Feral cats on Stewart Island/Rakiura

Population regulation, home range size and habitat use

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Grant A. Harper

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

ABSTRACT

Feral cats *Felis catus* are being controlled in alpine areas of Stewart Island/ Rakiura to reduce predation on endangered southern New Zealand dotterels *Charadrius obscurus obscurus*. In order to improve cat control, research on the population regulation and habitat use of cats was undertaken. Cat numbers were limited by the seasonal availability of rats, their primary prey, which contributed 81% of cats' diet by weight. More cats died of starvation or left their home ranges in late summer or autumn, when rat numbers were low, than at other times. Because of the seasonal depressions in prey availability, cats had very large home ranges of about 1100 ha for females and 2000 ha for males. As a consequence, the population density of cats was very low at around 0.2/km². Cats were using podocarp-broadleaf forest more than was expected by availability and used subalpine shrubland significantly less than podocarp-broadleaf forest. Selection of forest types was influenced by the need for shelter from wet weather.

Keywords: Feral cat, *Felis catus*, home range, habitat use, *Rattus* spp., predation, New Zealand dotterel, *Charadrius obscurus obscurus,* Stewart Island, Rakiura, New Zealand.

1. Introduction

House cats *Felis catus* were probably introduced to Stewart Island/Rakiura during the settlement of New Zealand by Europeans in the early 1800s, and eventually became feral (Wodzicki 1950). Feral cats are the largest mammalian predators on Stewart Island and three introduced species of rats—Pacific rats *Rattus exulans*, Norway rats *R. norvegicus*, and ship rats *R. rattus*—are now their primary prey (Karl & Best 1982). Cats, along with rats and the introduced brushtail possum *Trichosurus vulpecula*, are known predators of native birds, lizards and insects (Sadleir 2000; Innes 2001). Ground-nesting native birds are particularly vulnerable to predation by cats (Sanders & Maloney 2002). On Stewart Island/Rakiura, cats were the principal predator of adult kakapo *Strigops habroptilus*, before the surviving 61 birds were transferred to cat-free islands by 1992 (Powlesland et al. 1995). Similarly, predation by cats is probably the main reason the endemic brown teal *Anas aucklandica chlorotis* has become extinct (Hayes & Williams 1982), and weka *Gallirallus australis scotti* have almost been extirpated on the island (Harper 2002).

Feral cats are also thought to be the chief predator of the endangered Southern New Zealand dotterel *Charadrius obscurus obscurus* (Dowding & Murphy 1993) that nests on mountain heathland above the tree-line on Stewart Island/Rakiura. Southern New Zealand dotterels once bred in the mountains of the South Island and Stewart Island/Rakiura, but introduced predators and hunting have restricted them to Stewart Island/Rakiura (Barlow 1993; Heather & Robertson 1996). Dotterel numbers continued to decline, down from more than 300 birds in the 1950s (Barlow 1993) to around 60 birds in 1994. However, control of cats using poison was initiated in 1992, and dotterel numbers began to increase immediately (Dowding 1999).

The poisoning operation to control cats has been carried out at four sites on the mountains of Stewart Island/Rakiura every spring and summer since 1992. Poison bait was presented in bait stations at the tree-line, at an altitude of about 500 m. Because of the prevailing wet and windy conditions, the bait was replaced every two weeks, and each re-baiting took about six days to complete at all four sites. The operation was thus expensive and very time-consuming. Consequently, more efficient use of time and resources was desired, and this required better knowledge of the population regulation of cats, their habitat use, and abundance. This report summarises the study that was carried out to obtain this information.

1.1 POPULATION REGULATION OF CATS

Some indications of responses of cats to changes in prey abundance could be inferred from other studies of predators, the Felidae in particular. Most predator populations are food limited and densities of predators will fluctuate along with periodic changes in prey abundance (King 1983; Korpimaki & Norrdahl 1991; Angerbjorn et al. 1999). Predators respond to prey abundance in two ways: numerically (changes in demographics) and functionally (changes in behaviour)

(Korpomaki & Krebs 1996). Numerical responses involve changes in rates of survival, reproduction, immigration and emigration (Kopimaki & Noordhahl 1991; Norbury et al. 1998a; Angerbjorn et al. 1999). Functional responses often include 'prey switching' to alternative prey when preferred prey numbers become low (Angerbjorn et al. 1999; Helldin 1999; Lode 2000).

Feral cats will use alternative prey, which enables them to maintain their abundance when one prey type is not available (Moors & Atkinson 1984). Use of alternative prey is well recorded in the Felidae, especially for the lynx *Lynx lynx* and the associated snowshoe hare *Lepus americanus* cycle (O'Donoghue et al. 1998). Lynx will switch from snowshoe hares to red squirrels *Tamiasciurus hudsonicus* when hares are scarce (O'Donoghue et al. 1998). Other cat species will also use alternative prey when preferred prey is in low abundance. For example, Lions *Panthera leo* preferentially use migratory, rather than resident, prey in the dry season (Viljoen 1993).

In periods of low prey abundance, mortality often occurs through starvation of adult and juvenile felids (van Ordsal et al. 1985; Bailey 1993). Increases in home range size and rates of emigration are also apparent when prey is scarce (Van Ordsal et al. 1985; Bailey 1993; Viljoen 1993).

Feral cats on Stewart Island/Rakiura could be expected to exhibit similar changes in mortality, emigration, and diet as prey abundance fluctuated. Although the diet of feral cats has been studied on Stewart Island/Rakiura (Karl & Best 1982), the authors did not relate cat diet to availability of preferred prey and possible changes in the abundance of cats. Therefore, the seasonal abundance of the principal prey near the cat control sites needed to be measured. These changes in abundance had to be linked to the diet of cats to investigate whether the cats were responding to scarcity of principal prey and switching to another prey type, birds for example. Knowledge of the fate of individual cats as prey abundance changed seasonally was also required, to show changes in rates of mortality or emigration.

1.2 HABITAT USE AND ABUNDANCE OF CATS

Dowding & Murphy (1993) suggested that the decline in the dotterel population was caused by a small number of cats visiting the breeding sites of the dotterel from forest or subalpine shrubland habitats at lower altitudes.

The key to understanding how an animal selects habitat within their home range often involves the identification of a few critical resources, such as prey abundance (Morrison 2001). Similarly, the home range size of a predator reflects the abundance of prey and the density of the predator population, and both these factors influence the behaviour of the predator (McNab 1963). Although prey availability is very important in determining densities and distribution in predators, other factors, like territoriality and shelter, also influence habitat use (Kruuk 1982; Sunquist & Sunquist 1989; Liberg et al. 2000).

Availability of shelter restricts cats' habitat use, particularly in wet and cool climates (Derenne 1976; Corbett 1979; Brothers et al. 1985). As little shelter is available in the alpine areas of Stewart Island/Rakiura, it was expected that cats

would use these areas more often during dry weather (Brothers et al. 1985). If cats are only using the alpine areas while dispersing, or when on occasional excursions during dry weather, control of cats should therefore be targeting the source population. Consequently, the aims of the study were:

- to find out if cats were occupying the alpine areas as residents or were occasional visitors from higher-density cat populations at lower altitudes.
- to investigate causal factors for any avoidance of alpine areas by cats and, if it occurs, preference for other habitats.

2. Methods

2.1 STUDY SITES

This study was carried in two parts. The initial research (testing trapping procedures for cats and rats) was done as a pilot study for two seasons, spring and summer 1999, in the Freshwater Valley and on Table Hill. The remainder of the research was carried out in the Rakeahua Valley (47ºS, 167º50'E; Fig. 1). Both valleys are low lying and consist of undulating low ridges separated by marshes and streams with *Leptospermum* shrubland or wetland vegetation. The Freshwater Valley has more wetland than the Rakeahua Valley.

Figure 1. Map of Stewart Island/Rakiura, the most southern of New Zealand's three main islands, showing location of study sites.
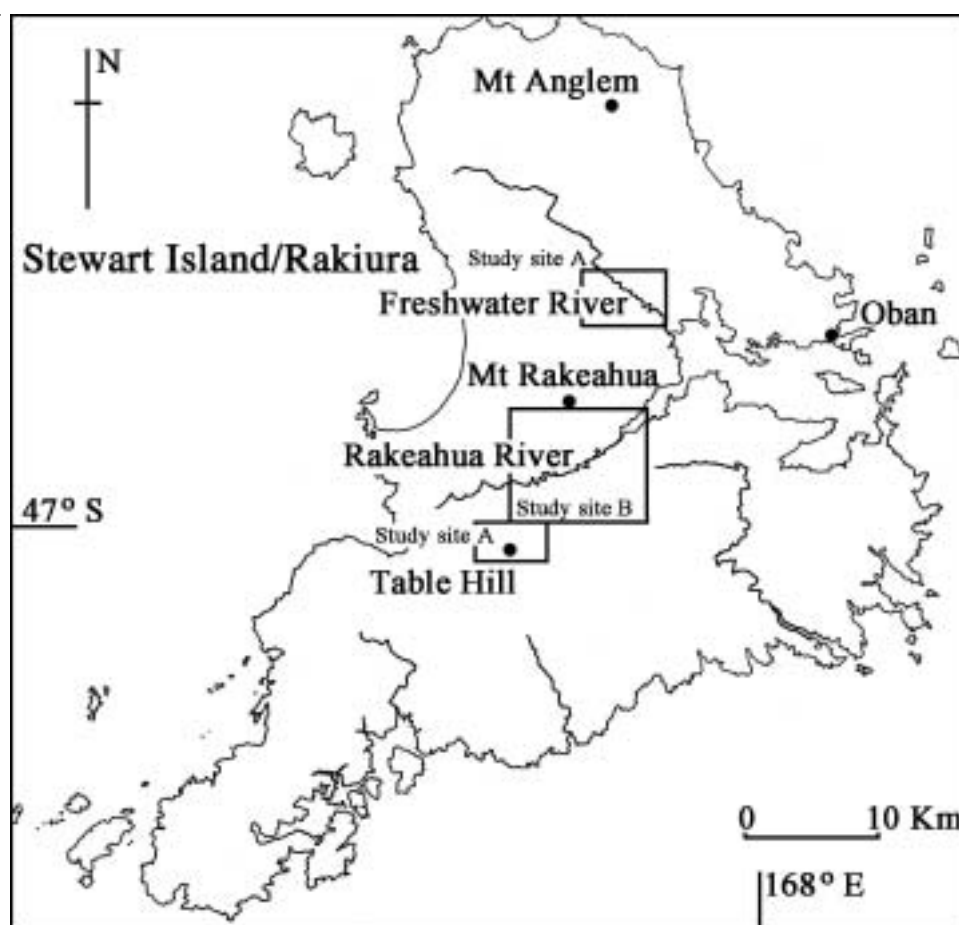
Both valleys are bounded by forested hills or escarpments rising to 716 m above mean sea level (a.m.s.l.). From 300 m a.m.s.l. the hills are covered in dense subalpine shrubland; and above 500 m, low-alpine heath. The soils of the valleys are derived from water-borne alluvium, peat and wind-blown sand and are generally of low fertility (Wilson 1987).

The climate is cool and wet with annual rainfall estimated at 2000 mm in the Rakeahua Valley (Wilson 1987; Meurk & Wilson 1989). Snow may lie to above 500 m in the winter and is occasionally recorded in the valley floor. To estimate the number of rain-days (rainfall < 0.9 mm/day: Sansom 1984) for the Rakeahua Valley, rainfall was recorded daily at an open area north of the DOC hut there. Four main vegetation types are recognised in the Rakeahua Valley (Wilson 1987; Harper 2002): riparian shrubland, *Leptospermum scoparium* shrubland, podocarp-broadleaf forest and subalpine shrubland.

