Habitat selection of feral cats (*Felis catus*) on a temperate, forested island

GRANT A. HARPER
Zoology Department, University. of Otago, Dunedin, New Zealand (Email: grant.harper@stonebow.otago.ac.nz)

Abstract   Habitat selection of mammalian predators is known to be influenced by availability and distribution of prey. The habitat selection of feral cats on Stewart Island, southern New Zealand, was investigated using telemetry of radio-tagged cats. Compositional analysis of the habitat selection of radio-tagged cats showed they were using the available habitats non-randomly. Feral cats avoided subalpine shrubland and preferentially selected podocarp-broadleaf forest. The avoidance of subalpine shrubland by cats was probably due to a combination of the presence of a large aggressive prey species, Norway rats *Rattus norvegicus*, and the lack of rain-impervious shelter there. Most cats also used subalpine shrubland more often in dry weather than in wet weather. Cats did not preferentially select all the other habitats with only smaller rat species, *Rattus rattus* and *Rattus exulans*, present however. Cats were probably further influenced by the availability of large trees, in podocarp-broadleaf forest, that can provide shelter. Cats were also more active in dry rather than wet weather which supports this conclusion. Home ranges of feral cats on Stewart Island were some of the largest recorded, probably because of limited primary and alternative prey.

Key words: diurnal activity, *Felis catus*, habitat selection, home range, prey, shelter.

INTRODUCTION

Although prey availability is very important in determining the population density and distribution of predators (McNab 1963; Morrison 2001), other factors, like territoriality and shelter, influence habitat use by affecting their ability to live and reproduce (Hall *et al.* 1997; Morrison *et al.* 1998; Liberg *et al.* 2001). The availability of shelter is an important influence on habitat use by mammals. Shelter is used for protection from extremes of weather and temperature (Buskirk 1984; Weber 1989; Palmer & Woinarski 1999) and as sites for resting and raising young (Lindenmayer *et al.* 1990; Lucherini *et al.* 1995; Halliwell & Macdonald 1996). Shelter is used for all these reasons by the smaller Felidae (Koehler 1990; Johnson & Franklin 1991; Palomares 2001) and has been identified as a key factor in the suitability of habitat for carnivores in general (Fernandez & Palomares 2000). Of the carnivores the feral cat *Felis catus* is a useful subject for understanding habitat preferences in the larger Felidae in particular, as feral cats are similarly cryptic, are often found in low densities and generally have a similar behavioural ecology to that observed in the bigger cats (Liberg *et al.* 2000).

Only six of the numerous studies on the home ranges of feral house cats have addressed habitat use (van Aarde 1979; Brothers *et al.* 1985; Edwards *et al.* 2002) and only three have used radio-telemetry

(Alterio *et al.* 1998; Daniels *et al.* 2001; Molsher *et al.* 2005). No studies of habitat selection by cats in mixed forests or forested islands have apparently been published. Moreover, only one has evaluated the effect of climatic variables on any aspect of cat biology (Daniels *et al.* 2001), which found that wind reduced cat activity. Adverse climate can profoundly affect cat populations. For example, there was high mortality of cats on subantarctic Kerguelen Island in winter 1988 due to poor climatic conditions (Say *et al.* 2002). Cats on this island regularly use seabird and rabbit burrows for shelter (Derenne 1976). Therefore, in sites where the climate is generally wet and cold, the availability of shelter is likely to influence habitat selection by cats.

On Stewart Island/Rakiura, New Zealand, feral cats are the largest carnivores present, and were introduced during settlement by Europeans in the early 1800s (Thomson 1922). Three introduced rat species, Pacific rats *Rattus exulans*, Norway rats *Rattus norvegicus*, and ship rats *Rattus rattus* are now the primary prey of cats on Stewart Island (Karl & Best 1982) and are distributed from sea level to the alpine tops (Harper *et al.* 2005). Evidence of cats are similarly found throughout the available habitats (G. Harper, pers. obs. 1999), which include substantial areas of forest and lowland shrub-land. However, the habitat preference of cats in the prevailing cool wet conditions is unknown. Availability of shelter restricts habitat use by cats, particularly in adverse climates (Derenne 1976; Corbett 1979; Brothers *et al.* 1985). As little shelter is available in the alpine areas of Stewart Island it was expected
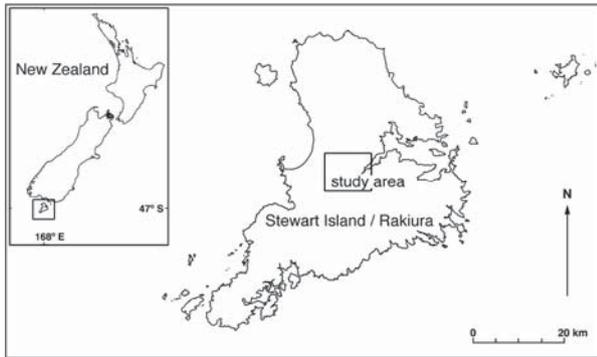
Fig. 1. Map of New Zealand showing the location of Stewart Island/Rakiura and the location of the study site.

