Use of Olfaction in Northern Brown Kiwi,

Apteryx mantelli.

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Abstract

The use of olfaction for territorial marking and prey detection was studied in captive Northern brown kiwi (*Apteryx mantelli*). Kiwi responded in a way that suggests they may use faecal odour to mark territories, and this is the first time that an avian species has been suggested to do so. Responses were observed to three types of faecal odour containers introduced into enclosures - with the resident kiwi's faeces, foreign kiwi faeces or empty controls. Juveniles were attracted more to foreign kiwi odour than adult birds, but showed significantly more escape behaviour from these odours than adults. This suggests that juveniles may use these odours to assess resident birds and to avoid confrontation with territorial adults. Adult males were repelled more than other kiwi from foreign kiwi odour, but showed significantly less escape behaviour. This suggests that they may avoid confrontations but supports the suggestion that males are the more territorial sex. Entering, roosting and defecation behaviours in roost boxes with different faecal odours were also studied. Kiwi did not purposefully defecate in boxes and did not countermark faeces from a foreign bird. This suggests that kiwi do not purposefully scent mark roost boxes using faeces, and that they may scent mark them instead from gland secretions left after roosting. This may explain why kiwi move from one roost site to another almost every day in the wild. Adult female kiwi roosted significantly more often in boxes than other kiwi, and roosted most often in boxes with foreign kiwi odour. This suggests that there is a behaviour difference between the sexes with females being more willing to roost in unfamiliar roost sites, possibly as a way of finding mates. Large boxes were also dug into enclosures to test the olfactory ability of kiwi to find subterranean prey. Kiwi do not appear to use olfaction as the primary sense to find subterranean earthworms, which is in direct contradiction to popular belief and to commonly cited literature. Kiwi were largely inaccurate in finding these prey and the ability of kiwi to find prey was not affected by the concentration of earthworms in a small area or the depth of the earthworms. Kiwi may instead use auditory of vibrotactile cues as the primary sense to find prey.

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Introduction: A Review of Avian Olfaction

PART ONE

Developments in Knowledge of Avian Olfaction

Olfaction is defined as the ability to perceive airborne chemical stimuli at a distance from their source, sometimes in extreme dilution (Kare and Mason, 1986; Clark, 1997; Roper, 1999). Olfaction plays many different roles in animals and can include information about food, sexual partners, associates, threats and the general environment (Le Magnen, 1963).

The olfactory sense has traditionally been considered the least well developed of the five common senses in birds and most early studies assumed that olfaction played only a small role in their everyday life (Stager, 1967). This is probably because the behaviour of birds does not suggest olfactory awareness (Wenzel, 1980).

Since the 1960s, however, evidence has accumulated of olfactory ability in a wide range of bird species (Roper, 1999). Bang (1960) was one of the first authors to suggest that birds possessing large olfactory organs may respond to chemical stimuli, either alone or in complex interactions with auditory, visual, vibratory, and other organs of special sense. Tucker (1965) was also convinced that the olfactory systems of birds were functional, and that such functionality was difficult to imagine without having biological significance.

The brains of living birds and mammals are approximately fifteen times larger than those of other vertebrates of the same body size (Pough *et al.*, 1996). The telencephalon and cerebellum make up the major areas of the brain in birds (Pough *et al.*, 1996), although the cerebellum can vary greatly in size (Cobb, 1960). The telencephalon is the most anterior part of the adult vertebrate brain and develops in association with the

olfactory bulbs (Wenzel, 1971a; Pough *et al.*, 1996). Although the avian olfactory system is very similar to that of amphibians, reptiles and mammals (Portmann, 1961; Roper, 1999), the olfactory lobes are usually very small in birds (Pough *et al.*, 1996) and the large optic lobes are one of the most characteristic features (Cobb, 1960). The kiwi brain, however, is exceptional in having extremely large olfactory bulbs and small optic lobes (Craigie, 1930) (Figure 1.1).
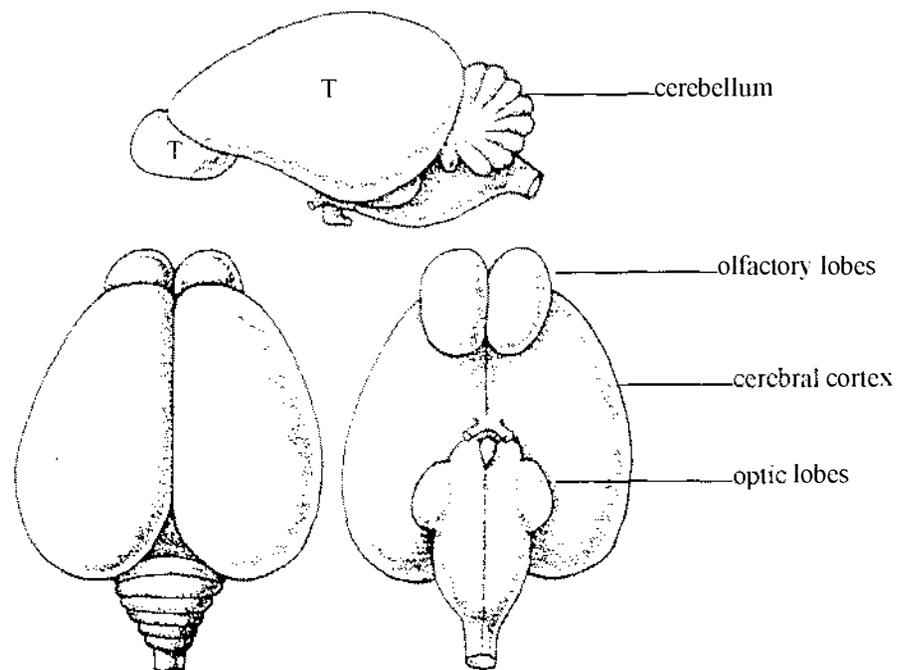
Figure 1.1: The kiwi brain, showing lateral, dorsal and ventral views. Note the large olfactory bulbs at the anterior of the brain. T = components of the telencephalon (after Hartwig, 1993).

Many authors assume that an increase in the size of a sensory system implies an increase in that sensory function (Bang, 1971; Kare and Mason, 1986). The size of the olfactory bulb is assumed to reflect the number of incoming olfactory nerve fibres, which in turn reflect the number of receptor cells of the olfactory mucosa (Wenzel, 1980). Even among birds, however, there is wide variation in the structure and development of olfactory bulbs (Cobb, 1960; Wenzel, 1971a; Benzo, 1986), and comparisons between avian species have been difficult to make.

Cobb (1960) showed that there is a marked decrease in the relative size of the olfactory bulb in more recently evolved bird species, suggesting a shift away from olfaction and towards a reliance on vision and hearing as the primary senses (Strong, 1911; Wenzel, 1971a; Clark, 1991). However, the olfactory ratio (the ratio between the longest diameter of the olfactory bulb and the longest diameter of the ipsilateral cerebral hemisphere of the brain (Cobb, 1960)) of birds varies about 13-fold, suggesting that there is a large difference in olfactory ability among avian species (Ioale and Papi, 1989). Eighty percent of birds with high olfactory ratios (25% or over) are generally ground nesting, water-associated, carnivorous/piscivorous and colonial breeding birds (Bang, 1971) but exceptions can be affected by species-specific ecological factors (Roper, 1999). Obviously the kiwi, with an olfactory ratio of 34% (Bang and Cobb, 1968), is one of these exceptions.

Healy and Guilford (1990) took a different approach to grouping species from Bang (1971), by taking into account the effect of increased body size and increased brain size on the size of the olfactory bulb. They suggested that birds living under low light conditions (e.g. nocturnal or crepuscular species) have significantly larger olfactory bulbs than diurnal species and that olfaction compensates when the effectiveness of vision is reduced. Healy and Guilford (1990) concluded that the time of day when a bird is active is the *only* character that accounts for the variation in olfactory bulb size between species.

Evidence of some olfactory capability has been found in every bird species tested, including those with relatively small olfactory bulbs (Ioale and Papi, 1989; Roper, 1999). Furthermore, olfactory abilities are often comparable to those of mammals such as rats and rabbits, which are considered to be macrosmatic (an animal with a good sense of smell) (Clark *et al.*, 1993). The amount of olfactory tissue, therefore, may not be a good indicator of odour discrimination in birds (Waldvogel, 1989) and it may not reflect the olfactory sensitivity of birds (Roper, 1999). An alternative suggestion is that olfactory bulb size is related to the ability to discriminate between a wide range of odours, and that birds with large olfactory bulbs may have a larger screen to compare olfactory information (Wallraff and Hund, 1982; Roper, 1999).

The Olfactory System

The airflow within the nasal cavity is initially influenced by the shape of the nostril (Proetz, 1941), and odours received during inspiration pass into the paired nasal chambers (conchae), which are separated by the nasal septum (Portmann, 1961). Odour molecules pass over the olfactory epithelium where they are processed by olfactory receptors. These connect, via paired olfactory nerves, to the olfactory bulbs of the brain (Roper, 1999).

The nasal chamber is divided into three areas; the anterior, maxillary and olfactory conchae (Bang, 1971). The first two conchae clean, warm and moisten the incoming air. The maxillary chamber, which is the main chamber, is the only chamber that opens to the buccal (mouth) cavity and allows some air to pass directly to the lungs (Roper, 1999). The olfactory chamber lies behind and slightly above the maxillary chamber (Stager, 1967), and it is the only part of the nasal cavity lined with sensory olfactory epithelium. The size and complexity of the olfactory chamber varies greatly between avian species (Parsons, 1971; Kare and Mason, 1986; Roper, 1999). In most birds its wall supports a projection called the olfactory concha (Bang, 1971), which is covered in olfactory epithelium (Parsons, 1971). The olfactory concha varies greatly in shape, and various scrolling, folding or branching patterns of the concha increase the surface area in various bird species.

Use of Olfaction in Avian Species

All birds possess olfactory organs. However, argument continues as to how important olfaction is in different species. A wide range of birds show olfactory ability and olfactory uses vary widely between species. The following is a short account of olfactory use in various bird species.

Vultures have long been thought to find prey by smell, but olfactory sensitivity differs greatly between species. The greater yellow-headed vulture (*Cathartes melambrotus*)

and the turkey vulture (*Cathartes aura*) are thought to use olfaction (Smith and Paselk, 1986; Gomez *et al.*, 1994), but the black vulture (*Coragyps atratus*) and king vulture (*Sarcoramphus papa*) are unable to locate food by smell (Stager, 1964; Houston, 1984).

In Passerines, the small size of the olfactory tissue makes their olfactory ability particularly interesting. Clark and Mason (1985) suggest that starlings (*Sturnus vulgaris*) use olfaction to distinguish fresh vegetation with high biocidal values, and use this vegetation to fumigate their nests (Clark and Mason, 1987; Clark, 1990; Clark, 1991). Olfaction may also play a role in the homing ability of starlings (Wallraff and Hund, 1982) and in the ability of Passerines to select antimicrobial or insecticidal objects to control skin parasites (Clark *et al.*, 1990; Clark, 1990). Harriman and Berger (1986) report that ravens (*Corvus corax*) are able to use olfaction to locate hidden prey. The ability of some Passerines to use olfaction suggests that simple olfactory tasks can be accommodated with even small amounts of olfactory tissue, and that in Passerines, at least, the relative allocation of brain tissue to olfactory function has little bearing on olfactory acuity (Clark *et al.*, 1993).

For centuries, Procellariiformes have been credited with a keen sense of smell. This stems mostly from reports of their being attracted over great distances to offal from fishing boats (Roper, 1999). Procellariiformes have well developed olfactory systems, with highly scrolled conchae, and large olfactory ratios of 27 to 37% (Roper, 1999). Most are nocturnal (Wenzel, 1980), and olfaction has been suggested as a means by which some species locate both colonies (Bang, 1966; Grubb, 1973) and specific nest burrows (Grubb, 1974; Minguez, 1997). Some seabirds also use smell to find surface prey (Grubb, 1972; Jouventin and Robin, 1984; Verheyden and Jouventin, 1994).

Domestic pigeons (*Columbia livia*) probably use olfaction for homing, especially from unfamiliar sites, and fly in the direction of odours that have been previously detected at the loft (e.g. Papi, 1982; Wallraff, 1982; Ioale *et al.*, 1990; Papi, 1991). However, Roper (1999) suggests that too little is known about atmospheric odours, and how pigeons may use these, to judge how plausible olfactory homing is.

Domestic chickens (*Gallus gallus*) also show olfactory awareness (e.g. Jones and Gentle, 1985; Burne and Rogers, 1996; Marples and Roper, 1996; Marples and Roper, 1997). Olfactory structures are evident in the domestic chick from the second day of incubation (Roper, 1999), but olfactory responsiveness is not fully developed until the day before hatching when the beak penetrates the air sac (Romanoff, 1960; Tolhurst and Vince, 1976).

It can no longer be doubted that birds possess a sense of smell. However, questions about how birds use this in their everyday lives, and about the extent to which reliance on olfactory cues varies between species, still remain to a large extent unanswered (Roper, 1999). Although birds have the potential to use olfactory cues for a wide variety of purposes, very little is known about whether, and especially how, they actually use them in natural situations (Roper, 1999).

PART TWO

The Kiwi

The kiwi is classified in both its own family (Apterigidae) and order (Apterygiformes), which is an uncommon distinction in avian nomenclature and reflects the unusual characteristics of kiwi. There were an estimated 12 million kiwi on mainland New Zealand before Maori and Europeans arrived (Peat, 1990). Terrestrial mammals, except for short-tailed and long-tailed bats, were lacking in New Zealand and in this relatively safe environment ratites, which include kiwi and moa, attained more diverse forms than in any other country (Peat, 1990).

Kiwi populations began to decline after humans arrived in New Zealand. Large areas of potential forest habitat, totalling two thirds of the original forest cover, were cleared by both Maori and Europeans (McCulloch, 1995; Department of Conservation and Ministry for the Environment, 1998). Thousands of kiwi were also killed in the 1870s for export to foreign museums and for use in the European fashion industry (Colbourne

and Robertson, 2000). By the early 1990s large-scale forest clearance had largely halted but kiwi numbers continue to decline to the current estimate of about 70,000 (Colbourne and Robertson, 2000).

The primary factor in the continuing decline of kiwi populations is now predation by introduced mammals (McLennan *et al.*, 1996). This includes dogs, cats and possums, but by far the biggest threat is predation by mustelids. Three species of mustelids (*Mustela erminea* (stoat), *M. nivalis* (weasel), and *M. furo* (ferret)) were introduced in the 1880s (King, 1995) to control increasing numbers of rabbits. Ferrets kill both juvenile and adult kiwi, but the main reason for the continuing decline in kiwi numbers is predation on young kiwi by stoats (McLennan *et al.*, 1996). Juvenile kiwi suffer exceptionally high mortality rates, with over 90% of juveniles dying before they reach adulthood (McLennan and Potter, 1993; McLennan *et al.*, 1996). Current studies indicate that numbers of Northern brown kiwi are declining by 5.8% per annum and the inevitable loss of the current adult population, as they die of old age, will result in many local extinctions (McLennan *et al.*, 1996).

Up to 1995, three species of kiwi were recognised – the great spotted kiwi (*Apteryx haastii*), the little spotted kiwi (*A. oweni*) and the brown kiwi (*A. australis*), with brown kiwi divided into three sub-species - the North Island, South Island and Stewart Island brown kiwi (McLennan and Potter, 1992). Following studies by Baker *et al.* (1995), brown kiwi have been treated as comprising two distinct species – Northern brown kiwi (*A. mantelli*), found in the North Island and Okarito, and Southern brown kiwi (*A. australis*), which occur south of Okarito.

Kiwi have many characteristics in common with mammals including the use of burrows, hairlike feathers, facial bristles, two functional ovaries, a lower body temperature than other birds, and the near absence of wings (Calder, 1978). Kiwi are omnivorous, opportunistic feeders taking whatever invertebrates are plentiful (McLennan, 1990; Miles, 1995). They eat mainly earthworms, cicada nymphs, insect larvae and various adult beetles (Reid *et al.*, 1982; Kleinpaste, 1990) but spiders, snails, centipedes, millipedes, crustaceans and small quantities of vegetable matter are also taken. Large seeds, such as hinau fruit, are consumed along with grit and stones to aid the break up of food in the crop (Reid *et al.*, 1982; Kleinpaste, 1990).

The tip of the upper mandible overlaps and protects the lower one while kiwi are probing (McLennan, 1990). Kiwi often exhale forcibly while probing, apparently to clear dirt from their nostrils and they also sniff loudly when approaching a strange object, suggesting that they perhaps test the air for olfactory clues as do mammals (McLennan, 1990). Kiwi are also assumed to have a good sense of hearing (Reid and Williams, 1975). The ear openings are obvious in all species and kiwi seem to listen for prey when they search for food (Yates, 1835; Haeusler, 1923; Peat, 1990; Johnson, 1996).

Historically, kiwi were assumed to have poor eyesight. Their eyes are small compared to those of other nocturnal birds and Reid *et al.* (1982) suggest the eyes have inadequate forward convergence to provide binocular vision, which is important for judging distances and positions of small items. However, Sivak and Howland (1987) suggest that kiwi are more like small-eyed nocturnal mammals. They studied refraction in the kiwi eye, and suggest that kiwi are more likely to be hyperopic (an inability to see near objects) rather than myopic (an inability to see distant objects) as historically assumed. Field observations also do not support the idea that kiwi are blind. Even in daylight, kiwi will negotiate their way though the bush at speed without crashing into anything and only panicked kiwi are likely to hit obstacles (Peat, 1990).

Olfaction in Kiwi

Kiwi have long been assumed to use smell over auditory or visual cues to find their prey. Most assumptions are based solely on anatomical evidence, given that kiwi have the second largest olfactory ratio (34%) of any known bird (Bang and Cobb, 1968). They are also the only extant bird with external nares at the tip of its bill (Parsons, 1971). Kiwi have a well developed olfactory bulb, with a similar structure to that of mammals (Reid and Williams, 1975). Associated with this is a much reduced optic lobe of the brain.

Instead of a single olfactory concha, kiwi have a series of five projections within the olfactory chamber (Parsons, 1971), and the olfactory chamber is enlarged in comparison to the respiratory parts (Portmann, 1961) (see Figure 1.2) Kiwi also have a pair of nasal valves lying across the roof of the nasal chamber, which may allow them to feed in water (Reid *et al.*, 1982; McLennan, 1990) and possibly prevent soil from entering the olfactory chamber (Peat, 1990). The olfactory epithelium begins just behind these nasal valves.
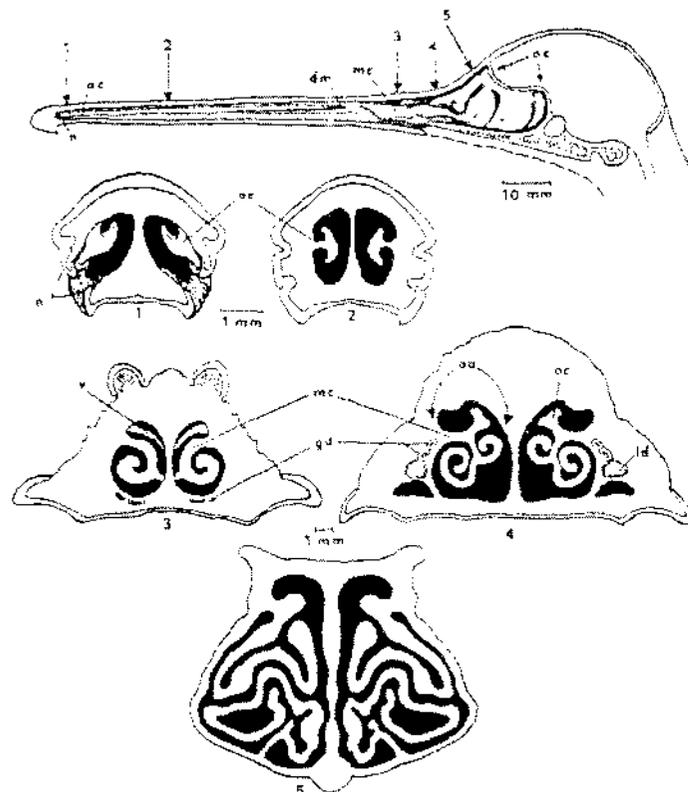
Figure 1.2: The kiwi nasal cavity. Numbered arrows on the top picture denote the levels of coronal sections shown – ac = anterior concha, dm = duct mouth, gd = gland ducts, ld = lacrimal duct, mc = maxillary concha, n = nostril, oa = olfactory atrium, oc = olfactory concha, v = nasal valve (from Bang, 1971).

Despite the wide-held belief that kiwi have a good sense of smell, there have been surprisingly few experimental studies on their olfactory ability. Benham (1906) was the first to publish olfactory experiments concerning kiwi, based on studies carried out by

the curator of Resolution Island on South Island brown kiwi. Earthworms were placed in shallow buckets, and covered with four inches of soil, with control buckets only containing soil. Benham (1906) stated that kiwi promptly probed the worm-containing buckets and ignored the control buckets, and concluded that this afforded some evidence that kiwi have a keen sense of smell.

Strong (1911) attempted to repeat Benham's (1906) work at the London Zoological Gardens, but failed to obtain positive results. Flower pots were partly filled with soil and placed at one end of an enclosure containing three kiwi. One of the pots contained earthworms, although details are not given. Only one kiwi approached the pots and on several occasions it did not discover the prey, although contact with the worms must have been made. Eventually the worms were located, apparently by hit or miss probing, and Strong (1911) concluded that there was no evidence of the acute sense of smell described by Benham (1906). Haeusler (1923) also reported that kiwi often did not detect prey that was directly in front of them and suggested that the sense of smell played a very unimportant role in prey detection. Instead, Haeusler (1923) suggested that the bill acted as a highly sensitive organ of touch and observed that as soon as the tip of the bill came into contact with something edible, the kiwi would invariably seize and consume it.

Wenzel (1968; 1971b) was the first to study kiwi olfaction in detail. Experiments were carried out using five kiwi, which were held in groups in two aviaries. The experiments were designed to test the ability of kiwi to locate their regular food under conditions that eliminated the use of visual, tactile, taste or auditory cues (Wenzel, 1971b). Three feeding stations, each consisting of a slightly tapering aluminium tube, were sunk into the ground in each aviary soon after dark. A ring around the top of each tube held an infrared light source and a detecting photocell, so that each approach by kiwi to the tube was recorded when the lightbeam was broken.

Food was placed in two of the aluminium tubes, and moistened soil in the third. Experiments varied with the amount of food in each tube, and all tubes were covered with nylon mesh that the kiwi could puncture. In certain experiments, the nylon mesh was covered with up to one inch of soil. Wenzel (1968; 1971b) states that the air space between the contents and the nylon mesh prevented the contents from being identified

by licking the top of the screen. This is an amazing suggestion considering that the rigid tongue of kiwi measures about 17 mm and never protrudes outside the 90-145 mm long beak.

Wenzel (1968; 1971b) gives no details about the number and specific type of experiments performed, but states that in a total of ten tests perfect performance was achieved with two pairs of kiwi, who only punctured the nylon mesh in tubes containing food. Tubes containing soil were visited and inspected closely, but the nylon mesh was never punctured. In a few experiments, Wenzel (1968; 1971b) used sections of giant earthworm and whole common earthworms. Although kiwi found the giant earthworm sections, they never found the whole earthworms and instead probed tubes containing their usual artificial food. Wenzel (1968) concluded that the performance of kiwi in tests to locate food was completely convincing. However, because kiwi were not under totally natural conditions, it cannot be inferred whether kiwi regularly locate their food by smell in the wild, although evidence strongly suggests they are capable of doing so (Wenzel, 1971b).

Flinn (1995) also repeated work similar to Wenzel's (1968; 1971b) experiments. Experiments were performed to test the ability of kiwi to find their normal artificial diet beneath different depths of soil, using PVC tubing pushed into the soil. Kiwi often did not detect the food and many of the control tubes were probed when no food was present. Flinn (1995) suggested that the inability of kiwi to distinguish between tubes with and without food could be because: (1) kiwi were interested in the freshly disturbed ground around each tube; (2) the tubes containing food may have encouraged the kiwi to check all of the other tubes; and (3) kiwi were only able to tell if the tube was empty after probing through the soil.

Despite the failure of many experiments to produce positive results, most authors still assume that kiwi have an excellent sense of smell (e.g. Reid and Williams, 1975; Stoddart, 1980; Reid *et al.*, 1982; McLennan *et al.*, 1987; Peat, 1990; Johnson, 1996; Robertson, 1996). Waldvogel (1989) even states that Wenzel's (1968; 1971b) results demonstrate that kiwi are macrosmatic, and that their highly developed sense of smell is the primary sense used in foraging. However, in contrast to most authors, Roper (1999) notes that all experiments performed so far on kiwi olfaction have been descriptive

rather that quantitative, and that the assumption that kiwi have a good sense of smell still relies on indirect evidence and remains to be convincingly demonstrated.

Finally, McLennan *et al.* (1987) suggested that kiwi may use odour to mark territories. Kiwi possess a well-developed uropygial gland at the base of the tail, which secretes preening oil (Jacob, 1982) and both the birds themselves and their faeces have a distinct, pungent smell. This odour often lingers in burrows for days or even weeks after the birds have left them and McLennan *et al.* (1996) suggest that this strong odour may play an important role as a signal for the maintenance of territories. All wild kiwi use a large number of dens scattered throughout their ranges, so it is also possible that these may act as scent posts to advertise occupancy.

The Importance of Understanding Kiwi Olfaction

Olfactory studies on a single species, such as the kiwi, can yield very different results and various interpretations have possibly been affected by pre-emptive assumptions in the past. Knowledge of an animal's sensory abilities is an essential prerequisite for understanding almost every aspect of its behaviour, and is particularly relevant to issues of management, conservation and welfare (Roper, 1999).

Understanding how a kiwi finds its food, and how it marks its territory, if in fact it does so, is essential to understanding its ecology, including intraspecific interactions which may affect the survival of released birds. Knowledge of the food finding ability of kiwi may also improve captive management through providing a more enriched environment and improving natural foraging activities. Territorial marking may also be important in ensuring successful pair bonding in captive kiwi.

Thesis Aims and Layout

The primary aims of this thesis are to: (1) determine whether kiwi respond to faecal odours in a way that suggests they may use these to mark territories, (2) determine whether kiwi respond to roost box odours in a way that suggests they may use roost burrows as scent posts in their territory, and (3) determine whether kiwi use olfaction as the primary sense in finding prey. This thesis is divided into five chapters, and each chapter is intended to be read as a separate unit.

Chapter Two investigates the responses that kiwi make to faecal odour placed in their enclosure. Both the kiwi's own faeces and foreign kiwi faeces were introduced into the enclosure. Six containers were placed in each enclosure – two with the kiwi's own faeces, two with foreign kiwi faeces and two empty as controls. Resident kiwi were observed and responses recorded for four hours each night over three consecutive nights.

Chapter Three investigates the responses of kiwi to faecal odour within roost boxes. Three roost boxes were introduced into each enclosure for six trial nights. Each night one roost box had the kiwi's own faeces, one had foreign kiwi faeces, and one was empty as a control. Analysis included which roost boxes kiwi entered, which boxes kiwi roosted in, defecation by the resident kiwi in the roost box, and the order the roost boxes were entered.

Chapter Four investigates the ability of captive kiwi to detect subterranean prey by smell. Earthworms were set into large boxes, each containing 15 small containers, dug into the soil of the enclosure. The amount, concentration and depth of prey was altered between four experiments. Differences in the number of cells probed, the proportion of probes into cells, and the number of earthworms taken were analysed.

Finally, **Chapter Five** includes a discussion on the major findings of this thesis and the implications for captive management of kiwi. Future research is also discussed.

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Chapter Two: Responses of Captive Northern Brown Kiwi to Faecal Odours

Responses of Captive Northern Brown Kiwi to Faecal Odours

ABSTRACT

Responses of captive Northern brown kiwi were observed towards containers with faeces from the resident kiwi, a foreign kiwi, and empty controls. The age and sex of the kiwi significantly affected the likelihood of approach to foreign kiwi odour and the responses that were made to odour types. Juvenile kiwi approached odours significantly more often than adult kiwi, suggesting that juveniles use faecal odours to assess other kiwi in the area. Juvenile kiwi and adult female kiwi were attracted significantly more than adult male kiwi to foreign kiwi odour, suggesting that adult male kiwi are repelled from foreign odours, thereby possibly avoiding encounters with territorial neighbours. Kiwi also showed significantly more response to foreign kiwi odour, by running away from the odour and probing less often around these odour containers. Juvenile males showed more extreme responses than adult males, suggesting that they express escape behaviour from an area that contains a foreign kiwi odour to avoid confrontation with resident adults. Results suggest that kiwi respond to faecal odours in a way consistent with the hypothesis that they use faeces to mark territories.

INTRODUCTION

Kiwi have long been assumed to have a well developed sense of smell. Most assumptions are based on anatomical evidence, given that kiwi are the only extant bird with external nares at the tip of its bill (Parsons, 1971) and they have the second largest olfactory ratio (34%) of any known bird (Bang and Cobb, 1968). The olfactory bulb in the kiwi brain is well developed and has a similar structure to that of mammals (Reid and Williams, 1975).

New Zealand birds share many characteristics with mammals. The long isolation of New Zealand and the lack of native terrestrial mammals has led to frequent niche shifts, gigantism, extended life histories and low reproductive rates in endemic birds (Daugherty *et al.*, 1993). Many have evolved to fill ecological niches that are occupied by mammals elsewhere. Kiwi, in particular, exhibit several mammalian characteristics, including their use of burrows, nocturnal habits, aggressive maintenance of year-round territories, and their use of smell (Wenzel, 1968; 1971; Daugherty *et al.*, 1993). It follows that these birds may also communicate in similar ways to mammals, using visual, auditory and olfactory cues (Kappeler, 1998). Kiwi and their faeces have a distinct, pungent smell, which lingers in burrows for some days after the kiwi have used them (McLennan *et al.* 1987), suggesting that kiwi may use this scent to advertise occupancy of a territory. McLennan *et al.* (1987) also suggest that kiwi may use dens scattered throughout their range as scent posts. During a study on kiwi in Hawke's Bay, McLennan *et al.* (1987) found that several birds used dens excavated by resident birds when they entered the territories of other kiwi. They reasoned that the only way such kiwi were able to find the well-disguised dens was by smell.