2.2   SCAT ANALYSIS

Cat scats were collected, during the course of other field work, each season (winter: June; spring: September; summer: December; and autumn: March) from September 1999 to June 2001. For the first two seasons, scats were collected in the Freshwater Valley, and thereafter in the Rakeahua catchment (Fig. 1). Four walking tracks—one along each of the valleys, one up each of Mt Rakeahua and Table Hill—were searched daily for scats during the course of other field work. The majority of scats were apparently not buried and were often found in the centre of tracks, in the top of grasses or sedges (*Microlaena avenacea*, *Gahnia procera*, *Uncinia* spp., *Carex* spp.) or on prominent moss clumps. Scats could often be found at the same location over several seasons. Only fresh or relatively fresh scats were collected; freshness being ascertained by the smell and lack of mould. Scats obtained during each field trip were regarded as being from the previous season unless they were obviously fresh. Most scats were collected in the first few days after arrival at the study site.

Scats were stored in separate 'ziplok' bags marked with the date that they were found. The location, normally the closest cat or rat trap or cat-tracking point, was also recorded. Scats were dried at 60ºC for 24 hours and stored, following Reynolds & Aebischer (1991), as soon as possible after finishing the field work for a season.

Scats were later soaked overnight in water then teased apart over a 355-mmm sieve. Any bones, feathers, arthropod exoskeleton or plant material found was recorded. The remains from each scat were stored in 5-mL vials in 75% alcohol. Rat remains were mainly identified by the presence of molar and incisor teeth. A minimum number of rats per scat were estimated from the number of molars of a certain age class (Karnoukhova 1971, i.e. four molars of an equivalent degree of wear were regarded as coming from one rat.). Other mammals were identified from bones and hair (Brunner & Coman 1974). Birds were mainly identified from feather remains (Day 1966) and some bones. Insects were grouped by Order according to the exoskeleton remains. Plant material and microscopic material were not included for analysis. The data from all scats collected during a season were pooled to investigate seasonal differences.

The data were analysed to obtain two measures: frequency of occurrence of prey items (percentage of scats containing a prey item); and percentage by weight of prey species. The two measures are used because the former does not take into account prey weight and its relative contribution to the cats' daily food intake (Fitzgerald & Karl 1979). Frequency of occurrence has been used in a number of published studies of cat diet (see, for example, Fitzgerald & Karl 1979; Konecny 1983; Liberg 1984) and is, therefore, useful for comparative purposes (Reynolds & Aebischer 1991).

Estimates of percentage by weight of individual prey types for each season were based on previously collected data on local prey species (e.g. seasonal weights of trapped rats) (Fitzgerald & Karl 1979; Karl & Best 1982). Unless remains could be identified to species, generic characteristic weights were assigned to prey types. For example, a mean bird weight of 50.45 g was used for bird remains unless they could be readily identified to species. This weight was derived from the 13 passerine species known to be common in the area (Karl & Best 1982). Remains of birds were not generally identified to species as this had been done previously (Karl & Best 1982) and was not the focus of the research. Lizard weights of 4 g, weta weights of 1.7 g, and beetle weights at 0.1 g were used for other prey weight estimates. Large prey items (greater than 500 g) are assumed to have provided more than a single meal for a cat and are, therefore, presented as 185 g per scat (Harper 2002).

2.3 RELATIVE ABUNDANCE OF RATS

Seasonal changes in relative abundance of the three species of rats present—Pacific rat, ship rat, and Norway rat—were investigated using standard trap lines. Rat trapping was carried out in two areas. Consequently, some trapping methodology changed between the study sites as the trapping procedure was refined for the main part of the study in the Rakeahua Valley.

The first site was the pilot study area in the Freshwater Valley and on Table Hill. Trapping was carried out in September and December 1999. Single trap lines were run in three vegetation types: Podocarp-broadleaf forest, *Leptospermum scoparium* shrublands and subalpine shrubland. Rats were trapped using a standard method (Cunningham & Moors 1996). Twenty-five pairs of 'Ezeset' snap-traps were set for three nights at 50-m intervals beside walking tracks in each vegetation type. The traps were protected with 12-mm-square mesh covers to exclude non-target species. The traps were baited with a mixture of peanut butter and rolled oats. The traps and mesh cover were secured with wire stakes to prevent their removal. All traps were checked daily. Any rat caught was removed and processed later in the day. Any traps that were sprung or had bait taken were noted and then re-baited and / or set. The traps were sprung, cleaned, dried and stored between trapping sessions.
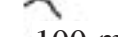
From March 2000 to June 2001, two lines, each having seven pairs of traps, were set out in each of four vegetation types (riparian shrubland, *Leptospermum* shrubland, podocarp-broadleaf forest and subalpine shrubland) in the Rakeahua Valley. The traps were set for a minimum of nine days in each of the four seasons (Fig. 2).

The paired trap lines were all a minimum of 350 m apart. All trap lines were set out adjacent to walking tracks.

Figure 2. Map of the Rakeahua Valley, showing the location of the rat-trapping lines.
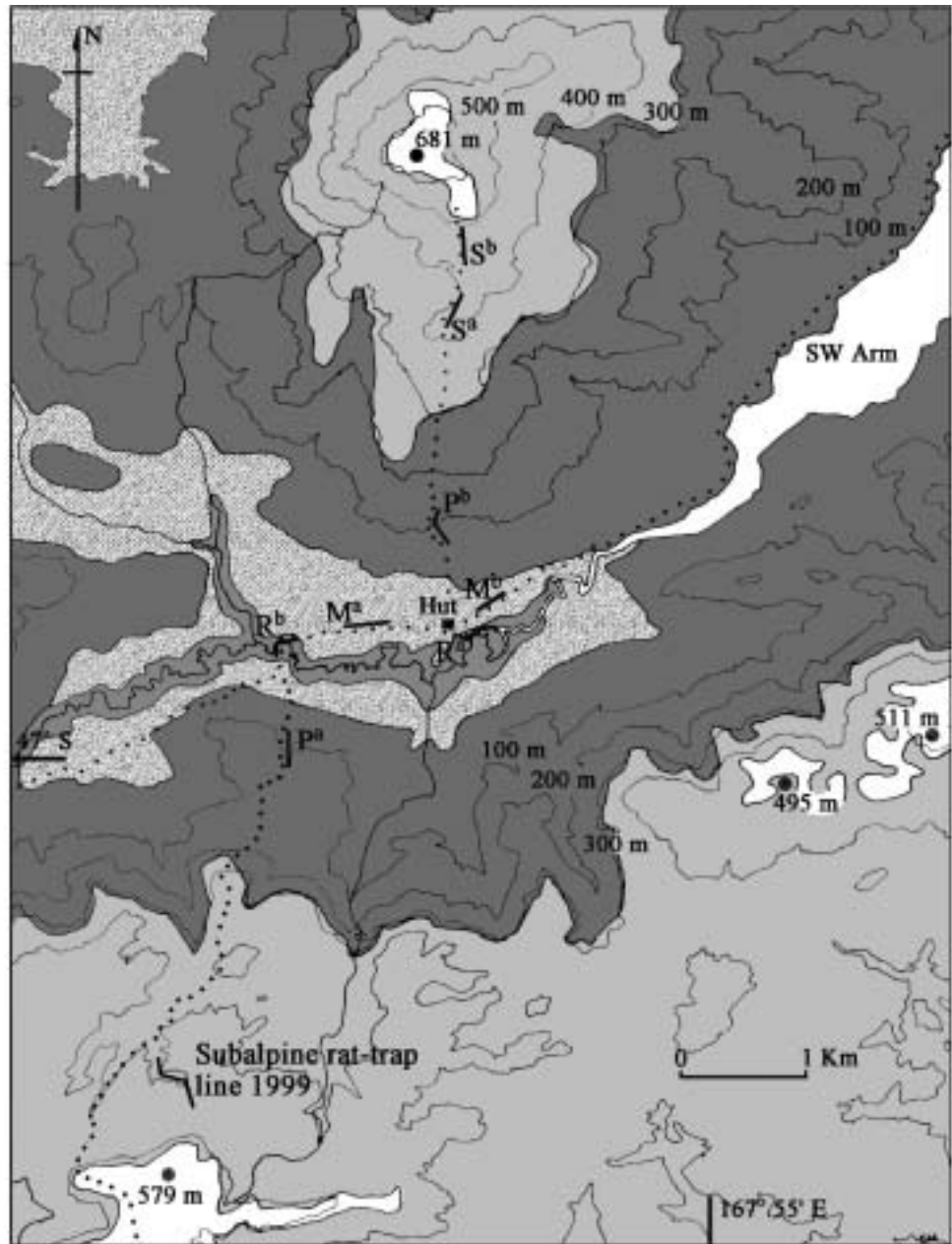
Key:

Riparian shrubland		Rat trap line	
Leptospermum shrubland		Track	
Podocarp-broadleaf forest		681 m Summit	
Subalpine shrubland		100 m Contour lines	
		Alpine heath	

Details of captured rats' species and weight were recorded on the day of capture. A mean weight of rats for each season was calculated using the weights of all rats captured, regardless of species or sex.

A mean seasonal rat abundance index was obtained from the pooled rat captures from the trap lines. The rate of rat capture was defined as the number of rats (R) caught (C) per 100 trap nights (TN) corrected for sprung traps (Nelson & Clarke 1973) and notated as R/100CTN (Cunningham & Moors 1996).

2.4   RADIO-TRACKING CATS

To investigate cats' response to changes in rat abundance, cats were trapped and fitted with radio-transmitters (n = 22). This gave information on possible cat deaths or emigration from the study area. The cats were captured in Victor 1.5 Soft Catch traps in dead-end sets against the base of trees (Veitch 1985). The traps were baited with thawed frozen fish. Trap lines were set 2–3 m off two walking tracks. One track was on the valley floor and the other ascended to the bush line (c. 500 m a.m.s.l.) through all forest types (Fig. 2). Traps were checked every morning. Each cat trapped was fitted with a two-stage transmitter attached to a collar (Sirtrack, Havelock North,). The transmitters had two pulse rates: an 'active' pulse at 60 pulses per second, and a 'resting' pulse at 40 pulses per second. The signal would change from active to resting after five minutes of inactivity, and back to 'active' immediately the cat became active.

Fixes on locations for radio-collared cats were obtained by radio-tracking daily for a month each season from March 2000 to June 2001. These fixes were obtained by triangulation. Cats were assumed to have a settled home range if they were regularly located within the study area for at least two consecutive seasons. Emigration was assumed to have occurred when a cat was either tracked leaving the study area, or was not located within the study area at the start of a field season, and was subsequently never located again within the study site. If a cat recorded a 'resting' pulse for more than two days it was located to see if it was dead. Dead animals were checked for possible causes and approximate dates of death.

2.5   HOME RANGE DETERMINATIONS

The home ranges of radio-collared feral cats (n = 11) were studied using radio-telemetry for six periods of up to four weeks each season (summer: December, autumn: March, winter: June, spring: September) from February 2000 and June 2001. Bearings were obtained by a single experienced observer, using a folding hand-held yagi directional antenna (Sirtrack, Havelock North) and a portable receiver (Telonics TR4). Bearings were obtained during daylight hours in all weather. Bearings on radio-collared cats were obtained once a day and occasionally twice a day, morning and evening, with a minimum of eight hours between fixes. Bearings were obtained from fixed points located using a GPS system. The time each bearing was taken, the weather, and whether the signal was on 'active' or 'resting' pulse was noted. A fix was obtained with a minimum of three bearings taken within 10 minutes of each other to reduce errors due to animal movement (Withey et al. 2001). On three occasions cats that had left the study area were located using an aircraft.

