scavenge a carcass that they encountered, but this was not so.

Carcasses provide scavengers with a more valuable food resource in winter than in other months, in part because the decay and desiccation processes are slower, but also because maggot abundance and size increased more slowly and they therefore consumed less flesh. In this study no carcasses were left out for longer than 4 weeks, but it is likely that, during winter, they would have remained in a palatable state (i.e., a decay rating of 2 or less) for at least 1 – 2 months and even longer in shaded areas that remained frosty for most of the day.

Assessing the true maintenance status of ferrets requires that they are able to maintain Tb in the absence of external sources of infection. However, because both natural and experimental possum and hedgehog carcasses were available in the study area, the frequency of ferrets feeding on ferret carcasses would have been offset by their feeding on these other carcass types. In an area where possum numbers had been controlled, higher rates of ferret-ferret feeding would be expected and therefore the possibility of maintenance more likely.

This study demonstrates that ferrets are not averse to feeding on other ferret carcasses, and that they make no strong distinction between these and other carcass types (although they may show a slight preference for possum carcasses). The implications of these observed scavenging rates for the maintenance of Tb in ferrets are discussed in chapter 5.

Chapter 4
SCAVENGING BEHAVIOUR OF CAPTIVE FERRETS.

4.1 Introduction

The field trials reported in Chapter 3 provide data on wild ferrets' encounter and scavenging rates and general preference for different carcass types. However, it is not as feasible to study the relative preference of individual ferrets to different carcass types in the field. It is also difficult to study sexual differences in scavenging behaviour of wild ferrets, and the typical sequence of scavenging behaviour exhibited by individual ferrets (which may shed light on the likely routes of infection). Therefore, this chapter reports on a pen study that investigated several aspects of the scavenging behaviours of ferrets that were not amenable to field assessment. These aspects included carcass preference, the typical sequence of scavenging behaviour, and sexual differences in the propensity to scavenge.

4.2 Methods

The study was conducted in an outdoor, 12x3 m enclosure located near Springston, central-Canterbury, New Zealand. The enclosure was made of 25x50 mm wooden framing covered with 30mm galvanised wire mesh, with 1200 mm high walls buried 300mm into the ground. A 300 mm internal overhang around the top of the enclosure prevented ferrets escaping. A single 350x300x200 mm den box was attached to one end of the enclosure by an 800x100 mm plastic tunnel.

Wild ferrets were trapped from around the Springston area using cage traps (Grieve Wireworks, Christchurch), and were individually housed in outdoor holding pens until

required for an experiment. Holding pens were 1000x550x500 mm wooden-frame, wire-mesh cages with a den box attached in the same manner as the main enclosure.

While in the holding pens, ferrets were fed 'Buster' dog roll (Vital Pet Foods, Christchurch). This dog roll is made almost entirely of mutton and lamb trimmings and has very little cereal added. This food was chosen because it was cheap, easy to obtain, and had already been used for several years raising three successive generations of ferrets with good results (*pers. obs.*).

The response of 10 adult ferrets (five of each sex) to ferret, hedgehog and possum carcasses was assessed by placing a new, fully-thawed carcass in the main enclosure with one study ferret and filming the resulting feeding behaviour using a time-lapse video recorder. The carcass was secured by one back leg to a metal stake using bailing twine, which allowed the ferret to manipulate the carcass while preventing the carcass from being moved out of the camera's field of vision. Ferrets were introduced to the enclosure 1 week before the start of each experiment to allow them to acclimate to their surroundings. Ferrets continued to be fed until the day before the introduction of the carcass, but were not fed during the trial. Before, and after each experiment the study animals were weighed using spring balance scales (10 g precision). Each study animal was involved in three trials (one with each carcass type), with the sequence of carcass types randomised and a minimum period of 6 weeks between successive trials.

Initially, filming continued until the carcass was entirely consumed or until no further feeding had taken place over 2 days. However, when several trials ran for more than 10 days, it became obvious that the time necessary to run all the experiments, acclimate the ferrets and analyse the video footage would be prohibitive. Consequently, the remaining

experiments were run for 3 days from the time at which each ferret first encountered the carcass.

4.2.1 Analysis

The following parameters were calculated from the video footage for each trial: number of investigations; number of feeding bouts; mean time spent investigating the carcass; mean time spent feeding on the carcass; total feeding time; feeding duration per investigation; and average number of feeds per investigation.

An investigation was considered to have begun when the ferret paused at or interacted with the carcass within the field of view of the camera. For example, on first encountering a carcass a ferret might stop and stare, or circle the carcass. Investigation was considered to end when the study animal left the carcass for at least 30 seconds, or became occupied in an activity clearly unrelated to the carcass for at least 30 seconds. The time recorded for the end of an investigation was the point at which the ferret left the carcass (i.e., not the including the 30-second break).