Territorial scent marking is a form of olfactory communication using chemical signals to mark an individuals' territory. It is usually effected through excretory products (i.e. urine and faeces) and/or gland secretions. In mammals, scent marks are placed on conspicuous objects, or on the ground, in an individual's range or territory and thus often involve a cost in time and energy to produce (Johnson, 1973; Gosling and Wright, 1994). If the costs of scent marking the territory (in terms of time and energy and perhaps

increased vulnerability to predators) are lower than the costs of actively defending the territory from intruders, then the use of scent marks can become an economic strategy for territorial defence (Gosling, 1982). Scent marks may remain in the environment for some time, providing an effective and reliable means of advertisement (Rich and Hurst, 1999).

The function of olfactory signals varies between species and may include information on species, group, sex, and individual identity, reproductive state, age and social status (Eisenberg and Kleiman, 1972). Scent marking is also involved in intrasexual competition and mate attraction in some species (Kappeler, 1998). Gosling (1982) suggests that the meanings of social odours are no less diverse than visual or auditory signals.

Kiwi have a territorial situation similar to that described for aardwolves by Richardson (1991). Thus, kiwi defend large territories, so the detection rate of intruders is probably low, and the costs of intrusion are low enough to allow regular intrusion by neighbours and non-territorial birds. This is also apparent from the extent of range overlap of kiwi reported in several areas (Taborsky and Taborsky, 1995). However, kiwi are very aggressive when defending territories, and it is expected that intruders should escape if detected. If kiwi do scent mark their territories using faeces, then a slight repellent effect of foreign kiwi odours might be expected, along with escape behaviour. The following study aimed to determine whether kiwi respond to faecal odour in a way consistent with faeces being used to scent mark territories.

Although most studies on scent marking involve mammals (e.g. Hurst, 1990; Richardson, 1991; Gosling and Wright, 1994; Heymann, 1998; Kappeler, 1998; Sillero-Zubiri and MacDonald, 1998; Allen *et al.*, 1999; Heymann, 2000), there have been a few studies on territorial marking in amphibians (e.g. Simons *et al.*, 1997), and reptiles (e.g. Carpenter and Duvall, 1995; Aragon *et al.*, 2000). In several avian species, smell has been suggested to be used for navigation (e.g. Bang, 1966; Grubb, 1972; Grubb, 1974; Jouventin and Robin, 1984; Verheyden and Jouventin, 1994), homing (e.g. Papi, 1982; Wallraff, 1982; Ioale *et al.*, 1990; Papi, 1991; Wallraff, 1993), learning (e.g. Calvin *et al.*, 1956; Michelson, 1960; Stattelman *et al.*, 1975), and prey finding (e.g. Harriman and

Berger, 1986; Smith and Paselk, 1986; Clark *et al.*, 1993; Gomez *et al.*, 1994; Roper, 1999). However, I know of no previous studies involving territorial scent marking by any avian species.

METHODS

Kiwi Used

A total of 43 kiwi were observed in 27 enclosures. All were captive held in nocturnal houses and outside enclosures at institutes throughout New Zealand (for details see Table 2.1). The adult kiwi tested included ten pairs, seven single adults and two male kiwi held together. Juvenile kiwi tested included three groups (one of five, one of three, and one of two), two juvenile females held together, two juvenile males held together, and four single juveniles. Nocturnal house kiwi used included two single adults, one adult pair, three juvenile groups (described above), two juvenile females held together, two juvenile males held together, and two single juveniles. Kiwi housed outside included two adult males held together, five single adults, nine pairs, and two single juveniles.

Table 2.1: Details of the kiwi used at each institute (total = 43). The number of kiwi held in each enclosure type (total number of enclosures = 27), and the number of kiwi held in nocturnal houses (total = 16) and outside enclosures (total = 27) are given. Numbers in brackets represent kiwi that did not encounter the odour containers over the trial, so their data were excluded. Juveniles were 3 years of age or younger. Pair enclosures held one adult female and one adult male. Same sex pairs involved either adult or juvenile birds. All groups involved only juveniles and included a group of two, a juvenile male and a juvenile female so could not be classified under a paired status.

Institute	Number of kiwi used:				Number of kiwi held as a:				Number of kiwi housed in:	
	Juvenile Female	Juvenile Male	Adult Female	Adult Male	Single	Pair	Same Sex Pair	Group	Nocturnal House	Outside Enclosure
Auckland Zoo	0	2	1	1	0	2	2	0	2	2
Otorohanga Kiwi House	2	1	4	5	1	6	2	3	4	8
Rainbow Springs	2	0	1	3	4	0	2	0	3	3
Westshore Wildlife Reserve	2	0	1	2	3	2	0	0	0	5
Orana Park	1	2	2	2	1	4	0	2	2	5
Willowbank Wildlife Reserve	5 (2)	1 (1)	3 (1)	4	2	6 (1)	0	5 (3)	8 (3)	5 (1)

Odour Containers

Odour containers comprised clear plastic sample vials 45 mm in diameter and 55 mm deep. A 4 mm diameter hole was drilled in the centre of the container lid and a 4 mm diameter soft galvanised wire rod, approximately 155 mm long, was inserted through this hole to use as an anchor for the odour containers. The rod was threaded at one end, then fixed to the container lid with two 4 mm hexagonal nuts, on either side (Figure 2.1a). Approximately 7 mm of the rod, and one nut, was exposed on the inside of the container lid. Hot glue was used to keep the nuts from loosening. This glue was odourless to humans once dry.

Thirteen holes, each measuring 3 mm diameter, were drilled in the bottom of the container using a pre-made pattern, so they were evenly distributed over the bottom surface. Eight holes, also 3 mm diameter, were drilled in the side of the container. These were spaced evenly around the side, centred approximately 18 mm from each other and 5 mm from the bottom.
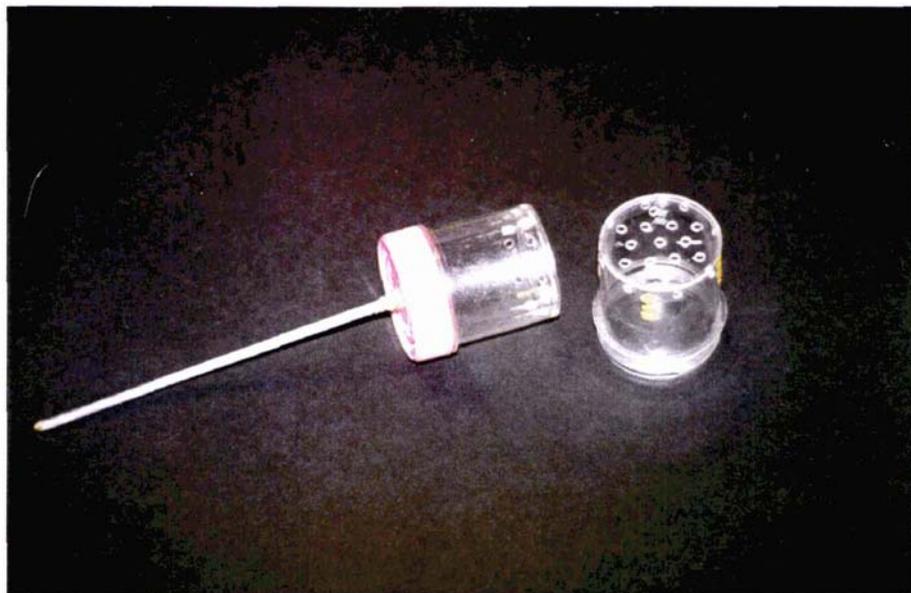
Figure 2.1a: Odour containers, showing the holes drilled at the top and in the sides of the containers to allow odour to diffuse. Note the anchoring rod attached to the container lid and reflective tape on the sides of the container nearest the holes.

Small pieces of reflective tape, approximately 3-4 mm square were used to identify and differentiate the containers according to the odour present. Tape was placed equidistantly at 4 points around the side of the container. A single piece of tape, placed at each point, indicated a container with the resident kiwi's faeces, two pieces indicated a container with foreign kiwi's faeces, and three pieces indicated a control container without odour.

Containers were placed upside-down in the enclosure with the wire rod pushed into the enclosure soil so that the container lid was flush with the ground and the container itself was above ground (Figure 2.1b).

Figure 2.1b: View of an odour container pushed into the soil of a kiwi enclosure, showing the holes at the top. This container is a control container, with three pieces of reflective tape, and contains no kiwi faeces.

Positioning Odour Containers in Enclosures

All faeces and odour containers were handled using disposable latex gloves. Approximately 3 g of fresh faecal matter was placed on the inside of the lid of the upturned container, just prior to arranging the containers in the enclosure. The container was then screwed tightly onto the lid. A total of six containers were placed in each enclosure for three consecutive nights. Two containers contained the resident kiwi's faeces, two contained faeces of a foreign kiwi, and two containers were left empty as controls. Containers were arranged in a line with approximately 1.5 m between each container. If enclosures were small, the line of containers was curved so that no container was closer than 1.5 m to another. At times containers had to be further apart so that I could view each of them from the observation point. Containers were also placed in the open rather than under or behind plants, so they could be viewed easily.

The order in which odour containers were placed was randomised. Clean containers holding fresh faeces were used each day and the order they were presented in was randomised again. All containers were washed after each use, using dish detergent and cold water, and left to dry. No odour could be detected by humans after washing.

Observing Kiwi

Kiwi housed in pairs or groups were identified by individual characteristics or leg bands. Those in nocturnal houses were observed directly from the public observation areas. On a few occasions this meant that I could not see the kiwi momentarily when the public obstructed my view. If possible, I moved so observations could continue, but these disruptions were ignored, and it was assumed that they did not bias data. Kiwi held outside were observed using an ITT Night Vision Night Enforcer nightscope. I sat in the enclosure, as far away from odour containers as possible, but where I could still observe all six containers. No kiwi appeared agitated by my presence.

Kiwi were observed for four hours once activity commenced. On one occasion, while observing a group of three juveniles in a nocturnal house, observations were stopped after 129 encounters were recorded in two hours.

Recording Behaviour

An encounter was scored when the head of the kiwi was within 30 cm of the odour container. Any responses within this distance were most likely a reaction to the nearest odour container rather than to an adjacent container. Encounters were recorded whether kiwi purposefully approached the container, or passed it without apparent purpose. Encounters were not recorded if the kiwi was running in a panic (i.e. being chased by another kiwi or after a fright) and recording was stopped after 10 encounters if the kiwi paced a path near the odour containers (this behaviour was only seen in nocturnal house kiwi).

The following four behaviours were scored after a kiwi encountered a container:

No Response (NR):
The kiwi approached the container without purpose, either at a walk or a trot, and did not change gait within the encounter zone of the container. They showed no apparent interest in the container by sniffing, purposeful touching or otherwise. On some occasions kiwi walked over the containers, without seeming to notice that they had done so.

Walked Away (W):
The kiwi approached the container with or without purpose then stopped and either touched the container with the bill, sniffed the container, or turned the head towards the container. They then walked away from the container.

Ran Away (R):

The kiwi approached the container with or without purpose then stopped and either touched the container with the bill, sniffed the container, or turned the head towards the container. They then ran away from the container.

Probed (P):

The kiwi approached the container with or without purpose and probed the soil within the encounter zone (i.e. within 30 cm). This could happen after acknowledging the presence of the container, or approaching the container while already probing the soil, and not acknowledging the container.

Only one response was recorded for each encounter. An individual had to exit the encounter zone first before another response to a specific odour container was recorded.

Data Analysis

Data are appended on the enclosed CD. Analysis was performed using SAS, Version 6.12, with a generalised linear model and a Poisson type1 distribution. The data were over dispersed (i.e. a large variance in the number of encounters by individual kiwi), so the model was adjusted using the dscale option in SAS, which estimates the scale parameter based on the deviance. Variables were considered significant if $P < 0.05$. Least significant means tests were performed using SAS, Version 8.0. Several variables were nested together, when every level of one factor occurs with only one level of another factor. The variable kiwi (the 43 individuals) was nested with age (juvenile (three years old or younger) or adult), sex (male or female) and housing (nocturnal house or outside enclosure) because an individual kiwi (or enclosure) could only be one age, one sex, and one housing type. The effect of the interaction between age and sex could not be included in the model because of the nested kiwi variable, and probe rates were compared between kiwi of different age and sex using means and standard errors alone. Several variables could not be included in the model because the mean parameter was

invalid or at a limit of its range. This occurred because of the number of zeros in the data, so the model did not converge. This included all three-way variables involving housing in the model used to assess the effect of trial day (day one, two or three), and the interaction between age-sex-odour-response in both models.

To determine whether kiwi encountered and responded differently to the odours on different trial days the number of encounters was used as the dependent variable in the Genmod analysis. This was compared to seven classes – kiwi, age, sex, housing, day, odour (the resident kiwi's faeces, foreign kiwi faeces, or control odour), response (no response, walked away, ran away, or probed), and combinations of these. These data were only used to investigate the effect of trial day because of the large number of zeros in the dependent variable data. The relatively small sample size meant that only the effects of age, sex and housing were investigated for paired comparisons.

Data from the three trial days were subsequently pooled for each kiwi for further analysis. To determine whether kiwi encountered and responded differently to the odours, the number of encounters was used as the dependent variable in the Genmod analysis. This was compared to six classes – kiwi, age, sex, housing, odour, response, and combinations of these. Only the effects of age, sex and housing were investigated for paired comparisons because of the relatively small sample size.

RESULTS

Individual Variation

Only four kiwi never approached any of the containers over the trial period and their data were excluded. One was a paired female who never used the middle of the enclosure, where the odour containers were placed, while I was present. The other three birds were all juveniles in a group of five, held in a nocturnal house. These individuals generally stayed in particular areas of the enclosure, and only two of them used the area where the odour containers were placed.

Encounters by other individuals ranged from one (two adult males - one singly housed outside, and one paired male) to 254 (a nocturnal house juvenile male, housed with another juvenile male).

There was a significant difference ($\chi^2 = 1045$, DF = 39, 1417, P = 0.0001) in encounter rates between individual kiwi, giving an overdispersed distribution, and this is the reason why the fixed parameter was used in the SAS analysis. The number of encounters was also affected by the size of the enclosure (Figure 2.2).

Total Number of Encounters

A total of 1615 encounters were recorded. These included 398 encounters by 17 adult males (average = 23.4 encounters per individual, S.E. = 8.2), 316 encounters from 11 adult females (average = 28.7 encounters per individual, S.E. = 9.7), 390 encounters from five juvenile males (average = 78.0 encounters per individual, S.E. = 45.5) and 511 encounters from ten juvenile females (average = 51.1 encounters per individual, S.E. = 16.5).
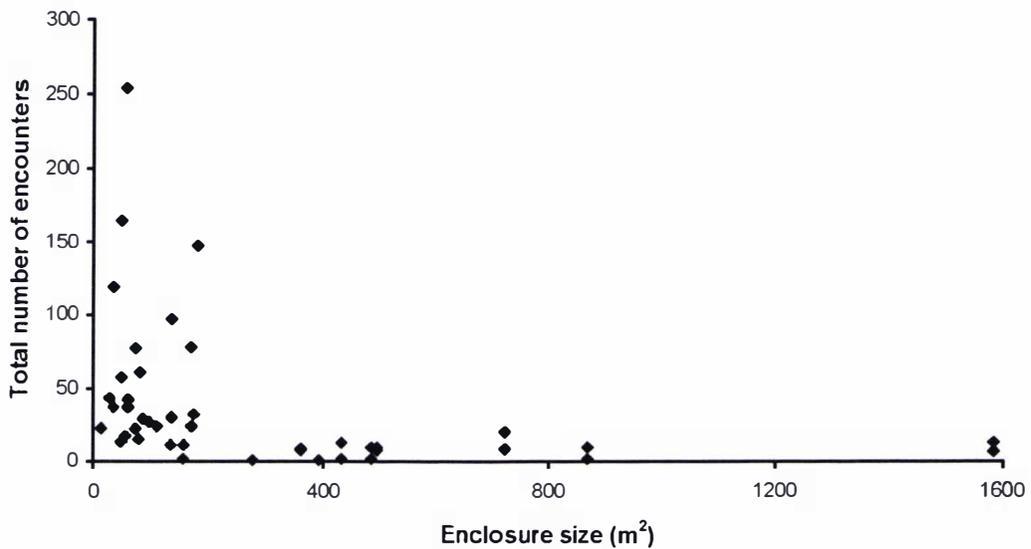
Figure 2.2: Total number of encounters to odour containers made over the trial by individual kiwi in enclosures of different size. Each trial was run over three consecutive days.

A total of 990 encounters were recorded from 16 nocturnal house kiwi in ten enclosures (average = 61.9 encounters per individual, S.E. = 17.0). A total of 625 encounters were recorded from 27 kiwi housed outside in 17 enclosures (average = 23.1 encounters per individual, S.E. = 5.9).

Effect of Trial Day

The data were overdispersed (deviance value = 2175.08, DF = 1417), but this was accounted for by estimating the scale parameter based on the deviance (see Methods for details). Likelihood ratio statistics are included in Table 2.2 and the variables used in this part of the analysis are denoted by ++ in this table.

Table 2.2: Likelihood ratio statistics for factors relating to the effect of trial day on odour encounters and responses made by kiwi. Variables used in this analysis are denoted in the table using ++. Other variables are analysed in the next section, after data for each day have been pooled for individual kiwi.

Source	NDF	ChiSquare	Pr>Chi
Odour	2	0.58	0.7477
Response	3	431.58	0.0001
Age	1	191.02	0.0001
Sex	1	5.14	0.0234
Housing	1	82.30	0.0001
Day ++	2	62.06	0.0001
Kiwi (Age-Sex-Housing)	39	1044.99	0.0001
Age-Day ++	2	19.01	0.0001
Age-Odour	2	11.77	0.0028
Age-Response	3	103.79	0.0001
Sex-Day ++	2	27.94	0.0001
Sex-Odour	2	10.00	0.0067
Sex-Response	3	12.26	0.0065
Housing-Day ++	2	0.79	0.6728
Housing-Odour	2	19.69	0.0001
Housing-Response	3	28.36	0.0001
Odour-Response	6	54.69	0.0001
Day-Odour ++	4	3.13	0.5364
Day-Response ++	6	22.33	0.0011
Day-Odour-Response ++	12	7.78	0.8018
Age-Odour-Response	6	23.33	0.0007
Sex-Odour-Response	6	12.23	0.0571
Age-Day -Odour ++	4	20.08	0.0005
Age-Day-Response ++	6	9.68	0.1388
Sex-Day-Odour ++	4	20.71	0.0004
Sex-Day-Response ++	6	5.91	0.4332

Kiwi made significantly higher numbers of encounters on the first day than on the second or third days (average number and standard errors are shown in Table 2.3).

Table 2.3: Average number (± S.E.) of encounters made by kiwi on each trial day.

Day	Average No. of Encounters	(+) S.E.	(-) S.E.
Day 1	7.39	1.74	1.41
Day 2	6.52	1.16	0.98
Day 3	6.04	1.12	0.94

Juvenile kiwi encountered odour containers significantly more often than adults on each day but they also showed a decrease in encounter rates on the second day that adult kiwi did not (Figure 2.3). There was also a significant difference between the encounter rates made by adult and juvenile kiwi to particular odours over the trial (Figure 2.4). There was no significant difference in the responses made by kiwi of different ages over the trial.

Female kiwi showed a significant decrease in encounter rates on the second day, which males did not show (Figure 2.5) and different sexes also encountered odours at significantly different rates over the trial (Figure 2.6). Female kiwi showed a decrease in encounter rates to all odours on the second day and, as a percentage of total encounters, female kiwi encountered kiwi odours (either their own or a foreign kiwi odour) more than the control odour. In contrast, male kiwi encountered the controls most often on the first two days. There was no significant relationship between trial day and the types of responses shown by kiwi of different sexes. There was no significant different between kiwi of different housing in the number of encounters made over the trial period.
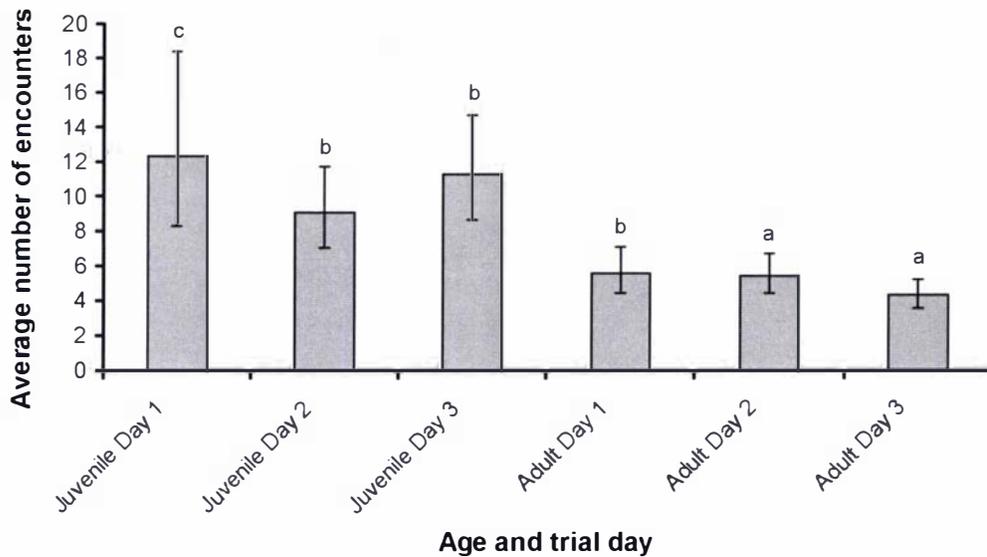
Figure 2.3: Average number of encounters (± S.E.) made on different trial days by kiwi of different ages. Each trial was run over three consecutive days. Different letters on the graph denote significantly different values.
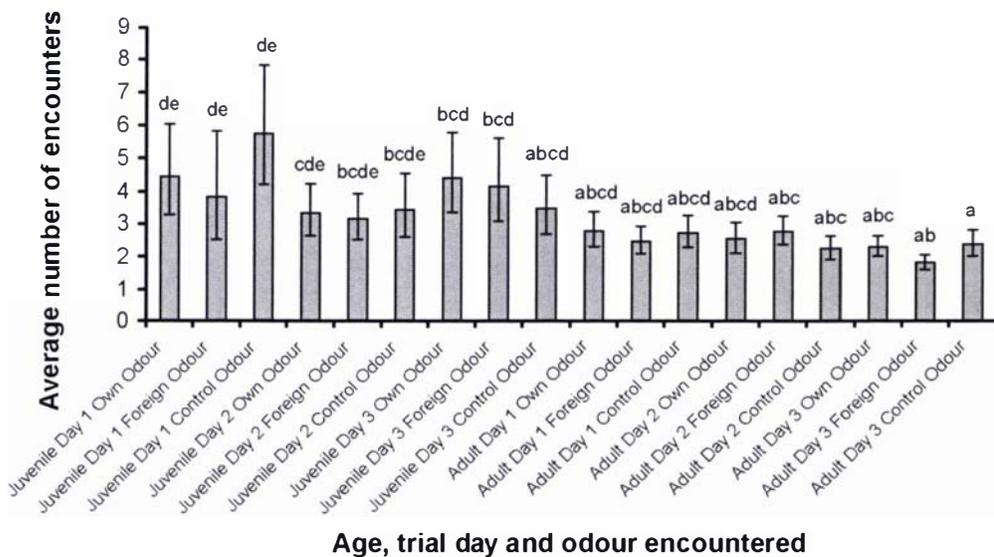
Figure 2.4: Average number of encounters (± S.E.) made to different odours on various trial days by kiwi of different ages. Each trial was run over three consecutive days. Different letters on the graph denote significantly different values.
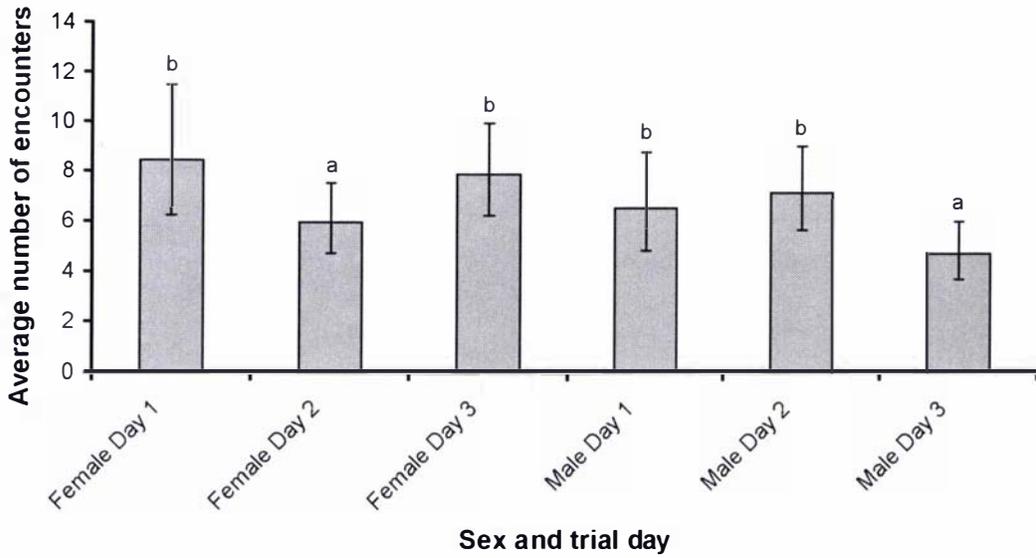
Figure 2.5: Average number of encounters (± S.E.) made on different trial days by kiwi of different sexes. Each trial was run over three consecutive days. Different letters on the graph denote significantly different values.
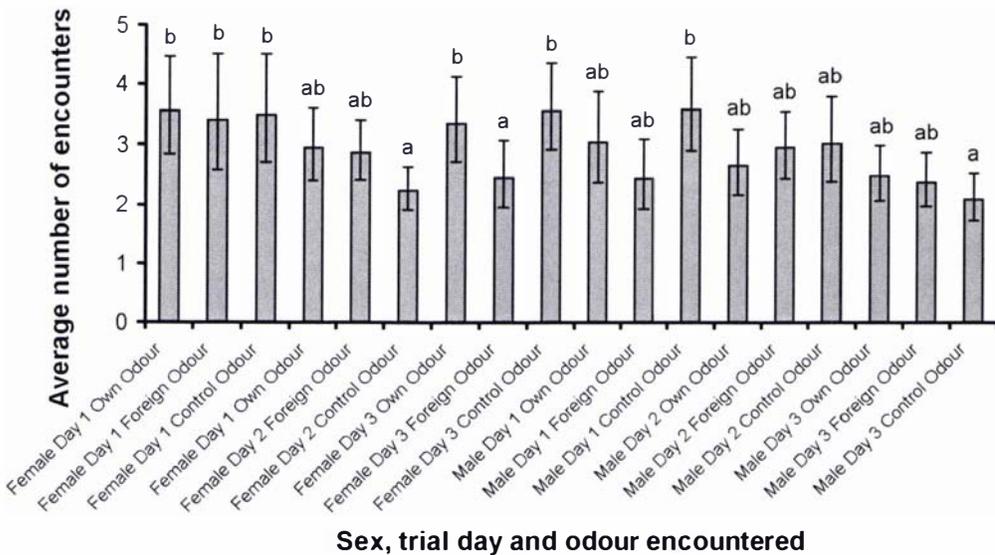
Figure 2.6: Average number of encounters (± S.E.) made to different odours on various trial days by kiwi of different sexes. Each trial was run over three consecutive days. Different letters on the graph denote significantly different values.

Encounter rates to different odours over the three trial days did not differ significantly, but there was a significant difference in the type of responses shown over the trial (Figure 2.7). As a percentage of response types shown on each trial day, there was a general decrease in the percentage of 'ran away' responses during the trial, and an increase in the percentage of 'probed' responses. Responses shown to specific odours did not change over trial days.

Encounters and Responses Made

The data were overdispersed (deviance value = 1000.06, DF = 424), but this was accounted for by estimating the scale parameter based on the deviance (see Methods for details). All other likelihood ratio statistics are included in Table 2.4.

Table 2.4: Likelihood ratio statistics for factors relating to effects on odour encounters and responses made by kiwi.