2.6 HABITAT AVAILABILITY

The area occupied by each vegetation type was obtained by marking vegetation features on a 1 : 50 000 topographic map and then using the map to estimate the area occupied by each type (NZMS 260: C49, D49). A landuse map was generated from this map with GIS software Arcview 3.0, and the areas of available forest types within the study area were determined using the geo-processing extension of Arcview. The principal species and differences in structural components (e.g. canopy height, diameter of tree at breast height) of each forest type were ground-truthed by a field survey (Harper 2002).

2.7 DATA ANALYSIS

A test for significant differences in the seasonal contribution of rats, by weight, to the diet of cats was carried out using a *G*-test (Sokal & Rohlf 1995). To investigate whether there was a relationship between the relative abundance of rats per season and the numbers or biomass of rats or birds found in scats in the same season, a randomisation test was carried out (Sokal & Rohlf 1995), as the sample sizes were small (n = 6 seasons). Initially, a correlation between the observed relative abundance of rats (log-transformed to normalise the data) and one of the four observed sets of variables was obtained. Then simulated values were generated, and correlated with the observed relative abundance of rats, which was repeated 2000 times. The number of times that the observed correlation matched the simulated correlation was counted, and divided by the number of repeats (2000). This gave an approximate proportion of bootstrapped samples with a lower correlation coefficient. The same randomisation procedure was used to obtain the probability that the numbers of cats dying or leaving the study area (a numerical response) in each season were related to the relative abundance of rats in those seasons (n = 6 seasons).

The positions of cats were calculated by triangulation and these locations were then used for home range analysis using RANGES V software package (Kenward & Hodder 1996). The resulting plots were transferred to ARCVIEW 3.0 for home range and habitat use analysis. It is suggested that for home range analysis two methods or more should be used (Harris et al. 1990), as all methods of home range and habitat analysis vary in their precision and in their underlying assumptions about how animals use space. Two methods were used: minimum convex polygon and kernel analysis.

Habitat availability was defined as the proportion of each vegetation type within the entire study area. The general technique for estimating the use of a vegetation type by an individual animal involves laying a plan of its home range over a vegetation map of the area occupied by the animal. The area of the home range that intersects with a particular vegetation type is measured and is then expressed as a proportion of the animal's overall home range area. This was done for cats in this study by using the intersection overlay of the geo-processing extension of Arcview 3.0. The total area of a cat's home range was calculated as the sum of the areas of the various vegetation types within the home range.

Compositional analysis (Aebischer at al. 1993) was used to test whether cats' use of habitats was non-random. Statistical analysis of habitat use was carried out using SYSTAT 10. Overall non-random habitat use was tested using multivariate analysis of variance of the resulting matrix of habitat pair by habitat pair log ratios against a test statistic, Wilk's Λ. Wilk's Λ has an approximate chi-square distribution with k–1 (number of habitats – 1) degrees of freedom, and is evaluated for significance using this test. If overall non-random use of habitats is indicated by Wilk's Λ, subsequent tests on the mean of the habitat use/availability log ratios for each cat can be carried out, against the distribution of t, for levels of significance and subsequent rankings of preference for each forest type (Aebischer et al. 1993).

2.8 DIURNAL ACTIVITY PATTERNS AND THE AFFECT OF CLIMATE ON HABITAT USE

Diurnal activity of cats was recorded, based on the 'active' or 'resting' transmitter pulse recorded when a bearing was taken on each cat. The weather was also recorded each time a bearing was taken, so the activity of a cat when the weather was wet (raining at the time the bearing was taken) or dry (not raining) was known. A G-test on the frequencies of active and resting pulse rates recorded from radio-collared cats during wet or dry weather was conducted. The null hypothesis was that the frequency of active or resting pulse rates recorded during wet and dry weather would be equal.

As feral cats were thought to prey on southern New Zealand dotterels nesting on alpine heath (Dowding & Murphy 1993), investigation of factors restricting cats' use of the subalpine shrubland, which borders alpine heath, was important. Wet weather was expected to inhibit cats' use of subalpine areas, as annual rainfall in the subalpine shrubland zone is thought to exceed 3200 mm (Sansom 1984). To investigate whether cats were using subalpine shrubland on dry days more than was expected by chance, a randomisation test on cat location data from the subalpine shrubland was carried out. Initially, a 2×2 table of observed frequencies of locations of each cat, in subalpine shrubland and podocarp-broadleaf forest, on wet (> 0.9 mm/day, Sansom 1984) and dry days (0 mm/day), was constructed, using rainfall data taken in the Rakeahua Valley. The marginal totals of this table were used to construct a table of expected frequencies if no difference in use on wet and dry days was expected between the forest types. Simulated values were generated, within the range of the marginal totals of the expected frequencies, and the probability of getting these totals compared to the observed values was repeated 2000 times. This gave the probability of getting the observed distribution of locations for each cat in the subalpine shrubland on wet and dry days by chance.

Shelter can affect the use of habitat by cats (Calhoon & Haspel 1989), and cats are known to use hollow trees as den sites (Fitzgerald & Karl 1986; Langham 1990). To investigate whether some vegetation types were more likely to have trees that were suitable as shelter from rain, whether as hollow trees or simply fallen trees, the circumference of trees were measured in each vegetation type. Four trees with the largest apparent circumference were selected from within a 20-m-diameter plot at every second rat-trap on rat-trapping lines (Harper 2002). Thirty-two trees were measured in each vegetation type in the study area.

The mean circumference of the trees in each vegetation type was then compared with the circumference of a single sleeping 3.5-kg domestic female cat. Vegetation types with trees that had a mean circumference larger than the circumference of the cat were assumed to provide more shelter than forest types with trees that had a mean circumference smaller than the cat's.

3. Results

3.1 DIET AND NUMERICAL RESPONSES OF CATS

Two hundred and nineteen cat scats were gathered during eight seasons over two years. Rats were the most important food either by frequency of occurrence (Table 1) or by weight (Table 2). Abundance of rats varied seasonally with a low in abundance in early summer to early autumn (Fig. 3). This trend occurred through all the vegetation types (Harper 2002).

There was little seasonal difference in the frequency of occurrence of rats in cat diet. A mean (± 95% CI) of 1.08 (± 0.08) rats were found per scat. The mean weight for rats varied seasonally (Table 2), with an overall mean weight (± 95% CI) of 123.0 g (± 6.6 g), but there was no significant seasonal difference in the

TABLE 1.   SEASONAL DISTRIBUTION, ACTUAL AND PERCENTAGE OCCURRENCES OF PREY ITEMS IN THE SCATS OF FERAL CATS FROM THE FRESHWATER AND RAKEAHUA VALLEYS, STEWART ISLAND/RAKIURA, 1999–2001.

SEASON	NO. OF SCATS/SEASON	NO. OF SCATS CONTAINING PREY ITEM (% OF TOTAL)						
		RAT	BIRD	WETA	BEETLE	LIZARD	POSSUM	OTHER
Sep 1999	5	5 (100)	2 (40)	1 (20)	–	–	1 (20)	1 (20)
Dec 1999	29	22 (76)	6 (27)	6 (21)	9 (31)	–	–	–
Mar 2000	20	18 (90)	6 (30)	2 (10)	2 (10)	–	1 (5)	–
Jun 2000	47	31 (66)	22 (47)	4 (9)	–	2 (4)	2 (4)	5 (11)
Sep 2000	56	51 (91)	6 (11)	1 (2)	1 (2)	1 (2)	–	2 (4)
Dec 2000	26	26 (100)	7 (27)	5 (19)	3 (12)	–	–	2 (8)
Mar 2000	21	17 (81)	7 (33)	4 (19)	2 (10)	–	–	3 (14)
Jun 2000	15	12 (80)	3 (20)	5 (33)	–	–	–	1 (7)
Total items	219	182	59	28	17	3	4	14
% of total (95% CI)		83 (75–90)	27 (22–34)	13 (9–18)	8 (5–12)	1 (1–4)	2 (1–5)	6 (4–10)

TABLE 2. SEASONAL AND OVERALL ALLOCATION OF WEIGHTS OF PREY OF FERAL CATS IN THE FRESHWATER AND RAKEAHUA VALLEYS, INCLUDING THE PERCENTAGE CONTRIBUTION OF THE PRINCIPAL PREY ITEMS.

SEASON	RATS			BIRDS		WETA		BEETLES		LIZARDS		POSSUMS		OTHER		TOTAL
	MEAN Wt (g) ± 95% CI	No.	Wt (g) (% OF TOTAL)	No.	Wt (g) (% OF TOTAL)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	Wt (g)
Sep 1999	133.5 ±10.8	6	801 (88)	2	100.9 (11)	3	5.1	0	–	–	–	–	–	Snail	2	909
Dec 1999	144.7 ±26.2	29	4196.3 (89)	6	332.3 (7)	11	18.7	9	0.9	–	–	1	185	–	–	4733.2
Mar 2000	86.8 ±25.1	21	1822.8 (88)	5	252.3 (12)	2	3.4	2	0.2	–	–	–	–	–	–	2078.7
Jun 2000	107.4 ±10.4	46	4940.4 (70)	23	1220.0pp (17)	4	6.8	0	–	2	8	1	185	3 fish baits spider, deer	740.5	7100.7
Sep 2000	120.8 ±17.3	56	6764.8 (87)	6	302.7 (4)	1	1.7	1	0.1	1	4	2	370	Fish bait kitten	370	7813.3
Dec 2000	146.1 ±30.4	36	5259.6 (82)	7	1147.0pk (18)	5	8.5	3	0.3	–	–	–	–	Caddis moth larvae, cockroach	0.2	6415.6
Mar 2001	145.9 ±24.1	17	2480.3 (71)	6	937.3k (28)	6	10.2	2	0.2	–	–	–	–	2 spiders, fly	0.6	3478.6
Jun 2001	100.3 ±14.3	17	1705.1 (89)	4	201.8 (11)	9	10.2	0	–	–	–	–	–	Spider	0.5	1917.6
Total no.		228		59		41		17		3		4		14		
Total weight	Mean: 122.8 ±6.6		27970.3		4544.3		64.6		1.7		12		740		1113.8	34446.7
% of total			81		13		<1		<<1		<<1		2		3	100

Wt = weight; p = 1 × red-crowned parakeet (*Cyanoramphus novaezelandiae*): 80 g; k = 1 × kereru / NZ pigeon (*Hemiphaga novaeseelandiae*): 720 g