Feeding bouts were considered to have begun when the ferret began chewing on the carcass. Tugging at the carcass in an attempt to remove it was not considered feeding. 'Feeding' was a subset of 'investigation', in that all feeding occurred within an investigation period. As before, feeding was considered to end when a 30 second break occurred, and did not include the 30-second break. If a ferret immediately left the carcass, for example when disturbed by a noise, the feeding and investigation periods were considered to have ended simultaneously. Similarly, the investigation and feeding periods could begin simultaneously if an arriving ferret immediately began feeding.

The effects of carcass type, carcass sequence, study animal sex, and season on scavenging behaviour were examined using a general linear model (PROC MGLM in Systat Version 6, Spss Inc, 1996). The individual study animals were specified as a repeated measures effect.

Seasons were defined as consecutive 3-month periods, starting with September, December, March and June for spring, summer, autumn and winter, respectively.

4.3 Results

Only 27 of the planned 30 trials were run. One trial was missed due to a ferret dying in captivity before its final trial could begin, and the other two trials were disrupted by wild ferrets breaking into the enclosure. (It was not possible to reliably distinguish between the study animal and the intruder on the videotape). In addition, five carcasses were dragged beyond the view of the camera so data from these trials were incomplete. One ferret demonstrated surprising intelligence by repeatedly chewing through the rope that held the carcass in place.

Ferrets did not appear to be disturbed by the sudden appearance of a carcass in the pen, regardless of carcass type or the sex of the ferret and, in some cases, upon first encountering the carcass the ferret immediately began feeding on it.

There was no effect of the sequence in which the carcasses were presented on any of the behaviours ($p > 0.05$) and this factor is not discussed further.

Twenty-three of the 27 carcasses were fed on during the 72-hour observation period. All four of the carcasses on which no feeding took place were ferret carcasses; in three of these four cases there were minor amounts of tugging of the carcass, and in all cases the carcasses were frequently visited and investigated.

Licking, sniffing, nuzzling under, and rolling around carcasses of all types was common, particularly early in each experiment. This behaviour was not quantified, but did appear to be more pronounced in the trials that involved a ferret carcass. Licking that appeared unrelated to feeding took place on ferret carcasses in around a quarter of trials.

Ferret and hedgehog carcasses tended to be more extensively consumed than were the possum carcasses, which reflects the large size of possums and the limited timeframe of the experiments. It was not possible to reliably determine the mass of each carcass eaten due to differing rates of decomposition and desiccation in the various seasons. Parts of carcasses were also removed by study animals and found stored and uneaten in the den boxes. In one case, an entire possum head was unaccounted for, having perhaps been buried in one of the numerous tunnels that the ferrets dug.

Ferrets appeared to have some difficulty breaking through the skin of a carcass to gain access to the flesh, although there were no cases where ferrets that attempted to feed were unable to do so eventually. Nevertheless, some ferrets returned to the carcass multiple times before obtaining access. It took seven ferrets more than 20 minutes of attempts (averaging 5 visits), before they gained access. Ferret carcasses appeared to be less problematic than possum or hedgehog carcasses, with access usually obtained within several minutes. However, it took one male ferret 61 minutes (in 3 visits) to gain

access to a ferret carcass. It was not always possible to accurately differentiate between unsuccessful and successful attempts to feed with the video camera, particularly when initial access to the carcass had just been made, so quantitative analysis of carcass access times was not possible. There was, however, no obvious difference in the access times of male and female ferrets.

The typical feeding sequence was similar for all three carcass types. Initial entry to carcasses was made via the neck in approximately 80% of trials. Often a second entry was then made through the abdomen (or pouch if the carcass was a female possum). Alternatively, the initial opening was widened until it reached the abdomen. The only other entry point observed was on the inside of the legs, but it was not always possible to distinguish between entry sites beginning from the legs or those proceeding from the gut cavity down to the legs. This sequence took at least 2 days in most cases, but was not quantified because the openings could not always been seen from the video footage.

In cases where the neck was the initial entry point, there was usually extensive removal of flesh from around the neck, and under and inside the jaw (including the tongue). Feeding then typically proceeded down into the chest cavity via the neck with most of the removed tissue being muscle. Approximately 70% of carcasses then had the heart and lungs eaten, although in several carcasses it was not possible to determine precisely what had been eaten due to infestations by fly maggots. Most carcasses (70%) also had some or all of the intestines and fleshy organs eaten, but only 45% of carcasses had the kidneys eaten.

Muscle was the main flesh consumed in 90% of trials, typically eaten outwards from inside the neck or gut cavity down to the elbow or knee joints.

There did not appear to be any consistent difference between sexes of ferrets regarding the parts of the carcass eaten or the order in which they were consumed.