Source	NDF	ChiSquare	Pr>Chi
Odour	2	0.38	0.8276
Response	3	280.87	0.0001
Age	1	124.32	0.0001
Sex	1	3.35	0.0674
Housing	1	53.56	0.0001
Kiwi (Age-Sex-Housing)	39	680.07	0.0001
Age-Odour	2	7.66	0.0217
Age-Response	3	67.55	0.0001
Sex-Odour	2	6.51	0.0386
Sex-Response	3	7.98	0.0465
Housing-Odour	2	12.82	0.0016
Housing-Response	3	18.46	0.0004
Odour-Response	6	35.59	0.0001
Age-Odour-Response	6	14.62	0.0234
Sex-Odour-Response	6	8.76	0.1874
Housing-Odour-Response	6	8.24	0.2208
Age-Sex-Odour	2	8.60	0.0136
Age-Sex-Response	3	18.80	0.0003
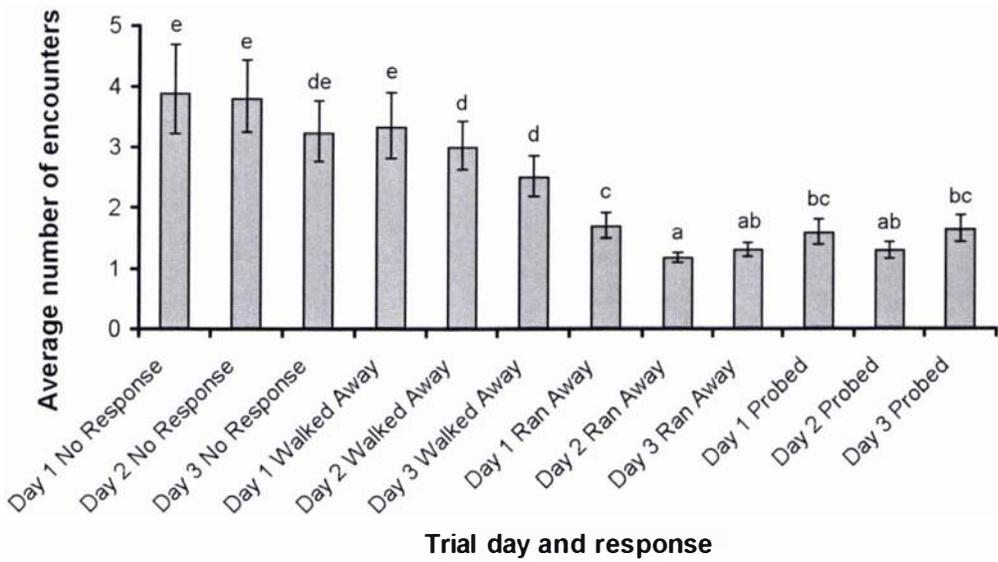
Figure 2.7: Average number of responses (± S.E.) made by kiwi on different trial days. Each trial was run over three consecutive days. Different letters on the graph denote significantly different values.
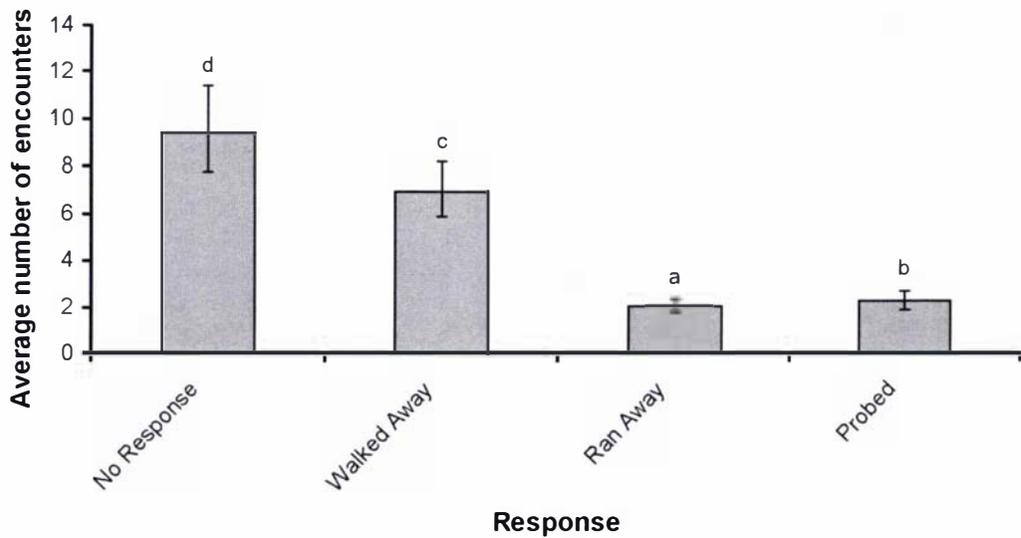
Figure 2.8: Average number of responses (± S.E.) made by individual kiwi. Different letters on the graph denote significantly different values.

Overall, there was no significant difference in the number of encounters made to each odour type. However, the type of responses made upon encountering the odour containers differed significantly (Figure 2.8). The type of response also showed a significant relationship with the type of odour encountered (Figure 2.9). Responses to a kiwi's own odour and to the control odour were not significantly different, but there were significantly more 'ran away' and significantly less 'probing' responses to foreign kiwi odour than to either of the other odour types.

Juvenile kiwi encountered odours significantly more often than adult kiwi. The average number and standard errors are shown in Table 2.5. Kiwi of different ages showed a significant difference in both the encounter rate to particular odours (Figure 2.10), and the type of responses made (Figure 2.11). Juvenile kiwi responded to odour containers more often than adult kiwi and, as a percentage of total responses, showed 'no response' less often than adults. Juveniles also showed more extreme responses (i.e. 'ran away' or 'probed' responses) than adult kiwi.

Table 2.5: Average number ($\pm$ S.E.) of encounters made by kiwi of different ages.

Age	Average No. of Encounters	(+) S.E.	(-) S.E.
Juvenile	34.79	12.01	8.93
Adult	14.79	3.51	2.84

Juvenile and adult kiwi also differed significantly in their responses to different odours (Figure 2.12). There was no significant difference in the way they responded to their own odours and to control odours, but adult kiwi responded to foreign odours more often than to their own or control odours. As a percentage of total encounters, both ages ran away more often, and probed least often, around foreign odours (adults probed only 0.5% of encounters to foreign odours, compared with 5.3% to their own odour and 4.9% to control odours).

Figure 2.9: Average number of responses (± S.E.) made by kiwi to different odours. Different letters on the graph denote significantly different values.
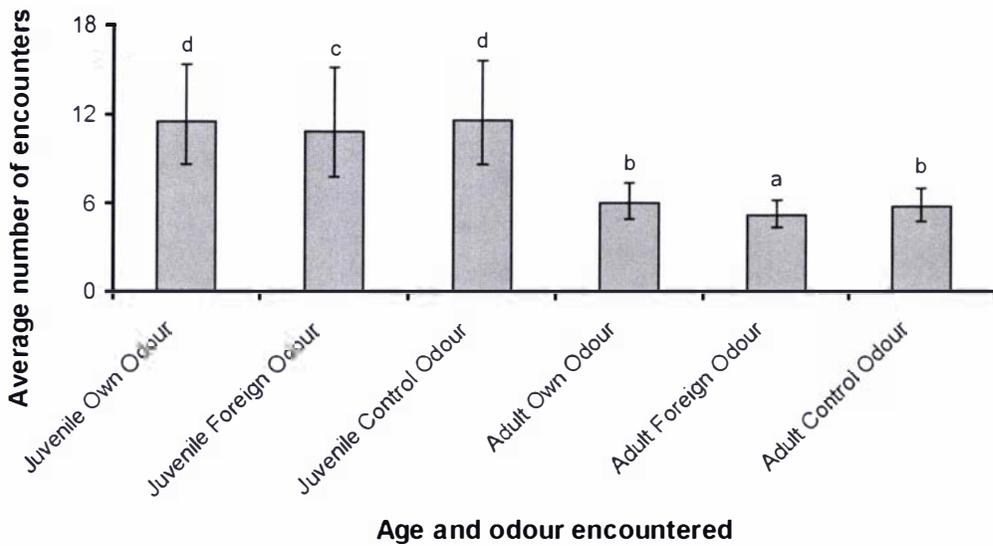
Figure 2.10: Average number of encounters (± S.E.) made to different odours by kiwi of different ages. Different letters on the graph denote significantly different values.
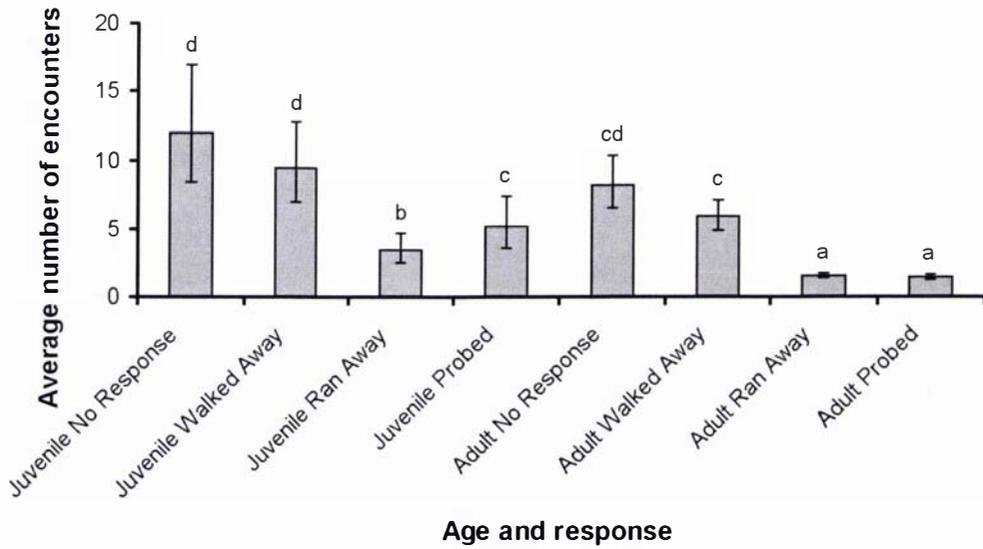
Figure 2.11 : Average number of responses (± S.E.) made by kiwi of different ages. Different letters on the graph denote significantly different values.
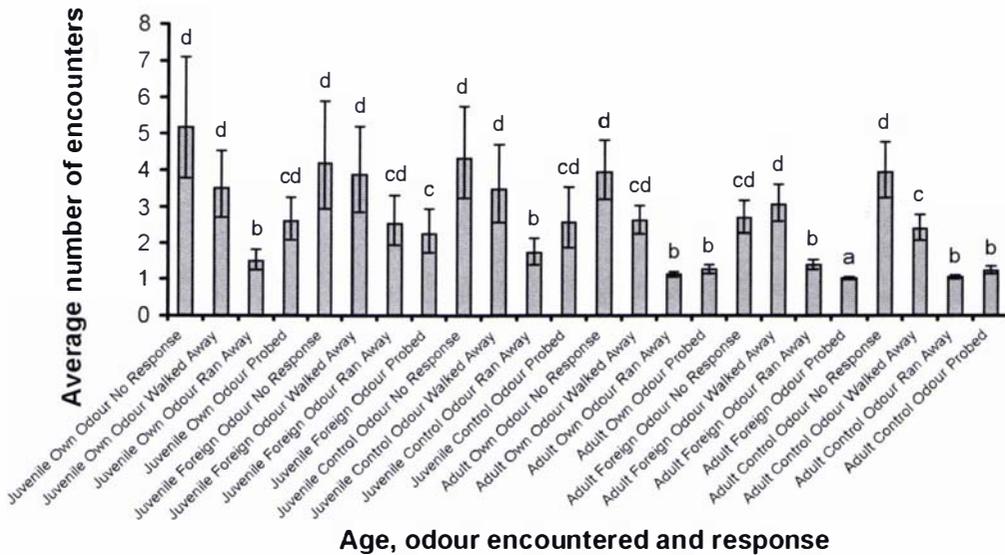
Figure 2.12: Average number of responses (± S.E.) made to different odours by kiwi of different ages. Different letters on the graph denote significantly different values.

There was no significant difference between the encounter rates shown by male and female kiwi, but there was a significant relationship between odours encountered and the sex of the kiwi. Female kiwi encountered their own odour slightly more often than foreign odours or controls, and male kiwi encountered foreign odours less often than their own odour or controls, and also less often than female kiwi.

Significantly different responses were made by kiwi of different sex (Figure 2.13), although the difference is only just significant, and the graph does not shown any obvious differences. There was no significant difference in the type of responses shown to particular odours by kiwi of different sex.

Male and female kiwi of different ages differed significantly in their encounter rates to different odours (Figure 2.14). Juvenile kiwi of both sexes encountered all odour types more often than adult kiwi. Juvenile males also encountered foreign kiwi odour more often than their own odour, whereas adult males encountered foreign odours least often, and significantly less often than all other kiwi.

Significantly different responses were also made by kiwi of different ages and sexes (Figure 2.15). Juvenile kiwi showed all responses more often than adult kiwi did. As a percentage of total encounters, all kiwi showed 'no response' and 'walked away' responses more often than they ran away or probed next to odour containers and juvenile females ran away from odours more often than juvenile males. Juvenile males responded more often to odours and, as a percentage of total responses, probed around odour containers more often than all other kiwi. Adult male kiwi responded least often of all kiwi.
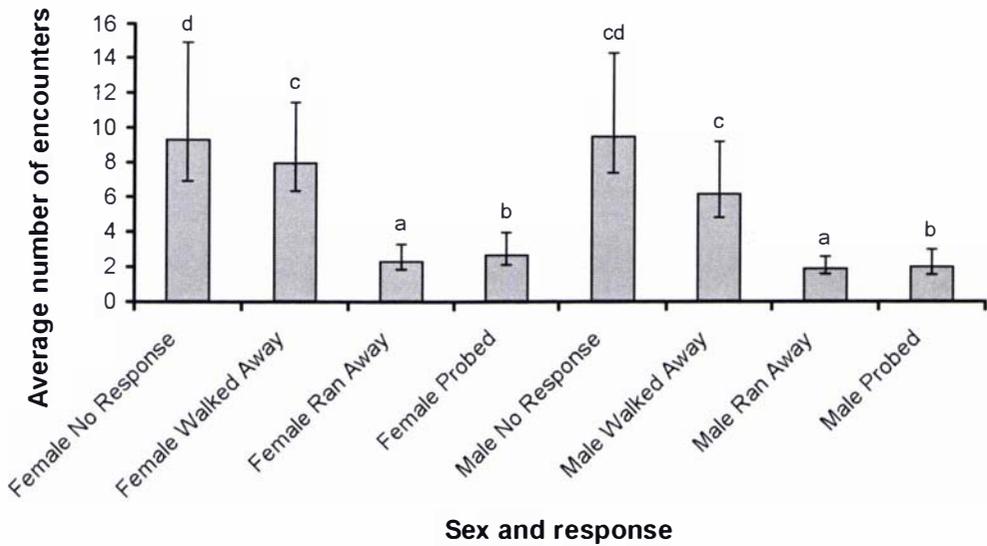
Figure 2.13: Average number of responses (± S.E.) made by kiwi of different sexes. Different letters on the graph denote significantly different values.
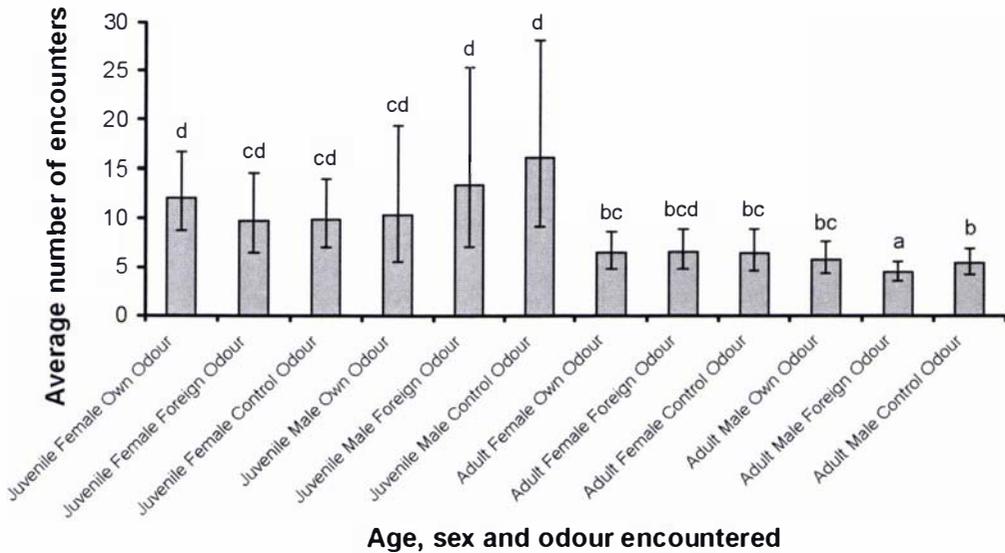
Figure 2.14: Average number of encounters (± S.E.) made to different odours by kiwi of different ages and sexes. Different letters on the graph denote significantly different values.
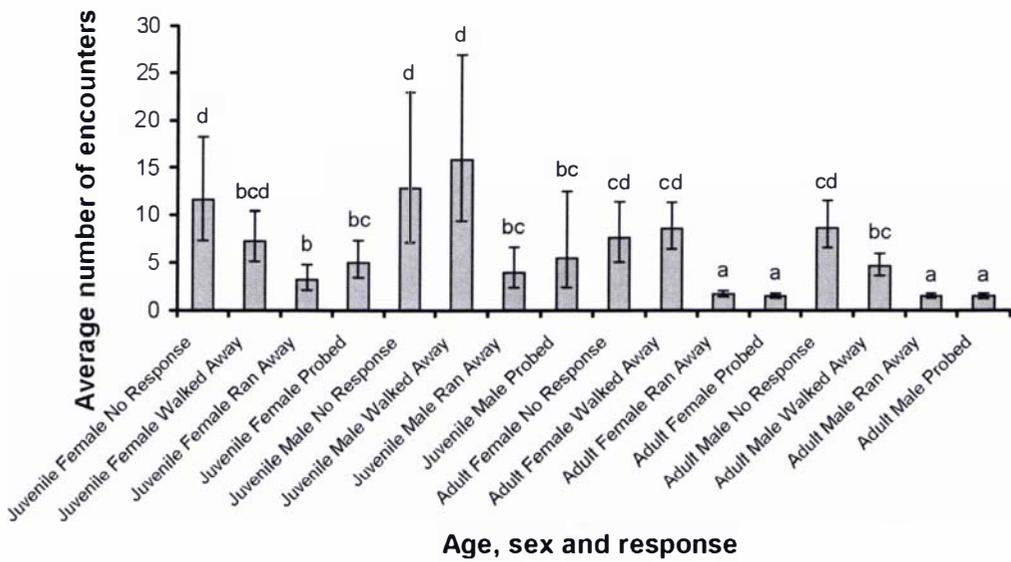
Figure 2.15: Average number of responses ($\pm$ S.E.) made by kiwi of different ages and sexes. Different letters on the graph denote significantly different values.

Nocturnal house kiwi made significantly more encounters to odours than kiwi housed outside. The average number and standard errors are shown in Table 2.6. The housing variable was assessed in the model after the age variable, indicating that the way kiwi are housed is significant even after age has been taken into consideration. Outside housed kiwi also encountered foreign odour significantly less often than their own odours or controls (Figure 2.16). Nocturnal house kiwi encountered all odours equally.

Table 2.6: Average number ($\pm$ S.E.) of encounters made by kiwi kept in nocturnal houses and outside enclosures.

Housing	Average No. of Encounters	(+) S.E.	(-) S.E.
Nocturnal House	37.38	12.04	9.11
Outside Enclosure	13.74	3.22	2.61

Nocturnal house kiwi showed all responses more often and, as a percentage of total encounters, ran away and probed significantly more often then outside housed kiwi (Figure 2.17). The type of housing had no significant effect on the type of responses made to particular odours.
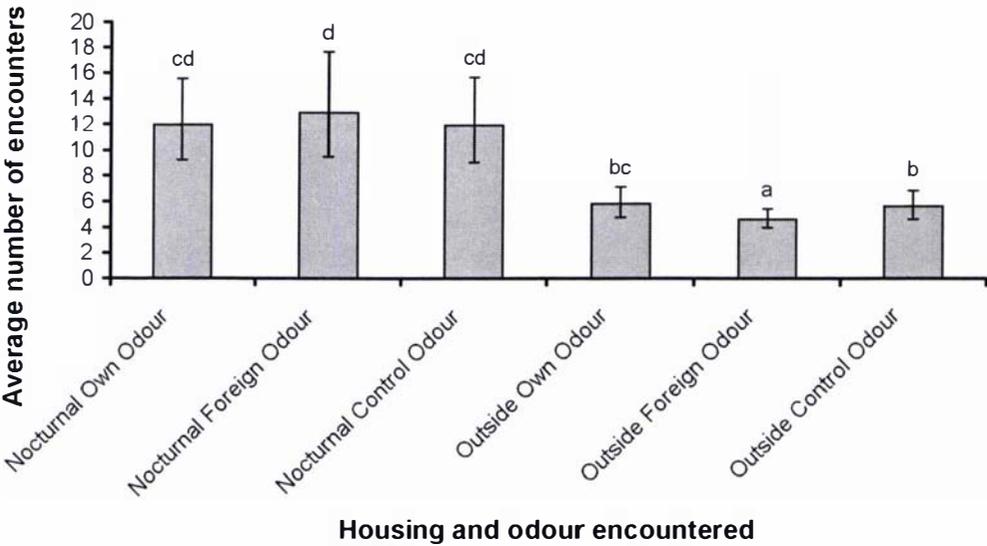
Figure 2.16: Average number of encounters (± S.E.) made to different odours by kiwi of different housing. Different letters on the graph denote significantly different values.
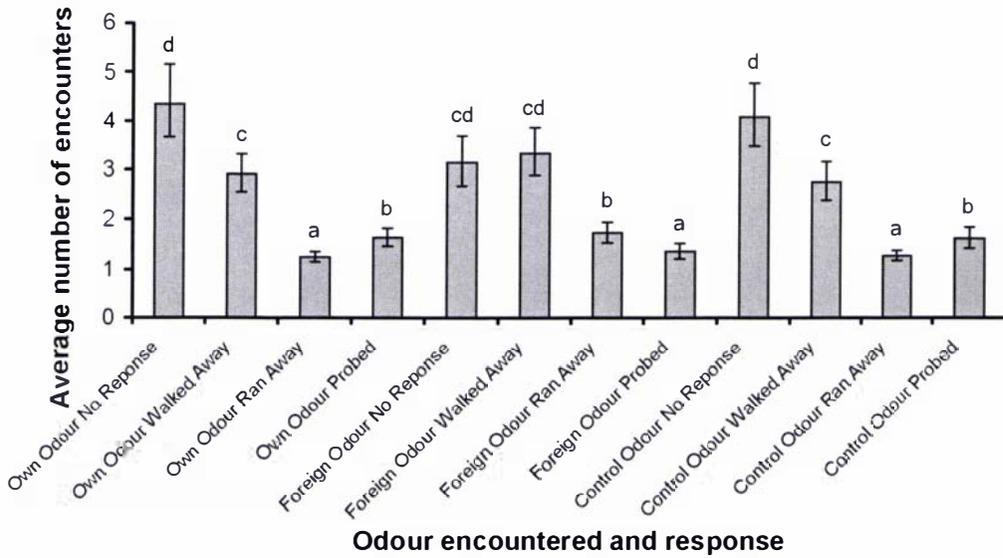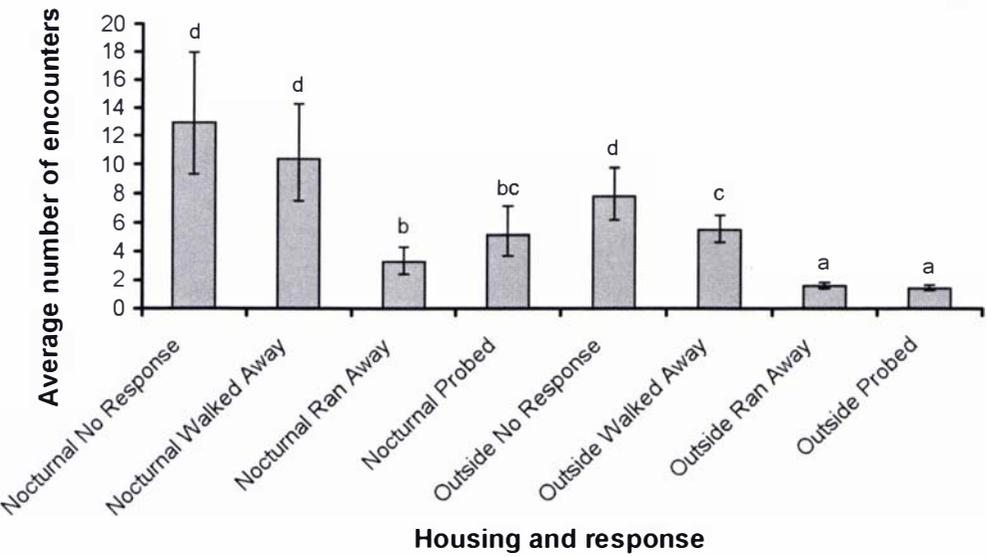

Figure 2.17: Average number of responses (± S.E.) made by kiwi of different housing. Different letters on the graph denote significantly different values.

DISCUSSION

The results of this study suggest that kiwi respond in a way consistent with the hypothesis that they use faecal odour to mark territories. Overall, there were no differences in the number of encounters to containers that held faeces and empty control containers and there was a high percentage of unresponsive encounters, suggesting that kiwi were neither attracted to kiwi faeces nor to the odour containers.

It was long assumed that marking behaviours were involved in direct territory defence. Early hypotheses assumed that scent marks aided in keeping intruders away and the scent marks themselves were assumed to intimidate and threaten intruders prior to any encounters with the resident individual (see review in Gosling, 1982). However, this hypothesis was questioned because, in many species, intruders were undeterred in entering territories of other individuals (e.g. Gorman and Mills, 1984; Richardson, 1991; Simons *et al.*, 1997; Sliwa and Richardson, 1998).

An alternative hypothesis for scent marking was suggested by Gosling (1982), whereby territory residents provide scent marks so that intruders can assess their own status with respect to the residents' status in any subsequent encounter. Gosling (1982) suggested that the cost of an encounter between an intruder and the territory holder is reduced through prior assessment by the intruder of the likely outcome. Gosling (1982) further suggested that territory marking provides an olfactory association between the resident and the defended area, allowing intruders to identify the resident when they meet, and respond appropriately. Because the resident is more likely to escalate encounters, intruders usually withdraw (Gosling, 1982) so the resident does not have to establish dominance over every intruder.

In order for Gosling's (1982) hypothesis to hold, the intruder must judge the costs of intrusion (risk of detection and possible attack) against the benefits of intrusion (using the defended resources). Costs are partly dependent on the competitive ability of the intruder and the costs and benefits of intrusion into defended territories will vary between species and with different local contexts. Richardson (1991) reported that intruding

aardwolves (*Proteles cristatus*) showed different behaviour from that predicted by Gosling's (1982) hypothesis. Aardwolves live in pairs in large territories, so residents have difficulty monitoring all intrusions. Nevertheless, most animals that approach intruders will be the territory owners and Richardson (1991) argues for an extension to Gosling's (1982) hypothesis, suggesting that scent marking is also used to assess asymmetry of contest. Richardson (1991) suggests that in species where territorial encounters are relatively rare, olfactory scent marks by residents should also act as a direct physical threat to intruders and must be reinforced by the behaviour of the resident when they encounter intruders. The presence of scent marks in a territory can act as evidence that the territory is occupied, while the density of scent marks may advertise the level of commitment by the owners to defend it. The density of marks will also advertise the intensity of use and thus the chances of encountering the resident (Richardson, 1991).

My results agree with the predictions of Gosling's (1982) hypothesis, which suggests that intruders into a territory assess scent marks with respect to the territory holder, and act accordingly. Kiwi do not avoid areas that are marked by other kiwi, but they do show increased escape behaviour from unfamiliar kiwi odours. This lack of avoidance is probably because intrusion into other kiwi territories is unlikely to be detected very often due to the large territories kiwi hold. Intruders that are found, however, are threatened aggressively by the resident kiwi. Results also suggest that faecal odours may act as a direct threat to intruders, especially to adult male kiwi, and may be used to avoid agonistic encounters. This is in accordance to Richardson's (1991) hypothesis.

The high rate of individual variation suggests that kiwi differ in their willingness to approach new objects in their enclosure and the amount of interest shown in these objects. Encounter rates and responses may also depend on the type of odour presented as the foreign kiwi odour. The faeces used in the present study were of mixed gender origin, as they were often collected from enclosures that held more than one kiwi. Further studies on scent marking in kiwi should concentrate on manipulating foreign odour types to assess kiwi responses to intruders of particular age and sex.

The greater number of encounters that kiwi made with odour containers on the first trial day suggests that this was due to a new object being in their enclosure. Kiwi generally showed inquisitiveness to anything new placed in their environment and, as they did not respond differently to containers with faeces and empty control containers, this suggests that the high number of encounters on the first day was a response to the presence of new objects in their enclosures, rather than to the presence of kiwi odour.

The decrease in foreign odour encounters shown by juveniles on the second trial day suggests that this is retreat behaviour in response to foreign kiwi odour. In a natural situation this would perhaps be to avoid meeting unfamiliar kiwi, which would most often be the territorial adult. The return of juvenile kiwi to the foreign odour on the third day suggests that additional visual or auditory signs may be required to maintain avoidance. The decrease in encounter rates shown by female kiwi on the second day was not in conjunction with an avoidance of foreign kiwi odour, suggesting they do not retreat from areas containing this odour as juveniles do. Overall, kiwi did not show a decrease in the proportion of encounters made to odours from a foreign kiwi over the trial, but there was a decrease in the percentage of running away responses. This indicates that there is a decrease in panic responses, rather than an avoidance of areas with this odour. Together with the increase in the percentage of probing responses over the three days, this also suggests that kiwi became accustomed to odours over the trial.

The increased encounter rates shown by adult males on the second trial day suggests that males increase their activity on this day, possibly because of the foreign kiwi odour in their territory. Male kiwi are more territorial than females (Taborsky and Taborsky, 1992), so such increased activity is likely to increase their chance of detecting possible intruders. Despite this increased activity on the second trial day, adult males still avoided foreign kiwi odour more than female kiwi, suggesting they were still repelled by foreign kiwi odour.

