

Numerical and functional response of feral cats (*Felis catus*) to variations in abundance of primary prey on Stewart Island (Rakiura), New Zealand

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Abstract. Few studies of populations of feral cats have simultaneously monitored the seasonal abundance of primary prey and the possible ‘prey-switch’ to alternative prey when primary prey abundance declines. On Stewart Island, when the abundance of feral cats’ primary prey, rats (*Rattus* spp.), was very low, significantly more cats died or left the study area than when rats were abundant. Cats preferentially preyed on rats regardless of rat abundance. Birds were the main alternative prey but cats did not prey-switch to birds when rat abundance was low, possibly owing to the difficulty of capture, and small mass, of birds compared with rats. On Stewart Island numbers of feral cats are restricted by seasonal depressions in abundance of their primary prey, coupled with limited alternative prey biomass.

Introduction

Feral house cats (*Felis catus*) are opportunistic predators with a wide spectrum of prey (Bonner 1984; Pearre *et al.* 1998), which has made them successful colonisers of islands throughout the world (Apps 1983). When the main prey of cats, which are often native species, are not available, cats will use alternative prey, which enables them to maintain their numbers during any seasonal changes in abundance of a variety of prey (Moors and Atkinson 1984; Molsher *et al.* 1999). The perpetuation of cat numbers by alternative prey can maintain predation pressure on the cats’ main prey and eventually lead to the extinction of the main prey species (Kirkpatrick and Rauzon 1986; Fitzgerald 1988). As a consequence, feral cats are controlled, or in some cases eradicated, from islands where they have had significant impacts on native species (Bester *et al.* 2000; Veitch 2001; Algar *et al.* 2002).

Ground-nesting birds are particularly susceptible to predation by cats (Sanders and Maloney 2002) and cats have been implicated in the decline or extinction of birds throughout New Zealand (Fitzgerald and Veitch 1985; Giradet *et al.* 2001), although Giradet *et al.* (2001) found no significant increase in bird numbers on Little Barrier Island after cats were eradicated there. On Stewart Island (47°S, 168°E) (Fig. 1), where Europeans had introduced cats by the late 18th Century (Karl and Best 1982), cats were the principal predator of adult kakapo (*Strigops habrotilus*), an endemic ground parrot that is now highly endangered. All the remaining 61 kakapo have been transferred to cat-free islands (Powlesland *et al.* 1995). Similarly, predation by cats, and possibly Norway rats, is probably the main reason the endemic brown teal (*Anas aucklandica chlorotis*) is now extinct on Stewart

Island and the weka (*Gallirallus australis scotti*), a large native rail, has been almost extirpated (Harper 2002).

Southern New Zealand dotterels (*Charadrius obscurus obscurus*) once bred throughout the South Island but, owing to predation by introduced predators, they now nest only on the alpine tops of Stewart Island where feral cats are the chief predator (Dowding and Murphy 1993). By 1992 the population was estimated to be ~60 birds, down from ~350 birds in the 1950s. Control of cats using poison was initiated in 1992, and dotterel numbers began to increase immediately (Dowding and Murphy 2001). The operation was, however, expensive and very time-consuming, so more efficient use of time and resources was needed. This required better knowledge of population regulation of feral cats and whether cats ate more birds when their primary prey, rats (Pacific rat, *Rattus exulans*; Norway rat, *R. norvegicus*; and ship rat, *R. rattus*) were scarce (Karl and Best 1982). Rabbits, the preferred prey of cats on mainland New Zealand, are absent from Stewart Island.

