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POPULATION BIOLOGY OF SMALL MAMMALS IN PUREORA FOREST PARK: 1. CARNIVORES (*MUSTELA ERMINEA, M. FURO, M. NIVALIS,* AND *FELIS CATUS)*

Summary: Populations of four species of carnivores were sampled over the five years 1983-87 at Pureora Forest Park, by regular three-monthly Fenn trap index lines supplemented with occasional control campaigns by shooting and additional traps. Stoats were the most frequently collected (63 captures), followed by weasels (18), cats (15) and ferrets (13). Stoats ranged throughout the mosaic of forest types but especially the older exotic blocks, hunting rabbits, rats, possums and birds. The mean age of 55 stoats trapped was 15 months, and their maximum life span about 5 years. The age-specific mortality rate of first year stoats was about 0.76, and the proportion of older stoats (>1 year) declined from 52% of 21 killed in summer/autumn of 1983 to 27% of 22 killed in the same seasons of 1984-87. Weasels were collected mainly from habitats favouring mice, such as a young plantation and the road verges, and 40% of 15 non-empty weasel guts contained mice. Cats and ferrets hunted the native forest blocks where their main prey, rats and possums, were abundant. The body sizes and reproductive patterns of mustelids at Pureora were similar to those recorded in podocarp-broadleaf forests elsewhere in New Zealand.

Keywords: Pureora Forest Park; cat; stoat; weasel; ferret; diet; body size; reproduction; kokako; predator management; competition.

Introduction

Pureora Forest Park covered (at the time of our study) 75 000 ha of the ranges west of Lake Taupo, on the volcanic plateau of the central North Island, New Zealand. The indigenous forests of Pureora have considerable conservation value, because they support one of the last surviving mainland populations of kokako (*Callaeas cinerea wilsoni* Gmelin), an endangered native wattlebird, and a comparatively intact indigenous biological community (Imboden, 1978; Leathwick, 1987). Now that logging has been stopped, the main threats to the continued survival of the kokako, and other vulnerable native species sharing the same forest community, are seen to be competition with and predation by introduced mammals (Innes and Hay, 1991, 1995).

The nine species of introduced small mammals in the park that are predatory to some degree are the stoat (*Mustela erminea*[1]), weasel (*M. nivalis*) and ferret (*M. furo);* ship rat *(Rattus rattus)* and Norway rat (*R. norvegicus);* the feral cat (*Felis catus),* hedgehog (*Erinaceus europaeus)* and house mouse (*Mus musculus);* and the Australian brushtail possum (*Trichosurus vulpecula*). The carnivores (stoat, weasel, ferret, feral cat) were regularly monitored with Fenn traps for five years from January 1983 to October 1987. Their abundance, distribution and habitat preferences, so far as these parameters could be determined from the trapping records, are analysed by King *et al.* (1996a), along with comparable records for the rodents from a parallel monitoring programme run from November 1982 to November 1987. In this paper we describe the physical characteristics such as measurements, population structure and reproduction of the carnivores collected, and companion papers (King *et al.*, 1996b; Innes *et al.*, in prep) do the same for the rodents. Hedgehogs and possums were recorded when captured but not collected for dissection.

The main aim of this study was to provide basic data on the population biology of potential predators of kokako and other fauna.

Study areas

Pureora State Forest Park (Fig. 1: for further details see King *et al.,* 1996a) supports a mosaic of native vegetation of various types in two main blocks, both including extensive tracts of indigenous forest interspersed with smaller areas of plantations of

[1] Nomenclature of mammals follows King (1990).