that cats would avoid these areas or use them more often during dry weather (Brothers *et al.* 1985). Consequently the aims of the study were (i) to investigate whether cats were occupying the alpine areas as residents or were moving up from forested areas; and (ii) to identify any habitat preferences, and examine possible reasons for these.

METHODS

Study area

The study was conducted in the Rakeahua Valley (47°S, 167°50′E) in the centre of Stewart Island (Fig. 1). The valley is low lying and consists of undulating low ridges separated by wetlands. Its south side is bounded by a steep forested escarpment and on its north and west sides by hills. The climate is cool (summer mean: 12.4°C, winter mean: 5.4°C) and wet (Mean annual rainfall: approximately 2200 mm (K. Tredea, National Institute of Water and Atmospheric Research, pers. comm. 2000)). 'Wet days' (rainfall ≥ 1.0 mm day^{-1}: Sansom 1984) were recorded on 77 out of 130 days in the field (59.2%). Snow often lies to above 500 m and occasionally in the valley floor in winter. Four main vegetation types were identified as follows:

Leptospermum scoparium *shrubland*

These shrublands almost covered the valley floor, where they were only absent in wetlands. The canopy and subcanopy was mainly 5–6 m high *Leptospermum scoparium*. Ground cover consisted mainly mosses, liverworts, *Empodisma minus*, fern patches.

Riparian shrubland

This forest type occurred on well-drained soils extending back from the main river edge for 20–30 m. This forest was flooded several times a year (G. Harper, pers. obs. 2000). The dominant canopy tree was *L. scoparium*. The understorey comprised numerous divaricating shrubs over thick ground cover.

Podocarp-broadleaf forest

This forest type was the dominant vegetation cover on well-drained valley sides from sea level to about 350 m above mean sea level (AMSL). The forest canopy, at 25 m high, consisted of emergent rimu *Dacrydium cupressinum* over a mix of broadleaf canopy trees. The midstorey included young canopy trees, shrubs and tree-ferns. Crown fern *Blechnum discolor* dominated the ground cover.

Subalpine shrubland

Subalpine shrubland existed mainly from 400 to 500 m AMSL on wet and well-drained sites. This 2–3 m high shrubland was generally very dense but was unlikely to inhibit cat movement. It was dominated by *L. scoparium* and leatherwood *Brachyglottis colensoi*. The tussock sedge *Gahnia procerum* and mosses, liverworts and small herbs provided groundcover.

Habitat availability

The distribution of the vegetation types was obtained from vegetation features drawn on a 1:50 000 topographic map (NZMS 260: C49, D49), and confirmed by survey. A land use map was generated from this map with GIS software ARCVIEW 3.0, and areas of available vegetation types within the study area were determined using the geo-processing extension of ARCVIEW.

Cat capture

Cats were captured with Victor 1.5 Soft Catch traps (Woodstream Corporation, Lititz, USA) placed against the bases of trees and baited with thawed frozen fish. Trap lines were set 2–3 m off two walking tracks, one in the valley floor and one to the bushline (about 500 m AMSL) through all vegetation types. Traps were checked every morning. Captured animals were sedated with an injection of Domitor (0.23 mL kg^{-1}). They were measured, weighed and

sexed. Cats above 1 kg body mass were fitted with a two-stage transmitter (160–161 MHz) attached to a collar with a whip aerial (SIRTRACK, Havelock North, New Zealand). The transmitters had two pulse rates, 'active' and 'resting'. The signal changed from 'active' to 'resting' after 5 min of inactivity, returning to 'active' once activity resumed. Battery duration was 17 months (33 g transmitter) or 21 months (45 g). Heavier transmitters were only fitted to cats above 3.0 kg. The transmitters never exceeded 3.3% of a cat's body mass. Cats were then injected with Antisedan to reverse the effects of the sedative and released. The rate of cat capture was defined as the number of cats caught per 100 trap nights (TN), corrected for sprung traps (Nelson & Clarke 1973). The correction factor was applied because of trap interference by possums (*Trichosurus vulpecula*) and rats.