Availability of prey, not territorial behaviour, regulates population density in feral cats (Liberg *et al.* 2000), and other felids (Kruuk 1982; Lawhead 1984; Pierce *et al.* 2000). In periods of low prey abundance cats often starve (van Ordsal *et al.* 1985; Bailey 1993). Home-range size and rates of emigration also increase when prey is scarce (Lawhead 1984; van Ordsal *et al.* 1985; Bailey 1993), and these demographic changes in rates of survival, immigration and emigration are termed ‘numerical responses’ (Solomon 1949). Behavioural responses by predators to changes in prey densities are known as ‘functional responses’ and are often manifested as ‘prey-switches’ from primary prey to alternative prey when preferred prey reach low numbers

(Holling 1965). Use of alternative prey is recognised as important for the maintenance of predator communities and is well recorded in the Felidae. For example, in the lynx (*Lynx lynx*) and snowshoe hare (*Lepus americanus*) cycle, lynx will switch to red squirrels (*Tamiasciurus hudsonicus*) when hares are scarce (O'Donoghue *et al.* 1998).

The aim of this paper was to examine the effect of seasonal changes in abundance of primary prey on the population demographics of feral cats in an island situation and to determine whether cats switched to alternative prey when preferred prey became less abundant.

Methods

Study area

The study area was located in the Freshwater and Rakeahua Valleys on Stewart Island, separated by Mt Rakeahua (Fig. 1). Cat control was carried out on the mountains adjacent to these valleys. The initial research was carried out for two seasons (spring and summer 1999) in the Freshwater Valley and on Table Hill, and subsequent research (autumn 2000 to winter 2001) in the Rakeahua Valley. Both valleys are low lying, with undulating low ridges separated by marshes and streams with *Leptospermum scoparium* shrubland or wetland vegetation. The Freshwater Valley has more wetland than the Rakeahua Valley. Both valleys were bounded by hills or escarpments, covered in tall podocarp–broadleaf forest, that rise steeply to 716 m above mean sea level (AMSL). From 300 m AMSL the hills are covered in dense sub-alpine shrubland and above 500 m, low alpine heath. The soils of the valleys are generally of low fertility (Wilson 1987). The climate is cool and windy (Wilson 1987), with rainfall of ~2265 mm year (K. Tredrea, NIWA, personal communication). Snow often lies above 500 m in the winter and occasionally is recorded on the valley floors.

Scat analysis

Cat scats were collected 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. The single walking track along each of these valleys and two walking tracks, one each up Mt Rakeahua and Table Hill, were searched for scats every day for four weeks in each season. Most scats were 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. Many scats were repeatedly deposited in the same place, and these sites were always rechecked each season. Old scats were discarded, and could be identified by being mouldy, with poor cohesiveness and a lack of smell. Firm, non-mouldy scats with an obvious smell were collected. Collection of scats at repeat deposit sites showed that scats would remain 'fresh' for 2–3 months. Most scats were found within the first week of collection each season, and scats collected during a field trip were regarded as being from the previous season unless obviously deposited in the previous 24 h.

Scats were stored in separate 'Ziplok' plastic 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 60°C for 24 h and stored in individual plastic bags 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- μ m sieve. Any bones, feathers, arthropod exoskeletons or plant material found was recorded. The remains from each scat were stored in 5-mL vials in 75% alcohol. Rat remains were identified largely by the presence of molar and incisor teeth. A minimum number of rats per scat was estimated from the number of molars of the same age class (Karnoukhova 1971) (i.e. four molars [2 upper, 2 lower] of an equivalent degree of wear were regarded as coming from one rat). Other mammals were identified from bones and hair (Brunner and Coman 1974). Birds were mainly identified from feather remains (Day 1966) and some bones. Insects were grouped by order, depending on the exoskeleton remains. Plant material and microscopic material were not included for analysis. The data from each scat from a season were pooled to investigate seasonal differences.

Results were expressed in two ways: (1) frequency of occurrence (percentage of scats containing a prey item), and (2) percentage by weight of prey species. The two methods are used because the former does not take into account prey weight and its relative contribution to the cats' daily food intake (Fitzgerald and Karl 1979). The frequency of occurrence method has been used in most published studies of cat diet (*inter alia* Fitzgerald and Karl 1979; Konecny 1987; Molsher *et al.* 1999) and is therefore useful for comparative purposes (Fitzgerald 1988).