4.3.1 The effect of carcass type on scavenging behaviour

The overall encounter rates during the study did not vary between carcass types ($p>0.05$), which is unsurprising given the small size of the enclosure. Ferrets fed more frequently on possum carcasses than on the other carcass types (Fig. 4.1; $p=0.006$); there was no significant difference in the number of feeding events on hedgehog and ferret carcasses. Extended feeding on possum carcasses could have been a consequence of the relatively large amount of flesh on each possum carcass, so that ferrets could continue to feed on these carcasses, whereas after an equivalent time they would have removed most of the readily accessible flesh from a hedgehog or ferret carcass. However, only five hedgehog and ferret carcasses had all the flesh removed and even when these five cases were omitted, the analysis still indicated that there were significantly more feeds on possum carcasses ($p=0.025$). No possum carcasses had all the flesh removed within the trial period.

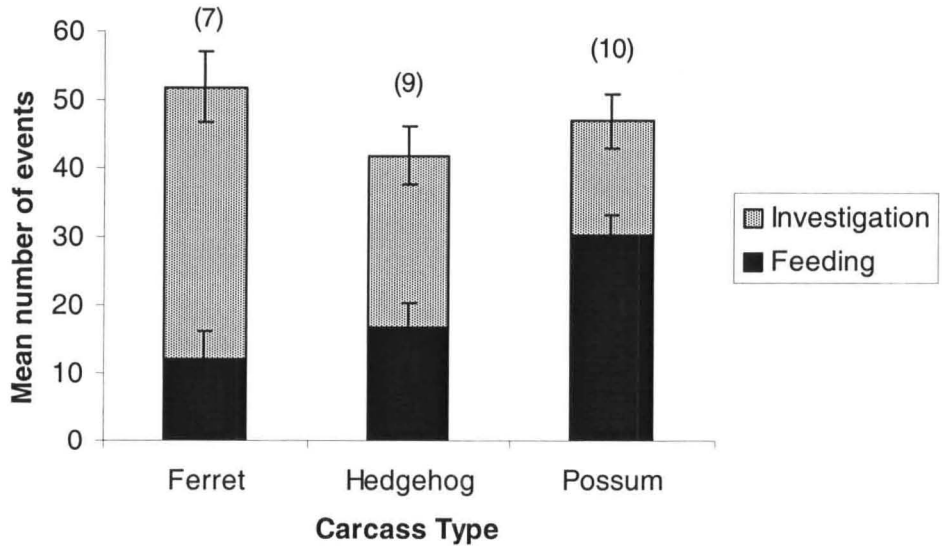

Figure 4.1: Mean number of ferret investigations and feeding bouts on different carcass types during the 72-hour study period. Solid bars indicate the proportion of investigations during which feeding took place. Means are presented ± SE; values in parentheses indicate the number of carcass trials.

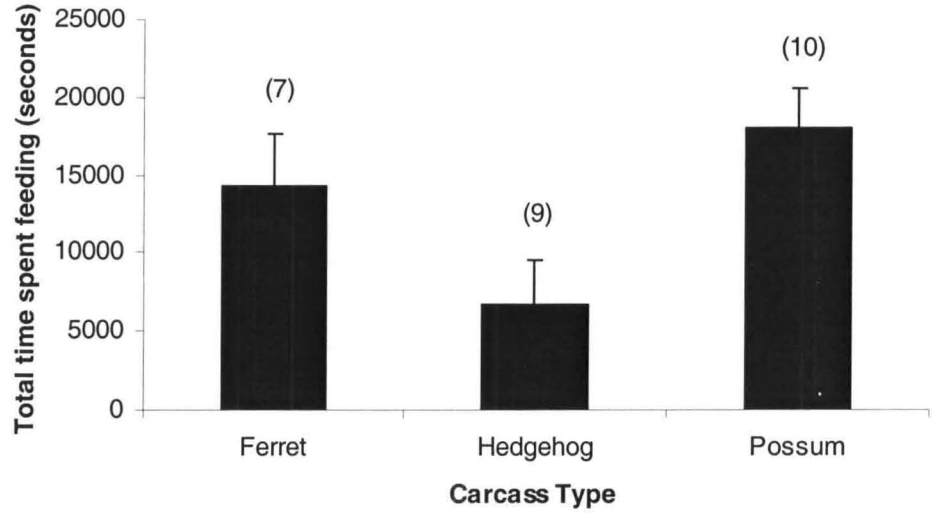

Figure 4.2: Total time spent feeding on different carcass types during 72 hour trial period. Means are presented ± SE; number of carcass trials are given in parentheses.

The total duration of feeding over the 72 hour study period was shorter for hedgehog carcasses than for ferret or possum carcasses ($p=0.031$; Fig. 4.2). Study animals feeding on ferret carcasses tended to intersperse their feeding with short periods of nuzzling and

rolling, whereas feeding tended to be more sustained on the other carcass types. The '30-second break' criterion used to indicate the termination of a feeding bout did not accurately reflect this situation because these breaks were often shorter than 30 seconds, which makes it difficult to compare the ferret mean in Fig. 4.1 with other means. In comparison, the difference between hedgehog and possum carcasses in Fig. 4.1 did seem to be a biological rather than methodological effect.