The responses to odours differed in relation to age and sex in kiwi. This has been reported in many other species (e.g. Johnson, 1973; Hurst, 1990; Gosling and Wright, 1994; Drickamer, 1995; Zuri *et al.*, 1997; Heymann, 1998; Kappeler, 1998; Sillero-Zubiri and MacDonald, 1998; Heymann, 2000). Juvenile kiwi were much more

inquisitive and reacted more often to odour containers than adults. The behavioural differences shown by juveniles and adults suggests that the behaviour toward foreign kiwi odour changes as kiwi mature. The attraction shown by juvenile kiwi to the odour from a foreign kiwi, and the escape behaviour they display suggests that juveniles use odour to possibly assess whether a territory is occupied, and whether other kiwi have been in the area recently. Juveniles often live within adult kiwi territories, and are tolerated to a degree by the territory holders (Colbourne and Kleinpaste, 1983). Possibly these juveniles are attracted to foreign kiwi odour in order to assess the territory holder, as occurs in other animals (Gosling, 1982). Most juveniles used in the present study were held in nocturnal houses, where they show more boredom behaviour than kiwi housed outside. The high amount of probing shown by juveniles appears to be a form of play, and a few of the juveniles in nocturnal houses pulled odour containers completely out of the soil.

In the wild, the majority of adult kiwi live in permanent monogamous pairs and hold stable territories (Taborsky and Taborsky, 1991; 1992). The way adult male kiwi were repelled from foreign kiwi odour suggests that this is a means of avoiding territorial neighbours and therefore avoiding unnecessary encounters. The low encounter rates shown by male kiwi to foreign kiwi odour suggests that avoidance of foreign kiwi odour is more important to male kiwi because males are more territorial (Taborsky and Taborsky, 1992). This avoidance is important when one considers that kiwi territories often overlap each other, so a strategy that avoids areas where neighbours have recently been could be advantageous. Taborsky and Taborsky (1992) found that neighbouring kiwi were seldom within 50 metres of each other. The differences in responses made by adult male kiwi, particularly the low percentage of times they ran away from foreign kiwi odour, suggests that although male kiwi are less likely to approach foreign faecal odours, they are also less likely to flee from the area. Such behaviour is to be expected from the more territorial of the sexes.

Adult females were attracted to a foreign kiwi odour but did not show the same retreat behaviour as juvenile kiwi. This suggests that females are interested in the odour from another kiwi, possibly to assess them as potential mates or as possible competitors. This also reflects the difference between adult and juvenile kiwi in territorial status, suggesting

that adult females are probably more confident within their enclosures. In the wild, paired female ranges overlap more than paired male ranges (Taborsky and Taborsky, 1992). Female Northern brown kiwi therefore have more opportunities to encounter other kiwi than males do (Taborsky and Taborsky, 1991). This is especially so when male partners are incubating eggs, which takes between 74 and 84 days (Calder, 1990). The attraction of females to foreign odour may therefore be because females are more likely than males to encounter foreign kiwi odour.

Most juvenile males were part of groups, and this may explain why juvenile males encountered control odour containers most often and avoided their own odour (which could also be that of an enclosure mate). Group-held individuals tend to stay in their own areas of the enclosure, often where they are away from most other birds. Juvenile males are possibly more territorial than juvenile females, and so attempt to control an area away from other individuals in the enclosure, but also away from odours of a foreign kiwi.

Nocturnal house kiwi encountered odour containers significantly more often than kiwi housed outside, for two possible reasons. Nocturnal house enclosures are generally smaller than outside enclosures so that nocturnal house birds make more encounters simply by chance in the smaller area. Second, nocturnal house kiwi showed more behaviours suggesting boredom than shown by kiwi housed outside. These behaviours included pacing and circling the bill against the glass and fences. I suggest that both factors play a role in increasing the encounter rates of nocturnal house birds. Kiwi held outside probably act more naturally by avoiding foreign kiwi odour to a large extent. They also responded to odours less often than did nocturnal house kiwi, which reflects the ability of outside housed kiwi to focus to a larger extent on the natural environment, which would be constantly changing, in contrast to the static environment of a nocturnal house.

Several problems arise when studying only captive kiwi. Most captive kiwi have been captive reared, so most have never encountered another adult kiwi in their territory, apart from mates. Although some juveniles are held in groups, most of these are separated before they reach adulthood. I therefore believe that most captive adult kiwi

have never had to defend their territory from other kiwi. Their responses may not represent those of wild kiwi, because the latter will meet neighbours and have to defend territories more often. The difficulties of studying kiwi in the wild, however, made the present study on captive birds a necessary first step. Future research should focus on the responses of wild kiwi, now that there is evidence that they respond to faecal odours.

One of the limitations of the present study was that it was not possible to move captive kiwi about in order to observe the behaviour of intruders in an unfamiliar area that was previously marked by another kiwi. Instead, responses were observed towards foreign kiwi odour placed into a resident kiwi territory. It was assumed that responses made by a resident kiwi to the odour of a foreign kiwi in their territory would be similar to the response of an intruder to the odour from a resident kiwi. It is probable, however, that such responses by the resident bird are not as strong. If possible, future work with captive birds should determine the responses shown by kiwi moved into an unfamiliar area that has been marked by another kiwi. Future research should also determine the effect of scent mark density on the responses of intruders.

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Chapter Three: Responses of Captive Northern Brown Kiwi to Roost Boxes Containing Faecal Odours
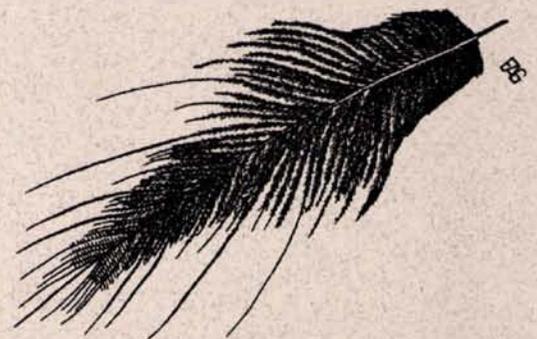
Responses of Captive Northern Brown Kiwi to Roost Boxes Containing Faecal Odours

ABSTRACT

Roost boxes containing resident kiwi odour, foreign kiwi odour, and an empty control were presented to 44 kiwi in 25 enclosures. Responses to the roost boxes included entry, roosting in the boxes, defecation in the boxes, and the order that kiwi entered the different boxes. When all ages and sexes of kiwi were analysed as a single group, they did not enter, roost, or defecate in relation to the odour that the roost box contained. Kiwi also did not enter roost boxes in any specific order in relation to the odour that the roost box contained. Instead, they were habitual in the way that they investigated their enclosure each night and entered the roost boxes as they encountered them, regardless of the odour that the boxes contained. Juvenile kiwi held in groups entered and roosted in the boxes significantly more often than all other kiwi. These juveniles were more likely to roost in boxes containing the control odour, suggesting that these individuals were attempting to roost away from other enclosure mates. Individually housed juvenile kiwi seldom roosted in unfamiliar roost boxes. Juvenile male kiwi were least likely to enter roost boxes and never roosted or defecated in them, suggesting that juvenile males are reluctant to enter unfamiliar roost sites and reluctant to leave signs of their occupancy. Individually housed female kiwi were more likely to enter roost boxes than male kiwi and paired kiwi. This may reflect a behavioural strategy adopted for mate finding, whereby female kiwi are more likely to seek out males that hold territories. Adult females were also more likely to roost in boxes containing foreign kiwi odour, suggesting that this may be a strategy to advertise sexual status as well as occupation of the territory. Adult males were less likely to roost in boxes than adult females, suggesting that they are less likely to roost in unfamiliar roost sites. Kiwi did not attempt to countermark foreign kiwi odour in roost boxes, suggesting that defecation is not the primary method used to

mark roost sites. Instead, the behaviour associated with roosting appears to be more important for marking roost sites, which may explain why kiwi frequently move from one roost site to another in the wild.

INTRODUCTION

Kiwi have the second largest olfactory bulb, in relation to the size of their brain, of any avian species known (Bang and Cobb, 1968). The olfactory chamber in the nasal cavity is also large in comparison with respiratory parts, and the olfactory epithelium is further increased by several folds of the chamber walls (Portmann, 1961). For this reason, it has long been assumed that kiwi have a good sense of smell, and several authors have suggested that olfaction is the primary sense used to find prey (Benham, 1906; Cobb, 1960; Wenzel, 1968; Wenzel, 1971; Reid and Williams, 1975; Waldvogel, 1989). However, other authors have questioned this olfactory ability (Strong, 1911; Roper, 1999), and Roper (1999) suggests that evidence for the olfactory prowess of kiwi remains surprisingly weak.

The olfactory bulb of the kiwi brain is very similar in structure to that of mammals (Craigie, 1930) and along with other mammalian characteristics, such as their use of burrows and nocturnal habit, it follows that kiwi may communicate in similar ways to mammals, including the use of olfactory communication. Kiwi hold stable year-round territories, and although encounters with intruders are sometimes aggressive (McLennan *et al.*, 1987; Taborsky and Taborsky, 1991; 1992), intruder detection is quite low because of the large size of these territories. McLennan and Potter (1992) found that kiwi in Hawke's Bay held stable territories, yet found little evidence that kiwi defended areas by overt aggression or vocal advertisement. This suggests that kiwi may use other forms of territorial marking.

As with many mammals, kiwi may use scent to mark their territories (McLennan and Potter, 1992). Odours play a significant role in the social and sexual communication of

mammals (Heymann, 1998), and are particularly important in some nocturnal species (Johnston *et al.*, 1997). It is widely accepted that many mammals scent mark their territories to advertise their occupation and ownership of the territory (Richardson, 1991) and although scent marks are unlikely to exclude all intruders (Johnson, 1973; Gosling, 1982), they often limit the degree to which the territory is intruded, and therefore indirectly protect the resources (Mills, 1987). The assumption is that only long-term residents of an area have the opportunity to heavily mark the territory (Gorman and Mills, 1984). An advantage of using scent marks is that they persist for some time in the environment in the absence of the sender (Eisenberg and Kleiman, 1972).

Although there have been many studies on the scent marking behaviour of mammals (e.g. Dietz, 1984; Hurst, 1990; Richardson, 1991; Fornasieri and Roeder, 1992; Gosling and Wright, 1994; Rosell and Nolet, 1997; Heymann, 1998; Kappeler, 1998; Sillero-Zubiri and MacDonald, 1998; Allen *et al.*, 1999; Heymann, 2000), and several on reptiles, amphibians, and insects (e.g. Johki and Hidaka, 1982; Carpenter and Duvall, 1995; Simons *et al.*, 1997; Aragon *et al.*, 2000; Gilbert *et al.*, 2001), I know of no other study on the use of territorial scent marking in any avian species.

Studies on mammals suggest that several strategies are used to mark territories. These involve either concentrated border marking (e.g. Bowen and Cowan, 1980; Richardson, 1991; Rosell *et al.*, 1998; Sillero-Zubiri and MacDonald, 1998; Allen *et al.*, 1999) or hinterland marking, which involves marking throughout the interior of the territory (e.g. Gorman and Mills, 1984). The different types of scent marking strategies are not necessarily species-specific alternatives, but instead may be in response to ecological conditions (Gorman and Mills, 1984; Roper *et al.*, 1993). Animals have a limited time budget and a finite supply of scent secretion (Gorman and Mills, 1984), so as territory size increases it becomes progressively more difficult to mark the border with the frequency necessary to maintain border marking. For example, Mills (1987) found that spotted hyaena (*Crocuta crocuta*) with large territories used hinterland marking but those that held small territories used border marking.

It is also possible that kiwi scent mark their territories and because territories are quite large, hinterland marking may be used. McLennan and Potter (1992) first suggested that kiwi may use the numerous roost sites within their territory as scent posts to advertise occupancy. Because kiwi and their faeces have a distinct smell, which lingers in the burrows for several days after they have left them, McLennan and Potter (1992) suggest that this odour may be used as a form of territorial marking. During a study of kiwi in Hawke's Bay, McLennan and Potter (1992) found that when kiwi intruded into another kiwi territory, they often used burrows that the resident kiwi had used several days previously. Several of these burrows were well disguised, suggesting that intruding birds located the burrows by smell.

Very few previous studies have focused on the scent marking of nests or burrows. Zuri *et al.* (1997) found that male blind mole-rats (*Spalax ehrenbergi*) scent marked their burrows in relation to the position of male neighbours, and that male scent marks inhibited excavation by male intruders. Richardson (1991) reported that aardwolves (*Proteles cristatus*) use dens at the border of their territory significantly more often than those in the middle region of the territory, and suggest that they use these as territorial signposts.

Many species, especially mammals (Johnston *et al.*, 1997), also countermark intruder odours by marking on top of a scent mark already present (Rich and Hurst, 1999). Countermarking is an attempt by the territory holder to obliterate the scent marks left by another individual (Gosling, 1982), thereby ensuring that marks within their territory are their own (Hurst, 1990). Johnston *et al.* (1997) found that female meadow voles (*Microtus pennsylvanicus*) preferred the top-scent male and suggest that countermarking may be an honest advertisement of a male's vigour, persistence and competitive ability. Countermarks from a challenger in a male's territory would indicate an inability to defend if effectively from competitors. Countermarking competition may be similar to sexual selection in influencing mate choice and reproductive success (Johnston *et al.*, 1997; Rich and Hurst, 1999).

It has already been determined in the previous chapter that kiwi respond in a way consistent with them using faecal odour to mark territory. The present study was

undertaken to determine whether kiwi use roost sites as scent posts to advertise occupancy of their territory. Results from the previous chapter suggested that, as a whole, kiwi were not repelled from a foreign kiwi odour, and that intruders may use scent marks to assess resident birds, as predicted from Gosling's (1982) scent-matching hypothesis. The results of the previous chapter also indicated that there is a slight repellent effect of foreign kiwi odour to adult males. This is also in accordance to Richardson's (1991) intimidation hypothesis, which predicts that in species where territorial encounters are relatively rare, the olfactory association provided by scent marks should act as a direct physical threat to intruders. Although it is predicted that kiwi will not be repelled from entering a roost box that contains the odour of a foreign kiwi, other behaviours may be dependent on the age and sex of kiwi.

METHODS

Kiwi Used

Captive kiwi were held in nocturnal houses and outside enclosures at institutes throughout New Zealand. Details of kiwi used are presented in Table 3.1. Kiwi were considered juvenile if they were 3 years of age or less at the time of observation. Three roost boxes, each with different scent, were presented to 44 kiwi in 25 enclosures for six nights each. Data could not be attributed to individual kiwi and were recorded for the enclosure as a whole. The kiwi involved in this trial were four juvenile females (two of which were held together), three juvenile males (two of which were held together), two adult females, and nine adult males (four of which were held in two same sex pairs). Eight pair enclosures and three group enclosures (a group of two, a group of three, and a group of five juveniles) were also used.

Roost Boxes

Roost boxes consisted of two separate components - the box, and the tunnel. The plastic box measured 300 mm by 335 mm and 280 mm deep. A square opening, measuring 165 mm by 165 mm, was cut out at the top of one of the 300 mm long sides. The box was placed open side down in the enclosure, forming a roost box with an earth floor.

The tunnel was made using untreated pine logs. The wood used was the top slice sawn off logs at a timber mill, so that each had a slightly rounded side. The majority of each log still had bark, which fell off naturally during use. The logs were cut into 425 mm lengths and three of these pieces were nailed together lengthwise. The two side pieces of the tunnel were cut along both edges so they were 155 mm wide, with both edges flat, and the untrimmed top piece of the tunnel was nailed to these side pieces using 100 mm galvanised nails. The final outcome was similar to a hollow log in appearance (see Figure 3.1). At the front end of the tunnel a fencing staple was nailed 30 mm from the bottom so that the cotton, attached to the timer magnet (described below), could be tied in place.

The inside surface of the tunnels were painted with three coats of Cabot's Crystal Clear Polyurethane so that the wood was less likely to absorb odours, and was easier to clean. The polyurethane was advertised as being low odour, and was odourless to humans when dry.

Table 3.1: Summary of the number of kiwi used at each institute (total = 44). The number of kiwi held in each enclosure type (total number of enclosures = 25), and the number of kiwi held in nocturnal houses (total = 18) and outside enclosures (total = 26) are given. Kiwi were considered juvenile if they were 3 years of age or younger. Pair enclosures held one adult female and one adult male. Same sex pairs involved either adult or juvenile birds and for analysis were classified as the age and sex of these two birds. Kiwi held in groups involved only juveniles and included a group of two, as this enclosure held a juvenile male and a juvenile female so could not be classified as a pair.

Institute	Number of kiwi sampled:				Number of kiwi held as a:				Number of kiwi housed in:	
	Juvenile Female	Juvenile Male	Adult Female	Adult Male	Single	Pair	Same Sex Pair	Group	Nocturnal House	Outside Housing
Auckland Zoo	0	2	1	1	0	2	2	0	2	2
Otorohanga Kiwi House	2	1	3	4	1	4	2	3	4	6
Rainbow Springs	2	0	1	3	4	0	2	0	3	3
Westshore Wildlife Reserve	2	0	1	2	3	2	0	0	0	5
Orana Park	1	2	2	2	1	4	0	2	2	5
Willowbank Wildlife Reserve	4	1	2	5	1	4	2	5	7	5

Figure 3.1: A roost box, showing the plastic box and wooden tunnel components.

Placement of Roost Boxes

The tunnel and box were placed together in each enclosure so that the tunnel was next to the opening that was cut in the box. The units were not physically attached to each other, but both units were covered with a single piece of black polythene so that the roost boxes were essentially dark during daylight hours. The polythene was pulled tightly around the roost box and weighted down on each side and at the back of the roost box using rocks or logs from the enclosure. A red house brick was placed on top of the roost box to prevent kiwi from knocking the roost box over when they were moving about inside it (Figure 3.2).

Figure 3.2: A roost box within a kiwi enclosure, showing the black polythene covering the box and tunnel components and the brick on top of the box. The timer can also be seen against the tunnel on the left-hand side.

Three identically coloured roost boxes were placed randomly in each enclosure. Placement was limited to flat areas that were relatively accessible so that odour changes could be made each day. Roost boxes were placed in enclosures at least two days before the odour trial began, so that kiwi became familiar with them. All kiwi entered at least one roost box on these first two nights. Roost boxes were kept in the enclosures for six consecutive nights once the odour trial started. Roost box tunnels and boxes were washed after each night with dish detergent and cold water, and left to dry within the enclosure. Any faecal matter left by the resident kiwi was also removed after each night.

Odour Containers

Odour containers comprised 90 ml clear plastic sample vials, 45 mm diameter and 55 mm deep, with a 4 mm diameter hole drilled in the centre of the container lid. A 4 mm diameter soft galvanised wire rod, 155 mm long, was inserted through this hole and used to anchor the odour containers to the ground. The rod was threaded at one end, and was fixed to the container using two 4 mm hexagonal nuts on each side of the lid. Approximately 7 mm of the rod, and one nut, was exposed on the inside of the container lid. Hot glue was used to keep the nuts from loosening. This glue was odourless to humans once dry.

Thirteen evenly distributed 3 mm diameter holes were drilled in the bottom of the container. Eight holes, also 3 mm diameter, were drilled in the side of the container centred approximately 5 mm from the bottom. These were spaced evenly around the side, centred approximately 18 mm from each other.

Placement of Odour Containers

All handling of equipment was done using disposable latex gloves. Approximately 3 g of fresh faeces were placed on the lid of the upturned container, and the container screwed onto the lid, just prior to placing the odour containers in the roost boxes. The odour containers were placed upside-down in the enclosure with the wire rod pushed into the enclosure soil so that the lid was flush to the ground and the rest of the odour container was above ground. Each roost box held two odour containers, with the same odour. Odour containers were placed in the top left corner of the roost box and halfway down the tunnel on the left hand side (see Figure 3.3). Roost boxes were assigned odours randomly so that one roost box contained the resident kiwi's faeces, one contained faeces from a foreign kiwi, and one roost box contained empty control containers. Roost box odours were changed after each night and reassigned randomly, such that over the trial each roost box contained each odour for two nights. Odour containers were replaced with clean containers and fresh faeces after three nights.
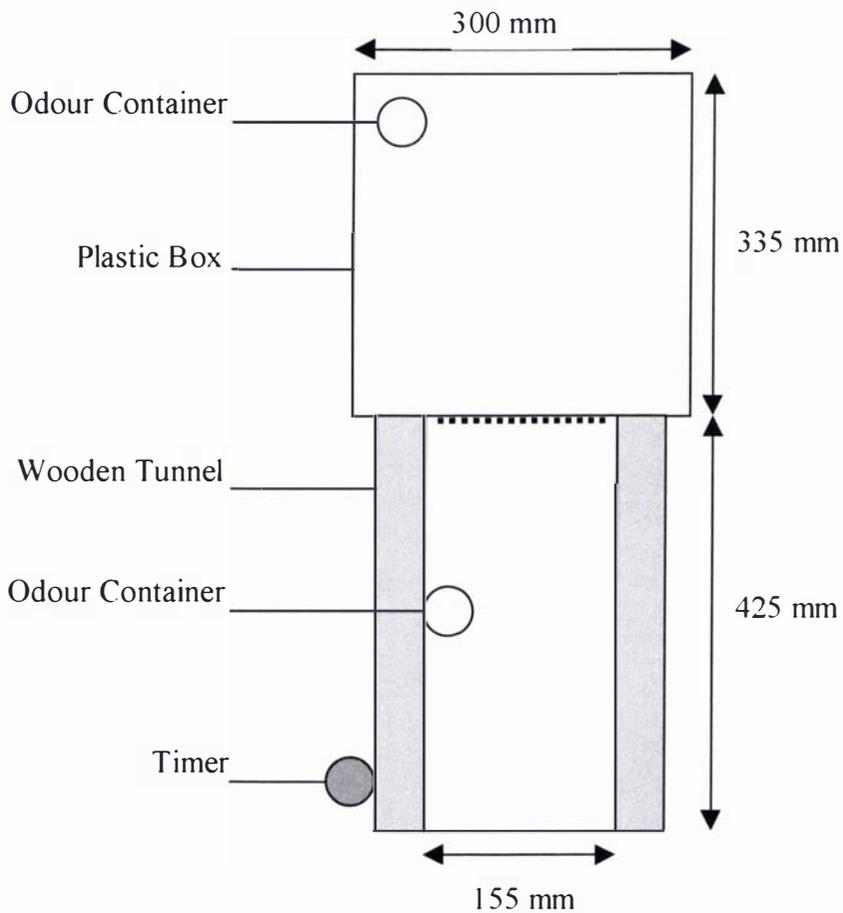
Figure 3.3: Diagram of a roost box, showing position of odour containers in the box and tunnel components and position of timer on the outside of the tunnel.

Roost Box Timers

The timers used are described in detail by Jenness and Ward (1985) and are accurate to the nearest five minutes. Each timer consists of two integrated circuits, powered by three AA size batteries. The first circuit is an oscillator and a 14-stage binary divider; the second is a 7-stage divider. Outputs from the divider chain power light-emitting diodes (LEDs), which indicate the status of the dividers when a magnet is placed across the circuit.

Each timer was encased in a 90 ml clear plastic container, with a screw-cap and a 5 mm breather hole drilled in the base to prevent moisture condensing inside. A small galvanised plate was glued on the outside of the container next to the timer's reset switch. The plate held a small magnet bar on the outside of the container, which kept the timer switch closed and the counter at zero. The timer operates when the magnet (attached to the cotton) is pulled away from the timer. This opens the circuit and the timer starts counting.

The time that has elapsed after the magnet was pulled away is obtained by placing the same magnet across a second switch, which closes the circuit and operates the LEDs. The eight LEDs have a binary weighting: $D_1 = 1 \times 5$ minutes, $D_2 = 2 \times 5$ minutes, $D_3 = 4 \times 5$ minutes, $D_4 = 8 \times 5$ minutes, etc. The total minutes shown by the LEDs are added together and the time that the kiwi entered the roost box for the first time is obtained by subtracting this from the interrogation time.

The timer magnet was attached to the roost box tunnel using cotton tied to the fence staple at the front of the tunnel. The cotton was placed across the tunnel entrance at a height of about 30 mm, and the magnet was set on the galvanised plate to hold the timer closed. The position of the cotton meant that kiwi pulled the magnet away from the timer when they entered the tunnel, thereby starting the timer counting. The timer unit sat on the opposite side of the tunnel from the staple and was placed next to the tunnel to prevent it being knocked over. Kiwi did not appear to notice the cotton when entering the tunnel.

Recording Behaviour

Kiwi were not observed directly during the trial. Data were instead recorded each morning or at the end of each dark cycle in nocturnal houses. Data included whether each roost box had been entered (i.e. whether the cotton across the entrance had been displaced). If so, the current interrogation time and LED display were recorded, allowing entrance times to be determined later. Data were also recorded on whether kiwi were roosting in the box, the identity of these kiwi, and whether the resident kiwi had defecated in the roost box.

If kiwi were roosting in experimental roost boxes, they were removed and placed in their own roost boxes so that the experimental roost boxes could be cleaned and reset. A pilot study had shown that removing kiwi from experimental roost boxes did not affect their entering and roosting in experimental roost boxes on subsequent nights. Removing kiwi during the daytime was preferred because it avoided human disturbance after activity commenced.

Data Analysis

Data are appended on the enclosed CD. Entrance, defecation and entrance order could not be attributed to individual kiwi so data were recorded for the enclosure as a whole. For this reason, paired kiwi and group-held kiwi were classified as a 'sex' for the purpose of analysis, so that the sex category includes four types - male, female, pairs and groups. Enclosures that held two kiwi of the same age (juvenile (three years of age or younger) or adult) and sex were classified under the particular age and sex of those kiwi. Data analysis was performed using a generalised linear (Genmod) model in SAS, Version 6.12. Variables were considered significant if $P< 0.05$.

Four models were run using the dependent variables of roost box entrance, roosting, defecation and entrance order. For the entrance, roosting, and defecation models a binomial type1 distribution was used. Roosting and defecation data gave a Poisson

distribution, so standard errors were calculated using log transformed data and then transformed back before graphing. This lead to asymmetric error bars on many of the graphs. A normal type1 distribution was used for modelling the dependent variable of the entrance order.

Several variables were nested together, when every level of one factor occurs with only one level of another factor. An individual kiwi (or enclosure) could only be one age, one sex and one housing type (nocturnal house or outside enclosure) so it was nested with these three variables (Kiwi(Age-Sex-Housing)). All kiwi held in groups were juveniles in nocturnal houses, and all paired kiwi were adults in outside enclosures, so sex was nested with age and housing (Sex(Age-Housing)). By nesting these variables, the model takes into consideration that there are no adult or outside housed groups and no juvenile or nocturnal house pairs. The variable age-sex could not be included in the models because the effect of the nested kiwi variable meant that the age-sex variable did not have any degrees of freedom. It was therefore analysed using the means and standard errors alone.

Similar analysis problems occurred in all four models. Least significant means tests could not be run because the model was too saturated. The model was therefore run with group-held kiwi and paired kiwi data progressively excluded to determine possible trends in the data. Certain variables could not be included in the model when pair and/or group data were excluded because the model became too saturated and the goodness of fit could not be assessed. These variables were eliminated from the model and are denoted by an asterix (*) in Tables 3.2 and 3.5. The variables Kiwi(Age-Sex-Housing-Day) and Kiwi(Age-Sex-Housing-Box) could not be assessed in the roosted model because the model was too saturated. Kiwi(Age-Sex-Housing-Odour) also could not be included in the defecation model.

Roosting occasions were determined as a percentage of the possible roosting occasions. This was the total possible number of roosting occasions for all kiwi in the enclosure. Thus, individually housed kiwi were only capable of roosting in one roost box each night. Paired kiwi (or kiwi housed with another kiwi of the same age and sex) were capable of roosting in two roost boxes each night. Group-held kiwi were capable of roosting in

roost boxes according to the number of kiwi in the group, obviously to a maximum of three roost boxes placed in the enclosure.

Entrance order could only be assessed for the first entrance into each roost box, as this was when the timer was triggered. On about 18% of occasions the timers used did not work and for this reason the number of observations used in the model are fewer than the observation numbers used for the other roost box analyses

RESULTS

Entrance Rates to Experimental Roost Boxes

Over the trial a total of 257 roost boxes (57.1% of a possible 450) were entered by kiwi and the number of roost boxes entered in each enclosure over each six-day trial period varied from two (11.1%) to 18 (100%). The model was underdispersed, indicating that there was less spread in the data than expected from the model. The deviance values of the Genmod model, the degrees of freedom, the number of observations used, and the likelihood ratio statistics for all variables are shown in Table 3.2.

Table 3.2: Likelihood ratio statistics for factors relating to entrance behaviour to roost boxes, where kiwi of different ages, sexes and housing were given a choice of three roost boxes, each with different faecal odour.

Source	Including All Data			Excluding Group Data			Excluding Group & Pair Data		
	DF	ChiSquare	Pr>Chi	DF	ChiSquare	Pr>Chi	DF	ChiSquare	Pr>Chi
Odour	2	5.55	0.0624	2	6.23	0.0445	2	1.69	0.4302
Age	1	15.21	0.0001	1	1.78	0.1818	1	0.37	0.5428
Housing	1	2.24	0.1344	1	0.00	0.9462	1	0.25	0.6187
Sex(Age-Housing)	7	69.15	0.0001	6	55.30	0.0001	5	52.41	0.0001
Day	5	7.49	0.1864	5	8.70	0.1217	5	5.47	0.3617
Kiwi(Age-Sex-Housing)	15	85.08	0.0001	13	79.63	0.0001	6	44.43	0.0001
Age-Odour	2	0.38	0.8264	2	0.68	0.7109	2	1.54	0.4631
Housing-Odour	2	2.41	0.3003	2	1.77	0.4119	2	0.24	0.8885
Sex(Age-Housing-Odour)	14	9.13	0.8227	12	8.90	0.7112	10	2.79	0.9860
Day-Odour	10	8.08	0.6206	10	9.58	0.4780	10	7.58	0.6696
Kiwi(Age-Sex-Housing-Odour)	30	25.50	0.7002	26	16.80	0.9149	12	8.03	0.7830
Age-Day	5	2.74	0.7404	5	2.10	0.8358	5	4.14	0.5297
Housing-Day	5	8.86	0.1148	5	7.47	0.1883	5	2.39	0.7934
Sex(Age-Housing-Day)	35	44.42	0.1321	30	42.67	0.0627	25	30.59	0.2029
Kiwi(Age-Sex-Housing-Day)	75	107.90	0.0077	65	100.76	0.0030	30	43.17	0.0566
Kiwi(Age-Sex-Housing-Box)	50	170.19	0.0001	44	155.02	0.0001	*	*	*
Goodness of Fit Deviance Value		50.35			50.35			140.19	
Goodness of Fit DF		190			166			130	
Number of Observations Used		450			396			252	

When all sexes of kiwi were analysed as a single group, there was no significant difference in the number of times they entered roost boxes with different odours, although roost boxes containing foreign kiwi odour were entered slightly less often than other boxes. When kiwi held in groups were excluded, roost boxes with foreign odour were entered significantly less often. Means and standard errors are shown in Table 3.3. When paired kiwi were also excluded from the model, the P-value was not significant.