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 and Karl 1979; Karl and 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 each separate group of bird remains in a scat unless they could be readily identified. Bird remains were separated by individual beaks, or paired wing and/or leg bones. This weight was derived from the 13 passerine species known to be common in the area (Karl and Best 1982). Remains of birds were not generally identified to species as this had been done previously (Karl and Best 1982). 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. This weight was derived using the following reasoning. The daily calorific requirement for a cat is 80 Kcal day⁻¹ kg⁻¹ of bodyweight (MacDonald and Rogers 1984), which for a 3.36-kg adult male cat (the average weight of an adult male cat caught on Stewart Island) is 268.8 Kcal day⁻¹. Females will usually require less, owing to their smaller weight, except when pregnant or lactating when they require 170–250 Kcal day⁻¹ kg⁻¹ of bodyweight (Scott 1968). I have used the mean adult male weight to

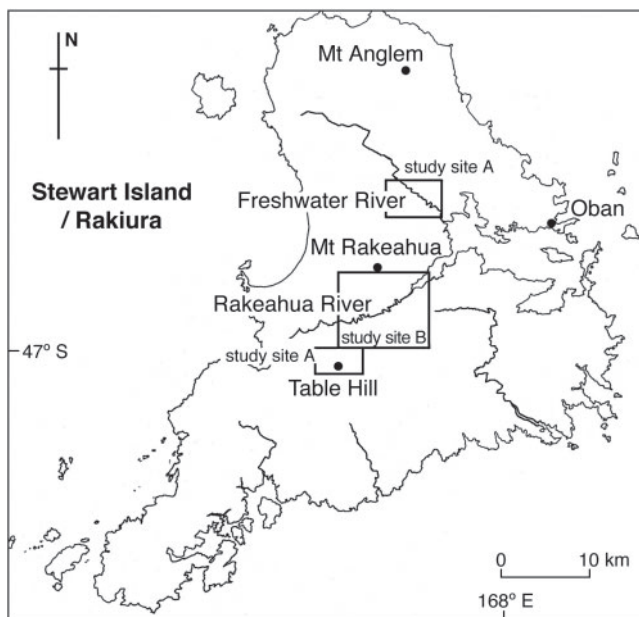


Fig. 1. Map of Stewart Island, southern New Zealand, showing the location of the two study areas.

account for the variations in the female requirements throughout the year. The available calorific value of a rodent (the field vole, *Microtus agrestis*) is estimated to be 1.46 Kcal g⁻¹ of fresh weight (Hansson and Grodzinski 1970). If the mean weight of a rat, the cats' primary prey, is assumed to provide the same amount of calories then the average rat on Stewart Island (weight: 123 g) will provide 179.6 Kcal for a cat. The daily requirement of 268.8 Kcal was divided by the available calories from an average rat of 179.6 Kcal, which equals 1.5. This means that an average adult male cat will require 1.5 rats per day to satisfy its calorific requirements. 1.5 rats multiplied by the mean weight for a rat on Stewart Island equals 184.5 g. This is slightly higher than amounts recorded for domestic cats elsewhere (Howard 1957; Fitzgerald and Karl 1979), but less than that required at some other locations where the mean weights of the cats were larger than in the Rakeahua Valley (Jones 1977; Liberg 1982a).

Relative abundance of rats

Seasonal changes in relative abundance of the three species of rats present were investigated using standard trap lines. Rat trapping was carried out in two areas. The first area was 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 and Moors 1996). Twenty-five pairs of 'Ezeset' snap-traps were set for three nights at 50-m intervals beside walking tracks in each forest type. From March 2000 to June 2001 two lines, each of seven pairs of traps, were set out in each of four vegetation types (riparian forest, *Leptospermum* shrubland, podocarp–broadleaf forest and subalpine shrubland) in the Rakeahua Valley and set for a minimum of nine days in each of the four seasons, to increase the number of trap-nights. The paired trap lines were all a minimum of 350 m apart. This distance is greater than the maximum recorded home-range length of any of the rat species in New Zealand at the time (Moors 1990) to ensure independence of trapping data. The traps were protected with (12 mm)² 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 removal of traps. All traps were checked daily. Any rat caught was removed, killed and autopsied later in the day. Any traps that were sprung or had bait taken were noted and then rebaited and/or set. The traps were set off, cleaned, dried and stored between trapping sessions.