Movement patterns and home range determinations

The feral cats were tracked using radio-telemetry for six periods of up to 4 weeks each season (summer: December; autumn: March; winter: June; spring: September) from February 2000 to June 2001. Locations of cats were obtained by triangulation using a folding yagi directional antenna (SIRTRACK) and portable receiver (TR4, Telonics Corp., USA). Bearings were obtained once a day and occasionally twice a day during daylight hours from fixed points, with a minimum of 8 h between fixes. The time each bearing was taken, the weather, and whether it was an 'active' or 'resting' signal were noted. Fixes were obtained with a minimum of three bearings taken within 10 min of each other to reduce errors due to animal movement (Withey *et al*. 2001). Site-specific error measurements for triangulated radio fixes were obtained (Withey *et al*. 2001), by constructing 'minimum error polygons' based on the size of polygons formed by three or more bearings on a known location of a cat. The bearings were made on radio-collared cats later found either dead or recaptured. The locations of these cats were fixed using a GPS. The area within the polygon boundary is an estimate of the area of error around a fix, measured in hectares.

Rat trapping

A standard trapping method was used to obtain indices of abundance of rats in the four forest types (Dowding & Murphy 1994; Cunningham & Moors 1996). Two rat-trapping lines of seven paired traps were set in each forest type for a minimum of 9 days in each of the four seasons from March 2000 to June 2001. This yielded 126 uncorrected TNs from each

line per season and a measure of variability of rat distribution among habitats. Traps were set at 50 m intervals.

Paired transects were set at least 350 m apart, to preclude sampling the same population. 'Ezeset' snap-traps, baited with a peanut butter and rolled oats mix, were placed under 12 mm-square mesh covers. Traps and mesh cover were secured with wire stakes. Traps were checked daily and rats removed and processed later. Sprung or empty traps were noted and re-baited and/or set. The capture rate was defined as the number of rats (R) caught per 100 TNs, corrected for sprung traps (CTN) (Nelson & Clarke 1973) and notated as R/100CTN (Cunningham & Moors 1996).

Data analysis

The positions of cats were calculated by triangulation and converted to Universal Transverse Mercator units. These locations were used for home range analysis using RANGES V (Kenward & Hodder 1996). Resulting plots were transferred to ARCVIEW 3.0 for home range and habitat use analysis. The 100% minimum convex polygon method (MCP) is used for comparisons of home range size across all studies (Harris *et al*. 1990). It requires at least 30 or more fixes for home range size estimation (Kenward 2001). For habitat selection analysis a kernel method was used (Worton 1989; Kenward 2001). The fixed kernel combined with a least squares cross validation for smoothing has the least biased estimates of home range size (Seaman & Powell 1996) and was used. The 95% kernel isoline, which encompasses 95% of the fixes, was used to define the study area and home ranges (Kernohan *et al*. 2001).

To estimate the use of a forest type by an individual, its home range was laid over a vegetation map of the area. The home range area that intersects with a vegetation type was measured and expressed as a proportion of the animal's overall home range area. The intersection overlay of the geo-processing extension of ARCVIEW 3.0 was used to do this. The total area of a cat's home range was the sum of the areas of the various forest types within the home range.

Compositional analysis was used to determine habitat use (Aebischer *et al*. 1993). Where the proportion of a home range in a particular habitat was zero, a value of 0.001 was substituted (Aebischer *et al*. 1993; Elston *et al*. 1996). 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, Wilks λ. Wilks 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 Wilks λ, subsequent tests on each pair of habitat log ratios were carried out, using *t*-tests for levels of significance and subsequent rankings of preference for each forest type (Aebischer *et al.* 1993). Statistical analysis of habitat use was carried out using SYSTAT 10.

Rat abundance between habitats

The abundance of small rodents can differ between apparently similar habitats (Morris 1984; Dowding & Murphy 1994). An ANOVA was used to test whether the mean abundance of rats differed between vegetation types over each season.