4.3.2 Sexual differences in feeding behaviour

Females were typically less active feeders than males in terms of duration of investigations, number of feeds, feeding duration, total feeding time, number of feeds per investigation and feeding duration per investigation, although these differences were not statistically significant (Table 4.1). Females did, however, tend to investigate carcasses more frequently than did males but this was also not significant. These sex differences were evident with all carcass types, but appeared to be most pronounced during encounters with ferret carcasses. Three of the four ferret carcasses that were uneaten were also in trials involving female ferrets. There are insufficient data to make any strong inference about sex-related differences in propensity to scavenge, but the lower scavenging indices associated with female ferrets may be worthy of more study.

Table 4.1: Differences by sex in scavenging behaviour; all durations are in seconds.

	Male (n=5)	Female (n=5)	Significance
Mean no. of investigations	38.5	54.3	0.27
Mean. duration of investigations	591	210	0.26
Mean no. of feeds	26.7	16.3	0.49
Mean duration of feeds	646	495	0.73
Total duration of feeding	19825	6919	0.25
Mean feeding duration/investigation	513	153	0.29
No. feeds/investigation	0.58	0.44	0.65

4.3.3 Seasonality of scavenging behaviour

Season had a significant effect on the number of feeding bouts during each experiment ($p=0.036$), with ferrets feeding more often during autumn and winter than spring or summer (Fig. 4.3). However, although there were more feeding bouts during these seasons, the duration of feeding was shorter (Fig. 4.4). This may simply reflect ferrets' aversion to being out of the den box in poor weather. It was certainly apparent, although not quantified, that rain deterred ferrets from coming out of their dens.

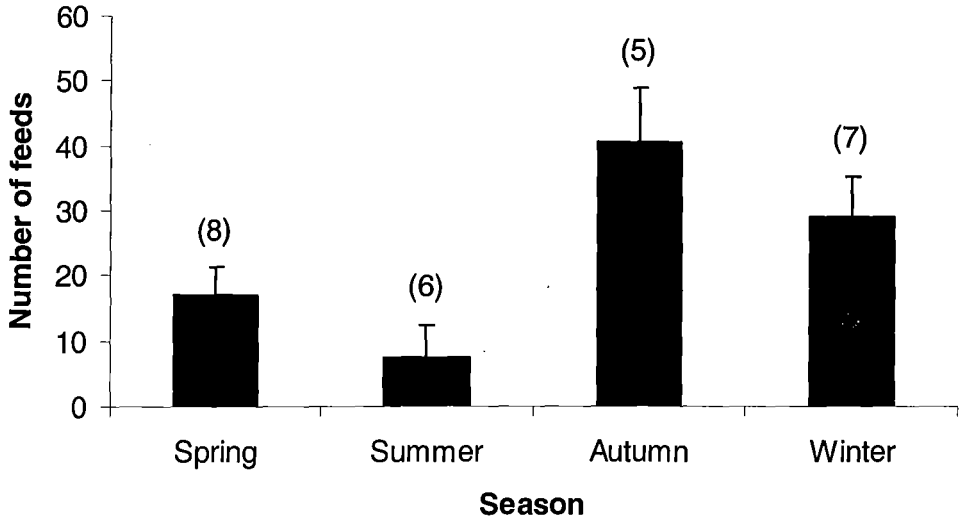

Figure 4.3: Mean number of feeds by ferrets feeding on ferret, hedgehog or possum carcasses during each season. Means are presented ± SE; number of carcass trials in parentheses.

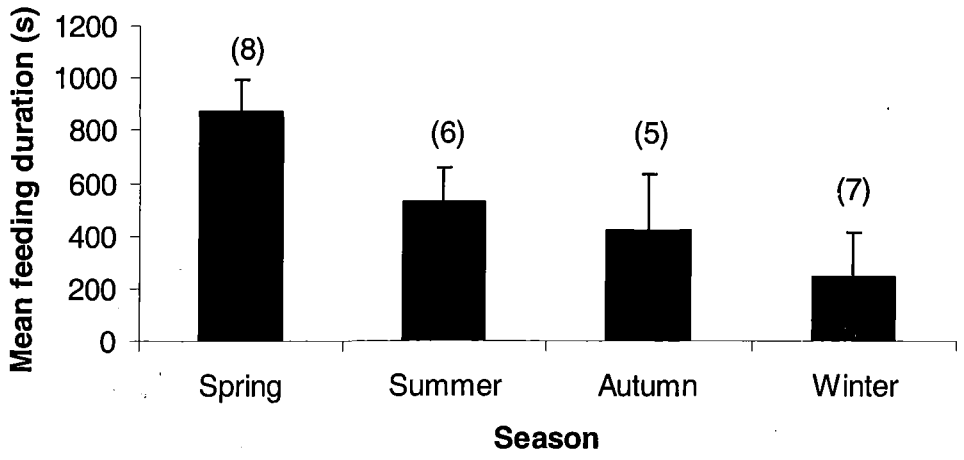

Figure 4.4: Mean feeding duration of ferrets feeding on ferret, hedgehog and possum carcasses during each season. Means are presented ± SE; number of carcass trials in parentheses.