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 and Clark 1973) and recorded as R/100CTN (Cunningham and Moors 1996). A mean weight of rats for each season was calculated using the weights of all rats captured, regardless of species or sex. The mean weight of rats was used as a basis of calculations of the contribution of rats to cat diet by weight as previously discussed. This assumes that cats are eating rats in approximately the same ratios as rats were trapped.

Monitoring cat emigration and mortality

To test cats' response to changes in rat abundance, cats were trapped and fitted with radio-transmitters. The cats were captured in Victor 1.5 Soft Catch traps (Woodstream Corporation, Lititz, USA) in dead-end sets against the base of trees, as described in Veitch (1985). Thirty-five traps were set for 21 days each season. The traps were 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 bush line (~500 m AMSL) through all forest types. Traps were checked every morning. Captured animals were sedated with an injection of DomitorTM (0.23 mL kg⁻¹). Cats were given AntisedanTM (0.12 mL kg⁻¹) to reverse the effects of the sedative and released when recovered. The cats were fitted with a two-stage

transmitter (160–161 MHz) with a whip aerial, attached to a collar (Sirtrack, Havelock North, New Zealand). The cats were wearing movement-sensitive radio-collars that switched pulse rates depending on whether the cat had moved or not over a 5-min period. The transmitter battery duration varied from 17 to 22 months.

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 taking consecutive bearings on separate cats from fixed points within 30 min of each other to reduce errors owing to cats moving. 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 within the study site. If bearings from a radio-tracking point changed little over a 2–3-day period and the pulse rate remained on 'resting' pulse rate it was assumed that the cat had died. The cat was located and retrieved as soon as possible and its possible cause and date of death noted.

Analysis

Tests for significant differences in the seasonal contribution of principal prey types to the diet of cats was carried out using G-tests (Sokal and Rohlf 1995). The probability that the number of cats dying, or leaving the study area, was related to the relative abundance of rats was determined using a randomisation test (Sokal and Rohlf 1995). An initial correlation between the observed abundance of rats, log-transformed, and the observed variables was obtained. Simulated values were then generated and correlated with the observed relative abundance of rats, repeated 2000 times. The number of times 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 functional response of the cats to rats and birds was based on the biomass of rats and birds in scats in relation to the relative abundance of rats. Exponential decay and asymptotic curves were fitted to the functional response of cats using non-linear regression models. Maximum-likelihood estimates of regressions coefficients were calculated using a least-squares loss function (SYSTAT 10.0 for Windows).

Results

Ship rats were the dominant rat species, numerically and spatially. Of the 173 rats caught, 54% were ship rats, caught in all forest types. A further 26% of the rats were Pacific rats, largely limited to the *Leptospermum* shrublands, and 20% of captures were Norway rats, mainly trapped in subalpine shrubland.

In total, 219 cat scats were collected from September 1999 to June 2001. Rats were the most important food either by frequency of occurrence (Fig. 2) or by weight (Fig. 3). Abundance of rats varied seasonally, through all the forest types, with a low in abundance in early summer to early autumn (Fig. 3).

There was little seasonal difference in the frequency of occurrence of rats in cat diet. An average of 1.08 rats (95% CI: ±0.08) were found per scat. The mean weight for rats varied seasonally, with an overall mean weight of 123.0 g (95% CI: ±6.6 g) but there was no significant seasonal difference in the contribution of rats, by weight, to cat diet ($G = 1.68$, d.f. = 3, $P > 0.1$).