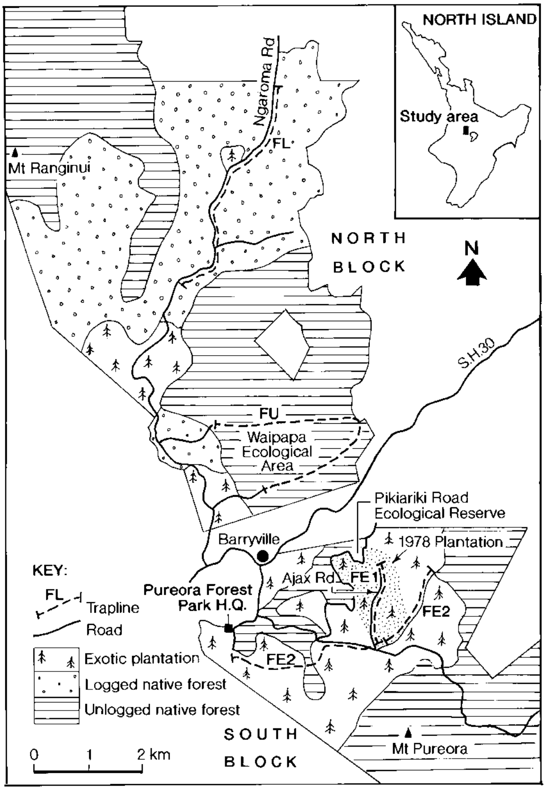

Figure 1: *Map of the study area. Pureora Forest Park boundaries are shown as they were during the field work. The Forest Park Headquarters includes the Visitor Centre and the meteorological station. The former settlement at Barryville is now deserted except for the old sawmill (closed). Traplines are identified by their codes, as described in Table 1.*

exotic conifers of various ages. At the time of our study (January 1983 to October 1987), the North Block retained both logged and unlogged indigenous forest, generally consisting originally of podocarps of varying density, principally rimu (*Dacrydium cupressinum*)[2] and matai (*Prumnopitys taxifolia*) emergent over a diverse, multi-tiered canopy dominated by tawa (*Beilschmiedia tawa*) and kamahi (*Weinmannia racemosa*). The South Block was a patchwork of coniferous plantings of different species and ages at the lower altitudes, plus unlogged indigenous forest on higher ground, e.g., on Mt Pureora and the adjacent Mt Titiraupenga.

[2] Nomenclature of plants follows Allan (1961) and Connor and Edgar (1987).

We distinguished three main habitat types in the park, all within 12 km of Pureora Forest Park Headquarters, at altitudes ranging from 550 to 700 m asl, and set extensive traplines to sample logged native forest, unlogged native forest and exotic forest.

The spatial and temporal distributions of two of the principal prey of carnivores, feral house mice and ship rats, were documented by three-monthly rodent traplines (King *et al.,* 1996a). Mice were fewest in unlogged native forest, more abundant in road edge cutover forest, and most abundant in a young exotic plantation (planted in 1978), but virtually absent in older (closed-canopy) exotic forest. Ship rats were abundant in all native forest regardless of logging history, and present in older exotic forest, but absent from the young plantation. Other prey such as possums, rabbits and birds were not indexed, but casual observations suggested that rabbits were probably more common in and around the exotic forests.

Methods

Three lines of Fenn traps sampled the three habitat types (Table 1). The 122 traps were placed singly in wooden tunnels to protect non-target species, baited with fish-based catfood, and inspected daily. After 1984 we fixed two horizontal wires across the tunnel entrances in an effort to reduce interference by possums. A single female stoat, caught in a rat trap along the rodent line in the logged forest, is included among the carcases analysed but excluded from the density estimates. Another five stoats, two weasels, two ferrets and seven cats were collected, usually during control operations by rangers, at various times and places other than on the regular Fenn trap lines, and these are also included with the carcases for analysis.

All animals caught were returned to the laboratory frozen, and later examined for a standard list of physical attributes. Stoat carcases were put through an abbreviated version of the routine developed during previous studies (King and Moody 1982). As described therein, we recorded weight, head and body length, and tail length; emptied the guts for analysis of diet (from identification of prey remains, mostly hair, feathers and insect/lizard parts); recorded the condition of the nipples of females and reproductive organs of both sexes; and removed the head and baculum for cleaning.