Table 3.3: Average number ($\pm$ S.E.) of roost boxes with different odour (n = 6) entered. Kiwi held in groups were excluded.

Roost Box Odour	Average No. Roost Boxes Entered	$\pm$ S.E.
Own Odour	3.41	0.35
Foreign Odour	2.64	0.41
Control Odour	3.45	0.36

Juvenile kiwi ($\bar{x}$ = 12.63, S.E. = 2.03) entered significantly more roost boxes than adult kiwi ($\bar{x}$ = 9.18, S.E. = 1.12). When group-held kiwi were excluded this difference was not significant because kiwi held in groups showed significantly higher entrance rates ($\bar{x}$ = 16.00, S.E. = 1.15) than individually housed juveniles ($\bar{x}$ = 10.60, S.E. = 2.89). Kiwi of different housing did not enter roost boxes at significantly different rates.

Kiwi held in groups also entered roost boxes significantly more often than all other sexes of kiwi, and individually housed female kiwi entered roost boxes significantly more often than males and paired kiwi. Means and standard errors are shown in Table 3.4. Juvenile female kiwi had a high entrance rate, similar to that of groups of kiwi (Figure 3.4), but juvenile male kiwi were least likely to enter roost boxes. Individually housed adult females, adult males and paired kiwi entered roost boxes at similar rates.

Table 3.4: Average number (± S.E.) of roost boxes (n = 18) entered by kiwi of different sexes and grouping.

Sex	Average No. Roost Boxes Entered	± S.E.
Female	12.80	2.27
Male	8.67	1.70
Pair	8.38	1.56
Group	16.00	1.15

Overall, kiwi did not enter roost boxes at significantly different rates on different trial days and there were no significant differences in entrance rates made by kiwi of different ages, sexes, and housing during the trials. Kiwi of different ages, sexes, and housing also showed no significant difference in entrance rates with regard to odour of the roost box and they did not show significant differences in the percentage of times they entered roost boxes with different odours on different trial days.

Individual kiwi varied markedly in their behaviour, and there was significant individual variation in both entrance rates (Figure 3.5) and how this changed during the trials. Individual kiwi also entered certain boxes at significantly different rates, but they did not enter roost boxes significantly differently in relation to the odour the boxes contained.
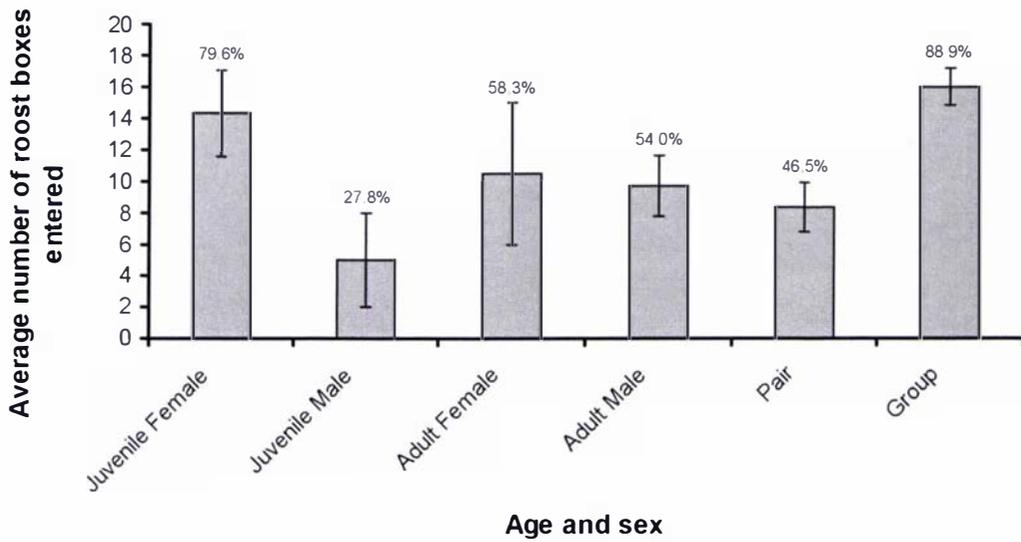
Figure 3.4: Average number of roost boxes entered (± S.E.) by kiwi of different ages and sexes. Percentages shown on the graph are the percentage of the total number of roost boxes entered by kiwi of different ages and sexes.
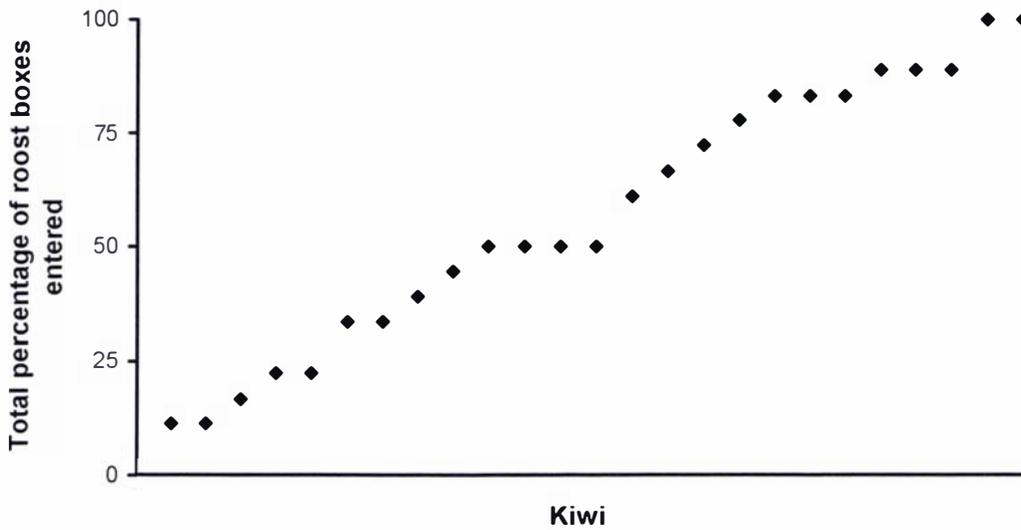
Figure 3.5: Total percentage of roost boxes entered by individual kiwi, shown in ascending order.

Roosting Behaviour in Experimental Roost Boxes

Fifteen kiwi in 10 enclosures roosted in boxes on 32 occasions. These included six juvenile females (four held as part of juvenile groups, and two held together), two juvenile males (both held as part of juvenile groups), four adult females (two paired females and two held individually), and three adult males (all held individually). Roosting behaviour was recorded for the enclosure as a whole, so group and pair data were still included in the sex category even though individual kiwi were identified. Therefore, a total of 29 roosting occasions were used in the model for analysis. The model was underdispersed, indicating that there was less spread in the data than expected from the model. The deviance values of the Genmod model, the degrees of freedom, the number of observations used, and the likelihood ratio statistics for all variables are shown in Table 3.5.

When all kiwi were considered together, they showed no significant difference in the rates that they roosted in boxes with different odours. However, as a percentage of total roosting occasions, roost boxes with foreign kiwi odour were roosted in most often. When group-held kiwi data were excluded this difference was significant, because this decreased the number of occasions when roosting occurred in control odour roost boxes. Means and standard errors are shown in Table 3.6. When paired kiwi data were also excluded, the P-value was not significant, but roost boxes with foreign odour were still roosted in most often as a percentage of roosting occasions.

As a whole, kiwi of different age did not have significantly different roosting behaviour, but when group-held kiwi were excluded, then juvenile kiwi ($\bar{x}$ = 1.25, S.E. = 0.25) used roost boxes significantly less often than adult kiwi ($\bar{x}$ = 1.66, S.E. = 0.25). There was only one juvenile roosting occasion, by two juvenile females housed together, once group data were excluded.

Table 3.5: Likelihood ratio statistics for factors relating to roosting behaviour in roost boxes, where kiwi of different ages, sexes and housing were given a choice of three roost boxes, each with different faecal odour.

Source	Including All Data DF	ChiSquare	Pr>Chi	Excluding Group Data DF	ChiSquare	Pr>Chi	Excluding Group & Pair Data DF	ChiSquare	Pr>Chi
Odour	2	4.45	0.1081	2	7.21	0.0272	2	5.48	0.0645
Age	1	0.09	0.7671	1	5.07	0.0243	1	4.43	0.0354
Housing	1	3.90	0.0483	1	0.52	0.4692	1	0.68	0.4084
Sex(Age-Housing)	7	16.99	0.0175	6	7.30	0.2944	5	7.21	0.2058
Day	5	2.08	0.8384	5	1.75	0.8823	5	1.80	0.8755
Kiwi(Age-Sex-Housing)	15	49.04	0.0001	13	39.75	0.0002	6	10.56	0.1030
Age-Odour	2	11.84	0.0027	2	1.17	0.5558	2	0.92	0.6318
Housing-Odour	2	1.66	0.4369	2	1.66	0.4366	2	1.49	0.4746
Sex(Age-Housing-Odour)	14	6.98	0.9356	12	5.30	0.9473	10	4.97	0.8930
Day-Odour	10	10.57	0.3918	10	18.13	0.0529	10	11.41	0.3263
Kiwi(Age-Sex-Housing-Odour)	30	19.91	0.9189	26	14.15	0.9710	12	6.58	0.8842
Age-Day	5	14.05	0.0153	5	6.50	0.2603	5	8.31	0.1399
Housing-Day	5	5.25	0.3857	5	6.95	0.2247	5	11.29	0.0460
Sex(Age-Housing-Day)	35	24.20	0.9150	30	29.97	0.4674	*	*	*
Goodness of Fit Deviance Value		44.12			12.98			15.28	
Goodness of Fit DF		315			275			185	
Number of Observations Used		450			396			252	

Table 3.6: Average number (± S.E.) of roosting occasions (n = 6) shown in roost boxes with different odour. Kiwi held in groups were excluded.

Roost Box Odour	Average No. Boxes Roosted in	(+) S.E.	(-) S.E.
Own Odour	1.20	0.11	0.10
Foreign Odour	1.31	0.14	0.13
Control Odour	1.07	0.05	0.05

Adult and juvenile kiwi also roosted at significantly different rates in roost boxes with different odour (Figure 3.6a). Juvenile kiwi did not roost in any roost boxes containing their own odour, and adult kiwi were least likely to roost in boxes that contained the control odour. When group data were excluded, the difference was not significant, largely because of a lack of data for juveniles (Figure 3.6b). When all data were included, there was a significant difference in roosting rates between kiwi of different ages on different trial days (Figure 3.7). However, the differences were not obvious so the roosting behaviour of group-held juveniles was probably responsible for the significance result. When group-held kiwi were excluded, the difference was non-significant.

Nocturnal house kiwi ($\bar{x}$ = 2.14, S.E. = 0.50) roosted significantly more often than outside housed kiwi ($\bar{x}$ = 1.47, S.E. = 0.21) when all data were included. When group data were excluded the difference between housing types was not significant, indicating that it was the high rate of roosting behaviour of group-held kiwi that explained a large number of roosting occasions shown by nocturnal house kiwi. Housing was not significantly related to the roosting behaviour shown with respect to odour or trial day.

Significantly different roosting rates were shown by kiwi of different sex, but when data from kiwi held in groups were excluded the difference was not significant. There was no relationship between sex and roosting behaviour in boxes with different odours or roosting behaviour on different trial days.
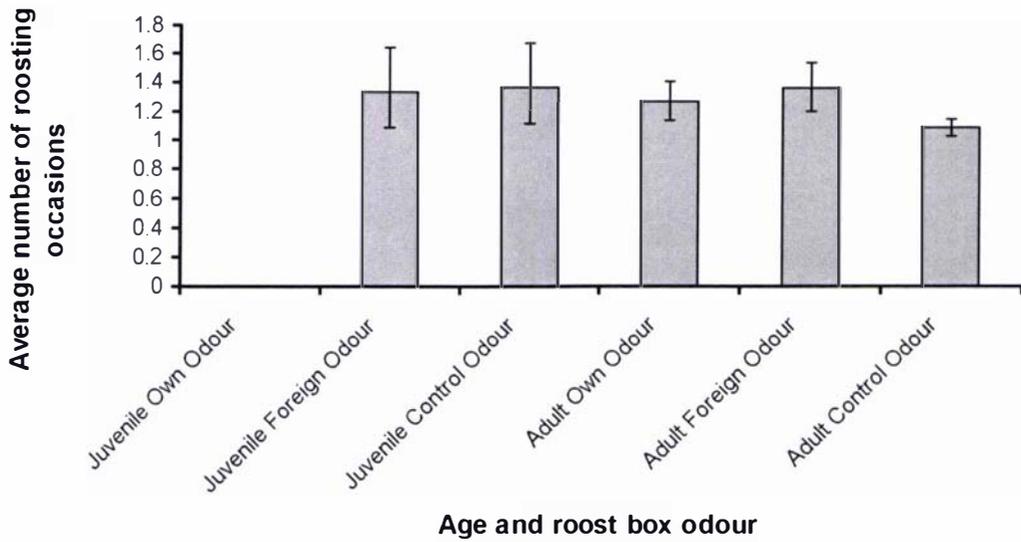
Figure 3.6a: Average number of roosting occasions shown (± S.E.) by kiwi of different ages in roost boxes of different odour.
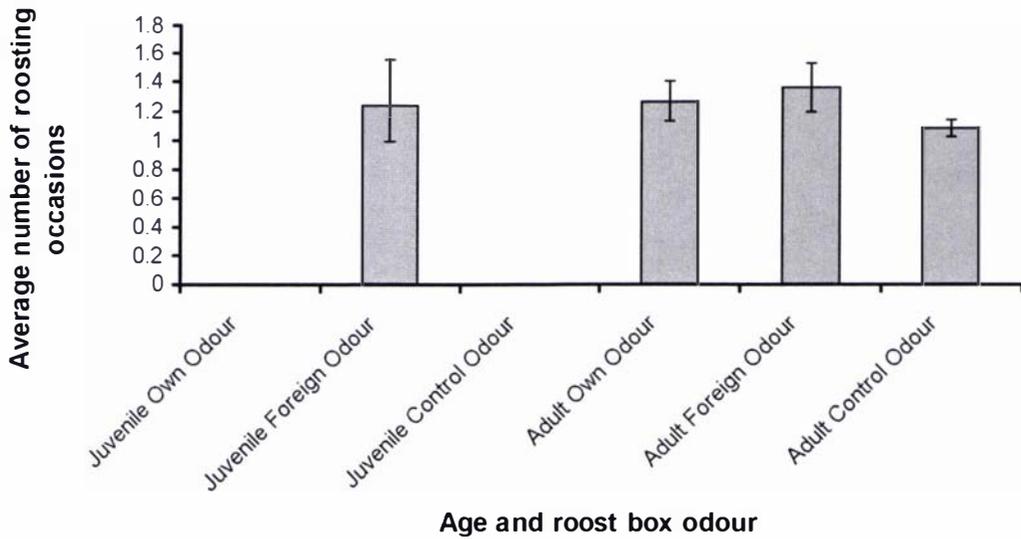
Figure 3.6b: Average number of roosting occasions shown (± S.E.) by kiwi of different ages in roost boxes of different odour, excluding kiwi held in groups.
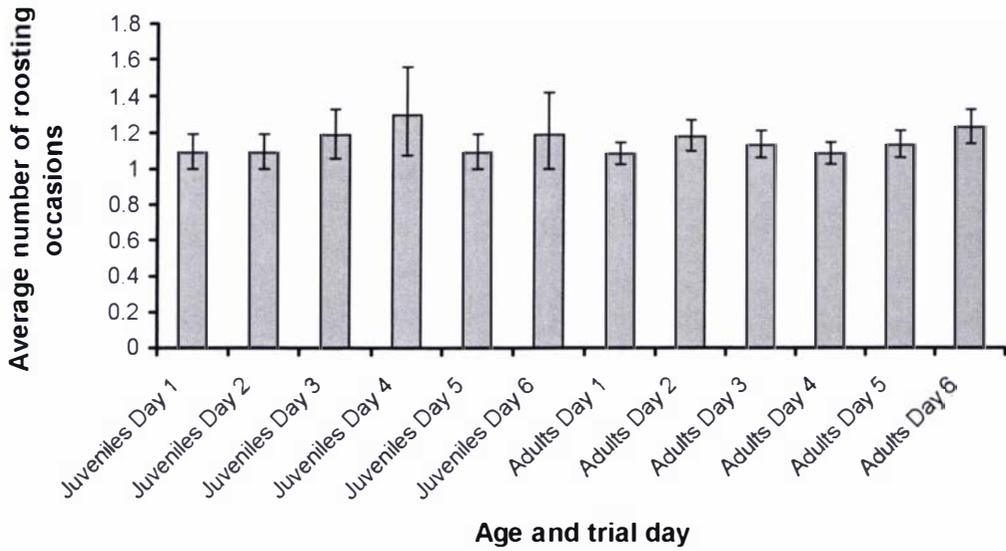
Figure 3.7: Average number of roosting occasions shown (± S.E.) by kiwi of different ages on different trial days.
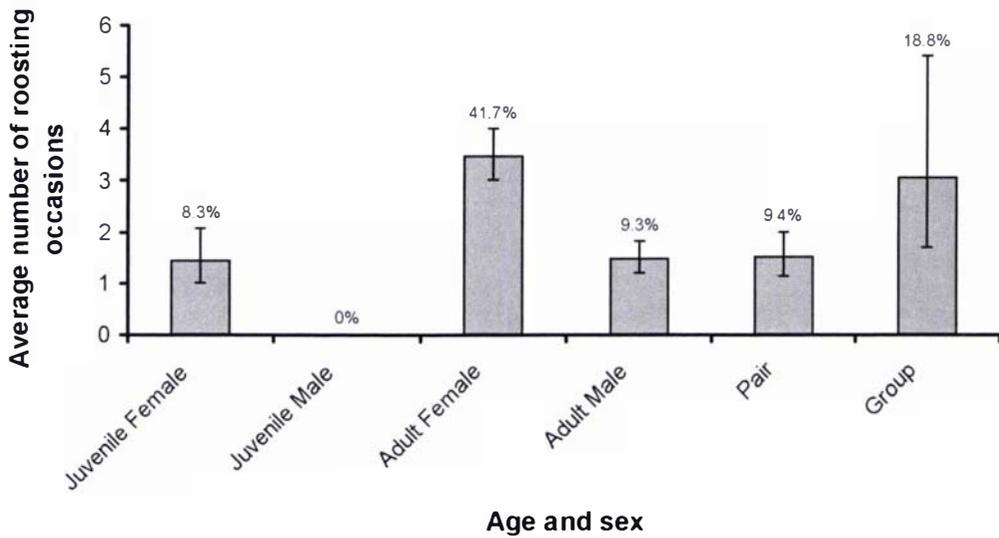
Figure 3.8: Average number of roosting occasions shown (± S.E.) by kiwi of different ages and sexes. Percentages shown are the number of roosting occasions in relation to all possible roosting occasions.

Differences in the roosting behaviour of kiwi of different ages and sexes were also investigated, although this analysis was not included in the model (see Methods for details). Individually housed adult female kiwi were most likely to roost in boxes (Figure 3.8) and kiwi held in groups also showed a higher number of roosting occasions compared to other kiwi. Adult females were also more likely to roost in boxes that contained a foreign kiwi odour (Figure 3.9).

Overall, there was no significant relationship between the number of roosting occasions and trial day and roosting rates in roost boxes of different odour were not significantly different over the trial. Individual kiwi showed significantly different roosting rates from each other, and their roosting rates varied on different trial days. Individual kiwi did not show significantly different roosting behaviour in relation to the roost box odour.

Defecation in Experimental Roost Boxes

Faeces were only found in the box component of the roost boxes and never in the tunnel. A total of 44 defecations were made by kiwi in five nocturnal enclosures and five outside enclosures (in 17.1% of the roost boxes entered). Kiwi in nine of these enclosures also roosted in the boxes and only one adult pair defecated in the boxes without roosting in them. Defecations were made in roost boxes by a pair of juvenile females, two adult females, two adult males, three paired adults, and two groups of kiwi (a group of three and a group of five). The model was underdispersed, indicating that there was less spread in the data than expected from the model. The deviance values of the Genmod model, the degrees of freedom, the number of observations used, and the likelihood ratio statistics for all variables are shown in Table 3.7.
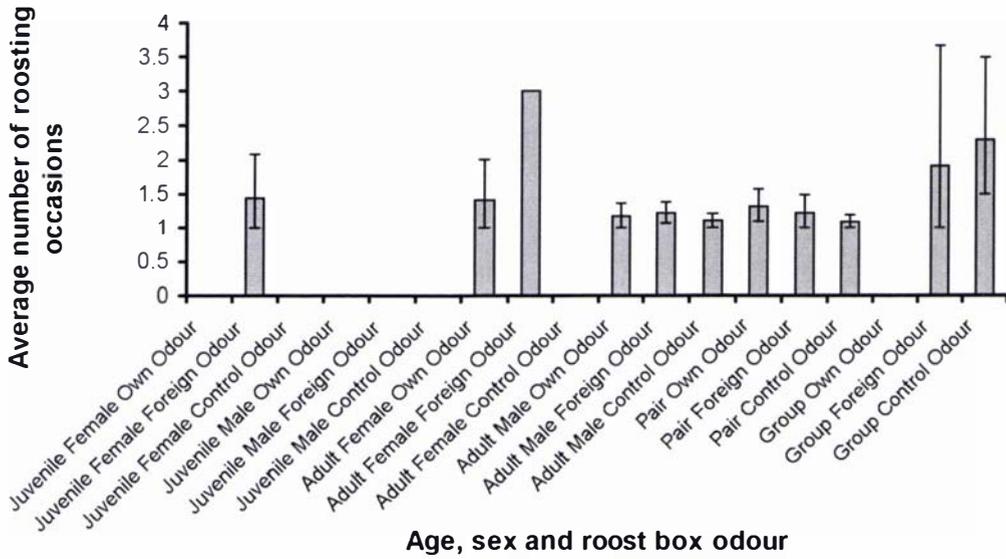
Figure 3.9: Average number of roosting occasions shown (± S.E.) by kiwi of different ages and sexes in roost boxes with different odour.

Table 3.7: Likelihood ratio statistics for factors relating to defecation in roost boxes, where kiwi of different ages, sexes and housing were given a choice of three roost boxes, each with different faecal odour.

Source	Including All Data DF	ChiSquare	Pr>Chi	Excluding Group Data DF	ChiSquare	Pr>Chi	Excluding Group & Pair Data DF	ChiSquare	Pr>Chi
Odour	2	1.63	0.4433	2	2.82	0.2445	2	1.15	0.5630
Age	1	2.69	0.1009	1	0.73	0.3931	1	0.55	0.4568
Housing	1	21.60	0.0001	1	13.94	0.0002	1	19.39	0.0001
Sex(Age-Housing)	7	19.75	0.0061	6	15.55	0.0164	5	10.03	0.0744
Day	5	0.88	0.9714	5	1.94	0.8571	5	0.84	0.9743
Roosted	1	80.59	0.0001	1	57.38	0.0001	1	18.65	0.0001
Kiwi(Age-Sex-Housing)	15	29.06	0.0158	13	22.84	0.0437	6	13.00	0.0430
Age-Odour	2	0.46	0.7936	2	1.36	0.5071	2	1.49	0.4738
Housing-Odour	2	0.05	0.9771	2	0.03	0.9848	2	0.72	0.6980
Sex(Age-Housing-Odour)	14	13.23	0.5082	12	10.73	0.5524	10	9.30	0.5042
Day-Odour	10	20.66	0.0236	10	18.19	0.0518	10	9.80	0.4580
Age-Day	5	5.73	0.3337	5	20.75	0.0009	5	18.06	0.0029
Housing-Day	5	11.90	0.0362	5	4.06	0.5401	5	3.37	0.6435
Sex(Age-Housing-Day)	35	44.84	0.1231	30	14.71	0.9913	25	12.23	0.9846
Goodness of Fit Deviance Value		35.09			27.45			11.09	
Goodness of Fit DF		344			300			171	
Number of Observations Used		450			396			252	

Faeces produced by resident birds showed no relationship to the roost box odour. The number of defecations was also unrelated to the age of the kiwi. The age-day variable was significant when group data were excluded from the model (Figure 3.10), and was caused by a lack of data from other juveniles. As a percentage of roost boxes entered, adults left more faecal deposits than individually housed juveniles.

Nocturnal house kiwi ($\bar{x}$ = 3.24, S.E. = 0.97) defecated significantly more often than outside housed kiwi ($\bar{x}$ = 1.46, S.E. = 0.21), but there was no significant difference in the way these kiwi defecated in relation to the odour the roost box contained. When all data were included, kiwi of different housing showed significantly different defecation rates with respect to trial day. However, these differences were not obvious so defecations by group-held juveniles were responsible for the significance, as with the roosting behaviour. When group-held kiwi were excluded, the difference was not significant.

Kiwi held in groups defecated more often than other kiwi and individually housed females defecated significantly more often than individually housed male kiwi and paired kiwi. Means and standard errors are shown in Table 3.8. Kiwi of different sex did not defecate significantly differently in relation to the odour the roost box contained, or on different trial days.

Table 3.8: Average number (± S.E.) of defecations (n = 18) made by kiwi of different sexes.

Sex	Average No. Defecations	(+) S.E.	(-) S.E.
Female	2.17	0.94	0.66
Male	1.42	0.40	0.31
Pair	1.79	0.61	0.46
Group	3.98	3.99	1.99
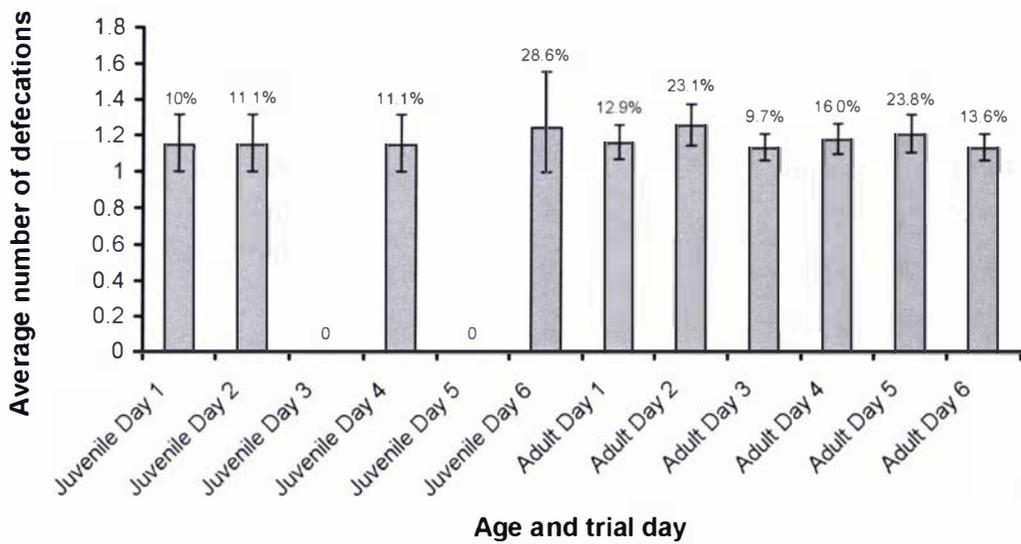
Figure 3.10: Average number of defecations made (± S.E.) by kiwi of different ages on different trial days. The percentage of roost boxes that kiwi of different ages entered and defecated in are shown.

Defecations by resident kiwi were also investigated after separating kiwi by age and sex, although the analyses were not included in the model (see Methods for details) (Figure 3.11). Individually housed juvenile males never defecated in roost boxes. Adult females were more likely to defecate in boxes than adult males, and they were also more likely to defecate in boxes that contained their own odour (Figure 3.12). Juvenile female kiwi defecated most often in boxes that contained either foreign kiwi odour or control odour. As a percentage of the number of roost boxes entered, paired kiwi were more likely to defecate in boxes that contained foreign kiwi odour, whereas kiwi held in groups were less likely to leave deposits in roost boxes that contained foreign kiwi odour.

When all kiwi were considered together, they showed no significant difference in the number of defecations with respect to trial day. Although there was a significant difference in the number of defecations made in roost boxes of different odour on different trial days, the differences were not obvious and it was probably a function of the small number of samples.