Figure 3. Contribution by weight (percentage ± 95% CI) of rats and birds to the seasonal diet of cats, in relation to the seasonal abundance of rats, Stewart Island/Rakiura, 1999–2001.
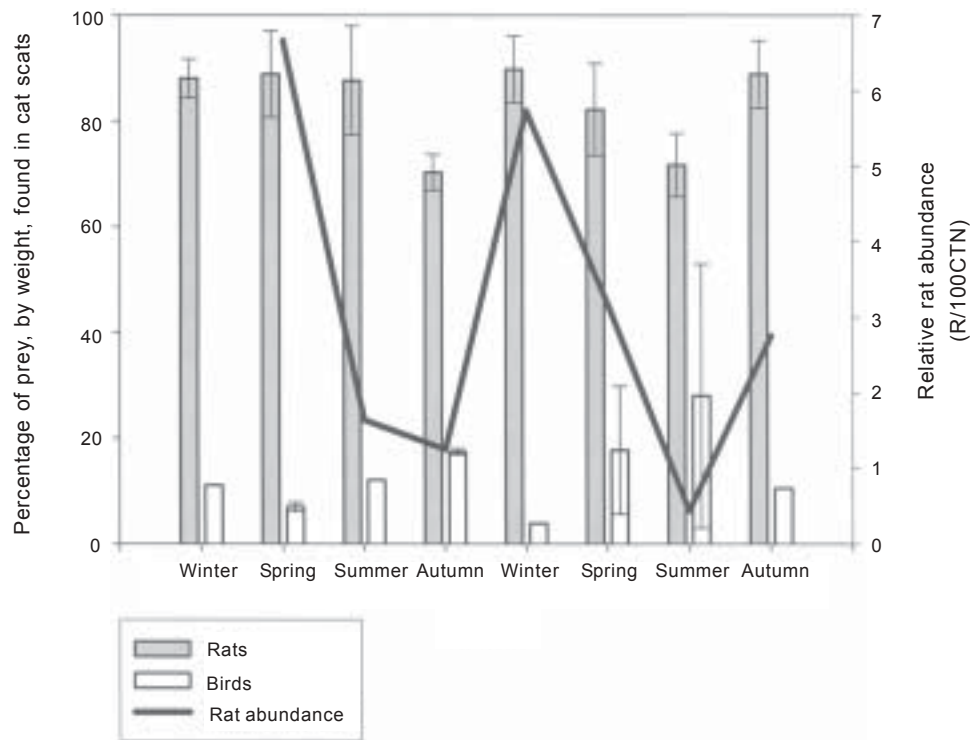
contribution of rats, by weight, to cat diet (Table 2; $G = 1.68$, d.f. = 3, $p > 0.1$). The overall contribution by weight of rats was 81.2% of total prey taken. The randomisation test showed only a weak positive relationship between the relative abundance of rats and the numbers of rats found in scats. A strong positive relationship between the relative abundance of rats and the biomass of rats in scats was evident, with the proportion of bootstrapped samples being significantly higher than if the data had been randomly assigned (Table 3). Consumption of rats by cats continued even when rat abundance declined.

Birds were the next most important prey item, occurring in 26.9% of scats, although they only contributed 13.2% of cat diet by weight. The randomisation test showed a statistically significant, and strong, inverse relationship between the relative abundance of rats and the numbers or biomass of birds found in scats (Table 3). Cats were eating more birds, or bird biomass, as rat abundance declined. The use of biomass rather than individual prey items takes into account the weight of the prey, and hence a general idea of the calorific return a cat would get per capture (Cumberland et al. 2001). The seasonal changes in prey mass are also taken into account.

The mass of all other prey items (mainly other categories and possums) combined contributed only 5.6% by weight to annual cat diet (Table 2).

TABLE 3. RELATIONSHIP BETWEEN THE SEASONAL RELATIVE ABUNDANCE OF RATS AND BIOMASS OF RATS OR BIRDS FOUND IN CAT SCATS, STEWART ISLAND/RAKIURA. (p = PROPORTION OF BOOTSTRAPPED SAMPLES WITH A LOWER CORRELATION COEFFICIENT).

|	OCCURRENCE OF RATS IN SCATS	BIOMASS OF RATS IN SCATS	OCCURRENCE OF BIRDS IN SCATS	BIOMASS OF BIRDS IN SCATS
Correlation	0.24	0.78	–0.75	–0.87
P	0.71	0.95	0.014	0.0005

3.2   CAT MORTALITY AND EMIGRATION

The number of cats that died of apparent starvation (n = 7) or other unexplained reasons (n = 1), and the number of cats that left the study area were also recorded (Details on numbers, sex and age of captured cats are presented in Appendix 1). Most cats died in the autumn (63% of recorded deaths), two (25%) died in late summer, and one (12%) died in the spring. Male cats also dispersed from the study area when rat abundance was low during the late summer and early autumn. Four males out of eight radio-tagged males (50%) left the study area in early 2000, and two out of six (33%) in early 2001.

The randomisation test showed that the numbers of cats dying or migrating were strongly inversely correlated with rat abundance, and the proportion of bootstrapped samples were significantly lower than if the data had been randomly assigned ($R = -0.77$, $p = 0.015$). Most cats died or migrated when the relative abundance of rats declined below 2 rats per 100CTN (Fig. 4). Of the cats that died, one male cat had lost 1.59 kg (40% of original capture weight) between its capture at 4.09 kg and when it was found freshly dead 35 days later. A post mortem could not find any obvious cause of death, which suggests that the cat had starved. One female cat died when rat abundance was above 3.5 rats per 100CTN, but she had been caught three to four days earlier in poor physical condition with obvious infestations of external parasites.

3.3   CAT CAPTURE

In total, 22 cats, 14 males (including two juveniles) and eight females (including one juvenile), were caught over seven seasons in the Rakeahua Valley. Four cats were re-caught within the study area at least once. Most cats were caught at night, except one female cat that was caught in a trap in an afternoon after the

Figure 4.   Percentage of radio-collared cats (n = number of radio-collared cats in different study periods) dying or emigrating from the study area, in relation to the relative abundance of rats, March 2000 – June 2001, Rakeahua Valley, Stewart Island/Rakiura.
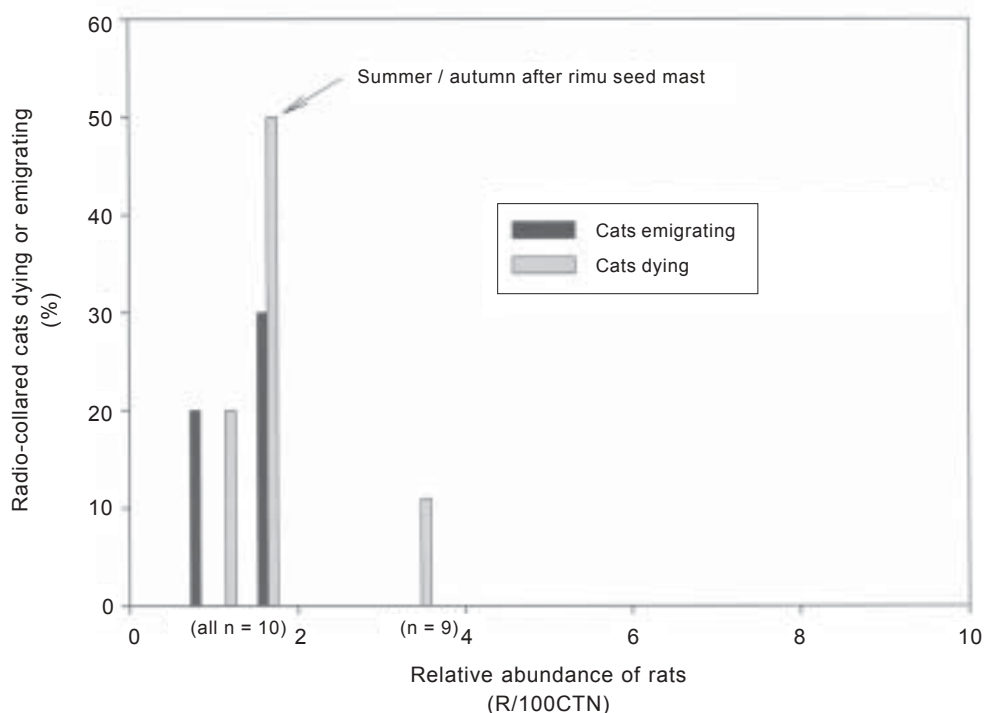
trap had been checked. During the course of the research 11 cats died, and five cats left the study area. A sufficient number of fixes for kernel analysis were obtained for only 11 of the cats caught.

3.4 HOME RANGES

More than 30 fixes each were obtained for seven cats (three female, four male), which enabled 100% MCPs (minimum convex polygons) to be calculated for them. 95% kernels were calculated for eleven cats (Fig. 5a–c). The mean (± SE) female home range sizes were 1109 (± 52.9) ha and 1065 (± 241.6) ha for 100% MCP and 95% kernel respectively. The mean (± SE) male home range sizes were 2083 (± 457.3) ha and 1815 (± 360.3) ha for MCP and 95% kernel respectively. The average female home ranges were 53% and 59% of the size of the mean male home ranges using MCP and 95% kernel methods respectively.

There was substantial inter- and intra-sexual overlap in fully utilised home ranges. Using the 95% kernel method, mean overlap between home ranges for all cats was estimated at 36 ± 3%. There was little variation in overlap between sexes. Male cats had home ranges that overlapped with other males by an average of 36 ± 4%, and females had mean home range overlaps with other females of 31 ± 5%. Individual home ranges of all cats overlapped with a mean (± SE) of 7 (± 2) other cats.

3.5 HABITAT USE

Eleven cats had more than 15 fixes each and were used for kernel analysis.

A Dixon test for outliers (Sokal & Rolf 1995) showed that there was a significant difference in habitat use between F2 and other cats (p < 0.05 for podocarp-broadleaf forest and $p < 0.01$ for *Leptospermum* shrubland), so F2 was removed from the analysis and is discussed later.

The total area utilised by the cats in this study area, as revealed by the 95% kernel analysis of the combined home ranges of all ten cats, was 41 457 ha. Of this area, 62.9% (26 058 ha) was podocarp-broadleaf forest, 21.1% (8744 ha) was subalpine shrublands, 10.7% (4434 ha) was *Leptospermum* shrublands, and 5.4% (2221 ha) was riparian shrubland. The breakdown of vegetation types within each cat's home range is shown in Table 4.

Compositional analysis showed that overall use of the four vegetation types within the 95% kernel home ranges of 10 feral cats was non-random when compared with vegetation type availability (Wilk's Λ = 0.321, c^2 = 11.363, 3 d.f., $p < 0.01$). Podocarp-broadleaf forest was used statistically significantly more than subalpine shrubland based on the use of the habitat versus availability ($p < 0.05$). Rank order of use of habitat versus availability is shown in Table 5. No cats were recorded in alpine heath, although one was recorded 300 m from the boundary of the subalpine shrubland and alpine heath.

Figure 5a. Map of the home ranges of three female cats (F2, F7, F8) in the Rakeahua Valley, Stewart Island/Rakiura, as calculated using the 95% kernel method. See Fig. 2 for explanation of vegetation types indicated by shading.

3.6 LARGE-SCALE MOVEMENTS AND DISPERSAL

Two male cats moved the length of their home range within 24 hours. One male cat (M8) was recorded moving the length of his home range, 7 km in a straight line, over 23 hours. This was at a mean pace of 300 m per hour. A second male cat (M9) also moved the length of his home range, 5 km in a straight line, in 20 hours. This was at an average speed of 250 m per hour. A straight-line track for cat M9 also entailed his travelling over two 300-m-high ridges.