In addition, one canine tooth from each adult stoat was extracted and sectioned in order to reveal the cementum annuli and allow construction of a frequency table of year classes. We first set aside all males under 10 months old and all females under 6 months old, which can be distinguished from skeletal morphology (King and Moody, 1982). The slides were prepared by Matson's Laboratory (Montana, USA), and read both by Gary Matson and by Helen Grue. Grue and King (1984) and King (1991b) confirmed that the ages estimated from cementum annuli are reliable. In the North Island, few young are ever caught before early December, so age structures derived from this material exclude all individuals that died before the age of independent dispersal (2-3 months).

For analyses of age distributions, we first tested (chi-square) for differences in the age distributions of males and females captured. Year-classes were defined in "stoat-years", commencing on 1 October (King and Moody, 1982). We assumed that the distribution of ages among the animals trapped was the same as in the living population (ie, the raw data were tabulated by the second method described by King 1989:173).

We estimated p_x, the proportion known to have been alive at age x that survived to age x+1, using Caughley's (1977) Method 4, which does not require that $r = 0$. Caughley cautioned that use of this method for cohorts not sampled with equal intensity each year can introduce errors in estimates of p_x; but at Pureora our sampling was effectively constant in all years. Finally, we developed a preliminary l_x and q_x table.

We report the body measurements of stoats in three age classes based on physical maturity rather than chronological age, which are different in the two sexes (defined in Table 2).

Weasels and ferrets were treated in the same way as stoats except that their ages could not be determined by cementum annuli, because we have no known-aged reference sections for those two species. Instead, we distinguished between adults and young on cranial and baculum anatomy, as illustrated by King, O'Donnell and Phillipson (1994).

Cats were sent whole to Lower Hutt for examination. Their diet was analysed by BMF according to a standard routine described in Fitzgerald and Veitch (1985). They were divided into two age classes; juveniles had milk teeth, and adults had permanent teeth. The permanent dentition is completed by the time the animals weigh about 1.6-2.0 kg. Carcases were also scored for condition, defined from fat deposits.

Results

Stoat

Almost half of the Pureora stoats were collected in the older exotic forests of the South Block, where the density index for stoats was higher than in any other sample area, significantly so compared with unlogged native or in young exotic forest (Table 1).

Table 1: *Configurations of Fenn traplines in Pureora Forest Park, and distributions of 109 carnivores captured. Traps were set at 300m spacing in the last weeks of January, April, July and October 1982-87 inclusive, but were of variable length depending on the extent of suitable habitat available. Positions of traplines marked on Fig. 1. The five-year means of capture rates (captures per 100 trapnights, with number of captures in parentheses) given for all species by area are adjusted for local variation in capture rate by season and year using the General Linear Model (GLM). Values in any row followed by the same letter do not differ significantly at* P=*0.05; rows without letters were not tested because of small sample size. "Extras" were collected away from the standard lines and are used for carcase analysis but not for density estimation. For further details, see King* et al. *(1996a).*

HABITAT	UNLOGGED NATIVE FOREST	LOGGED NATIVE FOREST	EXOTIC FOREST			
			planted 1978	planted >1966		
Fenn trapline label (see Fig. 1)	FU	FL	FE1	FE2		
Length (km)	9.9	11.4	3.0	12.6		
N sites	32	39	10	41		
MEAN DENSITY INDICES (n)					**EXTRAS**	**TOTALS**
Stoat	0.16 a (10)	0.19 ab (15)	0.05 a (1)	0.37 b (30)	(6)	63
Weasel	0	0.09 (7)	0.14 (3)	0.07 (6)	(2)	18
Ferret	0.08 (5)	0.05 (4)	0	0.02 (2)	(2)	13
Feral cat	0.06 (4)	0.01 (1)	0.10 (2)	0.01 (1)	(7)	15
Total captures						**109**
Total corrected trapnights	6281	7746	2079	8166		**24 272**