Defecation was significantly related to roosting occasions and half of the defecations were made in conjunction with roosting. On 22 (75.9%) occasions, kiwi defecated in the roost box they roosted in. Individual kiwi also differed significantly in their rates of defecation.
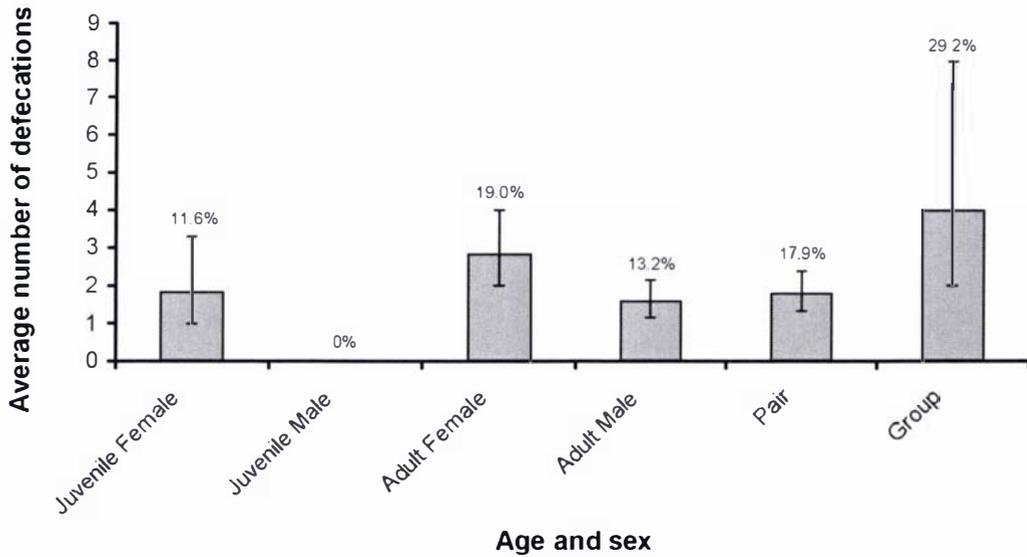
Figure 3.11: Average number of defecations made (± S.E.) by kiwi of different ages and sexes. The percentage of roost boxes that kiwi of different age and sex entered and defecated in are shown.
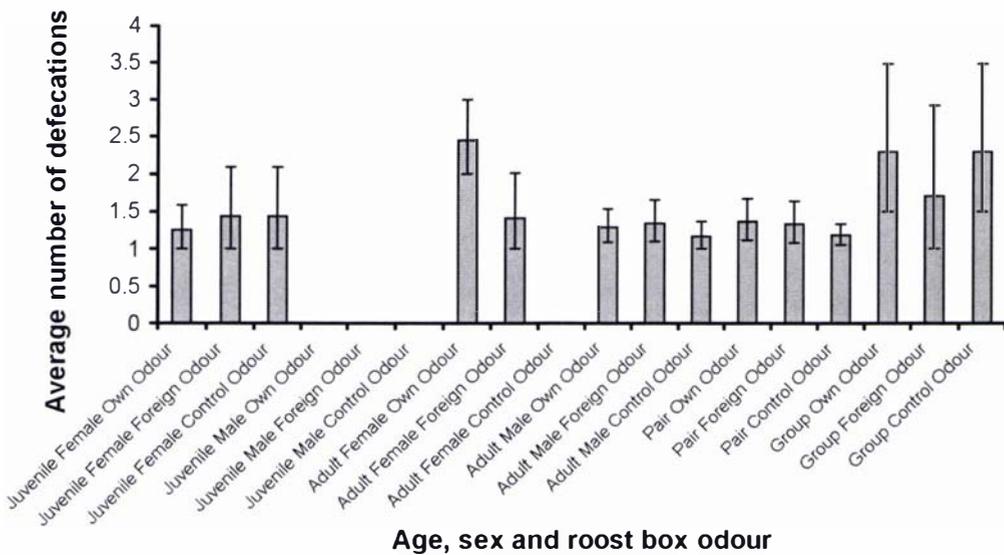
Figure 3.12: Average number of defecations made (± S.E.) by kiwi of different ages and sexes in roost boxes with different odour.

Order of Entrance into Roost Boxes

The deviance values and degrees of freedom suggest that the values predicted from the model were dispersed in a similar way to the actual data. The deviance values of the Genmod model, the degrees of freedom, the number of observations used, the missing values, and the likelihood ratio statistics for all variables are shown in Table 3.9. There was no significant relationship between the order that kiwi entered roost boxes and the odour these boxes contained. There was a significant difference in the way kiwi of different ages and sexes entered roost boxes of different odour, but there were no obvious trends in the data. The significance is most probably due to the lack of data from juvenile males, and the high level of individual variation. Kiwi of different housing showed no significant preferences for boxes of different odour and kiwi did not enter roost boxes with different odour in a significant order on particular trial days.

There was no significant difference in the way individual kiwi entered roost boxes of different odour, but individual kiwi did show a significant preference for entering certain boxes within the enclosure, regardless of which odour the roost box contained. Kiwi of different ages, sexes and housing also showed a significant preference for the order they entered roost boxes of different odour on particular trial days, but no consistent patterns were evident.

Table 3.9: Likelihood ratio statistics for factors relating to entrance order to roost boxes, where kiwi of different ages, sexes and housing were given a choice of three roost boxes, each with different faecal odour.

Source	Including All Data			Excluding Group Data			Excluding Group & Pair Data		
	DF	ChiSquare	Pr>Chi	DF	ChiSquare	Pr>Chi	DF	ChiSquare	Pr>Chi
Odour	2	5.32	0.0701	2	3.48	0.1753	2	2.68	0.2620
Age-Odour	3	10.91	0.0122	3	3.03	0.3864	3	3.53	0.3173
Housing-Odour	3	5.07	0.1666	3	2.22	0.5277	3	0.29	0.9615
Sex(Age-Housing-Odour)	24	52.78	0.0006	18	40.26	0.0019	15	33.43	0.0041
Day-Odour	15	12.89	0.6107	15	15.04	0.4486	15	13.51	0.5629
Kiwi(Age-Sex-Housing-Odour)	42	57.58	0.0551	39	54.26	0.0530	18	23.84	0.1603
Kiwi(Age-Sex-Housing-Box)	50	153.86	0.0001	44	144.63	0.0001	28	109.78	0.0001
Age-Day-Odour	15	35.39	0.0022	15	33.16	0.0045	15	32.24	0.0060
Housing-Day-Odour	15	32.91	0.0048	15	25.91	0.0390	15	29.65	0.0132
Sex(Age-Housing-Day-Odour)	90	219.96	0.0001	68	161.15	0.0001	53	151.21	0.0001
Goodness of Fit Deviance Value		118.66			117.85			51.22	
Goodness of Fit DF		105			100			40	
Number of Observations Used		365			323			208	
Missing Values		85 (18.9%)			73 (18.4%)			44 (17.5%)	

DISCUSSION

Overall, the odour that roost boxes contained did not influence the likelihood of the box being entered, suggesting that kiwi were neither attracted to, nor repelled from, boxes containing foreign kiwi odour. Kiwi entered roost boxes as they came across them, regardless of the odour they contained. This suggests that captive kiwi are habitual in the way they investigate their territory each night. The timers used recorded only the first entrance into a roost box each night so future experiments should investigate the amount of time kiwi spend in each box, and the total number of times kiwi enter roost boxes of different odours.

Roosting and defecation was also unrelated to the odour the roost box contained when the responses of all kiwi were considered. I expected to find that kiwi countermarked a foreign kiwi odour in an attempt to mask an intruder's odour and to advertise their occupancy as the territory owner. There are several possible explanations for why this did not happen. First, faecal deposition may not play a role in territorial marking. This is unlikely, as the responses kiwi made to foreign kiwi odour, shown in the previous chapter, suggest that they probably do use faecal odour to mark territories. Second, the amount of foreign faeces placed in the roost boxes may not have been enough to warrant the resident kiwi countermarking the roost box. Again, this is unlikely considering kiwi responded to a single odour container in the open enclosure, as reported in the previous chapter. Qualitative rather than quantitative changes in scent are important in scent processes in other species such as lemurs (Fornasieri and Roeder (1992). Third, kiwi may not purposefully countermark an intruder's odour at roost sites.

The third option is supported given the low number of defecations in roost boxes. Sliwa and Richardson (1998) found that aardwolves (*Proteles cristatus*) did not countermark scent marks near dens they were using, but did sniff at them for long periods. The high number of defecations associated with roosting suggests that defecation is mainly related to the amount of time kiwi spend in the boxes and the difference in faecal deposition rates shown by nocturnal house kiwi and outside housed kiwi supports this. Personal observations suggest nocturnal house kiwi are more interested in the roost boxes as a

new object in their enclosure, and therefore spend more time in and around them. Outside-housed kiwi spend less time in roost boxes and are more interested in investigating the rest of their enclosure for daily changes as well.

Kiwi did not attempt to countermark roost boxes containing a foreign kiwi odour, suggesting that defecation is not the primary way kiwi scent mark roost sites. However, the type of foreign kiwi scent may have been important in this response. Sliwa and Richardson (1998) found that aardwolves over-marked more frequently and increased their scent marking rate more when they found scent marks of same-sex donors and males over-marked fewer female marks than vice versa to avoid discouraging females that were searching for mating opportunities. The faeces used in the present study were of mixed gender origin, as they were often collected from enclosures that held more than one kiwi. Further studies on scent-marking in kiwi should concentrate on manipulating foreign odour types to assess kiwi responses to intruders of particular age and sex.

It is also possible that kiwi do not purposefully mark roost sites at all. The threat from a challenger finding the resident at its den may be so strong that the resident does not give away its position by faecal marking (Sliwa and Richardson, 1998). Roosting behaviour observed by McLennan and Potter (1992) suggests that kiwi often find roost sites of other kiwi by smell, so it appears that roost sites are scent marked in some way. Scent from glands on various parts of the body may play a more important role in roost site marking and this may explain why kiwi shift from one roost site to another almost every day in the wild.

Results also suggest that there are behavioural differences between kiwi of different ages and sexes. The greater likelihood that juvenile kiwi enter roost boxes appears to be a consequence of juveniles more often being held in groups. Personal observations of juvenile groups suggest that each of these kiwi attempt to claim a small part of the enclosure as their own, even from a young age. This was especially apparent from observations of the two larger groups, suggesting that the high entrance rate to experimental roost boxes, regardless of the odour the roost box contained, may be a way of individuals staking their claim to roost sites.

Kiwi held in groups were also more likely to roost, and therefore defecate, in roost boxes than juvenile kiwi housed individually, suggesting that group-held kiwi were eager to roost separately from other individuals in the enclosure. Kiwi held in groups were most likely to roost in boxes that contained a control odour and never roosted in experimental roost boxes that contained odour from their own enclosure, which supports this. The only other juvenile kiwi to roost in experimental roost boxes were two juvenile females housed together and it is likely that this single roosting occasion may also have been an attempt by one of the kiwi to roost singly for the night. This suggests that the desire of group-held kiwi to roost away from others in the group overpowered the unwillingness of individually housed juveniles to roost in unfamiliar roost boxes. When experimental roost boxes were not in the enclosures, group-held kiwi would mostly roost together, even though they had a choice of two enclosure boxes. The roost boxes seldom used may still have smelt of enclosure mates, so that kiwi did not use them as they did the freshly cleaned experimental roost boxes. This suggests that group-held juveniles should each be given clean roost boxes if they are to learn to roost singly before being released.

The fact that kiwi held in groups were less likely to roost in a box containing foreign kiwi odour suggests that such juveniles may be reluctant to roost in sites that contain an unfamiliar kiwi odour. Individually housed juvenile males were least likely to enter experimental roost boxes, regardless of the scent, and did not roost in boxes at all. These results may reflect a behaviour shown by juvenile kiwi, especially males, that prevents confrontation with adult birds in the wild. Adult territorial birds are likely to be heavier, stronger birds (Taborsky and Taborsky, 1991) and, as such, are more likely to escalate encounters with intruders (Gosling and McKay, 1990). Territorial kiwi may be particularly aggressive towards intruding males, which may represent a larger threat to territory holders, because intruding males are more likely to attempt to establish their own territory. No individually housed juveniles left faeces in roost boxes, which suggests that juveniles avoid leaving tell-tale signs of where they were within adult territories. Roper *et al.* (1993) also reports that sexually immature badgers rarely defecated or urinated at latrines, and Hurst (1990) suggests that dominant males will not tolerate the presence of subordinates if they deposit marks that signal their dominance.

Adult birds are more likely to act as territory holders than juveniles and their high entrance rates to roost boxes suggest they were not as timid as juveniles were at entering unfamiliar roost sites. Individually housed kiwi were attracted slightly more to roost boxes with foreign kiwi odour than were paired kiwi, suggesting that they may assess intruder odours for sexual reasons as well as territorial reasons.

Although single females may still hold territories, single males are more likely to hold larger territories and attempt to attract females into their territories by calling (Taborsky and Taborsky, 1991). This may mean that females are more likely to seek out partners as they reach breeding age. The slightly higher entrance rates shown by adult female kiwi may represent an attempt to find partners and the fact that they roosted most often in boxes with foreign kiwi odour supports this. This may reflect a behaviour that females show to both assess intruder status and to advertise their own sexual status and occupancy of the area. McLennan *et al.* (1987) also reported that unmated females were significantly more likely to enter the ranges of other kiwi than paired females were, and this may explain why single females are more likely to enter and roost in boxes than paired females.

Surprising, few individually housed adult males roosted in boxes. Since male kiwi are the more territorial sex (Taborsky and Taborsky, 1992), it was expected that adult males would roost more often in boxes to advertise territory occupancy. The behaviour of adult males suggests instead a behaviour related to mate finding where they may be more comfortable roosting in a familiar roost box in order to attract possible mates. The majority of adult pairs studied were involved in courtship behaviour or had eggs at the time of the study, so they were probably less interested in unfamiliar roost boxes which had not been prepared by the male for courtship. Both of the paired birds that did roost were females, but in each case the male partner was incubating at the time. On only one night, was a paired male seen carrying twigs and leaves into an experimental roost box and covering the entrance with leaves. This was after the female had spent considerable time in the box. During incubation, male kiwi have low blood plasma levels of testosterone and very high levels of oestradiol so male aggression decreases (Potter and Cockrem, 1992). This may explain why these paired males did not show high territorial interest in roost boxes.

The behaviours shown by captive kiwi may not be shown by wild kiwi. Ward-Smith (1998) found that there were marked differences in the behavioural responses of captive and wild kiwi to various baits placed outside nests, suggesting that captive kiwi were more likely to feed on novel items. Hurst (1990) also found that house mice that were not defending territories and had no experience of territory invasion did not show strong territorial behaviours. Hurst (1990) suggested that because marks had been translocated in a novel situation, as was done in my study, that house mice may not have responded correctly as expected in a proper social communication situation. Because captive kiwi never have to defend territories, future research on wild kiwi will improve knowledge on scent marking of roost sites.

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Chapter Four: Olfactory Detection of Subterranean Prey by Captive Northern Brown Kiwi

Olfactory Detection of Subterranean Prey by Captive Northern Brown Kiwi.

ABSTRACT

Olfactory detection of subterranean earthworms by kiwi was tested using large subterranean plastic boxes, each with fifteen cells containing soil. Four different experiments were performed to determine if kiwi primarily locate prey using olfaction, and whether the distribution or depth of earthworms in soil affected probe rates. Kiwi probed boxes with prey significantly more often than boxes without prey, but they did not probe empty cells within boxes with prey significantly less often than cells with prey. Concentrating prey in the middle cell of the test box did not result in probing being concentrated there and there was no significant difference between the number of probes made in cells with or without prey. The depth of prey within the cell also did not significantly affect the number of cells probed. The amount of prey in the box was the only variable that significantly affected probing frequency. Kiwi were better able to detect earthworms and probed significantly more often when earthworms were in greater numbers. Kiwi also removed the largest percentage of prey from boxes with the most prey. Juvenile kiwi probed significantly more often than adult kiwi, and made more multiple probes to individual cells, suggesting that juvenile kiwi locate prey less quickly. Kiwi held in groups probed significantly more often than single housed or paired kiwi, and were more likely to make multiple probes into individual test cells. This suggests that the amount of probing was related to the number of individuals in the enclosure as well as to juvenile probing behaviour, and that kiwi held in groups copy the probing behaviour of other enclosure mates, regardless of whether the box contained prey or not. Male kiwi were least likely to probe and thus removed the lowest percentage of prey. Probing often occurred in the absence of prey, and earthworms were often not discovered. The overall results suggest that kiwi do not use olfaction as the primary

sense to find subterranean prey, and that other cues such as auditory or vibrotactile cues may play key roles.

INTRODUCTION

Many species of mammals and reptiles use odour to detect prey (e.g. Johki and Hidaka, 1982; Langley, 1985; Nicoletto, 1985; Apfelbach, 1986; Langley, 1988; Cooper and Habegger, 2000; Gonzalez and Claramunt, 2000) and olfaction is the primary sense used for prey detection in several mammals (e.g. Balakrishnan and Alexander, 1979; Huang, 1987). In contrast, olfaction was considered least well developed in birds, and most are considered to be microsmatic (having a poor sense of smell) compared with other classes of vertebrates (Waldvogel, 1989). This resulted because most birds do not show behaviour suggestive of olfactory awareness (Reid and Williams, 1975; Wenzel, 1980).

Since the 1960s, however, evidence has accumulated that a wide range of bird species use olfaction (see review by Roper, 1999). All birds possess olfactory organs, but the size of the olfactory bulb is generally small both compared to other vertebrates, and in comparison with their own optic bulbs (Cobb, 1960; Pough *et al.*, 1996). The olfactory lobes, which lie towards the anterior of the brain, are associated with the telencephalon (Wenzel, 1971a) and the size of the olfactory bulb varies greatly in birds. Using the ratio between the longest diameter of the olfactory bulb and the longest diameter of the ipsilateral cerebral hemisphere (telencephalon), Cobb (1960) showed that there was a marked decrease in the size of this olfactory ratio in more recently evolved bird species. This suggests that there has been a shift away from olfaction and towards a reliance on vision and hearing as the primary senses in these birds (Strong, 1911; Wenzel, 1971a; Clark, 1991).

Avian species with large olfactory ratios were often assumed to have better olfactory ability, but recent studies show that birds with moderate or even poorly developed olfactory systems have some ability to detect odour. Evidence includes a wide range of

birds, including pigeons, domestic chickens, hummingbirds, starlings, ravens, turkey vultures, petrels, shearwaters, and kiwi, that use olfaction for many different purposes (e.g. Benham, 1906; Calvin *et al.*, 1956; Stager, 1964; Wenzel, 1968; Wenzel, 1971b; Grubb, 1972; Grubb, 1974; Stattelman *et al.*, 1975; Tolhurst and Vince, 1976; Papi, 1982; Wallraff and Hund, 1982; Jouventin and Robin, 1984; Gentle, 1985; Jones and Gentle, 1985; Harriman and Berger, 1986; Ioale and Papi, 1989; Clark and Smeraski, 1990; Healy and Guilford, 1990; Ioale *et al.*, 1990; Clark, 1991; Papi, 1991; Clark *et al.*, 1993; Gomez *et al.*, 1994; Turro *et al.*, 1994; Verheyden and Jouventin, 1994; Burne and Rogers, 1996; Jones and Roper, 1997; Minguez, 1997; Roper, 1999). This suggests that the olfactory ratio may not be a good indicator of how good a bird is at detecting odour (Waldvogel, 1989), and that it may not reflect their absolute olfactory sensitivity (Roper, 1999). An alternative suggestion is that the size of the olfactory bulb relates to the ability to discriminate between a range of odours, and that species with large olfactory ratios have a larger screen to compare olfactory information (Wallraff and Hund, 1982; Roper, 1999).

Kiwi have an olfactory ratio of 34%, which is the second largest known for any avian species (Bang and Cobb, 1968). This is largely responsible for the assumption that kiwi possess a good sense of smell. Additionally, kiwi are the only bird with external nares at the tip of the bill (Reid and Williams, 1975) and certain foraging behaviours, such as their audible sniffing, also suggests that they are using smell. Despite these assumptions, there have been few studies on the olfactory ability of kiwi.

The first of these studies, by Benham (1906), was based on a study carried out by the curator of Resolution Island on South Island brown kiwi and involved covering earthworms with 10 cm of soil in shallow buckets. Benham (1906) noted that kiwi only probed buckets containing worms and ignored similar buckets without them, and concluded that this was evidence that kiwi have a keen sense of smell.

Strong (1911) attempted to repeat Benham's (1906) work at the London Zoological Gardens, using clay garden pots partly filled with soil, but failed to obtain positive results. Only one kiwi approached the pots, and on several occasions it did not discover the food even though it must have made contact with the worms. Strong (1911)

concluded that there was no evidence of the acute sense of smell, although its existence was not disproved. Haeusler (1923) also reported that kiwi often did not detect prey that was directly in front of them and suggested that the sense of smell was not important in prey detection. Haeusler (1923) observed that as soon as the tip of the bill came into contact with something edible, kiwi would invariably seize and consume the food, and suggested instead that their bill acts as a highly sensitive organ of touch.

Wenzel (1968; 1971b) used five kiwi in experiments designed to test their ability to locate their regular food under conditions that eliminated visual, tactile, taste or auditory cues. She reported that kiwi only punctured tubes that contained food and that their ability to locate food was completely convincing. However, there are no details on exactly how the experiments were done, the number of replicates performed, or on the performances of all kiwi. Despite the fact that kiwi did not probe tubes that contained earthworms, Wenzel (1968) concluded that kiwi are capable of locating food, both natural and prepared, by means of olfactory cues alone.

This lead most subsequent authors to assume that kiwi have a very good sense of smell (e.g. Reid and Williams, 1975; Stoddart, 1980; Reid *et al.*, 1982; McLennan *et al.*, 1987; Peat, 1990; Johnson, 1996; Robertson, 1996). Waldvogel (1989) even states that Wenzel's (1968; 1971b) results demonstrate that kiwi are macrosmatic, and that their highly developed sense of smell is the primary sense used in foraging. In contrast, Roper (1999) noted that all experiments performed so far on kiwi olfaction were descriptive rather that quantitative, and that the assumption that kiwi have a good sense of smell still relies on indirect evidence and remains to be convincingly demonstrated.

All previous studies on kiwi olfaction have relied on tests performed in largely unnatural situations. All tests involved small containers for holding prey, which were visually obvious in the enclosures, and most of Wenzel's (1968; 1971b) tests involved uncovered artificial food. It was not possible for me to study kiwi in the wild, so I therefore created a situation as natural as possible using captive kiwi and their natural prey (earthworms). The latter were held within large, inconspicuous boxes underground, and these were used to determine whether kiwi use olfaction as their primary sense to detect subterranean prey.

METHODS

Kiwi and Earthworms Used

A total of 50 kiwi, in 28 enclosures, were used for this study. Kiwi were captive held in nocturnal houses and outside enclosures at institutes throughout New Zealand. Details of kiwi used are presented in Table 4.1. These included five juvenile females (two of which were held together), two juvenile males (held together), two adult females, nine adult males (four of which were held in two pairs), eleven pairs, and three groups (a group of two, a group of three, and a group of five). Enclosures used included ten nocturnal house enclosures and 18 outside enclosures.

Kiwi were presented with live earthworms in underground boxes, each containing 15 individual cell containers, which were filled with commercial organic compost soil. Earthworms were bought commercially from an organic farm, and included a mixture of five species – *Lumbricus terrestris*, *L. rubellus*, *Aporrectodea longa*, *A. celigonosa*, and *A. trapesoides*.

Table 4.1: Summary of the number of kiwi used at each institute (total = 50). The number of kiwi held in each enclosure (total number of enclosures = 28) and the number of kiwi held in nocturnal houses (total = 21) and outside enclosures (total = 29) are given. Kiwi were considered juvenile if they were 3 years of age or younger. Pair enclosures held one adult female and one adult male. Same sex pairs involved either adult or juvenile birds and for analysis were classified as the age and sex of these two birds. Kiwi held in groups involved only juveniles and included a group of two, as this enclosure held a juvenile male and a juvenile female so could not be classified under a paired status.

Institute	Number of kiwi sampled:				Number of kiwi held as a:				Number of kiwi housed in:	
	Juvenile Female	Juvenile Male	Adult Female	Adult Male	Single	Pair	Same Sex Pair	Group	Nocturnal House	Outside Housing
Auckland Zoo	0	2	2	2	0	4	2	0	2	4
Otorohanga Kiwi House	2	1	4	5	1	6	2	3	4	8
Rainbow Springs	2	0	1	3	4	0	2	0	3	3
Westshore Wildlife Reserve	2	0	1	2	3	2	0	0	0	5
Orana Park	1	1	2	2	0	4	0	2	2	4
Willowbank Wildlife Reserve	5	1	3	6	2	6	2	5	10	5

Prey Boxes

The plastic prey boxes measured 340 mm by 555 mm and 235 mm deep (42 *l* volume), each with six holes (10 mm diameter) drilled in the bottom for drainage. Four wooden blocks, 85 mm high, were placed in the bottom corners of each plastic box and a segment of 8 mm plywood, 318 mm by 515 mm, was placed on top of them. This plywood formed a stage for holding the cell containers at the right height within the prey box.

A grid made from aluminium bars (25 mm by 3 mm) rested on top of each prey box. This grid measured 390 mm wide by 600 mm long and formed 15 square cells, each measuring 75 mm by 75 mm (Figure 4.1). The 20 cells around the edge were not used. The central cells were numbered one to fifteen from top left to bottom right of the box. The edges of the grid were shaped to fit snugly on the top of the prey box and all edges were rounded.

Figure 4.1: A prey box. These boxes were dug into the soil of the enclosure so that the top was level with the soil. Aluminium bars formed a grid that enclosed 15 central cells, each measuring 75 mm by 75 mm. Cells were numbered one to fifteen from top left to bottom right of the box.

Cell Containers

Cell containers were square black plastic pots measuring 70 mm by 70 mm and 160 mm deep. They tapered towards the bottom, which measured 55 mm by 55 mm. The bottom had a square section of black vinyl fixed to it, with a small hole in the centre to allow drainage. Each side of the container was drilled with 12 evenly spaced holes, 2 mm in diameter, to allow odour to disperse between cells (Figure 4.2a and 4.2b).

Figure 4.2a: A cell container. Each container measured 70 mm by 70 mm and 160 mm deep and tapered towards the bottom, which measured 55 mm by 55 mm. The bottom had a square section of black vinyl fixed to it, with a small hole in the centre to allow drainage. Each side of the container was drilled with 12 evenly spaced holes, 2 mm in diameter, to allow odour to disperse between cells.

Figure 4.2b: A cell container, showing the 12 holes drilled in the sides of each container, to allow odour to disperse.

Fifteen cell containers were placed in each prey box, where they were held within the aluminium grid (Figure 4.3). They were set up immediately prior to use with soil, paper dividers and earthworms (as described below). Latex gloves were used for handling of all equipment and prey. Cell containers were washed after each use with dish detergent and cold water, and left to dry.

Figure 4.3: A prey box, showing the placement of cell containers within the aluminium grid of the box.

Paper Dividers

Depending on the experiment, either two or three horizontal layers of paper were added within the soil in the cell containers to restrict earthworms to a certain depth and to help detect probing by kiwi. These were made of newsprint paper cut into squares (80 mm by 80 mm) to fit the cell containers. Cuts were also made 15 mm in from each corner at a 45 degree angle so that the edges of the paper could be folded up the side of the cell containers a short distance to seal in the earthworms. Twenty-five pin holes were made in each divider, over the area that lay flat to the soil. These holes were spaced 10 mm from each other in rows of five by five and were designed to allow odour to diffuse through into the adjacent soil. A pilot test showed that the paper dividers restrained the earthworms if set carefully with no gaps at the corners of the cell containers.

Placement and Filling of Prey Boxes

Four prey boxes were dug into each enclosure so that the top of the box was flush at ground level. The boxes were placed in relatively flat areas, which were also readily accessible for making changes between experiments. The prey boxes and cell containers were then filled with compost soil until a 5 mm layer of soil totally covered them. Soil from the same commercial source was used for each experiment, and was topped up as needed. The same soil was used for several trials, but fresh soil was used for each captive institute.

Experimental Set Up

Four different experiments were run in each enclosure and in the same order each time. On the first night of each experiment, kiwi were deprived of at least some of their artificial food, so that they had to forage to a larger extent in the enclosure. On the second night of each experiment kiwi were given their usual amount of food. This alternating feeding regime was continued for the duration of the trial and depended on captive institutions, as follows:

- The Auckland Zoo nocturnal house kiwi were given half their normal food on the first experimental nights for display reasons and kiwi housed outside had no decrease in food for breeding reasons.
- Kiwi in the Otorohanga nocturnal house had no decrease in food, but food was not available for most of their active period. Birds housed outside were given no food on the first experimental nights.
- All kiwi at Rainbow Springs were given no food on the first experimental nights, except for one kiwi, which was given half food because it had recently been moved to a new enclosure.
- All kiwi at Westshore Wildlife Park were given no food on the first experimental nights.

- Kiwi in the nocturnal house at Orana Park were given half their normal food on the first experimental nights for display reasons. Kiwi housed outside had no food on the first experimental nights.
- Breeding pairs of kiwi at Willowbank Wildlife Reserve were given half food on the first experimental nights, but all other kiwi were given no food.

Prey boxes were dug into the enclosure three to four days before prey trials began. The cell containers contained soil only, so that kiwi got used to the equipment before experiments began. Experiments 1, 2, and 3 were run consecutively, each over two days. These three tests were followed by a break of two days, during which the cell containers were filled with soil only. After this, Experiment 4 was run and the prey boxes were then removed. Details of the four experiments are as follows:

Experiment 1: Can kiwi detect earthworms in soil?

This tested whether kiwi could determine whether a prey box contained earthworms. Two prey boxes were provided with earthworms and the other two prey boxes had none. All cell containers had paper dividers at depths of 10, 40 and 50 mm and eight of the cells in the two experimental boxes were each provided with two earthworms. These were placed between the two lower paper dividers.

Experiment 2: Will kiwi probe more selectively near earthworms when more earthworms are concentrated within an area?