Birds were the next most important prey item, occurring in 26.9% of scats, although they contributed to only 13.2%

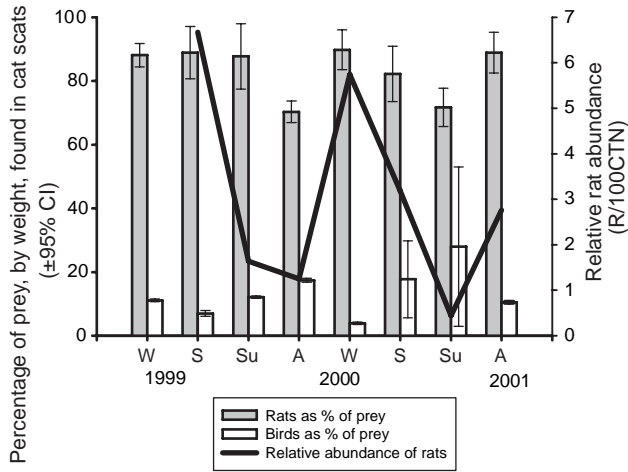


Fig. 2. Seasonal variation in the percentage occurrence of prey items in scats of feral cats on Stewart Island from September 1999 to June 2001 ($n = 219$). Numbers of scats are shown in parentheses. W = winter, S = spring, Su = summer, A = autumn. R/100CTN = rats caught per 100 trap-nights.

of overall cat diet by weight. Small native and introduced passerines were most commonly found, but four kakariki (*Cyanoramphus* spp.) and two kereru (*Hemiphaga novae-landiae*) were also identified. Cats ate more birds as rat abundance declined. The percentage biomass of birds in cat scats increased when rat abundance decreased below 3.5 R/100CTN (Fig. 4). The mass of all other prey items combined contributed only 5.6% by weight to an annual cat diet. These included weta (an endemic orthopteran) >1%, beetles >1%, lizards >1%, possums 2%, and other categories >3%, which included spiders, fish bait, a kitten, and deer (*Odocoileus virginianus* or *Cervus elaphus*).

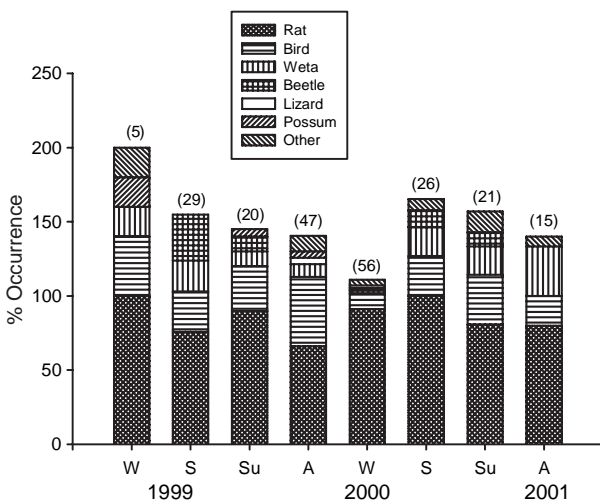


Fig. 3. Percentage contribution, by weight, of rats and birds to the seasonal diet of feral cats, in relation to the seasonal abundance of rats, on Stewart Island. W = winter, S = spring, Su = summer, A = autumn.