4.3.4 Weight maintenance in study animals

The duration of each trial time was restricted to 72 hours so weight gain probably indicates ferrets' relative propensity to gorge on food supplies rather than any change in body condition. Males had a significantly higher proportional increase in bodyweight than did females (Fig. 4.5; p=0.004).

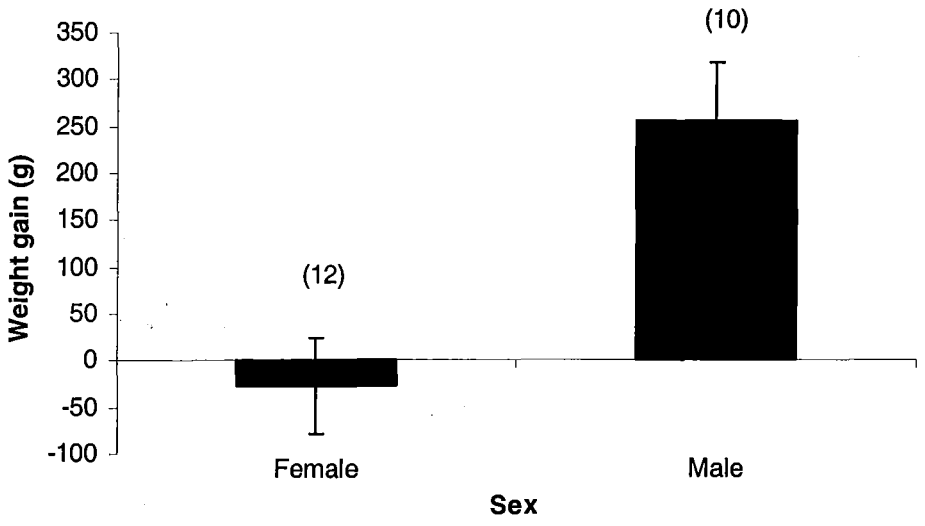

Figure 4.5: Mean change in weight of study animals over the 72 hour trial period. Means are presented ± SE; number of carcass trials in parentheses.

4.4 Discussion

Pen trials are somewhat artificial environments and results from them need to be interpreted cautiously in relation to the situation in the field. It is clearly not appropriate to directly compare encounter and scavenging rates from the pen trial with those of field trials, but the study does allow comparisons of relative indices of scavenging behaviours to be made.

The presentation of single carcasses in succession was chosen for the trial because these "acceptance" trials tend to be more representative of the field situation than "preference" trials where all carcass types are presented simultaneously (Johnston 1981). However preference trials have the advantage that they are more sensitive to differences in responses and they tend to give less variable results. Due to the small

sample size in this study a preference trial may have better identified overall carcass preference, but would have made investigations of other aspects of ferret feeding behaviour more difficult.

The maintenance diet fed to the ferrets in this study could have biased what they ate when they began feeding on carcasses. However, because this food had been used to raise three successive generations of captive ferrets it appears unlikely that there were any major dietary deficiencies that would have caused such a bias.

Most ferrets attempted to drag carcasses back to their den, but they were unable to do so due to the securing of carcasses. The behaviour of ferrets would inevitably have been somewhat different with unsecured carcasses. Some female ferrets are not able to drag a large possum carcass (*pers. obs.*) and, in any case, large carcasses may not fit into some dens, so eating carcasses in *situ* may be normal for some ferrets in at least some situations. Carcasses moved to dens would probably be eaten at a more leisurely pace, with longer feeding periods and fewer feeding bouts than observed in the present study. However, it is not likely that this would affect the sequence of feeding behaviour or the relative carcass preference.

Male ferrets show a greater propensity to gorge on carrion than do females. If this means they consume a larger infectious dose of *M. bovis,* they may face a stronger force of infection. This is consistent with the higher rates of infection found in male ferrets in the field (Ragg 1997), although other factors such as fighting and large home ranges may be more important determinants of this male-biased Tb prevalence.

Although four carcasses were not eaten during the experiment, it is not certain that they would not have been eaten had the experiment run longer. Many carnivores are opportunistic feeders, often gorging themselves when food is available and then going for periods without food. Lavers & Clapperton (1990) noted that one ferret remained in a rabbit burrow for three days after feeding, so it is possible the carcasses would have been eaten given more time. It is interesting that all four uneaten carcasses were ferret carcasses. This is one of several findings that suggest that ferrets are less prone to eat ferret carcasses than those of other species. If true, this would decrease the likelihood that ferrets can act as true maintenance hosts of Tb. This result may warrant further study.