Table 2: *Body and skull measurements of stoats from Pureora. Growing: males under 15 months old, females under 6 months. Fullgrown: males 16-35 months, females 7-35 months. Old: both sexes 36 months of age or older. Means estimated from a weighted means model which adjusts for uneven sample sizes, ± SE and n.*

Age group	Body weight (g)	Head-and-body length (mm)	Condylobasal length of skull (mm)
Females			
Growing	176 ± 10.0 (14)	238 ± 4.9 (11)	45.0 ± 0.34 (11)
Fullgrown	209 ± 13.2 (8)	243 ± 5.8 (8)	45.0 ± 0.40 (8)
Old	220 ± 26.4 (2)	250 ± 11.5 (2)	46.3 ± 0.80 (2)
Males			
Growing	281 ± 13.2 (17)	251 ± 6.8 (12)	48.9 ± 0.43 (12)
Fullgrown	308 ± 16.4 (11)	266 ± 7.5 (10)	49.6 ± 0.48 (10)
Old	338 ± 19.2 (8)	276 ± 8.4 (8)	49.8 ± 0.53 (8)
Range of local means from podocarp/broadleaved or mixed forests elsewhere[1] in New Zealand (from King, 1991a), with combined n			
Females			
Adult + old	179-224 (81)	247-259 (88)	45.0-46.0 (99)
Males			
Adult + old	288-341 (105)	275-284 (117)	48.3-49.7 (83)

[1] Urewera National Park (NP), Egmont NP, western side of Arthur's Pass NP, Westland NP, Milford Sound and Hollyford Valleys, Fiordland NP.

The mean body and skull measurements of Pureora stoats fell within the range recorded from similar habitats in other parts of New Zealand (Table 2).

Gut contents

After discarding all guts that were empty or contained trap bait only, a total of 52 guts with contents remained for analysis of diet (Table 3). With some reservations - since, when the records are broken down by season and sex, the samples become very small - we can say that stoats at Pureora ate mainly birds, rats, possums and lagomorphs. Insects were taken frequently but were not identified. The samples are too small to subdivide by habitat, and in any case individual stoats probably ranged widely throughout the mosaic of habitats at Pureora.

Reproduction

The smallest and youngest stoat collected was found alive at the side of the road during our preliminary surveys on 20 November 1982. It was a female, and weighed 73 g, with a head-and-body length of 178 mm. From the indicators of age summarised by King (1989), including the short tail (51 mm) with a very small black tail tip, and all four deciduous canine teeth present, it was estimated to be 4-7 weeks old, suggesting that it was born some time during the first half of October.

Of 12 full-grown (second-year or older) females collected, none was visibly pregnant. Six were collected in winter or spring, when virtually all females were in the apparently quiescent phase of delayed implantation. One of three caught in January 1983 showed signs of having suckled young in the recent season (nipples >4 mm long); one definitely had not bred recently (nipples still in the juvenile condition, invisible to the naked eye), and one was intermediate (nipples of 2 mm). Two adult females caught in January 1984 both had 4 mm nipples. The only one caught in 1987, on October 22, had probably just lost her litter (no lactation, nipples only 1.5 mm) and had the engorged uterus (0.58 g) typical of female stoats just before or just after oestrus (for full description of the female reproductive cycle, see King and Moody, 1982). No adult females were caught during the breeding seasons of 1985 or 1986.

Age structure

The age distributions of the two sexes (Table 4) were not significantly different (χ^2= 2.21, P>0.05 (2d.f., using 3 age classes <1, 1-3, 3+, n=61; test includes another 6 animals which could not be included in Table 4 because their ages were known to within one of these classes only). The mean life span of males (19.0 ± 18.65 months, n=33) was not significantly longer than that of females (9.5 ± 11.46 months, n=22). The two oldest individuals were both 5-year-old males caught in October, the season when males travel widely in search of mates.