Functional response

The biomass of rats in cat scats increased with increasing rat abundance, up to a plateau of ~85% biomass in scats (Fig. 4). The functional response was a Type II curve, best described with the equation:

$$y = ax/(1 + bx) + 0.625,$$

where y = biomass of rats in scats, x = rat abundance, $a = 0.25$ (s.e. = ±0.13) and $b = 0.75$ (s.e. = ±0.55). The addition of the constant 0.625 improved the fit of the curve. The curve accounted for 65% of the variance in the data, but the power of the analysis was low ($\alpha = 0.61$) so the relationship was not strong. The minimum rat abundance detected was 0.44 R/100CTN, which equalled one rat caught over 300 uncorrected trap-nights, so the shape of the curve below this abundance was unknown. However, the Type II curve was confirmed using a test described by Pech *et al.* (1992). The functional response of cats to birds in relation to rat abundance is best described by the equation:

$$y = axe^{(-bx)} + 0.08,$$

where y = biomass of birds in scats, x = rat abundance, $a = 0.27$ (s.e. = ±0.09) and $b = 0.79$ (s.e. = ±0.32). The addition of the constant 0.08 indicates that a minimum of 8% of bird biomass was expected in cat scats, even when rat abundance was above 5 R/100CTN. The curve accounted for 80% of the variance in the data ($P < 0.01$).

Cat mortality and emigration

Twenty-two cats were captured (14 male [2 juv.], 8 female [1 juv.]) with seven recaptures, over 1417 corrected trap-nights, an average of 2.75 cats caught per 100 trap-nights.

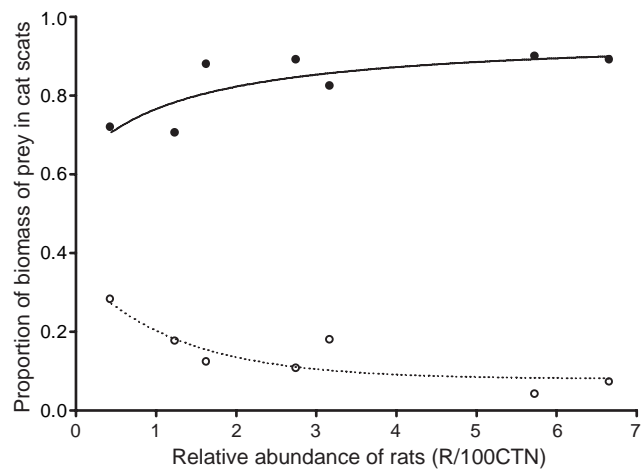


Fig. 4. Functional response of feral cats to rats and birds in relation to the relative abundance of rats, based on the derived biomass of rats and birds in cat scats (closed circles, rats; open circles, birds). The solid line is the equation: $y = ax/(1 + bx) + 0.625$ ($r^2 = 0.65$). The dotted line is the equation: $y = axe^{(-bx)} + 0.08$ ($r^2 = 0.8$). R/100CTN = rats caught per 100 trap-nights.

Trap success was corrected because of trap interference by possums (*Trichosurus vulpecula*) and rats. Eight (36%) radio-collared cats died during the study. Of these, seven died in late summer or autumn (88%), and one (12%) in the spring. Cats died 1–15 months after being radio-tagged (mean: 5.4 months \pm 1.8 s.e.). Male cats also dispersed out of the study area when rat abundance was low during the late summer and autumn. Four out of eight males (50%) left the study area in early 2000 and two out of six males (33%) emigrated 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 ($R = -0.77$, $P = 0.015$). All but one of the cats died or migrated when the relative abundance of rats fell below 2 R/100CTN. Of the cats that died, the cause of death could be determined for only two, as the others were too decomposed for autopsy. One male lost 1.59 kg (40% of original weight) between his capture at 4.09 kg and when he 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 >3.5 R/100CTN, but she had been caught 3–4 days earlier in poor physical condition with obvious infestations of unidentified external parasites.