The effect of rain on diurnal activity patterns and habitat use

Diurnal activity of cats in wet (precipitating when bearings were taken) or dry weather was noted, based on 'active' or 'resting' pulses recorded when a bearing was taken. A *G*-test was used to determine whether equal frequencies of active or resting pulse rates were recorded during wet and dry weather (Sokal & Rolf 1995).

To investigate whether subalpine shrubland was used more often on dry days than was expected by chance, a randomization test on cat location data from the subalpine shrubland was carried out. A 2×2 table of observed frequencies of locations of each cat, in subalpine and podocarp-broadleaf forest, on wet (≥ 1.0 mm day^{-1}, Sansom 1984) and dry days (0 mm day^{-1}) was constructed. The marginal totals of this table were used to construct a table of expected frequencies if there was no difference in use on wet and dry days between the forest types. A total of 2000 simulated values were generated, within the range of the marginal totals of the expected frequencies, to generate the probability of getting the observed values by chance.

Cats are known to use hollow trees as den sites (Fitzgerald & Karl 1986; Langham 1992). To determine whether some forest types had more trees suitable for shelter, like hollow and/or fallen trees, the circumferences of trees were measured in each forest. Four trees with the largest apparent circumference were measured in a 20 m diameter plot, at eight sites at 50 m intervals, in each forest type ($n = 32$ trees per forest). The mean circumference of trees in each forest type was compared with the circumference of a single sleeping 3.5 kg domestic female cat. Forest types with trees with a mean circumference larger than the 'cat circumference' were assumed to provide more shelter than forests with trees with a smaller mean circumference.

The four vegetation types were surveyed, using a Reconnaissance (RECCE) description (Allen 1992), on each rat-trapping transect to confirm the forest type and measure the presence and absence of fallen trees. Eight samples were obtained in each vegetation type. 'RECCE plots' of 20-m diameter were centred on alternate rat-trap sites at 100-m intervals (Allen 1992). Fallen trees were noted as present (1) or absent (0) at each site.

RESULTS

Cat captures

Twenty-two cats, 14 males (including two juveniles) and eight females (including one juvenile), were caught for radio-tagging over seven seasons and 1417 corrected TNs. Of 11 cats radio-tracked for more than two seasons, five (45%) were recaptured at least once. The cat capture rate was significantly higher at the start of the study, with the same trapping effort ($G_{adj.} = 55.0$, $P < 0.001$). Fifteen cats were caught in the first two seasons but only one was caught in the last two seasons. The mean capture rate of cats during the study period was 2.33 cats per 100CTN in podocarp-broadleaf forest, 1.16 in riparian forest, 1.06 in subalpine shrubland, and 1.03 in *Leptospermum* shrubland. There was no significant difference in the capture rate among forest types (Kruskal–Wallis = 6.13, d.f. = 3, $P = 0.11$).

The mean error polygons for transmitters located on dead or recaptured cats ($n = 12$) was 4.2 ha (SE $\pm$ 1.3 ha). This polygon size yielded an acceptable level of error at 0.2% of the smallest habitat area or 0.3% of the smallest home range (Saltz 1994).