The mean age (±SE) at capture was 15.2 ± 2.25 months (n=55), and the first-year mortality rate was

Table 3: *Foods of carnivores collected from Pureora (areas pooled), as percentage frequencies of occurrence of a given item in all guts containing any food. Since one gut could contain more than one item, especially of the smaller prey species, the percentages do not add up to 100 and cannot be summed. For definitions of categories and methods of identification, see King and Moody (1982). "Large mammals" includes possums, lagomorphs, and unidentified large mammals; "Lizards" includes both skinks and geckos. n = number of guts containing food.*

	Percentage frequency distributions						
	Mice	Rats	Birds	Insects	Large mammals	Lizards	n guts with food
Stoats (sexes separate)							
Pureora							
Males	19	22	28	50	47	3	32
Females	5	20	55	65	15	5	20
Sexes pooled	13	21	38	56	35	4	52
Other forests[1]	22	7	42	c.40	P13/L13/ ULM11*	S1/G2*	866
Weasels (all males)							
Percent	40	7	14	40	7	7	15
Ferrets (sexes pooled)							
Percent	0	20	0	10	80	0	10
Cats (sexes pooled)							
Juveniles	4 (66)	0	1 (16)	5 (83)	1 (16)	0	6
Adults	4 (57)	3 (43)	2 (28)	4 (57)	6 (86)	0	7

[1] Comparative data from King and Moody (1982). *They did not have a category "Large mammals" but calculated frequencies for possums (P), lagomorphs (L), and unidentified large mammals (ULM) separately, and likewise for skinks (S) and geckos (G). These figures cannot be added, since in theory one gut could contain more than one of these items; but *if* all occurrences had been separate, the pooled figures for Pureora and those from other forests would be similar.

Table 4: *Raw age frequencies by sex of stoats collected at Pureora, plus first estimates of mean age-specific survivorship probabilities (l_x) and mortality rates (q_x).*

Age (yr)	Numbers		l_x	q_x
	Males	Females	Sexes pooled	
0.2-1	16	15	1.00	0.76
1-2	8	5	0.24	0.42
2-3	3	0	0.14	0.42
3-4	1	2	0.08	0.38
4-5	3	0	0.05	0.60
5-6	2	0	0.02	
n	33	22		
total	**55**			

about 0.76. The proportion of stoats >1 year old caught at Pureora declined over the five years studied, from 52% of 21 collected in summer and autumn of 1983 to only 27% of 22 collected in the same two seasons of 1984-87.

Weasel

All 18 weasels collected came from areas of disturbed vegetation, either along the side of the Ngaroma Road through the logged native forest or in the exotic plantation (Table 1). All were males, and all but 2 of the 16 skulls and bacula cleaned were classed as belonging to reproductively mature adults. The distribution of male body weights (Table 5) was not different from that of weasels collected elsewhere in the country (t=1.104, d.f.=57, P>0.05: see King, 1990).

In the 15 guts available for analysis (Table 3), all but two items represented small prey - mostly mice and insects, plus one lizard. One rat (including an almost complete tail) could well have been scavenged from a trap, since substantial quantities of rat carrion were provided along our traplines during our field sessions.

Feral ferret

Unlike the weasels, the thirteen ferrets represented all ages and both sexes, and their local distribution was almost opposite to that of the weasels (Table 1). Five of the 13 were caught in the unlogged native forest which weasels avoided altogether. The ferret teeth were not sectioned, and the only distinguishable age class was that of the apparently still-growing young. Many of the skulls were smashed, and several carcases had to be discarded,

Table 5: *Measurements of weasels and ferrets collected from Pureora. Samples are too small to subdivide except by sex. Weights in grams, head/body lengths in millimetres.*

	Male weasels: body weight	Male weasels: head/body length	Male ferrets: body weight	Male ferrets: head/body length	Female ferrets: body weight	Female ferrets: head/body length
n	18	18	7	7	5	4
Minimum	105	195	690	338	269	270
Maximum	158	234	1273	416	768	345
Mean	132	214	973	376	576	320
SE	3.6	2.1	86.2	10.0	93.0	17.1

but the ages of nine were estimated; four of five males had bacula of juvenile shape, and one of four females had open sutures in the skulls (Table 5). None showed any evidence of breeding, although the presence of juveniles implies that some had bred, in Pureora or nearby.