This tested whether kiwi were more attracted to prey when more prey were present and when it was concentrated together. It also tested how accurate kiwi were at finding subterranean prey. All four prey boxes were set up identically with prey. All cell containers had paper dividers at depths of 10, 40 and 50 mm and five earthworms were placed between the lower two paper dividers in the middle cell of each box.

Experiment 3: Do kiwi probe selectively for subterranean prey at different depths?

This tested whether kiwi were attracted to, or had a preference for, prey at different depths. All four prey boxes were set up identically with prey. Five of the cells (cells 1, 4, 7, 10, and 13) were set as 'deep prey' cells. These cell containers had paper dividers at depths of 10, 80 and 90 mm and two earthworms were placed between the lower two paper dividers. Five of the cells (cells 2, 5, 8, 11, and 14) were set as 'shallow prey' cells. These had paper dividers at depths of 10, 20 and 30 mm and two earthworms were placed between the lower two paper dividers. The remaining five cells in each prey box were set without prey. These cell containers had paper dividers at depths of 10, 40 and 50 mm.

Experiment 4: Will kiwi probe preferentially beneath logs?

This tested whether kiwi preferentially probe under objects in their environment. All four prey boxes were set up identically without prey. All cell containers had paper dividers at depths of 10, 40 and 50 mm and two of the prey boxes had a log placed diagonally across the top of the soil from the top left to the bottom right of the prey box. The logs used were found within each enclosure, so that any responses were not due to a new object in the enclosure. These logs differed in species, with the most common type being tree fern (*Cyathea* or *Dicksonia* spp.).

Recording Probing Responses by Kiwi

Kiwi were not observed directly during these trials, but the number of probes made by them was determined from holes left in the paper dividers. Probing by individual kiwi could not be identified, so data were recorded for the enclosure as a whole. Data recorded included whether kiwi had probed a cell, which paper dividers were shredded (indicating multiple probes into the same cell), and the number of earthworms taken. Examples of damage to paper dividers are shown in Figure 4.4a and 4.4b. Any

earthworms missing were assumed to have been taken by kiwi, although some earthworms may have escaped from cells after kiwi had made holes through the paper dividers. Some worms were found in the bottom of the cell after kiwi had damaged the paper dividers, which suggests that they moved downwards if possible. Kiwi often completely uncovered the boxes and sometimes pulled paper dividers out of the cell containers (Figure 4.5a and 4.5b). In these cases, the cells were recorded as having been probed, but the paper dividers were not recorded as having been shredded.

Data Analysis

Data are appended on the enclosed CD. Analysis was performed using SAS, Version 6.12, with a generalised linear model and a binomial type1 distribution. Several variables were nested together, when every level of one factor occurs with only one level of another factor. The variable sex was nested with age and housing because there were no groups of adults, no groups were housed outside, and there were no juvenile pairs to compare data with. The variable kiwi (individual birds) was nested with age (juvenile (three years of age or younger) or adult), sex (male, female, pair or group) and housing (nocturnal house or outside enclosure) because an individual kiwi (or enclosure) could only be one age, one sex, and one housing type. For Experiment 1 and for analysis of the entire data set, cell type (whether the cell container held earthworms or not, and the depth of earthworms) was nested with box type (whether the prey box contained earthworms or not) so that empty cells in boxes with prey were distinct from empty cells in empty boxes. Variables were considered significant if $P < 0.05$. Least significant means tests could not be run using this model for undetermined reasons.

Figure 4.4a: Paper dividers recovered from one cell container after kiwi had probed the prey box during two experimental nights. This cell was probed through all three layers of paper. Note the cuts at the corners of the paper dividers to allow folding within the cells.

Figure 4.4b: Paper dividers recovered from one cell container after kiwi had probed the prey box during two experimental nights. These paper dividers were shredded by the kiwi, indicating multiple probes into the same cell.

Figure 4.5a: View of a prey box within a kiwi enclosure, covered by the darker soil. This photo was taken before kiwi had access to the box.

Figure 4.5b: View of the same prey box after kiwi had probed the box for two nights. The aluminium grid, cell containers and plastic box are well exposed.

Data Analysis for Experiment 1: Can kiwi detect earthworms in soil?

The ratio derived from the number of cells probed divided by the number of cell types present in each prey box was used as the dependent variable. This was compared to seven classes - box type, cell type, age, sex, housing, kiwi and kiwi-box.

Data Analysis for Experiment 2: Will kiwi probe more selectively near earthworms when more earthworms are concentrated within an area?

The ratio derived from the number of cells probed divided by the number of cell types present in each prey box was used as the dependent variable. This was compared to six classes - cell type, age, sex, housing, kiwi and kiwi-box.

Data Analysis for Experiment 3: Do kiwi probe selectively for subterranean prey at different depths?

The ratio derived from the number of cells probed divided by the number of cell types present in each prey box was used as the dependent variable. This was compared to six classes - cell type, age, sex, housing, kiwi and kiwi-box.

Data Analysis for Experiment 4: Will kiwi probe preferentially beneath logs?

The ratio derived from the number of cells probed divided by the number of cell types present in each prey box was used as the dependent variable. This was compared to five classes - log (whether the prey box had a log placed across it or not), age, sex, housing, and kiwi. The kiwi-box variable could not be assessed because the model became too saturated and would not assess the goodness of fit.

Data Analysis for Overall Trends

The ratio derived from the number of cells probed divided by the number of cell types present in each prey box was used as the dependent variable. This was compared to eight classes - box type, cell type, age, sex, housing, box (1, 2, 3, or 4), experiment (1, 2, 3, or 4), kiwi, and combinations of these. The effect of age-sex could not be included in the model because of the nested kiwi variable, and probe rates were compared between kiwi of different age and sex using means and standard errors alone.

Data were also analysed for the effect of enclosure size on the percentage of cells probed, to determine whether the number of times a kiwi encountered a prey box was related to the number of times a prey box was probed.

Data Analysis for Multiple Probing

When kiwi made multiple probes into the same cell, the paper dividers became shredded into several small pieces. This state of the cell was termed 'shredded', and was analysed as the dependent variable to assess rate of probing in different cells. This was compared to nine classes - experiment, box type, cell type, age, sex, housing, percentage of prey taken, kiwi, and kiwi-box.

Data Analysis for the Percentage of Prey Taken

The ratio of the number of prey taken divided by the number of prey presented was used as the dependent variable. This was compared to seven classes - experiment, cell type, age, sex, housing, kiwi and kiwi-box. Cells that did not contain prey were excluded from this analysis.

RESULTS

Each of the four tests showed similar effects of age, sex, housing, kiwi, and kiwi-box so data from the four tests were pooled and these variables were analysed over the entire data set.

Experiment 1: Can kiwi detect earthworms in soil?

The model was underdispersed (deviance value = 24.88, DF = 55), indicating that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.2. Prey boxes with earthworms were probed significantly more often than those without earthworms, but kiwi did not probe empty cells within boxes with earthworms significantly less than cells with prey. The percentage of cells probed and standard errors are shown in Table 4.3.

Table 4.2: Likelihood ratio statistics for factors relating to Experiment 1, where kiwi of different ages, sexes, and housing were given a choice of four prey boxes, each with 15 cell containers. Two boxes held earthworms in eight of the cells they contained (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Box Type	1	14.86	0.0001
Cell Type (Box Type)	1	0.01	0.9112
Age	1	10.21	0.0014
Housing	1	91.63	0.0001
Sex (Age-Housing)	7	326.18	0.0001
Kiwi (Age-Sex-Housing)	18	789.84	0.0001
Kiwi (Age-Sex-Housing-Box)	83	371.29	0.0001

Table 4.3: Average percentage (± S.E.) of cells probed in different cell types and box types for Experiment 1 (see Methods for details).

Cell Type and Box Type	Average % Cells Probed	± S.E.
Empty Cells in Empty Boxes	34.40	5.19
Empty Cells in Boxes with Prey	43.37	6.18
Prey Cells	43.75	6.04

Experiment 2: Will kiwi probe more selectively near earthworms when more earthworms are concentrated within an area?

This model was also underdispersed (deviance value = 41.57, DF = 111), indicating that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.4. The percentage of middle cells probed in each prey box, with five earthworms, was not significantly more ($\bar{x} = 36.61$, S.E. = 4.57) than the percentage of empty cells probed ($\bar{x} = 40.56$, S.E. = 4.15).

Table 4.4: Likelihood ratio statistics for factors relating to Experiment 2, where kiwi of different ages, sexes and housing were given a choice of four prey boxes, each with 15 cell containers. Each box had earthworms in the middle cell only (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Cell Type	1	0.69	0.4074
Age	1	34.43	0.0001
Housing	1	47.46	0.0001
Sex (Age-Housing)	8	355.87	0.0001
Kiwi (Age-Sex-Housing)	17	851.08	0.0001
Kiwi (Age-Sex-Housing-Box)	84	455.07	0.0001

Experiment 3: Do kiwi probe selectively for subterranean prey at different depths?

The goodness of fit parameters (deviance value = 27.48, DF = 222) indicate that the model was underdispersed and that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.5. Kiwi did not probe cells with prey that was deep or shallow at significantly different rates, and did not probe empty cells less often than cells with prey. Kiwi of different ages did not probe cells at significantly different rates, but the rest of the variables were significant and are analysed over the whole data set and included in the overall trends section below.

Table 4.5: Likelihood ratio statistics for factors relating to Experiment 3, where kiwi of different ages, sexes, and housing were given a choice of four prey boxes, each with 15 cell containers. Each box contained earthworms set at deep (80-90 mm) and shallow (20-30 mm) depths (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Cell Type	2	0.23	0.8894
Age	1	0.27	0.6063
Housing	1	15.5	0.0001
Sex (Age-Housing)	8	451.89	0.0001
Kiwi (Age-Sex-Housing)	17	1424.55	0.0001
Kiwi (Age-Sex-Housing-Box)	84	228.49	0.0001

Experiment 4: Will kiwi probe preferentially beneath logs?

The model was underdispersed (deviance value = 226.21, DF = 83), indicating that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.6. Kiwi probed a significantly smaller percentage of cells under logs ($\bar{x}$ = 43.45, S.E. = 5.67) than in boxes without logs ($\bar{x}$ = 55.71, S.E. = 6.29). Kiwi of different housing did not probe cells at significantly different rates, but the rest of the

variables were significant and are analysed over the whole data set and included in the overall trends section below.

Table 4.6: Likelihood ratio statistics for factors relating to Experiment 4, where kiwi were given a choice of four prey boxes, each with 15 cells and without earthworms. Two of the boxes had logs placed diagonally across them (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Log	1	25.32	0.0001
Age	1	6.27	0.0123
Housing	1	3.63	0.0568
Sex (Age-Housing)	8	330.39	0.0001
Kiwi (Age-Sex-Housing)	17	1214.95	0.0001

Overall Trends

The goodness of fit parameters (deviance value = 373.03, DF = 613) indicate the model was underdispersed and that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.7. The results from the entire data set, after data from all four experiments have been pooled, showed that kiwi probed a significantly greater percentage of cells in boxes that contained prey ($\bar{x} = 49.05$, S.E. = 1.84) than empty boxes ($\bar{x} = 44.52$, S.E. = 3.36). There was also a significant difference in the percentage of different cell types probed (Figure 4.6). Cells with deep and shallow prey were probed most often, followed by cells without prey. Cells with prey at 50 mm were probed least often.

Table 4.7: Likelihood ratio statistics for factors relating to data from all experiments combined (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Box Type	1	7.55	0.0060
Cell Type (Box Type)	4	110.39	0.0001
Age	1	30.20	0.0001
Housing	1	122.01	0.0001
Sex (Age-Housing)	8	1332.84	0.0001
Experiment	2	68.54	0.0001
Kiwi (Age-Sex-Housing)	17	3664.11	0.0001
Kiwi (Age-Sex-Housing-Box)	84	931.42	0.0001
Age-Experiment	3	48.00	0.0001
Housing-Experiment	3	60.09	0.0001
Sex (Age-Housing-Experiment)	24	240.77	0.0001
Kiwi (Age-Sex-Housing-Experiment)	51	446.73	0.0001
Age-Boxtype	1	10.15	0.0014
Housing-Boxtype	1	5.22	0.0223
Sex (Age-Housing-Boxtype)	8	56.82	0.0001
Kiwi (Age-Sex-Housing-Boxtype)	17	20.36	0.2563

Juvenile kiwi probed a significantly greater number of cells ($\bar{x} = 52.38$, S.E. = 3.08) than adult kiwi ($\bar{x} = 46.45$, S.E. = 1.90). Kiwi held in groups probed boxes significantly more often than individually housed and paired kiwi, and individually housed male kiwi probed prey boxes least often (Figure 4.7). Adult female kiwi probed significantly more often than other individually housed kiwi (Figure 4.8), and juvenile kiwi probed less often than adults of the same sex, indicating that the significantly higher probe rates shown by juveniles when kiwi are only separated by age is caused by the high probe rates of kiwi held in groups. Kiwi in nocturnal houses probed a significantly greater percentage of cells ($\bar{x} = 57.31$, S.E. = 2.70) than outside housed kiwi ($\bar{x} = 43.05$, S.E. = 1.99). The percentage of cells probed was greatest in Experiment 3 (Figure 4.9).
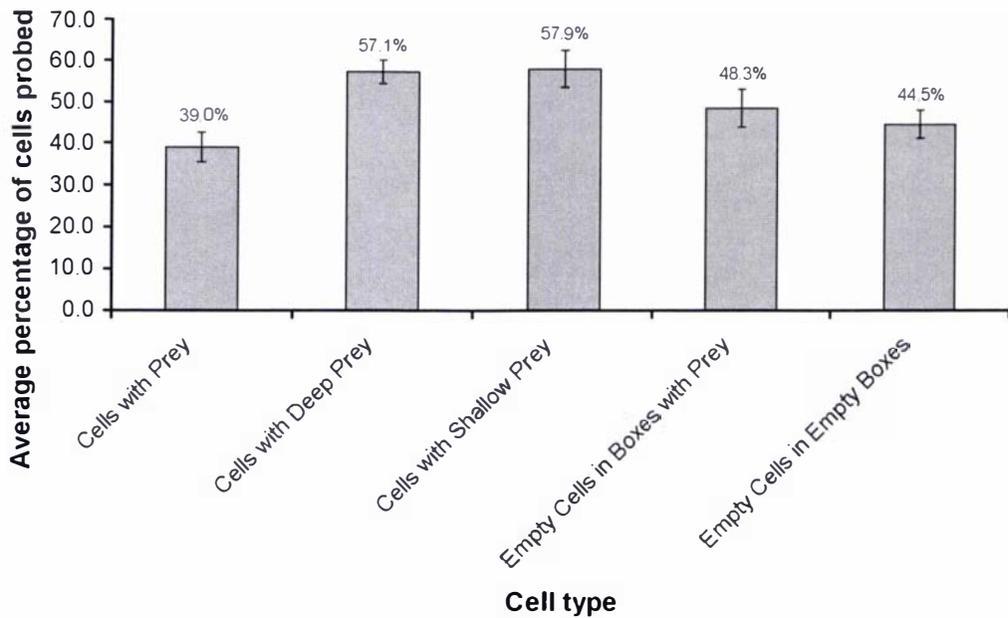
Figure 4.6: Average percentage (± S.E.) of different cell types probed. Data are from all experiments combined. Cells with Prey = prey at 40-50 mm, Cells with Deep Prey = prey at 89-90 mm, Cells with Shallow Prey = prey at 20-30 mm.
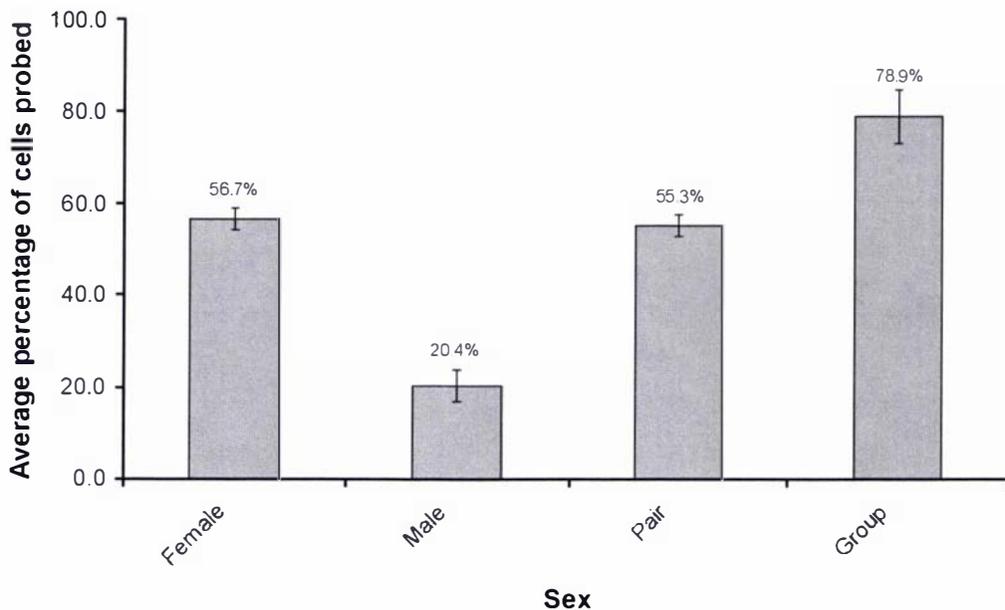

Figure 4.7: Average percentage (± S.E.) of cells probed by kiwi of different sexes. Data are from all experiments combined. Pair and group enclosure types are included in the sex category because probing by individual kiwi could not be identified.

Figure 4.8: Average percentage (± S.E.) of cells probed by kiwi of different ages and sexes. Data are from all experiments combined. Pair and group enclosure types are included in the sex category because probing by individual kiwi could not be identified.
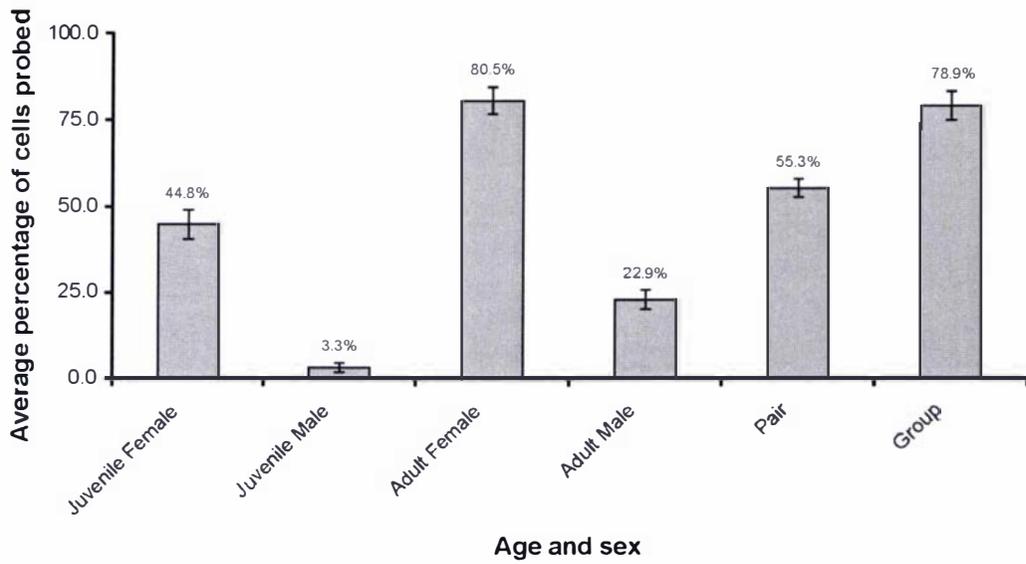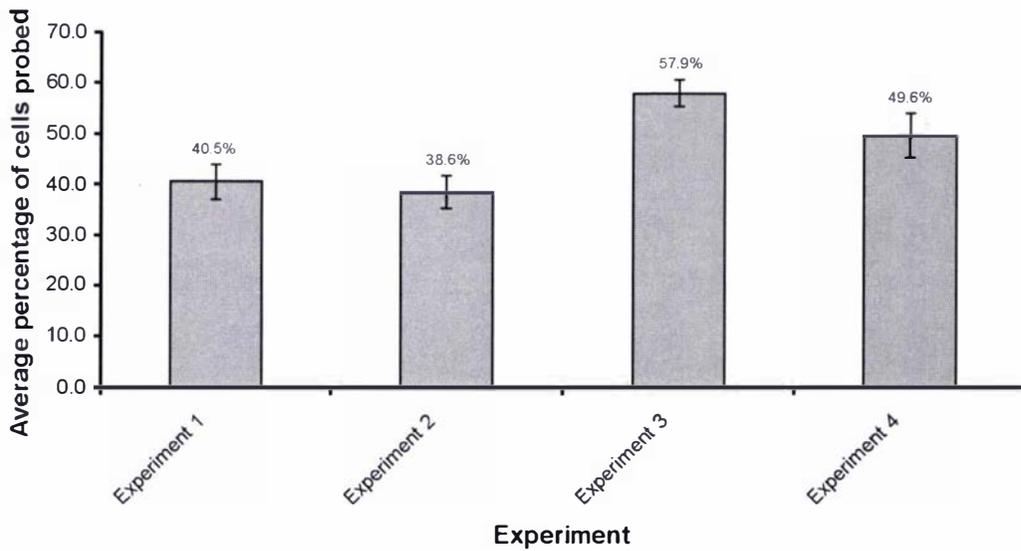

Figure 4.9: Average percentage (± S.E.) of cells probed by kiwi in different experiments. For details of experiments see Methods.

Individual kiwi also showed significantly different probe rates from each other (Figure 4.10) and showed significantly different probe rates in certain boxes.

Juvenile kiwi probed significantly more often than adults did in all tests except for Experiment 3 (Figure 4.11), when there was no significant difference between birds of different ages. Juvenile kiwi probed at similar rates over the entire trial, whereas adult kiwi probed a higher proportion of cells in Experiments 3 and 4. Kiwi held in groups probed at significantly higher rates than individually housed and paired kiwi (Figure 4.12), and they also probed at similar rates over the entire trial. Individually housed female kiwi probed significantly more often than individually housed male kiwi in each experiment, and all sexes of kiwi probed a higher percentage of cells in Experiment 3. Nocturnal house kiwi probed significantly more often than kiwi housed outside in each experiment, except Experiment 4 (Figure 4.13), when there was no significant difference between the housing types. Individual kiwi also probed cells at significantly different rates in different experiments, but there was no apparent pattern in this.

There was a significant difference in the percentage of cells probed by kiwi of different ages in boxes with and without prey. The average percentage of cells probed and standard errors are shown in Table 4.8. Kiwi of different sexes (Figure 4.14) and kiwi housed differently also probed at significantly different rates in boxes with and without prey. The average percentage and standard errors of cells probed by nocturnal house and outside kiwi are shown in Table 4.9. There was no difference in the probe rates between individual kiwi in boxes with or without prey.
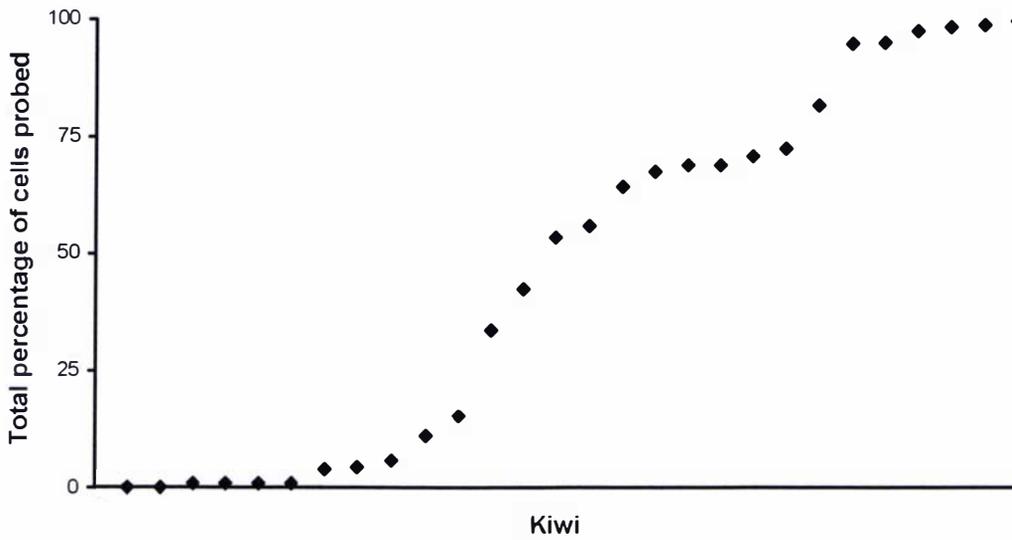
Figure 4.10: Total percentage of cells probed by individual kiwi, shown in ascending order. Data are combined from all experiments.
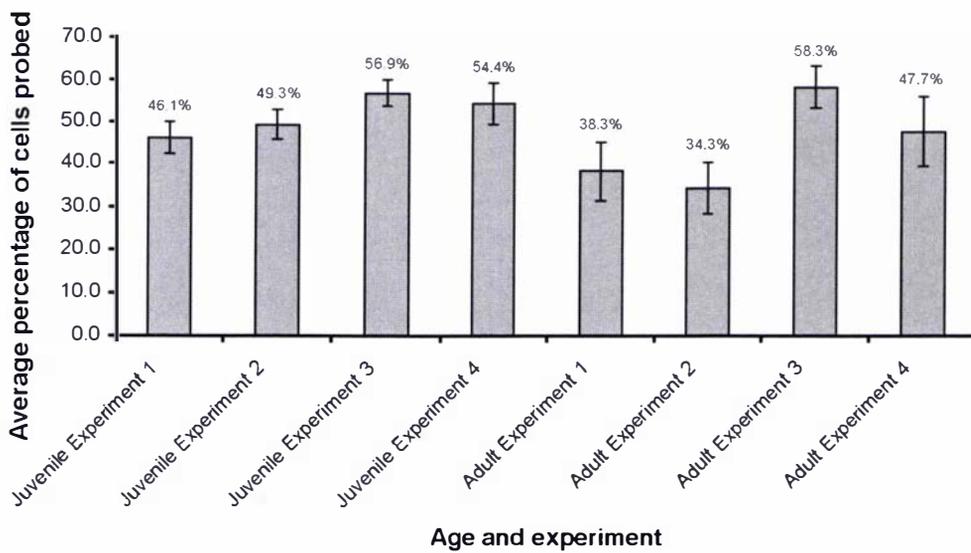
Figure 4.11: Average percentage (± S.E.) of cells probed in different experiments by kiwi of different age. For details of experiments see Methods.
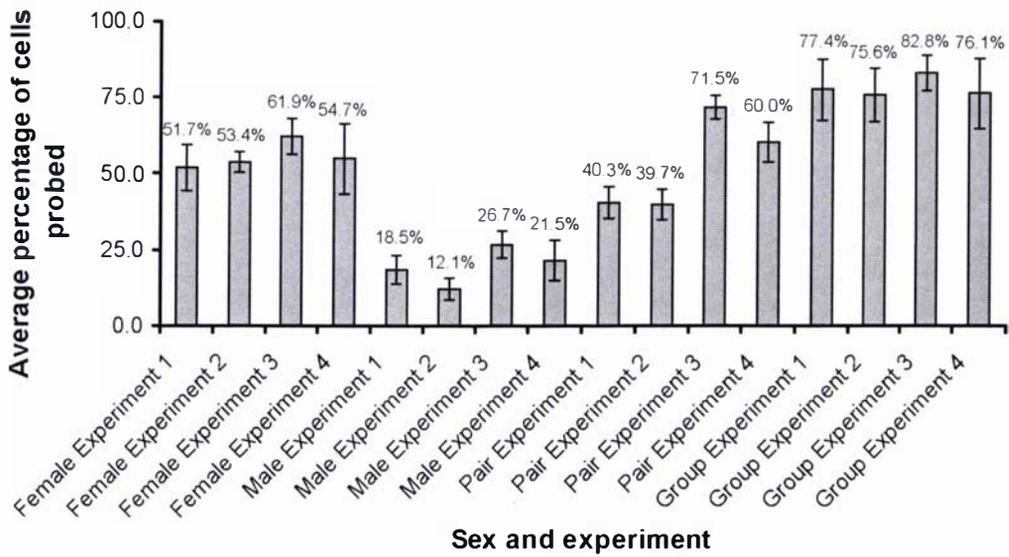
Figure 4.12: Average percentage (± S.E.) of cells probed in different experiments by kiwi of different sexes. Pair and group enclosure types are included under the sex category because probing by individual kiwi could not be identified. For details of experiments see Methods.
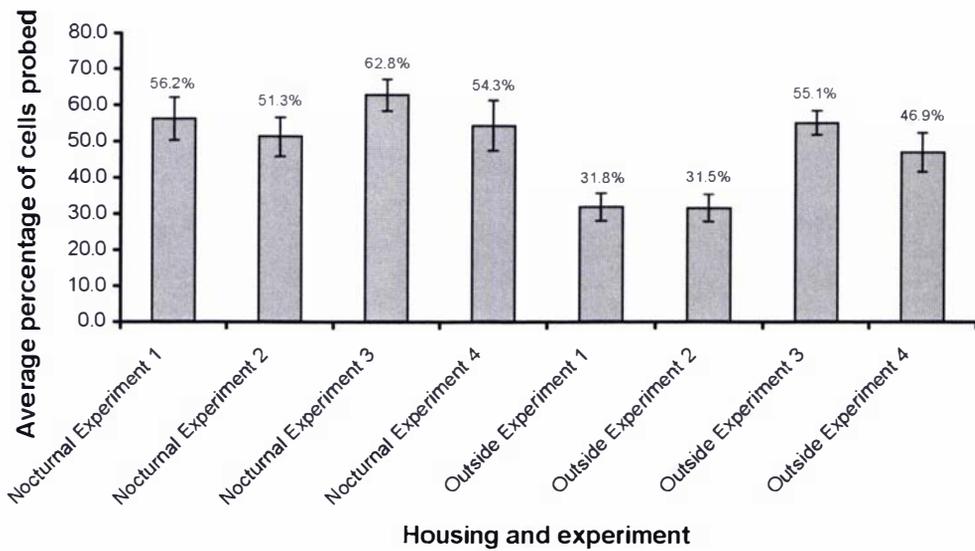
Figure 4.13: Average percentage (± S.E.) of cells probed in different experiments by kiwi in different housing. For details of experiments see Methods.
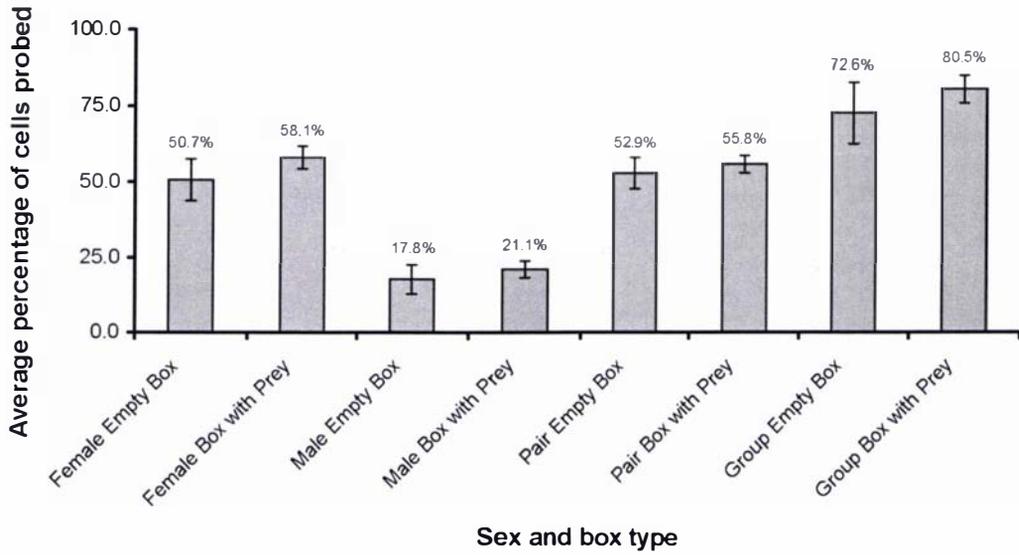
Figure 4.14: Average percentage (± S.E.) of cells probed in different box types by kiwi of different sexes. Data are from all experiments combined. Pair and group enclosure types are included in the sex category because probing by individual kiwi could not be identified.
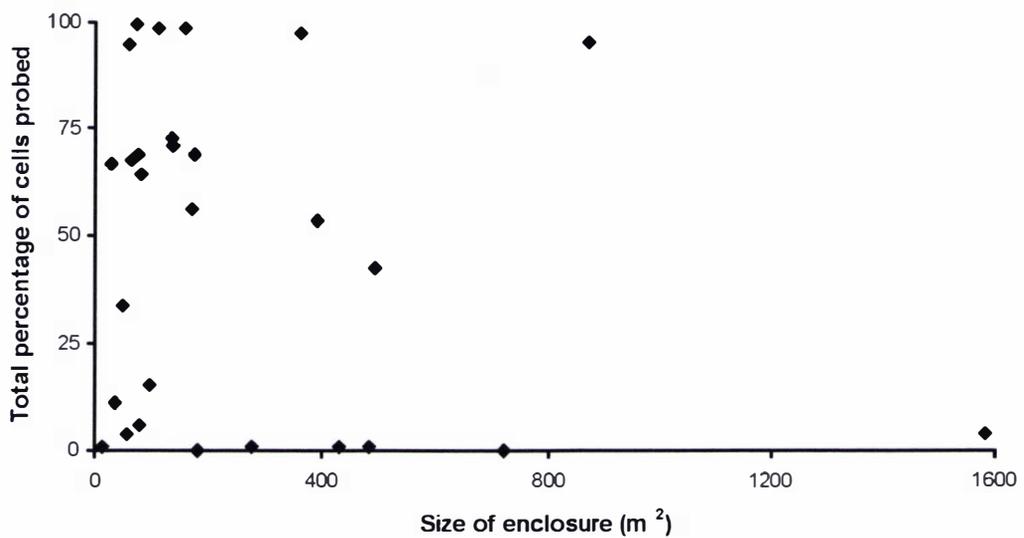
Figure 4.15: Relationship between the size of the enclosure (m^2) and the total average percentage of cells probed by kiwi in the enclosure. Data are from all experiments combined.