Home ranges

The 100% MCPs were calculated for seven cats (three ♀, four ♂) which each had more than 30 fixes, and the 95% kernel isoline was used to calculate home ranges for 11 cats (three ♀, eight ♂ Fig. 2a–c). A minimum sample size of 30 fixes is suggested for a fixed kernel (Seaman & Powell 1996), but this refers to kernels incorporating a utilization distribution, which produce a three-dimensional contour 'map' of home range use. This study required only a home range outline, and as the mean home range sizes, using 100% MCPs and 95% kernels for seven and 11 cats, respectively, were within ± 1SE of each other (see below), the sample size requirements for the 95% kernel isoline was set at 15. The mean female home range sizes were 1109 ha (SE $\pm$ 52.9 ha) and 1065 ha (SE $\pm$ 241.6 ha) for 100% MCP and 95% kernel respectively. The mean
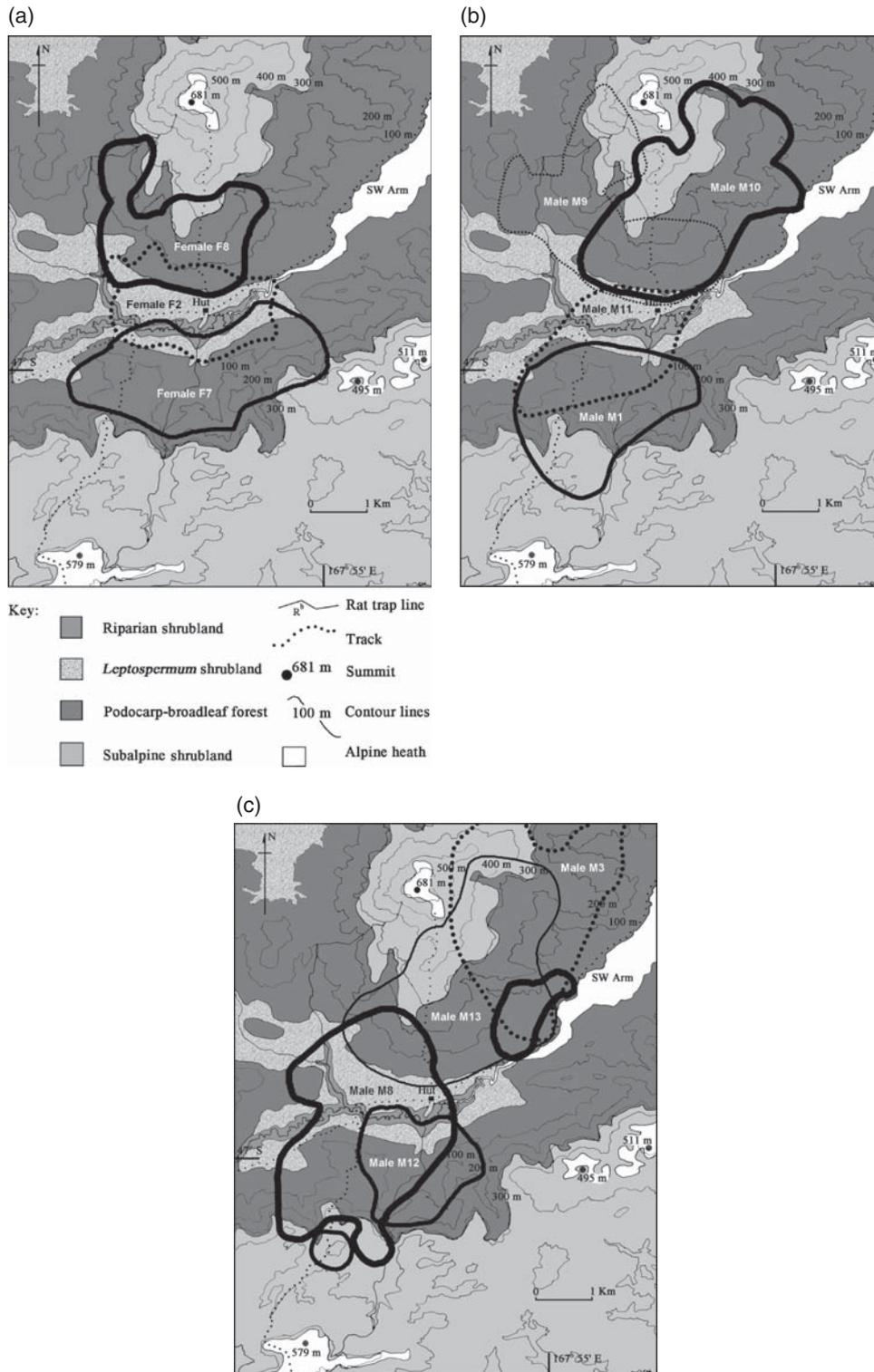
Fig. 2. (a) Map of the Rakeahua Valley, Stewart Island, showing the 95% kernel home ranges of three female feral cats (F2, F7, F8). (b) Map of the Rakeahua Valley, Stewart Island, showing the 95% kernel home ranges of four male feral cats (M1, M9, M10, M11). (c) Map of the Rakeahua Valley, Stewart Island, showing the 95% kernel home range of four male cats (M3, M8, M12, M13).

male home range sizes were 2083 ha (SE ± 457.3 ha) and 1815 ha (SE ± 360.3 ha) for MCP and 95% kernel respectively.

Density estimate

The density of cats was calculated on the assumption that all cats in the study area were radio-collared. This assumption was probably justified, considering the high recapture rate of collared cats and the low capture rate for un-collared cats in the last half of the study. Using 100% MCP, the study area for seven cats was estimated as 36.0 km², yielding a density of 0.19 cats per square kilometre. The 95% kernel isoline of the study area for 11 cats was estimated as 41.5 km², with a density of 0.27 cats per square kilometre.