If the carcasses in this experiment were to have *M. bovis* infection at sites typical of the disease in ferrets, most study animals would have eaten *M. bovis* infected material. Intestines, lungs, and neck were eaten in a majority of cases, making it likely that a variety of lymph nodes and other infected sites would have been consumed and therefore infection would have been likely.

If ferrets have to make multiple visits to a carcass before beginning to feed successfully, there is opportunity for other scavengers to feed on the entire carcass. This would reduce the potential infective dose of *M. bovis* bacilli but would increase the number of potentially infectious contacts with the carcass. Ragg *et al.* (2000) noted, however, that scavenging by harrier hawks (*Circus approxmans*) might be an important mechanism for providing access to carcasses for subsequent scavengers. The trade-off of increased carcass access and reduced flesh availability in terms of the overall chances of contracting Tb infection is unknown.

Males tended to be more active feeders in all respects except the amount of time spent investigating carcasses. If transmission of *M. bovis* is possible through the close contact with carcasses that occurs during investigation, females may face a higher force of infection than from feeding on carcasses alone. Infection in wild ferrets is predominantly found associated with the digestive tract, so the spread of Tb from carcasses is considered unlikely unless infected material is actually consumed (Lugton *et al.* 1997a). Nevertheless, in some areas up to 11% of ferrets exhibit open lesions (Ragg *et al.* 1995a). Consequently, *M. bovis* could be transmitted to ferrets that licked a carcass, or rolled on and around it – these behaviours were common in this study. Lesion distribution resulting from such behaviour would be similar to that arising from feeding on infected material. The significance of this intimate contact with carcasses for the spread of Tb is likely to be low because most carcasses are subsequently eaten anyway. However, there is potential for transmission of the disease even in cases where the carcass is not eaten or the carcass is taken by another scavenger before a ferret gains access to the flesh, so it is worth noting that the observed scavenging rate may underestimate disease transmission. In the present study four of seven ferret carcasses were not fed on, but in all cases there was close contact with these carcasses.

Hedgehogs are unlikely to be an important source of infection for ferrets. Ferrets appear to least favour hedgehogs of the three carcass types investigated in respect to the time they spent feeding, the time the spent investigating and the number of visits made. In addition, the prevalence of Tb in hedgehogs is low; at least in the area this study was conducted.

The major findings of the pen study were that ferrets prefer feeding on possum carcasses to other carcass types, that most ferrets ate sites on the carcass where Tb

lesions are commonly found and that males were more active feeders. These findings are similar to those of the field study (Chapter 3) and the results of Ragg (1997) and suggest that ferret scavenging behaviour in the pens was reasonably representative of that seen in the field.

Chapter 5
DISCUSSION

Disease transmission is extremely difficult to study in the field because it is not possible to observe all the behaviours or events that occur for any reasonable period of time and with satisfactory sample sizes. A definitive study of ferrets as a maintenance host in the field would require the complete absence of interspecific disease transfer and, clearly, this was not feasible in this study. Consequently, pen trials are often used, even though the results of such trials may not give an entirely accurate picture of the equivalent behaviour in the field. Inferences about the Tb maintenance status of ferrets have been made using sources of evidence that may be considered circumstantial, and it is only by the accumulation of additional pieces of evidence that the strength of such inferences can be improved. This study aimed to contribute such evidence.

The study used a dual approach in an attempt to draw on the relative merits of both pen and field data, and also to see whether the approaches were consistent in the trends they revealed. Both experiments indicated that ferrets scavenge on possum carcasses in preference to other carcasses. The importance of this finding depends on the relative densities and prevalence of Tb in possums and ferrets in an area. There is a belief by some farmers that, in semi-arid areas, possums are less common than ferrets or completely absent (Walker *et al.* 1993). However Caley *et al.* (1998b) found significant numbers of possums in such areas and suggested that a bias in visibility may be responsible for the belief. If ferrets do have an aversion to eating ferret carcasses (the data suggest so but are not conclusive on this point) then they would be unlikely to be maintenance hosts for Tb. Favouring possum carcasses does not, however, preclude them from eating ferret carcasses, particularly if possums are not available. The

experiments show that ferrets will eat ferret carcasses, at least when other food is not available.

The experiments also showed that ferrets visited ferret carcasses more often than other carcass types. Ferrets make repeated contact with other ferret carcasses even when not feeding on them, involving behaviours such as rubbing, nuzzling and licking of the carcasses. If the cause of death of these carcasses were generalised tuberculosis and they had open lesions, this behaviour could directly infect ferrets with *M. bovis* bacilli, or could transfer bacilli on to the fur and skin of ferrets, which could then cause infection by such behaviours as grooming. Ragg *et al.* (1995a) found that 11% of tuberculous ferrets exhibited open lesions but ferrets that died from generalised tuberculosis would be likely to exhibit even higher levels of open lesions. Infection in this manner would be consistent with the observed lesion distribution on ferrets, which suggests an alimentary infection route. This may mean rates of infection from carcasses are higher than the rates of actual scavenging on the carcasses. The extent to which this may occur is unknown and may be worthy of further investigation.