Discussion

Numerical responses by cats

Cats in the Rakeahua Valley exhibited numerical responses to reductions in relative rat abundance through increased dispersal and mortality, probably from starvation. The home-range size of cats will increase when prey numbers are low (Norbury *et al.* 1998) or cats will abandon an established home range altogether (Brothers *et al.* 1985; Jones 1977). Similarly, most cats died when rabbit numbers were depressed in winter on Macquarie Island (Jones 1977) and male cats will lose significant amounts of weight when rabbits are scarce (Liberg 1984). In feral cats worldwide, most deaths appear to occur in juveniles (Apps 1983; van Aarde 1984). Juvenile mortality is a significant restraint on population growth when prey is limited (van Aarde 1978; Jones and Coman 1982). When food is not limiting, cat numbers can increase quickly through improved survivorship of juveniles and subadults (Apps 1983). Larger felids are similarly affected by declines in prey abundances; for example, more lynx will die of natural causes when their primary prey, snowshoe hares, are in low abundance (Poole 1994).

Functional response

Cats on Stewart Island exhibited an inverse density-dependent response to increases in rat abundance. The response curve with the best fit suggested that cats would

continue to hunt rats at extremely low abundances. The curve crossed the y -intercept at $\sim 63\%$ rat biomass in scats even at a relative abundance below 0.1 R/100CTN. The amount of bird biomass was constant at $\sim 8\%$ in cat scats at high rat abundance, but increased when rat abundance declined, comprising almost 40% of biomass in cat scats at extremely low rat abundances.

Cats on Stewart Island are apparently not eating rats according to rat abundance, which mirrors the findings of Fitzgerald and Karl (1979), who found little variation in occurrence of rats in scats at low or high rat abundance. This may be due to the relatively small variation in rat abundance, tied with the likelihood that ‘... one rat is a substantial meal’ (Fitzgerald 1988). Although there was a trend for less mass of rats to be eaten as abundance of rats declined and a corresponding increase in the mass of ‘alternative prey’ (birds) consumed, the Type II response curve indicates a lack of prey switching to birds (Hassell *et al.* 1977). This is based on the assumption that the relative abundance of rats relates directly to density, and prey mass is linked to the number of individuals caught by cats (van Baalen *et al.* 2001). Similarly, 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 their prey (snowshoe hares and red squirrels). They concluded that virtually no secondary prey (squirrels) were killed when they comprised 30% or less of the available biomass of prey. This ‘prey switch’ occurred only when the proportion of secondary prey comprised 55% of the total available biomass. Indeed, the prey-switching threshold has recently been modified to include the calorific value, handling time and abundance of the alternative food (van Baalen *et al.* 2001).

The accessibility and calorific value of birds, the cats’ main alternative prey, probably limits their occurrence in cat diet. Volant forest birds (as opposed to ground-nesting birds) are probably not only difficult to catch, but are likely to return fewer calories (Konecny 1987) per unit of effort than a rat capture. 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 when rat abundance was reduced, this may be a function of increased foraging time for all prey types when rats are at low densities (Liberg 1982b).

Although feral cats generally take prey in relation to its density (Coman and Brunner 1972; Bloomer and Bester 1990), the primary prey, if it is easy to catch, is often the larger of the prey types available (Jones 1977; Liberg 1984; Bloomer and Bester 1990). Whereas prey are probably selected by means of their size (Jaksic *et al.* 1993), prey weight is a better surrogate for energy per prey unit (MacDonald and Rogers 1984; Piersma and Davidson 1991), which suggests that the perceived energy return of a prey item, as well as its capture difficulty, also influences prey selection by feral cats (Konecny 1987).

Diet of feral cats

The previous study of the diet of cats on Stewart Island (Karl and Best 1982) possibly sampled at least 50 individuals, as scats were collected from sites across the entire island, including coastal areas. The results of the current study were probably restricted to ~20 cats in a much smaller area (Harper 2002).

The contribution, by weight, of rats to cat diet was 79.7% in the study of Karl and Best (1982) and 81.2% in the current study. Similarly, birds were recorded, by weight, contributing 15.5% and 13.2%, respectively, to cat diet. The percentage occurrence for rats is less for this study but not significantly so: Karl and Best (1982) recorded 93.0% (95% binomial CI: 87.4–95.2%) occurrence of rats in cat scats whereas this study found 83.1% (95% binomial CI: 74.5–90.4%) occurrence of rats.