Habitat selection

Eleven cats with more than 15 fixes each were used for compositional analysis. A Dixon test for outliers (Sokal & Rolf 1995) showed that one female was using habitat significantly differently compared with other cats ($P < 0.05$ for podocarp-broadleaf forest and $P < 0.01$ for *Leptospermum* shrubland). This animal was removed from the analysis.

The study area encompassed 41 457 ha, using the 95% kernel isoline of the combined home ranges of 10 cats. Podocarp-broadleaf forest amounted to 62.9% (26 058 ha) of forest cover within the study area, with subalpine shrublands consituting 21.1% (8744 ha), *Leptospermum* shrublands 10.7% (4434 ha), and riparian forest 5.4% (2221 ha). The percentage compositions of vegetation types within each cat's home range are shown in Table 1.

Overall use of the four forest types within the cat's home ranges was non-random (Wilk's $\lambda = 0.321$, $\chi^2 = 11.363$, d.f. = 3, $P < 0.01$). Subsequent t-tests of each pair of habitat log ratios revealed podocarp-broadleaf forest was used significantly more than subalpine forest relative to availability ($P < 0.05$, Table 2). No cats were recorded in alpine heath. The Rakeahua River (4–6 m wide) did not appear to affect cat movement. Several cats, both adults and juveniles, were recorded on both sides of the river over the course of a few days of radio-tracking.

Rat abundance between habitats

The mean relative abundance index of rats (mean: 2.94 R/100CTN SE ± 0.63) did not differ between forest types ($F_{3,21} = 1.54$, $P = 0.23$). Ship rats were trapped in all forest types, and dominated podocarp-broadleaf forest and riparian shrubland. Pacific rats were most common in *Leptospermum* shrubland, and Norway rats dominated the subalpine shrubland (Harper *et al.* 2005).

The effect of rain on diurnal activity habitat use

Overall, active pulse rates were recorded on 76.2% (95% binomial CI 76.13%–76.20%, $n = 1545$ bearings) of the times a bearing was taken. Active pulse rates were recorded significantly fewer times in wet weather (68.1%, 95% binomial CI 67.95%–68.20%, $n = 389$ bearings) than in dry weather (77.5%, 95% binomial CI 77.42%–79.64%; $z = 3.65$, $P < 0.05$). There was a statistically significant departure from homogeneity for the four categories of active or resting pulse rates during wet or dry weather ($G_{adj.} = 17.82$, $P < 0.01$).

Examination of the weather on the days that eight adult cats (six ♂, two ♀) were located in subalpine shrubland suggested that six were using this forest type significantly more on dry days than wet days (Table 3).

Shelter and cats

The mean circumferences of the largest trees in *Leptospermum* shrubland, subalpine shrubland, and riparian forest did not differ significantly from one another (Fig. 3). The mean circumference of large trees in podocarp forest was significantly larger than riparian forest, the forest type with the next largest mean ($t = 10.61$, d.f. = 58, $P < 0.001$). Podocarp-broadleaf forest was the only forest type that had large trees with
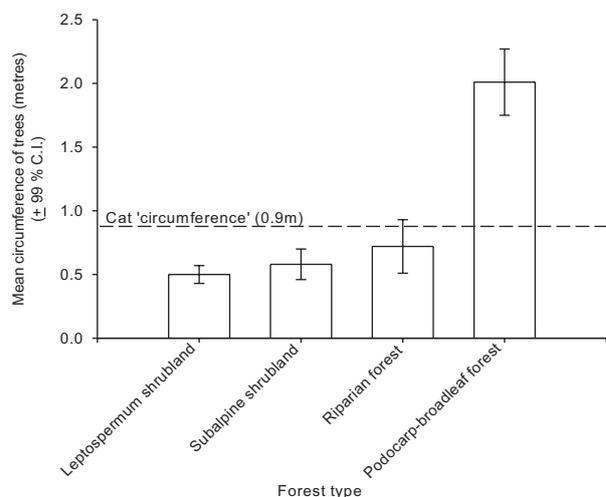

Fig. 3. Mean circumferences of trees in four forest types, Rakeahua Valley, Stewart Island, compared with the 'circumference' of a resting female cat. (ANOVA of differences of mean circumference between forest types ($n = 32$ trees in each forest type), $F_{3,124} = 116.4$, $P < 0.001$).