Cats were assumed to have dispersed from their home range if they were tracked leaving the area and / or were not subsequently found in the study area after being repeatedly located there. Seven cats left the study area; the fates of four of these were determined. The fate of one male cat (M5) is unknown, as he dispersed immediately and his transmitter was found 10 km from where he was trapped. Another male (M1) occupied a home range in the study area for at least

Figure 5b. Map of the home ranges of four male cats (M1, M9, M10, M11) in the Rakeahua Valley, Stewart Island/Rakiura, as calculated using the 95% kernel method. See Fig. 2 for explanation of vegetation types indicated by shading.
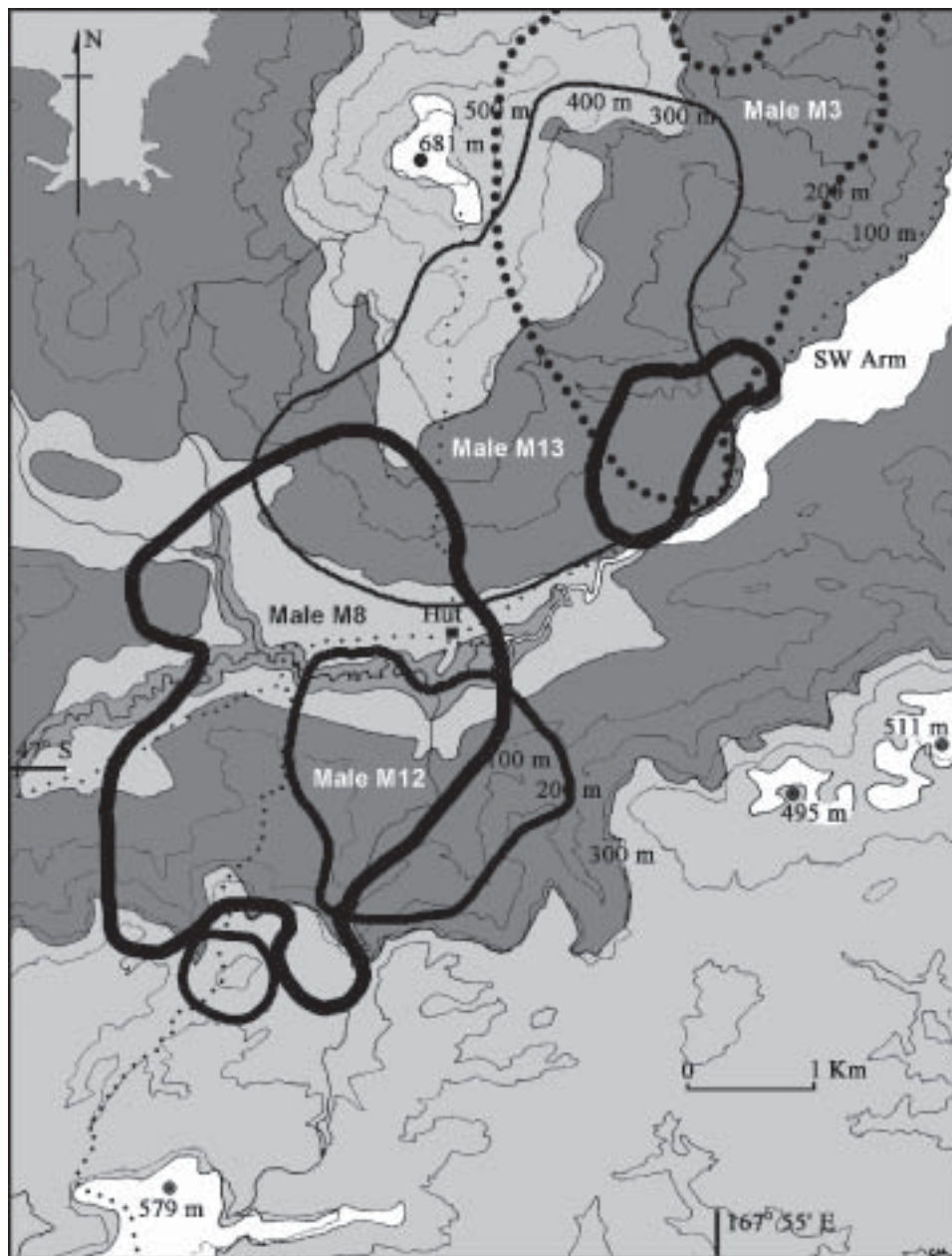
three months then left and was located alive, twice over the next year, in an area 11 km west of where he was first trapped. One adult male (M8) held a large territory in the valley for 12 months then dispersed and was later found dead just outside the study area. An adult female and a juvenile male were captured in one season and in the next season were also found dead outside the study area.

3.7 POPULATION DENSITY OF CATS

The population density of cats was calculated using the two home range methods, on the assumption that all the cats in the study area had been radio-collared. Using 100% MCP, the study area for seven cats was estimated as 36 km^2. The population density of cats was therefore 0.19 cats per km^2. When the 95% kernel method was used the study area was estimated as 41.5 km^2, with a density of 0.27 cats per km^2.

Figure 5c. Map of the home ranges of four male cats (M3, M8, M12, M13) in the Rakeahua Valley, Stewart Island/Rakiura, as calculated using the 95% kernel method. See Fig. 2 for explanation of vegetation types indicated by shading.
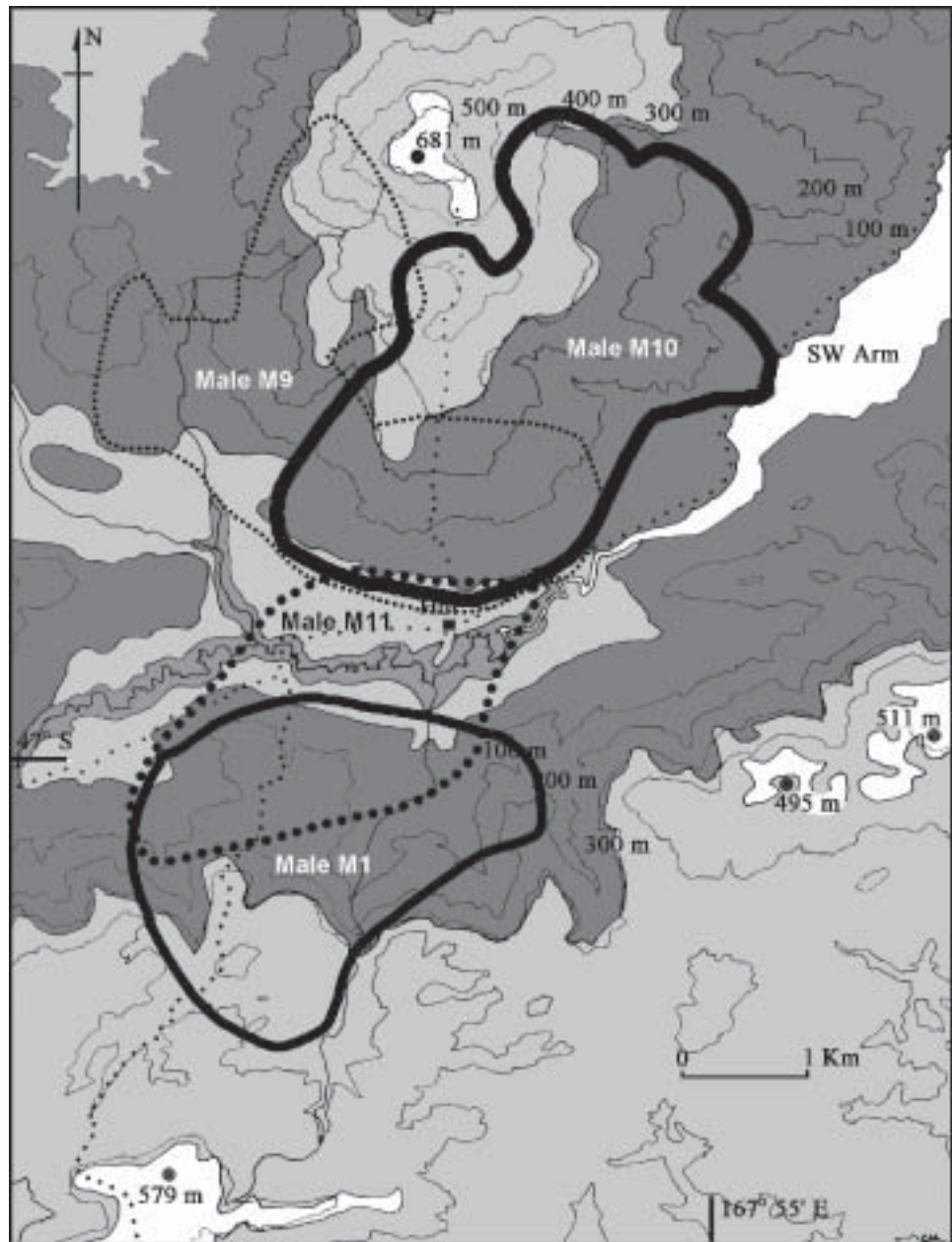
3.8 DIURNAL ACTIVITY AND THE EFFECT OF CLIMATE ON HABITAT USE

Overall, active pulse rates were recorded 76.2% (95% binomial CI: 76.1%–76.2%, n = 1545 bearings) of the times a bearing was taken on a radio-collared cat.

During wet weather, active pulse rates were recorded fewer times (68.1%, 95% binomial CI: 68.0%–68.2%, n = 389 bearings) than during dry weather (77.5%, 95% binomial CI: 77.4%–79.6%). Significant rain (> 0.9 mm) was recorded on 77 out of 130 of field days (59%). There was a statistically significant departure from homogeneity for the four categories of active or resting pulse rates during wet or dry weather (G_{adj} = 17.82, p < 0.01). The hypothesis that the proportion of active bearings taken in dry weather equalled the proportion of active bearings taken in wet weather was rejected (z = 3.65, p < 0.05).

Eight adult cats (six males and two females) used the subalpine shrubland and examination of the weather on the days that these cats were located in this vegetation type suggested they were using subalpine shrubland more on dry days than wet days. The probabilities that the distribution of locations of each cat in the subalpine shrubland on wet or dry days occurred by chance were estimated using randomisation tests (Table 6). Four cats used the subalpine shrubland on dry days significantly more often than expected by chance, and the probability of two cats' use of the subalpine shrubland occurring on dry days, when compared to chance, approached formal statistical significance ($p < 0.05$).

The circumferences of the largest trees in the *Leptospermum* shrubland, subalpine shrubland, and riparian shrubland did not differ significantly from one another (Fig. 6). The circumference of large trees in the four vegetation

TABLE 4. PERCENTAGE OF FOREST TYPES WITHIN EACH 95% KERNEL FOR TEN FERAL CATS, RAKEAHUA VALLEY, STEWART ISLAND/RAKIURA.

| FOREST TYPE | CAT | | | | | | | | | | AVAILABLE FOREST TYPE (% OF STUDY AREA) | MEAN USE OF FOREST TYPE (% ± SE) |
	M1	M3	M8	M9	M10	M11	M12	M13	F7	F8		
Podocarp broadleaf forest	67.9	53.1	63.4	73.6	72.4	63.9	71.3	53.1	72.4	77.4	62.9	68.0 ± 2.4
Subalpine shrubland	27.6	46.9	8.0	8.4	22.3	0.0	0.6	25.8	6.4	7.6	21.1	15.0 ± 4.7
Leptosp'm shrubland	4.0	0.0	15.0	17.3	5.2	17.9	11.9	0.0	11.4	15.0	10.7	11.0 ± 1.9
Riparian forest	0.5	0.0	12.6	0.7	0.0	18.2	16.2	2.3	9.9	0.0	5.4	6.0 ± 2.3
Total	100	100	100	100	100	100	100	100	100	100	100	100

TABLE 5. RANKING MATRIX OF MEANS AND STANDARD ERRORS OF LOG RATIO DIFFERENCES BETWEEN HABITAT CATEGORIES UTILISED BY FERAL CATS AND HABITATS AVAILABLE WITHIN KERNEL HOME RANGES. SIGNIFICANT DIFFERENCES ARE SHOWN IN BOLD. RANKING OF THE HABITATS IS SHOWN IN THE FAR RIGHT COLUMN, WHERE 1 = THE MOST PREFERRED HABITAT.