Table 4.8: Average percentage (± S.E.) of cells probed by kiwi of different ages in different box types.

Age and Box Type	Average % Cells Probed	± S.E.
Juvenile Empty Box	50.14	6.73
Juvenile Box with Prey	52.94	3.47
Adult Empty Box	42.49	3.91
Adult Box with Prey	47.42	2.17

Table 4.9: Average percentage (± S.E.) of cells probed by kiwi of different housing in different box types.

Housing and Box Type	Average % Cells Probed	± S.E.
Nocturnal Empty Box	52.89	5.65
Nocturnal Prey Box	58.41	3.07
Outside Empty Box	39.88	4.13
Outside Prey Box	43.85	2.27

There was no relationship between the size of the enclosure and the percentage of cells probed (Figure 4.15).

Multiple Probing

The model was underdispersed (deviance value = 1028.76, DF = 6601), indicating that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.10. There was a significantly higher percentage of cells with paper dividers shredded in Experiment 3 compared with other experiments (Figure 4.16). Cells in boxes with prey also had a significantly greater percentage of paper dividers shredded ($\bar{x} = 7.24$, S.E. = 0.40) compared with boxes without prey ($\bar{x} = 0.24$, S.E. = 0.10). The percentage of cells with paper dividers shredded was also significantly related to whether the cell contained earthworms or not, and the depth of the earthworms (Figure 4.17).

Figure 4.16: Average percentage (± S.E.) of cells with multiple probes to a maximum of 50 mm by kiwi in different experiments. For details of experiments see Methods.
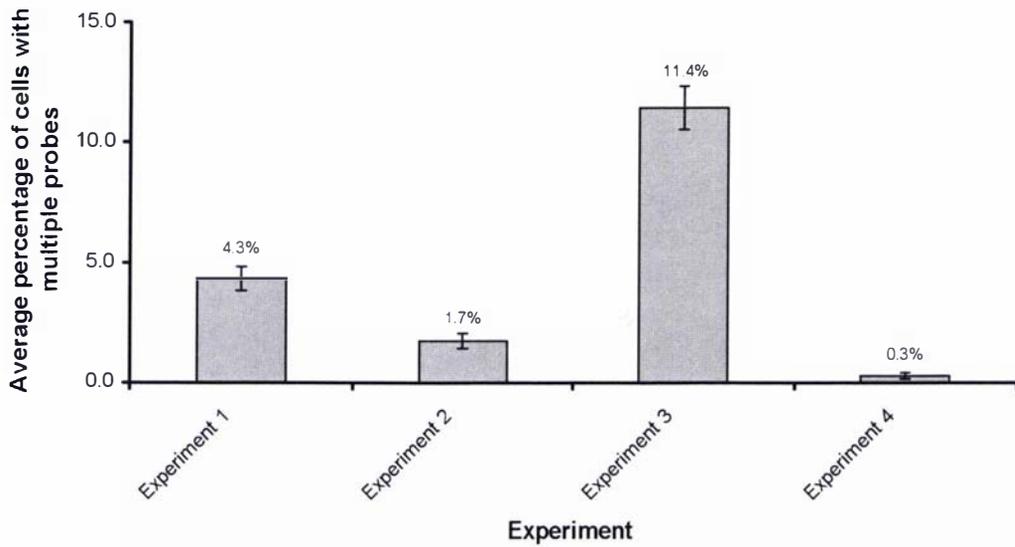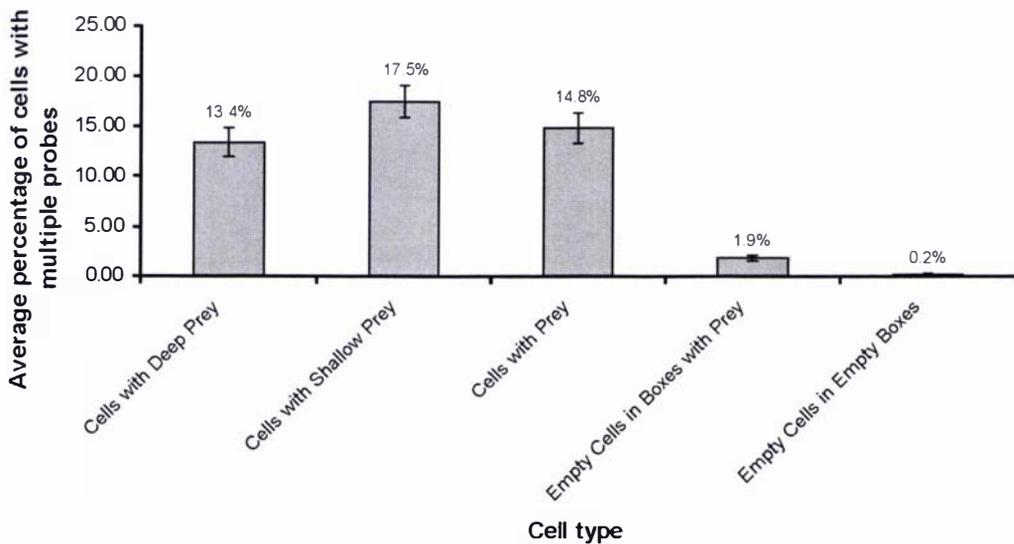

Figure 4.17: Average percentage (± S.E.) of paper dividers shredded by kiwi in different cell types. Data are combined from all experiments. Cells with Deep Prey = prey at 80-90 mm, Cells with Shallow Prey = prey at 20-30 mm, Cells with Prey = prey at 40-50 mm.

Shallow prey cells were shredded most often, followed by cells with prey at 50 mm and cells with deep prey. Cells without prey were shredded least often.

Table 4.10: Likelihood ratio statistics for factors relating to multiple probing. Data are from all experiments combined (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Experiment	3	312.59	0.0001
Box Type	1	93.77	0.0001
Cell Type (Box Type)	3	154.05	0.0001
Age	1	134.92	0.0001
Housing	1	26.77	0.0001
Sex (Age-Housing)	7	233.43	0.0001
Number of Prey Taken	6	243.95	0.0001
Kiwi (Age-Sex-Housing)	18	176.50	0.0001
Kiwi (Age-Sex-Housing-Box)	84	141.14	0.0001

Juvenile kiwi shredded a significantly higher percentage of paper dividers ($\bar{x} = 9.32$, S.E. = 0.66) than adult kiwi ($\bar{x} = 2.73$, S.E. = 0.24), and nocturnal house kiwi shredded more paper dividers ($\bar{x} = 8.13$, S.E. = 0.56) than outside housed kiwi ($\bar{x} = 2.66$, S.E. = 0.24). Kiwi held in groups shredded significantly more paper dividers than individually housed kiwi and paired kiwi. The average percentage and standard errors of cells with paper dividers shredded are shown in Table 4.11. Individually housed male kiwi shredded the least number of dividers.

Table 4.11: Average percentage (± S.E.) of cells probed by kiwi of different sexes with paper dividers shredded.

Sex	Average % Cells with Paper Dividers Shredded	± S.E.
Female	9.10	0.76
Male	0.26	0.12
Pair	2.88	0.33
Group	13.61	1.28

A significantly larger proportion of prey was taken from cells where the paper dividers were shredded ($\bar{x}$ = 91.60, S.E. = 1.43) than those that were probed but where the dividers were not shredded ($\bar{x}$ = 84.82, S.E. = 1.32). Individual kiwi also showed significant differences in the percentage of paper dividers they shredded, and the percentage of dividers shredded in certain prey boxes.

Percentage of Prey Taken.

The goodness of fit parameters (deviance value = 1304.09, DF = 1565) indicate that there was less spread in the data than expected from the model. Likelihood ratio statistics are presented in Table 4.12. The highest percentage of prey was taken in Experiment 3 (average percentage and standard errors shown in Table 4.13), but this was not significantly related to the depth the prey was set at. The average percentage and standard errors are shown in Table 4.14.

Table 4.12: Likelihood ratio statistics for factors relating to the percentage of prey taken. Data are from all experiments combined and cells without prey were excluded from the model (see Methods for details).

Source	DF	ChiSquare	Pr>Chi
Experiment	2	177.87	0.0001
Cell Type (Box Type)	1	3.01	0.0826
Age	1	0.74	0.3908
Housing	1	37.56	0.0001
Sex (Age-Housing)	7	662.78	0.0001
Kiwi (Age-Sex-Housing)	18	2011.76	0.0001
Kiwi (Age-Sex-Housing-Box)	84	640.25	0.0001

Table 4.13: Average percentage (± S.E.) of prey taken by kiwi in different experiments. For details of experiments see Methods.

Experiment	Average % of Prey Taken	± S.E.
Experiment 1	30.69	2.14
Experiment 2	31.43	4.25
Experiment 3	53.08	1.46

Table 4.14: Average percentage (± S.E.) of prey taken by kiwi from different cell types.

Cell Type	Average % of Prey Taken	± S.E.
Deep Prey Cells	51.25	2.05
Shallow Prey Cells	54.91	2.06
Common Prey Cells	30.84	1.91

Nocturnal house kiwi took a significantly higher percentage of prey ($\bar{x} = 51.20$, S.E. = 1.96) than outside housed kiwi ($\bar{x} = 42.59$, S.E. = 1.49), and kiwi held in groups took a significantly higher percentage of prey than all other kiwi. The percentage and standard errors are shown in Table 4.15. Individually housed male kiwi took the least amount of prey. Kiwi of different ages did not vary significantly in the percentages of prey they took.

Table 4.15: Average percentage (± S.E.) of prey taken by kiwi of different sexes.

Housing	Average % of Prey Taken	± S.E.
Female	53.56	2.54
Male	18.85	1.78
Pair	54.85	1.90
Group	67.72	3.26

Individual kiwi also differed significantly in the percentages of prey they took, and the percentage of prey taken by individual kiwi from certain boxes was also significantly different.

DISCUSSION

Kiwi did not locate prey accurately in this study. This contrasts with the results of Wenzel (1968; 1971b) and Benham (1906), who reported that kiwi were very accurate in finding prey and never probed tubes or buckets that did not contain prey. Kiwi in my study often probed boxes without prey, and this confirms the findings of Strong (1911), Haeusler (1923), and Flinn (1995), who reported that kiwi did not detect prey accurately, often probed areas that did not contain prey, and often found prey apparently by chance.

My study was performed to determine if kiwi could detect prey underground using olfaction. The aim was not to determine how captive kiwi find their artificial food, which is presented above ground or in tubes sunk into the ground but open to the air. Sight, smell and sound may all be used for detecting prey above ground and smell is likely to be involved to find the odorous artificial food provided in captive situations. The ability of kiwi to smell food on the surface may also be the reason why Wenzel's (1968; 1971b) results differed so much compared to mine, because most of the food used by Wenzel was uncovered. This is seldom the case for kiwi in a natural situation.

Kiwi probed prey boxes that contained prey significantly more often than those without prey, but their probe rates suggest that kiwi could not distinguish between the contents of the individual cells within each box, because they did not probe cells with earthworms significantly more often than cells without earthworms. The higher percentage of cells probed in boxes with earthworms probably resulted because kiwi continued to probe after finding some prey. When analysed over the whole data set, cells without prey were probed more often than cells that had earthworms at 40-50 mm deep. This was

irrespective of the distribution of prey within cells of a box, and even when all the earthworms were in the middle cell of the box (Experiment 2), the area probed by kiwi was not concentrated toward this cell. Concentrating the worms in one cell also did not affect the number of cells probed, which suggests that the ability of kiwi to find prey is not affected by the number of prey within a small area. Kiwi also did not show any preference for worms at a particular depth, but the order that prey was taken was not observed. Further research would benefit by determining the order in which cells are probed.

The frequency that cells without earthworms were probed suggests that it may be necessary for kiwi to first probe soil before determining whether there is prey nearby, as was also suggested by Flinn (1995). Kiwi found the majority of worms in cells once they had probed them and the number of cells with shredded paper dividers (indicating multiple probes into a cell) increased in relation to the number and concentration of prey within boxes. Paper dividers usually only became shredded in cells that contained earthworms, suggesting that kiwi are more likely to continue probing once they detect that prey is present in the cell. Multiple probing may occur because of an inability to locate prey accurately, or because kiwi may continue probing cells in the hope of finding more prey.

Kiwi probed significantly fewer cells under logs than in the open, yet some invertebrates are more likely to be found under logs and other objects. The pattern of probing in boxes with logs indicated that kiwi could not probe right under the log because the cell containers prevented them probing sideways through the soil. This probably resulted in the significant difference in probing rates between different boxes. My results suggest, however, that kiwi do not probe under objects any more often than in the open.

There are two possible explanations why kiwi showed high probing activity when logs were placed across the boxes, even though no prey was present. The first is that the placement of logs across two of the boxes increased probing activity in all boxes. The other is that kiwi learnt during the trial, and especially after Experiment 3 (where boxes held a large amount of prey), that there was prey in the boxes. Such learning is unlikely because of the two-day break after Experiment 3, when the cells contained only soil. If

kiwi remember what was in the boxes, then they should also learn during the break period that there was no prey in them. The fact that there was no general trend in the probing rates of individual kiwi over the trial also suggests that kiwi did not learn to look for prey in the prey boxes. It is therefore more likely that placing logs over two of the boxes increased interest by kiwi in all prey boxes, regardless of whether there were earthworms in them or not.

Flinn (1995) also suggested that kiwi probe objects out of curiosity and found that kiwi often probed tubes that did not have food in them. This suggests that kiwi may take an increased interest in prey boxes once a change is made to them and it is likely that the disturbed soil of the boxes, although kept to a minimum by covering the box with a thin layer of soil, attracted their interest. Once kiwi find prey in one box, they may probe all boxes in the hope of finding prey, as discussed above. This may not be an effective way of foraging, because it is not an effective use of foraging time, but it may be a characteristic of captive kiwi who do not have to forage for food. Wild kiwi may therefore not show the same behaviour, and may show more effective foraging activities.

The total number of earthworms in prey boxes had the most significant effect on both the number of cells probed, and the probing behaviour of kiwi. Kiwi were more able to detect earthworms when there were more of them in a larger area, as evidenced by Experiment 3, and they also found significantly more of the prey in such situations. Significantly more paper dividers were shredded in Experiment 3 than in any other experiment, suggesting that kiwi continue probing cells in the hope of finding more prey, and possibly because their location of prey is inaccurate.

The high probing rates by juveniles in empty boxes suggests that they are less able than adults to detect which boxes contain prey. The large number of paper dividers shredded by juveniles also suggests that they are less able to determine precisely where earthworms are within the cell. The shorter length of the bill in juveniles may also hinder prey extraction. However, the percentage of prey taken did not vary with the age of the birds, suggesting that juvenile kiwi show perseverance in finding their prey. These results suggest that kiwi learn how to find prey and that experience may be important for prey learning, as reported for several other bird species (e.g. Gochfeld and Burger, 1984;

Marchetti and Price, 1989; Desrochers, 1992). This is a particularly important consideration when preparing captive reared juvenile kiwi for release, and I suggest that it is important that such birds learn how to forage naturally.

The difference between the probe rates of male and female kiwi, and between individually housed and group-held kiwi, parallels differences from other experiments in this thesis. These differences reflect an overall pattern of interest in foreign objects, with female kiwi approaching foreign objects more often than male kiwi, as well as reflecting specific probing behaviour. The high number of cells probed by kiwi held in groups is related to the number of individuals in the enclosure and the large number of paper dividers shredded confirms that juvenile kiwi are less able to detect prey easily. Juvenile kiwi were also more inquisitive about equipment than adults, and juveniles held in groups may show more interest in probing prey boxes after observing others in the enclosure. The number of individuals in group enclosures also contributes to the higher number of cells that were shredded and the higher percentage of prey taken in relation to other kiwi, because the chance of finding prey by random is increased when more birds are present.

Individually housed adult female kiwi showed similar probing behaviour to that of paired kiwi, with respect to the number of cells probed, suggesting that the female probes prey boxes most often amongst pairs of kiwi. Adult females also found the same proportion of available earthworms as kiwi in pairs, but individual females were more likely to shred the paper, suggesting they were less able to detect prey quickly. This is most likely related to the age of the female kiwi studied, because all were juveniles except for one young adult and an adult female that had recently been moved out of a nocturnal house.

Individually housed male kiwi, especially juvenile males, were least likely to probe prey boxes and thus shredded the least number of paper dividers. They also recovered the lowest proportion of earthworms. Whether males are neophobic, or whether males and females feed at different depths, is not known.

Nocturnal house kiwi probed significantly more often than outside housed kiwi and thus were more likely to make multiple probes in individual cells. This suggests that nocturnal house birds were either less able to detect prey quickly or that they continue to

probe for longer than outside housed kiwi. Extended probing may be a boredom behaviour, because such behaviours are apparent in many captive animals, where the environment is static (e.g. Mitchell, 1983; Anderson and Visalberghi, 1991; Baker and Easley, 1996). Nocturnal house kiwi were more interested in prey boxes and spent more time probing in and around the boxes, thus resulting in more paper dividers becoming shredded. The higher percentage of prey recovered by nocturnal house kiwi is probably a result of the amount of time spent probing in the boxes, thus increasing the number of chance encounters to prey.

The huge range in probe rates exhibited by different kiwi suggests that captive kiwi are habitual in where they probe within their enclosures. The preference shown by individual kiwi for probing in certain boxes also suggests that they may spend a long time probing in one area of the enclosure regardless of whether there is prey there or not. This is probably because captive kiwi have a regular supply of food and thus do not have to forage extensively. Some captive kiwi may never have learnt to forage naturally, but this should be encouraged to relieve boredom (Mitchell, 1983; Anderson and Visalberghi, 1991) and increase the range of food types eaten by captive kiwi.

My results suggest that olfaction is *not* the primary sense used by kiwi to find prey underground, because they did not find prey accurately enough to suggest that they relied on olfaction. The fact that kiwi did not probe more accurately when prey was more concentrated, and that they appeared to find prey only by chance, even when it was numerous and very localised, also suggests they were not using smell. Although it is possible that the method of containing earthworms in this study affected odour dispersal, prey odour could be expected to disperse less between prey box cells than in natural situations, thus restricting any odour to the area directly above the cell. This suggests that if kiwi did detect prey primarily by olfaction, then they should have been more accurate in locating those cells that contained prey, and this was not the case.

It is most likely that kiwi primarily use other senses to find prey underground. I have observed kiwi stomping over the ground several times before stopping and cocking their head as if listening for prey. Kiwi always discovered prey after showing this behaviour, suggesting that they may use auditory cues for prey location, as do black-backed

magpies (*Gymnorhina tibicen*) and American robins (*Turdus migratorus*) (Floyd and Woodland, 1981; Montgomerie and Weatherhead, 1997). Kiwi may also use vibrations of the substrate to detect earthworms. Schwartzkopff (1973) suggests that birds are able to locate prey using substrate vibrations felt by corpuscles on the papillae of their feet, legs, or beaks. The beak is particularly sensitive in kiwi (Haeusler, 1923; Peat, 1990) and this suggests a possible sense used for prey location. The length of the beak may also increase vibrotactile sensation and the way that kiwi walk around the forest, with their beaks repeatedly touching the ground, also suggests that they may use their beak as a sensitive tool to detect prey movement. The way that earthworms were contained in this study possibly affected any auditory or vibrational cues produced by them, by dampening of these cues by the paper dividers or the cells themselves, and this may have affected the accuracy of finding prey. Kiwi may also use visual cues to locate prey, such as finding earthworm holes or earthworm castes, but this is unlikely because kiwi are longsighted and probably cannot see close objects very well (Sivak and Howland, 1987).

Further research is required on the behaviour of wild kiwi to further our understanding of their feeding ecology and to improve kiwi husbandry. I suggest that further research on the detection of prey by kiwi should include the use of auditory and vibrational cues produced by prey, to determine whether kiwi are more likely to use these cues as the primary sense in prey detection.

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Chapter Five: Conclusions, Recommendations and Future Research
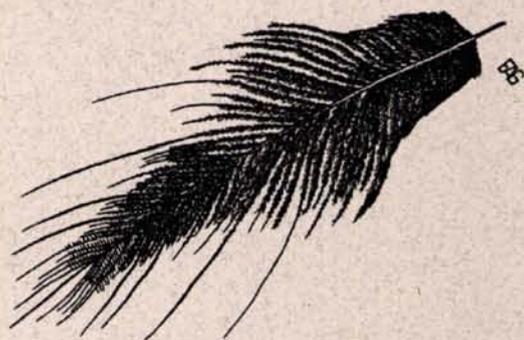
Conclusions, Recommendations and Future Research

Kiwi responded to faecal odours in a way that suggests they may use scent to mark territories. This is the first avian species identified that may scent mark their territory. Kiwi do not appear to purposefully mark roost sites with faeces, however, and they did not countermark faeces of other kiwi at roost sites. This suggests that they may be unwilling to give away their exact roosting positions. Although roost sites are not purposefully marked by defecation, they may still be scent marked by other means, including scent from body glands or by defecation that occurs during roosting. The process of marking roost sites, using gland secretions and/or defecation, may also explain why wild kiwi frequently move from one roost site to another.

Overall, kiwi were neither attracted to, nor repelled from, areas or roost sites that contained a foreign kiwi odour, but they did show more escape behaviour from open areas with these odours. Juvenile kiwi were more attracted to foreign kiwi odour than adults, suggesting they may use this scent to assess resident birds in the wild. Juveniles also showed more escape behaviour than adults from areas with foreign kiwi odours, suggesting that they are unwilling to confront unfamiliar kiwi. Juvenile males were more apprehensive than juvenile females in this respect, suggesting that they may be less tolerated by territorial adults, and may thus avoid areas where other kiwi have been. Single housed juvenile kiwi seldom roosted in unfamiliar roost sites, and this may also be a strategy to avoid confronting other kiwi. Juvenile male kiwi never roosted or defecated in the roost boxes, suggesting they are especially reluctant to leave signs of their intrusion.

Juveniles held in groups were more likely to roost in trial boxes, suggesting that these kiwi attempt to roost away from other enclosure mates when they can. It is recommended that juveniles held in groups be given sufficient clean roost boxes for individual use when they are introduced to the enclosure, and that all individuals should

be introduced at the same time into a shared enclosure. Juveniles will thus learn to roost singly, or at least be given the choice to roost away from other individuals in the enclosure, which is an important consideration if they are intended for release. My observations of nocturnal house kiwi suggest that these kiwi show much more boredom behaviour, including pacing and circling beaks against objects, than kiwi housed outside. Their increased interest in experimental equipment also suggested that most nocturnal birds are generally bored. This may not come as a surprise for some institutes, but I suggest kiwi are kept in nocturnal houses for only a short time, rather than years as has been common practice. Nocturnal house environments can also be enriched in many ways, and this needs to be addressed nationally.

Single female kiwi were more likely to roost in boxes than single males, and they also roosted in boxes with foreign kiwi odour most often. This may suggest a behavioural difference between males and females, where female kiwi are more likely to use unfamiliar roost sites, possibly as a way of finding a partner.

Adult males seldom roosted in the trial boxes. They were also repelled more than other kiwi from foreign kiwi odours, but they showed less escape behaviour when they did encounter foreign kiwi odours. This supports suggestions that males are the more territorial sex (Taborsky and Taborsky, 1992) and that they also avoid confrontations between territorial neighbours when possible. The effect of faecal odours decreased over the trial period, suggesting that visual and/or auditory signals may be needed to support territorial maintenance. The density of scent marks may also be important in responses made towards foreign kiwi odour. Further tests should explore the effect of scent mark density in a kiwi's territory.

It was not possible to move captive kiwi around to study the behaviour of an intruder into another kiwi's territory, but it is recommended that future captive research should include this, because it would allow better judgement of the behaviour of intruding birds. I only recorded the first entrance of kiwi into each roost box and future research should assess the time spent in roost sites with different odours, and the number of times they are entered.

Kiwi do not use olfaction as the primary sense to find subterraneous earthworms, because they did not find them accurately enough even when they were concentrated in a small area, and they often probed where there were no earthworms at all. Kiwi showed no preferences for earthworms at different depths, but future research should assess preferences in the order that prey is taken. It is more likely that kiwi use auditory and/or vibrotactile cues as the primary sense for detecting subterraneous prey and future research should assess the use of these cues.

Juvenile kiwi were less able to detect earthworms and less able to extract them than adults, suggesting that kiwi learn to forage successfully. Allowing juvenile kiwi to forage naturally is an important consideration in their captive management, especially if they are going to be released into the wild. I recommend that all captive kiwi be given the chance to forage naturally. This can be done by adding live prey to enclosures on occasions and sometimes not giving the kiwi artificial food for a night so that they are encouraged to forage naturally. My suggestion that kiwi learn to catch their prey is new, because probing and feeding behaviour of kiwi was assumed to be innate in the past. Further research is needed to determine how much of their feeding behaviour is learned by experience. There is also some suggestion that male and female kiwi may probe to different depths, and this may be connected to the differences in bill lengths of the sexes. This warrants further investigation.

Only captive kiwi were used in my research, and it is possible that the behaviours of captive kiwi may not truly reflect the behaviour of wild kiwi. Most captive kiwi have also been captive reared, so they have never encountered another adult kiwi, and they have never had to defend their territory from another kiwi. Therefore, they may not respond as wild kiwi do to foreign kiwi odour. Captive kiwi may also not forage in a similar way to wild kiwi, because they show more boredom behaviours and they do not have to forage in order to get food. Future research should assess how successful wild kiwi are at foraging in soil.

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