Table 1. Percentage of forest type compositions within each 95% kernel for 10 feral cats, Rakeahua Valley, Stewart Island

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 (±2.3)
Riparian shrubland	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)

Table 2. Ranking matrix of means (+SE) of log ratio differences between habitat categories utilized by feral cats, and habitats available within kernel home ranges

	Podocarp-broadleaf forest	*Leptospermum* shrubland	Riparian shrubland	Subalpine shrubland	Ranking
Podocarp-broadleaf forest					1
Leptospermum shrubland	1.51 ± 0.75				2
Riparian shrubland	2.17 ± 1.00	1.17 ± 0.94			3
Subalpine shrubland	**2.28 ± 0.84**	0.38 ± 1.41	0.17 ± 1.49		4

Significant differences ($P < 0.05$) are shown in bold. The values shown equal the relative differences (i.e. largest value = largest difference) between forest types and are used to rank the forest types in order of preference, where 1 = most preferred.

Table 3. Proportion of wet days relative to dry days that cats were located in podocarp-broadleaf forest and subalpine shrubland and the probability of each cats observed use of subalpine shrubland occurring by chance

	Cat							
	F7	F8	M1	M8	M9	M10	M12	M13
Podocarp-broadleaf forest	0.82	0.44	0.5	0.5	0.59	0.54	0.36	0.45
(n = no. of observations)	(22)	(54)	(12)	(44)	(22)	(50)	(22)	(11)
Subalpine shrubland	0.0	0.0	0.0	0.17	0.29	0.2	0.25	0.0
(n = no. of observations)	(5)	(1)	(3)	(6)	(7)	(10)	(4)	(3)
Probability of each cat's observed use of subalpine shrubland on wet *versus* dry days occurring by chance	0.01	0.27	0.06	0.03	0.21	0.01	0.07	0.05

a mean circumference that exceeded the 940 mm 'circumference' of a 3.5-kg female cat (Fig. 3). Five of 32 trees sampled in riparian forest had circumferences exceeding this circumference, and no large trees exceeding 940 mm were found in *Leptospermum* or subalpine shrubland. Podocarp-broadleaf forest had significantly more sites with fallen trees present (75%) than any of the other vegetation types (13% or less, Fisher's exact test: $P < 0.001$). In addition, many hollow trees, particularly southern rata, were noted in the podocarp-broadleaf forest.

DISCUSSION

Habitat selection: prey distribution and shelter

Compositional analysis and trapping results showed that cats in the Rakeahua Valley used podocarp-

broadleaf forest more than expected if the relationship were simply a reflection of habitat availability. This pattern could result from the accessibility and habitat use of rats or from the availability of shelter.

The three rat species were not distributed evenly across the study area (Harper *et al.* 2005). Norway rats, and some ship rats, were almost exclusively located in subalpine shrubland. This may explain, at least partially, why cats were not found in large numbers there. Cats avoid preying on large adult Norway rats because of their aggressiveness (Childs 1986; Brodie 1988; Fitzgerald *et al.* 1991), unless they are the main prey available (Dilks 1979). However, ship rats were also present in the subalpine shrubland, providing less aggressive prey. If habitat selection of cats was determined by rat distribution they should use *Leptospermum* and riparian shrubland, where both of the smaller species, Pacific rats and ship rats, were found. In this study cats probably selected habitats

with smaller rat species, but among those habitats, preferred podocarp-broadleaf forest.

Other studies have linked the distribution of feral cats to shelter (van Aarde 1979; Brothers *et al.* 1985; Calhoon & Haspel 1989), and the lack of shelter may reduce the survival of feral cats. The recent extinction of feral cats on Campbell Island, New Zealand may have been partially caused by a lack of shelter (P. Moore, pers. comm. 2000). Feral cats on subantarctic islands use a variety of sites for shelter including rabbit and seabird burrows (Derenne 1976; van Aarde 1979; Brothers *et al.* 1985), and will use abandoned buildings (Calhoon & Haspel 1989) and hollow logs (Fitzgerald & Karl 1986; Langham 1992; Fisher 2000; Edwards *et al.* 2001; Molsher *et al.* 2005). In an area like the Rakeahua Valley, shelter for feral cats protects them primarily from rain. Wetting the coat reduces thermal resistance in a mammal (Webb & King 1984). Cats probably prefer to stay dry in the Rakeahua Valley, where energy budgets may be finely balanced due to the seasonal limitation of prey (Harper 2005).