	PODOCARP-BROADLEAF FOREST	*Leptospermum* SHRUBLAND	RIPARIAN SHRUBLAND	SUBALPINE SHRUBLAND	RANKING
Podocarp-broadleaf forest		-1.51 ± 0.75	-2.17 ± 1.00	**−2.28 ± 0.84**	1
Leptospermum shrubland	1.51 ± 0.75		-1.17 ± 0.93	-0.38 ± 1.41	2
Riparian shrubland	2.17 ± 1.00	1.17 ± 0.93		-0.17 ± 1.49	3
Subalpine shrubland	**2.28 ± 0.84**	0.38 ± 1.41	0.17 ± 1.49		4

types were statistically significantly different ($F_{3,124} = 116.4$, $p < 0.001$), with the largest trees found in podocarp-broadleaf forest. Podocarp-broadleaf forest was the only vegetation type that had large trees with a mean circumference that exceeded the 940 mm 'circumference' of a sleeping 3.5-kg female cat (Fig. 6). The mean circumference of trees in riparian shrubland was less than the circumference of the sleeping cat, although five of the 32 trees sampled exceeded the 'cat circumference'. No trees greater than 940 mm in circumference were measured in the *Leptospermum* shrubland or subalpine shrubland. Impervious shelter from rain for cats (as provided by holes in trees or boles of large fallen trees), and especially for nursing cats with kittens, was mainly found in podocarp-broadleaf forest.

TABLE 6.   PROPORTION OF WET AND DRY DAYS THAT FEMALE AND MALE CATS WERE LOCATED IN SUBALPINE SHRUBLAND OR PODOCARP-BROADLEAF FOREST, AND PROBABILITY OF OCCURRANCE, RAKEAHUA VALLEY, STEWART ISLAND/ RAKIURA.

CAT	F7	F8	M1	M8	M9	M10	M12	M13
Podocarp-broadleaf forest (%)	8	44	50	50	59	54	36	45
(no. of observations)	(22)	(54)	(12)	(44)	(22)	(50)	(22)	(11)
Subalpine shrubland (%)	0	0	0	17	29	20	25	0
(no. of observations)	(5)	(1)	(3)	(6)	(7)	(10)	(4)	(3)
Probability of each cat's observed use of subalpine shrubland on wet v. dry days occurring by chance (%)	1	27	6	3	21	1	7	5

Figure 6.   Mean (± 99% CI) tree circumference in four forest types, Rakeahua Valley, Stewart Island/ Rakiura, compared with the mean 'circumference' of a resting female cat. (ANOVA of differences of mean circumference between forest types [n = 32 trees in each forest type], $F_{3,124} = 116.4$, $p \ll 0.001$)
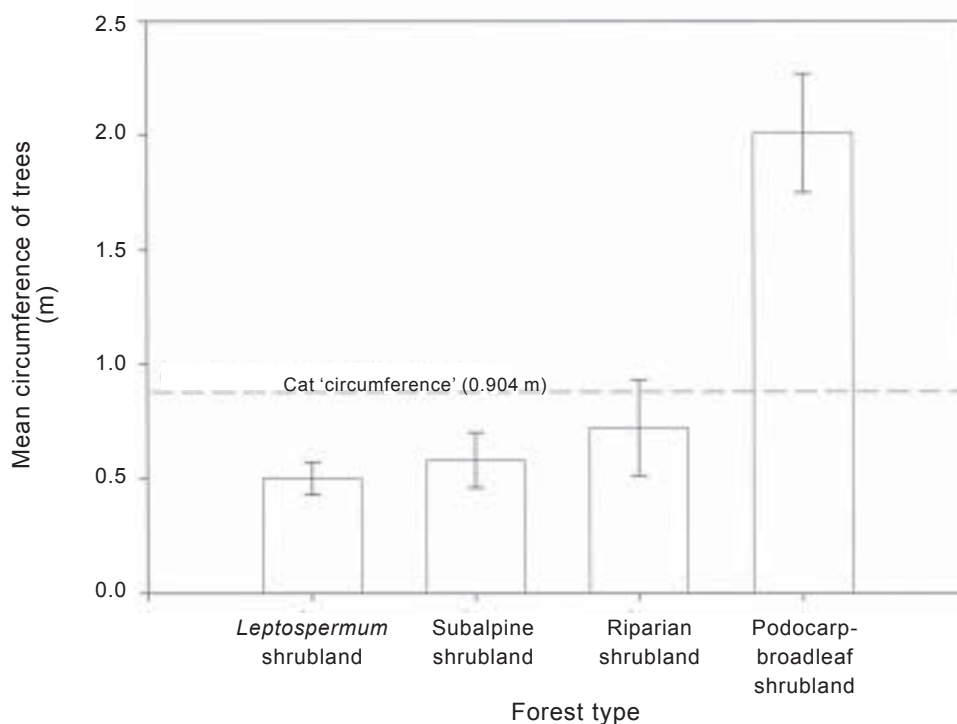
4. Discussion

4.1 NUMERICAL RESPONSE BY CATS

Cats tended to move out of the Rakeahua Valley when rat numbers decreased (Fig. 4). The home range size of cats is known to increase when prey numbers are low (Norbury et al. 1998a) or cats will abandon an established home range altogether (Jones 1977; Brothers et al. 1985). Correspondingly, cat mortality, probably from starvation, tended to be the greatest during periods of low relative abundance of rats (Fig. 4). Similarly, cats on Macquarie Island died most often in winter when rabbit numbers were low (Jones 1977), and Liberg (1984) found that male cats in Sweden lost significant amounts of weight during periods of low rabbit abundance. In feral cats worldwide, most deaths appear to occur in juveniles, because of starvation (Wodzicki 1950; Derenne 1976). Juvenile mortality is a significant restraint on population growth when prey is limited (van Aarde 1978; Jones & Coman 1982). When food is not limiting, cat numbers can increase quickly through improved survivorship of juveniles and sub-adults (Apps 1983). Survivorship of adult and juvenile cats may improve on Stewart Island/Rakiura during occasional rat plagues. The rat plagues have been recorded over the spring after multi-annual seed mast events of rimu *Dacrydium cupressinum* (Powlesland et al., 1995; GH pers. obs.). A temporary increase in cat density is likely during these plagues, and may persist until rat abundance decreases in the following summer. This may result in increased predation impact on native bird and lizard species when cats disperse. The numbers of cats dying and dispersing in the summer and autumn after a rimu mast season supports this. More cats dispersed and died in early 2000 after the rimu mast of early 1999 than in the following year (Fig. 4).

4.2 PREY SWITCHING

Cats on Stewart Island/Rakiura are apparently not eating rats in proportion to rat abundance, which mirrors the findings of Fitzgerald & Karl (1979) who found little variation in occurrence of rats in scats at low or high rat abundance. Nevertheless, there was a trend for a lower mass of rats to be eaten as abundance of rats declined, which corresponded to an increase in the mass of 'alternative prey' (birds) consumed. There was, however, no sudden change in the relative contribution of either prey type as rat abundance declined. If it is assumed that the relative abundance of rats relates directly to density, and prey mass is linked to the number of individuals caught by cats, then there is little evidence that cats on Stewart Island/Rakiura 'prey switch' (Hassell et al. 1977). Indeed, O'Donoghue et al. (1998) used relative biomass rather than abundance as an index to investigate prey switching by lynx because of the large differences in body size of prey, hares and squirrels. They concluded that virtually no secondary prey (squirrels), were killed when they made up 30% or less of the available biomass of prey. 'Prey switching' only occurred when the proportion of secondary prey was 55% of the total available biomass.

The accessibility and calorific value of birds—cats' main alternative prey—probably limits their occurrence in cat diet. Flying forest birds (as opposed to ground-nesting birds) are probably not only difficult to catch, but are likely to return fewer calories (Konecny 1983) per unit of effort than a rat. An 'average' rat (123 g) has 2.4 times the mass of an 'average' forest bird (50.45 g). Although more bird biomass was eaten during troughs in rat abundance, this may be a function of increased foraging time expended by cats, which likely increased the chances of other prey being encountered (Liberg 1982), rather than selection of birds as alternative prey. Cats are still relatively efficient rodent predators at very low prey densities (Pearson 1964), and when cats are foraging for longer periods, they have, where possible, fewer but larger meal sizes (McDonald & Rogers 1984).

4.3   CAT DIET

The previous diet study of cats on Stewart Island/Rakiura (Karl & Best 1982) recorded similar results to this study. The contribution by weight of rats to cat diet was 79.7% in the previous study and 81.2% in this study. Similarly, birds contributed, by weight, 15.5% and 13.2%, respectively, of cat diet. Possum remains made up 3.4% of a cat diet by weight in Karl & Best's study, and 2.1% in this study. Weta (Orthoptera) contribution was the same in both studies (0.2%). The percentage occurrence for rats is less for this study but not significantly so. Karl & Best (1982) recorded 93% (95% binomial CI: 87.4%-95.2%) occurrence of rats in cat scats. This study found 83.1% (95% binomial CI: 90.4%-74.5%) occurrence of rats.

A significantly higher percentage of birds was recorded in cat scats in the previous study (44.1%: 95% binomial CI: 37%-50.5%; Karl & Best 1982) than in this study (26.9%: 95% binomial CI: 21.8%-35.4%). The lower percentage recorded in this study may reflect the location of the study area, which had fewer ground-nesting birds (e.g. penguins) than that in the Karl & Best study, which included the coast of Stewart Island/Rakiura. Of the individual birds identified from cat scats by Karl & Best, 5.7% were penguins—blue penguins *Eudyptula minor* and a crested penguin *Eudyptes* spp. Another 11.3% of the birds identified by Karl & Best were sooty shearwaters *Puffinus griseus*. These shearwaters breed on islands off the coast of Stewart Island/Rakiura (Heather & Robertson 1996), and may be killed by cats if they inadvertently land on Stewart Island/Rakiura.

This study also recorded significantly fewer lizards, *Leiolopisma* spp., in the diet of cats (1.4% frequency of occurrence, 95% binomial CI: 2.8%-3.9%) than the earlier study (24% frequency of occurrence, 95% binomial CI: 19.1%-30.1%). This may be because many scats in the previous study were collected in southern Stewart Island, where the higher proportion of low scrub and exposed rock than in the present study area (GH pers. obs.) favours lizards. Cats will tend to take prey according to availability, which is likely to vary with vegetation types (Coman & Brunner 1972; Nogales & Medina 1996).

Fish, deer (*Odocoileus virginianus* or *Cervus elaphus*) and kitten remains were all found in scats. It is possible that the occurrence of kitten was a result of cannibalism, but this may be unlikely if cats rarely consume aggressive prey as

large as an adult Norway rat (Childs 1986). Remains of adult cats and kittens have occasionally been found in small numbers in the diet of feral cats (Hubbs 1951; Jones 1977; Bloomer & Bester 1990), and scavenging or cannibalism may occur more often during periods of nutritional stress (Paltridge et al. 1997). The presence of deer in a scat is probably the result of a cat scavenging on an animal shot by hunters. A deer carcase could provide food for a cat for many days. The fish remains are likely to be the bait from the cat trapping for this study.

Possums are preyed on by cats in New Zealand (Cowan et al. 2000) and remains in cat scats may indicate predation on juvenile possums by cats as well as scavenging of carcases (Fitzgerald & Karl 1979; Langham 1990). Invertebrates are eaten frequently, but provide little mass in cat diet. The preponderance of weta (Orthoptera) is not surprising. Orthopterans are often the dominant group in cat diets (Fitzgerald & Karl 1979; Jones & Coman 1982; Paltridge et al. 1997) despite their poor calorific value (Konecny 1983).