Both studies suggest that ferrets forage less actively in winter than other seasons. Ferret catch rates are typically low during winter and early spring (Moller *et al.* 1996), due, in part, to winter mortality and in part to reduced trappability (A. Byrom, *pers. comm.*). The reason ferrets may forage less in winter and spring is not clear but may be related to the abundance of young rabbits in spring, seasonally variable neophobia, or pregnancy (A. Byrom, *pers. comm.*). The result from the pen trial (in the absence of such factors) suggests that ferrets may simply exhibit an aversion to poor weather.

Tb in ferrets appears to predominantly be associated with the alimentary canal, so is most likely due to scavenging. Livingstone (1996) suggested an approach to estimate the scavenging rate per carcass required for Tb to persist at a steady level. The example proposed by Livingstone (1996) indicated that Tb could persist in a ferret population exposed to a regular supply of tuberculous possums provided 1.2 ferrets fed on each available tuberculous carcass. To estimate this value for a ferret population at typical ferret densities in North and South Canterbury, Livingstone's proposed model can be summarised as an equation:

$$n = \frac{N_f P_f}{N_f P_f S_f + N_p P_p S_p} \quad (1)$$

where n is the number of ferrets feeding on each carcass, f and p represent ferret and possums respectively, and N, P and S represent density km^{-2}, prevalence of Tb, and scavenging availability of carcasses respectively for each species.

The possum density estimate of 50 km^{-2} used by Livingstone was retained for both North and South Canterbury. Thomas (1997) estimated that possum densities at Scargill, North Canterbury, were similar to those found by Hickling & Thomas (1990) in South Canterbury (37-63 km^{-2}), and the habitat of both areas is similar (G. Hickling *pers. comm.*). Livingstone's assumption that 50% of all carcasses are available to be scavenged was also retained, but may be conservative.

At a low North Canterbury density of 1.5 ferrets km^{-2}, the equation suggests a prevalence of 15% could be maintained if 0.6 ferrets scavenged each available carcass; that is, not all available carcasses would need to be scavenged for Tb to persist. Somewhat counterintuitively, at a higher density of 3.1 km^{-2}, at least one ferret would need to scavenge each carcass to maintain a Tb prevalence of 15%.

The scavenging rates of ferrets on ferret carcasses observed in the field trial were 5% overall and 17% for autumn. According to Livingstone's model, a scavenging rate of 17% would be insufficient for Tb to persist at any level above 1%. Therefore, given that Tb persists in North Canterbury at levels well above 1%, either the assumptions of the model are incorrect, or there is additional transmission of disease occurring through other routes. Because the model is very simple and the epidemiology of Tb in ferrets supports oral infection, it is likely that the former is true. This approach cannot account for the Tb prevalences exceeding 60% that have been observed in some ferret populations. In addition, the model is not particularly helpful with regard to the question of whether ferrets are true maintenance hosts of Tb, because if possums are removed the equation simplifies to:

$n = \frac{1}{S_f}$, which simply means that if 50% of tuberculous carcasses are available for scavenging then 2 ferrets must scavenge each carcass to maintain levels of Tb; this is overly simplistic.

The ferret scavenging rates (50%) found by Ragg (1997) were notably higher than those found in the present study. A simple model was constructed to explore the implications of such pronounced differences in apparent scavenging and therefore potential disease transmission. The model, modified from Gillman & Hails (1997), assumed that the rate of change of Tb infected ferrets (I) in a population could be expressed as:

$$\frac{dI}{dt} = \beta SC - (\alpha + b)I \qquad (2)$$

where β is the transmission parameter coefficient encompassing two components: the frequency of contact (estimated from current study as 0.173 during autumn and from Ragg (1997) as 0.5); and the likelihood that the contact results in infection (assumed to

be 1 following Livingstone). S denotes the density of susceptible ferrets (assumed to be all ferrets regardless of age or sex) and C the density of infected carcasses. The instantaneous per capita death rates due to disease and other factors are expressed as α and b respectively. This is a simple single-species model where host population is considered to be a constant size and individuals are uniformly dispersed (homogeneous mixing).

For disease to persist in a population the rate of new infections must be greater than the loss of infected individuals, i.e., $\beta SC > (\alpha+b)I$

Therefore, $$\frac{\beta SC}{(\alpha+b)I} > 1 \qquad (3)$$

This expression is referred to as the basic reproductive rate of the disease, R_0, and this must be greater than 1 for infection to persist. Following Livingstone (1996), C was assumed to be 50% of the number of infected animals dying, i.e., $C = ((\alpha+b)I)/2$

Substituting this into the equation (3) gives an estimation of R_0 as $(\beta S)/2$.

Using data from North Canterbury (β=0.27 and S=1.7-2.5), the estimates of R_0 are 0.2 to 0.3, well below the threshold necessary for disease persistence. Estimates of R_0 from Otago (β=0.62 and S=5-8.4) are 1.6 and 2.6, which are above the threshold.