A significantly higher percentage occurrence of birds was recorded by Karl and Best (1982): 44.1% (95% binomial CI: 37.0–50.5%) compared with the current study (26.9%: 95% binomial CI: 21.8–35.4%). This may be related to the location of the study area. Few ground-nesting birds such as penguins were present in the Rakeahua Valley (present study) in contrast to the coast of Stewart Island. In all, 5.7% of the individual birds identified from cat scats by Karl and Best (1982) were penguins: blue penguins (*Eudyptula minor*) and a crested penguin (*Eudyptes* spp.). Another 11.3% of the birds identified by Karl and Best (1982) were sooty shearwaters (*Puffinus griseus*), which mainly breed on islands off the coast of Stewart Island.

This study also showed significantly fewer lizards, *Leiopisma* 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 found in southern Stewart Island. The higher proportion of low scrub and exposed rock in this area (author's observations) makes the habitat highly suitable for lizards.

Of the rat species available, cats were probably consuming mainly ship rats and Pacific rats. Although some very large rat remains were found that were possibly Norway rats, this latter species is mainly restricted to subalpine shrublands in the study area, which cats use less than other forest types (Harper 2002). Cats generally prefer smaller rats (Childs 1986; Fitzgerald *et al.* 1991) although they will take Norway rats when other prey is not available (Dilks 1979).

Kitten and white-tailed deer (*Odocoileus virginianus*) or red deer (*Cervus elaphus*) remains were all found in scats. It is possible that the occurrence of the kitten was a result of cannibalism, but this seems unlikely if cats rarely consume aggressive prey as large as an adult Norway rat (Childs 1986). Adult cats and kittens have been found in small numbers in the diet of feral cats in other studies (Jones 1977; Bloomer and 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 a deer shot by hunters. A deer carcass could provide food for a cat for many days.

Cats prey on possums in New Zealand and Australia (Molsher *et al.* 1999; Cowan *et al.* 2000) and remains in cat scats may indicate predation on juvenile possums by cats as well as scavenging of carcasses (Fitzgerald and Karl 1979; Langham 1990). Invertebrates are eaten frequently, but provide little mass in cat diet. The preponderance of weta, a nocturnal orthopteran, is not surprising. Orthopterans are often the dominant group of invertebrates in cat diets (Fitzgerald and Karl 1979; Jones and Coman 1982; Paltridge *et al.* 1997), despite the poor digestibility and low calorific return of each individual orthopteran (Konecny 1987). Despite the small energy return, the accessibility and ease of handling weta probably results in a net energy reward.

Management implications

On Stewart Island, where cats and rats have been present for at least 150 years, the decline and extinction of native birds appears to be due to hyperpredation, where the presence of exotic prey has increased the size of a predator population, thereby increasing the predation on indigenous prey (Courchamp *et al.* 1999a; Roemer *et al.* 2002). Controlling cats alone on Stewart Island, however, could result in meso-predator release, whereby ship rats, known predators of birds, increase in numbers and impact on remaining bird numbers (Courchamp *et al.* 1999b). Using the removal or control of the primary prey for control of cats on islands would therefore depend on the effect of the primary prey on indigenous fauna. If rabbits were the only exotic prey then their control would likely negatively impact cats with fewer deleterious flow-on effects to native birds and animals than if the exotic prey were also predators, such as rats. For example, on islands where seabirds are available as prey for only a few months every year, the absence of primary prey such as rats or rabbits provides a significant constraint on cat population growth (Stonehouse 1962).

Feral cats on Stewart Island appear to be under nutritional stress from late spring to early autumn and, like 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 is restricting cat numbers, but seasonal restriction in primary prey, coupled with limited alternative prey biomass. These conditions lead to increased dispersal and mortality in feral cats. Removal or reduction of cats' primary prey on Stewart Island, or indeed other islands with limited alternative prey, could substantially reduce or possibly even eradicate feral cat populations.

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