4.4 HOME RANGE AND DENSITY

Compared with other studies of feral cats, the home range sizes of cats in the Rakeahua Valley were the largest so far recorded worldwide for females and the second largest for males (Table 7). Home range size and population density in feral cats are inversely related (Liberg et al. 2000); consequently, the density of cats in the Rakeahua Valley was one of the lowest recorded anywhere. Densities of cats in the Rakeahua Valley were restricted by food supply; by seasonal restrictions in the abundance of primary prey in particular, as well as a lack of secondary prey. Food abundance, and especially seasonal minima in prey biomass, is thought to be inversely correlated with female home range size in solitary carnivores (Sandell 1989). Male home range size will, in turn, be influenced by both female distribution during the breeding season and food abundance (Sandell 1989; Liberg et al. 2000). In this study it appears that low food abundance was the primary reason for the large home ranges of males. The home ranges of male cats overlapped, and sometimes encompassed, the home ranges of females, so access to females was apparently not limited. The male cats abandoned their home ranges only when prey abundance was very low (late summer to early autumn), not when females were in breeding condition in the spring.

TABLE 7.   COMPARISON OF HOME RANGE SIZE AND DENSITY OF ADULT FERAL CATS IN THE SOUTHERN HEMISPHERE, USING MCP UNLESS STATED WITH *.

| MEAN HOME RANGE SIZE (ha) | | DENSITY $(cats/km^2)$ | LOCATION | REFERENCE |
ADULT MALE	ADULT FEMALE			
41	–	2.27–4.5	Macquarie Island*	Jones (1977)
155	84	1.1	North Island, N.Z.*	Fitzgerald & Karl (1979)
304	93	2.2–2.5	Galapagos Islands	Konecny (1983)
620	170	0.74–2.4	Victoria, Australia	Jones & Coman (1982)
189	249	0.6–1.4	South Island, N.Z.	Norbury et al. (1998a)
2083	1109	0.2	Stewart Island, N.Z.	This study
2211	–	0.1	Central Australia	Edwards et al. (2001)

Although the recorded home ranges were very large and mountainous, male cats were able to cross them within a day. These movements are common for cats and rates of travel of 513 m and 1000 m per hour have been recorded for cats in New Zealand (Gillies 1998; Sanders & Maloney 2002). Indeed, the topography of the Rakeahua Valley appeared to have little effect on how cats utilised space. Their home ranges were irregularly shaped and encompassed podocarp-broadleaf forest on moderately steep to steep sides of the valley (10°–30°). This is in contrast to a population of feral cats in the Orongorongo Valley of the southern North Island, New Zealand, which had linear home ranges largely restricted to the nearly flat valley floor, probably because prey was plentiful only in the bottom of the valley (Fitzgerald & Karl 1986). As with topography, the Rakeahua River (4–6 m wide) did not appear to affect the movement of cats. Several cats, both adults and juveniles, were recorded on both sides of the river over the course of a few days of radio-tracking.

4.5 HABITAT USE AND THE INFLUENCE OF SHELTER

Cats in the Rakeahua Valley used podocarp-broadleaf forest more than would be expected if the relationship were a simple reflection of habitat availability. If prey availability alone were affecting habitat selection, cats would be expected to be using the forest types approximately equally. As the relative abundance of rats was approximately equal between forest types (Harper 2002), then the availability of shelter was thought to be affecting the cats' use of habitat.

The distribution of feral cats has been linked to shelter directly (Calhoon & Haspel 1989) and indirectly (van Aarde 1979; Brothers et al. 1985). Indeed, a lack of shelter may even affect the survival of a feral cat population. It has been suggested that feral cats on subantarctic Campbell Island have recently died out because of the lack of shelter (P. Moore 1997, Department of Conservation, unpubl. report). Feral cats use a variety of sites for shelter, including rabbit and seabird burrows on subantarctic islands (Derenne 1976; van Aarde 1979; Brothers et al. 1985), abandoned buildings (Calhoon & Haspel 1989) and hollow logs (Fitzgerald & Karl 1986; Langham 1990). In an area like the Rakeahua Valley, which has a relatively high amount of rainfall and rain-days per year, shelter for feral cats is needed primarily to provide protection from rain. This study showed that wet weather also influenced cats' activity, as they rested more often in wet weather than in dry weather. A reduction in cat activity in wet weather has been recorded elsewhere (Derenne 1976). It is possible that rain affects the ability of cats to forage for prey. The high proportion of resting activity during wet weather gives a partial indication of the use of shelter, as cats were probably using shelter to rest under while it was raining. It may be an underestimation of shelter use in wet weather, as cats could be recorded as active if they are grooming, for example. Use of shelter by non-maternal cats may be largely opportunistic. Twenty-five cats studied in the central South Island used over 70% of their den sites only once during 287 days (Norbury et al. 1998b). One used the same den site eight times, however, which suggests a degree of selection of favourable shelter sites.

Shelter for cats, in the form of large hollow or fallen trees, was more likely to be present in podocarp-broadleaf forest than in any of the other vegetation types in the study area, which may explain why cats used this vegetation type more than would be expected. The thermal dynamics of the forest may also have favoured its use by cats. The interiors of some forest types are warmer and less windy than other vegetation types, which influences their use by small felids (McCord 1974). Thermoregulation may be particularly important in selection of shelter by females because of their smaller size and requirements for nursing kittens. Temperatures inside hollow trees oscillate less than outside (Fernandez & Palomares 2000) and, when occupied by cat-sized animals, hollows can be at least 17°C warmer than outside (Stains 1961). Whilst the size of a den will be related to the size of the animal because of access requirements (Lindenmayer et al. 1991), it may also reflect thermoregulatory efficiency, i.e. smaller holes are easier to heat than large ones (Lariviere et al. 1999). Female cats in our study probably did not use the *Leptospermum* and subalpine shrublands while raising kittens because of the lack of large trees. Riparian shrubland in the study area does, however, have some trees that are large enough to provide adequate shelter. This may explain the location of the home range of female F2.

Female F2 was the only cat out of 11 to use the riparian and *Leptospermum* shrublands in preference to podocarp-broadleaf forest (Fig. 5a). Her home range was smaller than those of the other two females, suggesting that prey was more abundant there than in the podocarp-broadleaf forest. Riparian shrubland may be a higher quality food source than podocarp-broadleaf forest because two prey species, ship rats and Pacific rats, are present (Harper 2002). (Only ship rats were present in podocarp-broadleaf forest; Pacific rats dominated the *Leptospermum* shrublands and Norway rats dominated in subalpine shrublands.) The quality of F2's home range was indicated by the fact that she gained weight (300 g) over three consecutive captures and was also thought to have weaned at least two kittens during the course of the study. It is possible that she was using the riparian shrubland, rather than *Leptospermum* shrubland, for raising young, as this forest type would have a few trees large enough to shelter a female and kittens from wet weather (Fig. 6).

Wet weather also influenced cats' use of subalpine shrubland, as the majority of cats were using this forest type more during dry weather than during wet weather. Six out of the eight cats located in the subalpine shrubland were male, which may be a function of the large size of their home range compared with female cats. When female cats were located in subalpine shrubland, they were on the edge of their home range and outside their 'core' ranges. Both these facts suggest that predation of nesting southern New Zealand dotterels in the alpine heath is mainly by male cats making excursions into the area during periods of dry weather.

5. Summary

Feral cats on Stewart Island/Rakiura appear to be under nutritional stress from late spring to early autumn and, as for many other predators, food supply is also the primary population regulatory mechanism for these cats. In this case, it is not overall low prey abundance *per se* that restricts cat numbers, but seasonal restriction in primary prey, coupled with limited alternative prey biomass. The limited prey availability and shelter are interacting to determine the selection of forest types by cats in the Rakeahua Valley. There is a climatic aspect to selection also, with subalpine shrubland being visited mainly when the weather is dry. Predation of adult male southern New Zealand dotterels by cats in the alpine heath probably occurs as chance events during excursions by male cats during periods of dry weather, particularly in the early spring when adult male dotterels are conspicuous or incubating.

6. Recommendations

As cats on Stewart Island/Rakiura respond numerically to the abundance of rats, and appear to survive winter conditions well, widespread large-scale control of cats is likely to be most effective during the summer, as rat numbers decline, and while female cats are also raising kittens.

Control of cats may need to be particularly intensive in the spring and summer following a rimu mast. There is some evidence for greater than usual rat abundance immediately after a rimu mast on Stewart Island/Rakiura (autumn), and survival of cats may improve as a consequence. Research on the response of rats to seed-masts in beech forest has been carried out, but little has been done on possible similar responses to mast-years in lowland podocarp-broadleaf forests. During the spring and summer following a mast, rat abundance will generally decline and more cats may therefore disperse in search of prey, although which forest types they move into appears to be strongly influenced by the prevailing rainfall conditions.

Cats should be controlled in concert with rats. Cat control by itself will allow rats to increase in abundance (meso-predator release), which is likely to be counter-productive, as rats are also effective predators of birds and nests. Reducing the numbers of rats in the subalpine shrubland may reduce the incentive for cats to move into this vegetation type, and hence, the likelihood of them depredating dotterels in the alpine heath during dry weather.

The importance of podocarp-broadleaf forest in providing shelter for cats could be investigated experimentally by the large-scale removal of rats from this forest type followed by monitoring of the consequent habitat selection of a population of radio-tagged cats. Although these sorts of experiments require resources that are far beyond the scope of this study, they may be able to be done in parallel with rat control operations.

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8. References

Aebischer, N.J.; Robertson, P.A.; Kenward R.E. 1993: Compositional analysis of habitat use from animal radio-tracking data. *Ecology 74(5)*: 1313–1325.

Angerbjorn, A.; Tannerfeldt, M.; Erlinge, S. 1999: Predator-prey relationships: arctic foxes and lemmings. *Journal of Animal Ecology 68*: 34–49.

Apps, P.J. 1983: Aspects of the ecology of feral cats on Dassen Island, South Africa. *South African Journal of Zoology 18(4)*: 393–399.

Bailey, T.N. 1993: The African leopard. Ecology and behavior of a solitary felid. Columbia University Press, New York.

Barlow, M. 1993: New Zealand dotterel: South Island historical notes and Southland coastal records. *Notornis 40(1)*: 15–26.

Bloomer, J.P.; Bester, M.N. 1990: Diet of a declining feral cat *Felis catus* population on Marion Island. *South African Journal of Wildlife Research 20(1)*: 1–4.

Brothers, N.P.; Skira, I.J.; Copson, G.R. 1985: Biology of the feral cat, *Felis catus* (L.), on Macquarie Island. *Australian Wildlife Research 12*: 425–436.

Brunner, H.; Coman, B.J. 1974: The identification of mammalian hair. Inkata Press, Melbourne.

Calhoon, R.E.; Haspel, C. 1989: Urban cat populations composed by season, subhabitat and supplementary feeding. *Journal of Animal Ecology 58*: 321–328.

Childs, J.E. 1986: Size-dependent predation on rats (*Rattus norvegicus*) by house cats (*Felis catus*) in an urban setting. *Journal of Mammology 67*: 196–199.

Coman, B.J.; Brunner, H. 1972: Food habits of the feral house cat in Victoria. *Journal of Wildlife Management 36(3)*: 848–853.

Corbett, L.K. 1979: Feeding ecology and social organisation of wildcats (*Felis silvestris*) and domestic cats (*Felis catus*) in Scotland. Unpublished PhD thesis, Aberdeen University, Aberdeen.

Cowan, P.; Clark, J.; Heath, D.; Stankiewicz, M.; Meers, J. 2000: Predators, parasites, and diseases of possums. *In*: Montague, T.L. (Ed.): The Brushtail Possum. Biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Lincoln, New Zealand.

Cumberland, R.E.; Dempsey, J.A.; Forbes, G.J. 2001: Should diet be based on biomass? Importance of larger prey to the American marten. *Wildlife Society Bulletin 29(4)*: 1125–1130.