Even at high densities, the disease transmission rates estimated from North Canterbury are insufficient to produce disease persistence. Comparison of this study with Ragg's (1997) data suggests that the transmission coefficient (β) is not constant and probably increases with higher ferret densities. Because there are only two estimates of the transmission coefficient, the relationship between ferret density and transmission rates

cannot be determined so the critical ferret density at which Tb maintenance may occur cannot be calculated using this method.

It appears that ferrets are not able to maintain Tb in North Canterbury, but could possibly do so in Otago because ferret densities and transmission rates are higher there. This finding is similar to that of Caley (2000) who predicted that Tb could not persist in a ferret population at densities below 5.3 ferrets km^{-2}, unless there was an additional external source of infection.

In both trials, hedgehog carcasses appear to be slightly less favoured by ferrets, although the difference was not significant. Given that no hedgehogs were infected with Tb in North Canterbury, it may be that they play no important role in the spread of Tb. However, it is worth noting that only 50 hedgehogs were examined in detail (P. Caley, *pers. comm.)* and, with that sample size, one can only be 95% confident that the true prevalence was below 6% (Cannon & Roe 1982). It is likely that at least some hedgehogs were infected in North Canterbury, given that hedgehogs become infected in the presence of infected possums (Lugton *et al.* 1995a). Because the home ranges of hedgehogs are relatively large in semi-arid areas and up to 50% of infected hedgehogs may exhibit pulmonary lesions, it is possible that hedgehogs may play an important role in maintaining Tb in an environment. Further wildlife surveys may be warranted to verify the presence and prevalence of Tb in hedgehogs in this area.

The question whether ferrets are true maintenance hosts for Tb needs to be addressed with caution. First, inferences drawn from one population of ferrets are not necessarily applicable to other populations. If ferrets are found to maintain Tb in one area, this does not necessarily imply that ferrets should be controlled everywhere, particularly given

that ferrets cost more to control than do possums. In all but a few areas of New Zealand, ferret control is unlikely to provide a 'magic bullet' solution.

In addition, the true maintenance host status of ferrets is not necessarily the most appropriate question to address. Given that possum control will not, in the foreseeable future, remove all the possums from an area and that hedgehogs and other wildlife will also be present with some level of background infection, the more appropriate question to ask is whether the system itself is maintaining Tb and what components of the system could most easily be managed for this disease cycling to break down. This is particularly difficult to assess, because the disease can remain latent for long periods of time in some species. Multi-species studies require better information about the ecology and epidemiology of Tb than we currently have, and funding for such research at a suitable scale is rarely available.

The oral route is currently considered 'the most important' route for ferret infection and, by implication, the other routes have received little attention. Yet, if oral infection accounts for 60-80% of all infections (Ragg 1997, Lugton *et al.* 1997b), then it follows that 20-40% of infections are being caused by other mechanisms. Ignoring this proportion of infection may be a serious omission. In addition, the pathology of oral infection does not preclude the possibility that some of the infection occurs through social activities or contact with carcasses other than scavenging.

The role of possums as maintenance hosts for Tb is accepted by most authors despite there being no single conclusive proof. The same cannot be said for the ferret's role in Tb maintenance and current opinion is strongly divided. The contradictory nature of evidence from the field suggests that if ferrets *are* maintenance hosts for Tb, then this is

true only in certain places at certain times. The inevitable 'background' level of possum Tb, makes inferences on ferret Tb maintenance more difficult than has been the case for possums. It is likely that much more evidence will be required before agreement is reached on the status of the ferret as a maintenance host for Tb.

In conclusion, this thesis cannot answer the question whether ferrets are true maintenance hosts for *M. bovis*. Encounter rates and subsequent scavenging rates of ferrets with different carcass types were investigated and were lower than expected. Ferrets feed more on possum carcasses than ferret or hedgehog carcasses, and it is possible that ferrets avoid feeding on ferret carcasses. These factors reinforce the belief that the majority of Tb infection due to scavenging is likely to be from possum carcasses. The encounter and scavenging rates observed do not appear to be sufficient for Tb to be maintained in a ferret population by scavenging alone. There appears to be sex-related differences in the feeding behaviour of ferrets, which may be partly responsible for the sex-biased Tb prevalence found in ferrets, however there was insufficient data to make a firm conclusion and further studies may be warranted.

Results from the present studies reinforce the notion that the behaviour, ecology and perhaps the epidemiology of Tb in ferrets varies dramatically in different areas of New Zealand and that caution should be taken when extrapolating results from one region to another.

Further large-scale manipulative studies such as those suggested by Caley *et al.* (1998b) are needed (and some are currently underway; P. Caley *pers. comm.*). These promise significant new insights into the role of the ferret in maintaining Tb in North Canterbury.

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Mum, I'm done!

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