Wet weather reduced cat activity, as they rested more often. This has been reported in other studies (Derenne 1976; Dunstone *et al.* 2002), possibly because rain affects cats' foraging abilities (Churcher & Lawton 1987). The proportion of resting during wet weather gives an indication of shelter use, but may underestimate shelter use, as cats could be active (e.g. grooming) while under shelter. Shelter, in the form of large circumference or fallen trees, was significantly more common in podocarp-broadleaf forest, which helps explain its preferential selection by cats. Thermoregulation may influence shelter selection by female cats as they are smaller and nurse young. Temperatures inside hollow trees are less variable and often warmer when occupied (Stains 1961; Fernandez & Palomares 2000), so although den size can restrict occupant size (Lindenmayer *et al.* 1990), smaller dens may also maximize thermoregulatory efficiency (Weber 1989; Lariviere *et al.* 1999).

Most cats used subalpine shrubland more often during dry weather. Six out of eight cats located in subalpine shrubland were male, possibly because of their large home ranges. Female cats home ranges generally only bordered subalpine shrubland. In the prevailing wet, cool conditions on Stewart Island habitat selection by feral cats appears to be influenced by a combination of shelter availability and the irregular distribution of their three main prey species.

Diurnal activity

As cats are often more active at night (Jones & Coman 1982; Page *et al.* 1992), home ranges of cats based on nocturnal fixes are often larger (Langham & Porter 1991; Barratt 1997), which suggests the home range

sizes in this research may be underestimates as they were derived from diurnal radio-fixes. However, the nocturnal-based studies were in either pastoral or urban areas, where humans were active and there was limited cover available. In these areas cats preferentially use cover during the day (Langham 1992; Alterio *et al.* 1998), and prefer to use open areas at night, possibly for hunting and/or to avoid humans (Langham 1992). In other sites with ample cover cats were equally active nocturnally and diurnally (Molsher *et al.* 2005). Similarly in the forested Rakeahua Valley, with very little human activity, cats were active both diurnally and nocturnally (G. Harper, pers. obs. 2000). This implies day-time foraging by cats and suggests cover availability and degree of human activity affects their temporal foraging behaviour. These conclusions also suggest that diurnal fixes in this study revealed the entire home range.

Home range and density

Home range sizes of cats in this study were the largest recorded for females and the second largest for males, using 100% MCP, when compared with other published home ranges (♀♀ 249 ha, Norbury *et al.* 1998; ♂♂ 2211 ha, Edwards *et al.* 2001). Home range sizes and density in cats are inversely related (Edwards *et al.* 2001); so the density estimate in this study is one of the lowest recorded. Cat numbers in the Rakeahua Valley were restricted by low abundance of both primary and alternative prey (Harper 2005). The mean relative abundance of rats in the Rakeahua Valley was less than half that in similar forest in other parts of New Zealand (6.22 R/100CTN (Innes *et al.* 2001) and 14.77 R/100CTN (Dowding & Murphy 1994)). Male home range size is influenced by both female distribution during the breeding season and by food abundance (Sandell 1989; Liberg *et al.* 2001). As male home ranges overlapped or encompassed female home ranges, access to females was not apparently limited. This suggests food abundance was the primary reason for large male home ranges, especially as males only abandoned their territories when prey were scarce, not when females were in oestrus (Harper 2005).

The Rakeahua Valley terrain had little effect on home range use, as cats regularly used forest on moderately steep to steep valley sides (10–30°). This contrasts with feral cats in the Orongorongo Valley of North Island, New Zealand, which had linear home ranges largely restricted to the nearly flat valley floor, probably because preferred prey was plentiful only in the valley bottom (Fitzgerald & Karl 1986).

These results suggest that shelter, as well as prey availability, influenced habitat use by cats. These conclusions appear applicable to other solitary carnivores like the larger felids. For example, lynx *Lynx lynx* and

bobcats *Lynx rufus* preferentially use habitats with substantial cover, for both protection from adverse weather and for maternal dens (McCord 1974; Koehler 1990; Fernandez & Palomares 2000). Moreover, lynx are also less active in wet weather (Schmidt 1999). This suggests future research should consider a larger suite of influences on the habitat selection of predators, especially in wet, temperate habitats.

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