Cunningham, D.M.; Moors, P.J. 1996: Guide to the identification and collection of New Zealand rodents. 3rd ed. Department of Conservation, Wellington.

Day, M.G. 1966: Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology (London) 148*: 201–217

Derenne, P. 1976: Notes sur la biologie du chat haret de Kerguelen. *Mammalia 40*: 531–595.

Dowding, J.E. 1999: Research on the southern New Zealand dotterels during the 1998–1999 season. Unpublished report, Department of Conservation, Invercargill.

Dowding, J.E.; Murphy, E.C. 1993: Decline of the Stewart Island population of the New Zealand dotterel. *Notornis 40(1)*: 1–14.

Fernandez, N.; Palomares, F. 2000: The selection of breeding sites by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation. *Biological Conservation 94*: 51–61.

Fitzgerald, B.M.; Karl, B.J. 1979: Foods of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington. *New Zealand Journal of Zoology 6*: 107–126.

Fitzgerald, B.M.; Karl B.J. 1986: Home range of feral cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Ecology 9*: 71–81.

Gillies, C. 1998: Aspects of the ecology and management of small mammalian predators in northern New Zealand. Unpublished PhD thesis, University of Auckland, Auckland.

Harper, G.A. 2002: Habitat selection by feral cats (*Felis catus*) and three rat species (*Rattus* spp.) on Stewart Island (Rakiura) and their impacts on native birds. Unpublished PhD thesis. University of Otago, Dunedin.

Harris, S.; Cresswell, F.J.; Forde, P.G; Trewhalla, W.J.; Wollard, T.; Wray, S. 1990: Home range analysis using radio-tracking data—a review of problems and techniques particularly as applied to animals. *Mammal Review 20*: 97–123.

Hassell, M.P.; Lawton, J.H.; Beddington, J.R. 1977: Sigmoid functional responses by invertebrate predators and parasatoids. *Journal of Animal Ecology 46*: 249–262.

Hayes, F.N.; Williams, M.J. 1982: The status, aviculture, and re-establishment of brown teal in New Zealand. *Wildfowl 33*: 73–80.

Heather B.; Robertson, H. 1996: The Field Guide to the Birds of New Zealand. Viking, Auckland.

Helldin, J.O. 1999: Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* 22: 324–336.

Hubbs, E.L. 1951: Food habits of feral house cats in the Sacramento Valley. *California Fish and Game 37*: 177–189.

Innes, J. 2001: Advances in New Zealand mammalogy 1990–2000: European rats. *Journal of the Royal Society of New Zealand 31(1)*: 111–125.

Jones, E. 1977: Ecology of the Feral Cat, *Felis catus* (L.), (Carnivora: Felidae) on Macquarie Island. *Australian Wildlife Research 4*: 249–262.

Jones, E.; Coman, B.J. 1982: Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia. III. Home ranges and population ecology in semiarid north-west Victoria. *Australian Wildlife Research 9*: 111–119.

Karl, B.J.; Best, H. 1982: Feral cats on Stewart Island; their foods, and their effects on kakapo. *New Zealand Journal of Ecology 9*: 287–294.

Karnoukhova, N.G. 1971: Age determination in brown and black rats. *Soviet Journal of Ecology 2*: 144–147.

Kenward, R.E.; Hodder, K.H. 1996: An analysis system for biological location data. (NERC: United Kingdom)

King, C.M. 1983: The relationship between beech (*Nothofagu*s sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary response of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology 52*: 141–166.

Konecny, M.J. 1983: Behavioral ecology of feral house cats in the Galapagos Islands. Unpublished PhD thesis. University of Florida, Gainesville.

Korpimaki, E.; Krebs, C.J. 1996: Predation and population cycles of small mammals. *Bioscience 46(10)*: 754–764.

Korpimaki E.; Norrdahl, K. 1991: Numerical and functional reponses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology 72(3)*: 814–826.

Langham, N.P.E. 1990: The diet of feral cats (*Felis catus* L.) on Hawke's Bay farmland, New Zealand. *New Zealand Journal of Zoology 17*: 243–255.

Lariviere, S.; Walton, L.R.; Messier, F. 1999: Selection by striped skunks (*Mephitis mephitis*) of farmsteads and buildings as denning sites. *American Midland Naturalist 142*: 96–101.

Liberg, O. 1982: Hunting efficiency and prey impact by a free-roaming house cat population. *Transactions of the International Congress of Game Biology 14*: 269–275.

Liberg, O. 1984: Food habits and prey impact by feral and house-based domestic cats in a rural area in southern Sweden. *Journal of Mammology: 65(3)*: 424–432.

Liberg, O.; Sandell, M.; Pontier, D.; Natoli, E. 2001: Density, spatial organisation and reproductive tactics in the domestic cat and other felids. *In*: Turner, D.C.; Bateson, P. (Eds): The domestic cat. The biology of its behaviour. Cambridge University Press, Cambridge.

Lindenmayer, D.B.; Cunningham, R.B.; Tanton, M.T.; Nix, H.A. 1991: Aspects of the use of den trees by arboreal and scansorial marsupials inhabiting montane ash forests in Victoria. *Australian Journal of Zoology 39*: 57–65.

Lode, T. 2000: Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*. *Austral Ecology 25*: 223–231.

McCord, C.M. 1974: Selection of winter habitat by bobcats (*Lynx rufus*) on the Quabbin Reservation, Massachusetts. *Journal of Mammalogy 55(2)*: 428–437.

McDonald, M.L.; Rogers Q.R. 1984: Nutrition of the domestic cat, a mammalian carnivore. *Annual Review of Nutrition 4*: 521–562.

McNab, B.K. 1963: Bioenergetics and the determination of home range size. *American Naturalist 97*: 133–139.

Meurk, C.D.; Wilson H.D. 1989: Stewart Island. *Biological Survey of Reserves Series No. 18*. Department of Conservation, Wellington.

Moors, P.J.; Atkinson, I.A.E. 1984: Predation on seabirds by introduced animals, and factors influencing its severity. *In*: The status and conservation of the World's seabirds. ICBP Technical Publication No. 2.

Morrison, M.L. 2001: A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management 65(4)*: 613–623.

Nelson, L.; Clark, F.W. 1973: Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammology 54(1)*: 295–298.

Nogales, M.; Medina, F.M. 1996: A review of the diet of feral domestic cats (*Felis silvestris* f. catus) on the Canary Islands, with new data from the laurel forest of La Gomera. *Zeitschrift fur Saugetierkunde 61*: 1–6.

Norbury, G.L.; Norbury, D.C.; Heyward, R.P. 1998a: Behavioral responses of two predator species to sudden declines in primary prey. *Journal of Wildlife Management 62(1)*: 45–58.

Norbury, G.L.; Norbury, D.C.; Heyward, R.P.; 1998b: Space use and denning behaviour of wild ferrets (*Mustela furo*) and cats (*Felis catus*). *New Zealand Journal of Ecology 22(2)*: 149–159.

O'Donoghue, M.; Boutin, S.; Krebs, C.J.; Murray, D.L.; Hofer, E.J. 1998: Behavioural responses of coyotes and lynx to the snowshoe hare cycle. *Oikos 82*: 169–183.

Paltridge, R.; Gibson, D; Edwards, G. 1997: Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research 24*: 67–76.

Pearson, O.P. 1964: Carnivore-mouse predation: an example of its intensity and bioenergetics. *Journal of Mammology 45(2)*: 177–188.

Powlesland, R.G.; Roberts, A.; Lloyd, B.D.; Merton, D.V. 1995: Number, fate and distribution of kakapo (*Strigops habrotilus*) found on Stewart Island, New Zealand. *New Zealand Journal of Zoology 22*: 239–247.

Reynolds, J.C.; Aebischer, N.J. 1991: Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review 21(3)*: 97–122.

Sadlier, R. 2000: Evidence of possums as predators of native animals. *In*: Montague, T.L. (Ed.): The brushtail possum: biology and impact of an introduced marsupial. Manaaki Whenua Press, New Zealand.

Sandell, M. 1989: The mating tactics and spacing patterns of solitary carnivores. *In*: Gittleman, J.L. (Ed.): Carnivore behavior, ecology, and evolution. Cornell University Press New York.

Sanders, M.D.; Maloney, R.F. 2002: Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year study. *Biological Conservation 106(2)*: 225–236.

Sansom, J. 1984: The climate and weather of Southland. *N. Z. Meteorological Service Miscellaneous Publication 115(15)*. Wellington.

Sokal, R.R.; Rolf, F.J. 1995: Biometry. The principles and practice of statistics in biological research. Freeman and Company, New York.

Stains, H.J. 1961: Comparison of temperature inside and outside two tree dens used by raccoons. *Ecology 42(2)*: 410–413.

Sunquist, M.E.; Sunquist, F.C. 1989: Ecological constraints on predation by large felids. *In*: Gittleman, G.L. (Ed.): Carnivore behavior, ecology, and evolution. Cornell University Press, New York.

van Aarde, R.J. 1978: Reproduction and population ecology of the feral house cat on Marion Island. *Carnivore Genetics Newsletter 3(8)*: 288–316.

van Aarde, R.J. 1979: Distribution and density of the feral house cat *Felis catus* on Marion Island. *South African Journal of Antarctic Research 9*: 14–19.

Van Ordsal, K.G.; Hanby, J.P.; Bygott, J.D. 1985: Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology* (London)*: 206*: 97–112.

Veitch, C.R. 1985: Methods of eradicating feral cats from offshore islands in New Zealand. *In*: Moors, P.J.; Atkinson, I.A.E. (Eds): Conservation of island birds. *ICBP Technical Publication No. 3*: 125–141.

Viljoen, P.C. 1993: The effects of changes in prey availability on lion predation in a large ecosystem in northern Botswana. *Symposium of the Zoological Society of London 65*: 193–213.

Weber, D. 1989: The ecological significance of resting sites and the seasonal habitat change in polecats (*Mustela putorius*). *Journal of Zoology* (London) *217*: 629–638.

Wilson, H.D. 1987: Vegetation of Stewart Island, New Zealand. Supplement: *New Zealand Journal of Botany*.

Withey, J.C.; Bloxton, T.D; Marzluff, J.M. 2001: Effects of radio tagging and location error in wildlife radiotelemetry studies. *In*: Millspaugh, J.J.; Marzluff, J.M. (Eds): Radio tracking and animal populations. Academic Press, San Diego.

Wodzicki, K.A. 1950: Introduced mammals of New Zealand. *D. S. I. R Bulletin No. 98*, Department of Scientific and Industrial Research, Wellington.

Wray, S.; Cresswell, W.J.; White, P.C.L.; Harris, S. 1992: What, if anything, is a core area? An analysis of the problems of describing internal range configurations. *In*: Priede, I.G.; Swift, S.M. (Eds): Wildlife telemetry—remote monitoring and radio tracking of animals. Ellis Horwood, Chichester, U.K.

Appendix 1

Measurements of adult feral cats *Felis catus* and age (A: adult, J: juvenile) of cats trapped in the Freshwater and Rakeahua Valleys, Stewart Island, September 1999 to March 2001.

	WEIGHT (kg)		HEAD-BODY LENGTH (mm)		TAIL LENGTH (mm)	
	M	F	M	F	M	F
Mean	3.36	2.63	518.1	460.7	275.4	257.1
s.e.	0.50	0.43	26.5	30.3	16.8	16.8
Range	2.68–4.09	2.16–3.25	460–560	435–500	250–305	230–280
n.	13	7	13	7	13	7

Age: males: 12A, 2J, females: 7A, 1J.