The guts of these ferrets (Table 3) contained only ten items, all but one of which were mammals of rat size or larger (seven possums, two rats, one lagomorph). Very few, if any, of these could have been taken as carrion, since possum trapping and road kills were scarce in Pureora at the time. The body measurements of the Pureora ferrets (Table 5) fell within the range for ferrets recorded elsewhere in New Zealand (Lavers and Clapperton, 1990).

Feral cat

Age, sex, size and coat colour

Eight cats were caught along the Fenn trap lines, and another seven were trapped, shot or found dead elsewhere in Pureora (Table 1), all in the first three years of the study. Thirteen of the cats were caught between January and May, one in July and one in October. Of the fourteen carcases retrieved for study, seven (five females, two males) were adults, and seven (three females, two males and two of unknown sex) were juveniles (Table 6). Most of the cats caught in Fenn traps were small - five were juveniles, two were adult females (one very thin, weighing only 1.14 kg), and one escaped. In three juveniles (1.3, 1.4 and 1.6 kg), the permanent teeth were beginning to show. The condition of ten cats was recorded; five adults were classed as medium and one as thin, and two juveniles as medium and two as thin. No cats were classed as fat.

Six of the cats were tabby (three striped, three blotched), seven were black, and one was black and ginger (tortoise-shell). Three had some white fur on the chest, belly and paws.

Gut contents

The 13 cat guts examined all contained food, consisting mainly of arthropods, rabbits, possums and mice plus to a lesser extent rats and birds (Table 3). Only three cats had eaten birds; one contained the

Table 6: *Measurements of feral cats collected from Pureora. Weights in kilograms, head/body lengths in millimetres. Two of the 14 carcases retrieved were too much damaged to measure.*

	Adult males		Adult females		Juvenile males		Juvenile females	
Date	Weight	Head/body length	Weight	Head/body length	Weight	Head/body length	Weight	Head/body length
11/3/85	2.7	743						
11/4/85	3.9	820						
13/4/83			1.14	610				
14/7/84			2.28	710				
30/3/85			2.95	680				
21/4/85			2.15	675				
18/5/85			1.80	630				
15/4/83					1.64	615		
1/4/85					1.41	640		
18/4/85					1.32	610		
12/1/84							0.70	480
16/1/84							0.81	504

remains of a blackbird, one a small passerine and the third the beak of a parakeet and feathers of a thrush. The 32 arthopods found were: weta, 5 *Turbottoplectron cavernae* plus an unidentified fragment (Rhaphidophoridae), 1 *Hemideina thoracica* (Stenopalmatidae); Lepidoptera, 4 geometrid larvae; Hymenoptera, 1 *Sphictostethus nitidus*, 1 *Priocnemis monachus* (spider wasps)(Pompilidae); Hemiptera, 3 cicadas (1 adult, 2 nymphs); Coleoptera, 3 *Dendroblax earlii* (Earl's stag beetle)(Lucanidae), 2 *Ochrocydus hutton* (kanuka longhorn), 6 *Prionoplus reticularis* (huhu beetle) (Cerambycidae), 2 *Stethaspis longicornis* (mumu chafer), 2 *Odontria* sp. (Scarabaeidae); and spiders, 1 *Miturga* sp. (large brown vagrant spider)(Miturgidae) (M.J. Meads, *pers. comm.*). Almost all the cats were collected in summer or autumn when arthropods are likely to be most common.

Juveniles ate mostly small items (insects and mice); adults took lesser numbers of these plus the much larger rats, rabbits and possums. Three juveniles weighing 0.7-0.95 kg contained 20 arthopods and one mouse, and three older juveniles (1.3-1.6 kg) seven arthropods, five mice, a blackbird and a fragment of bone from a rabbit or possum. Apart from this bone fragment, all of the rats, rabbits and possums recorded were eaten by adult cats. Of the seven adult cats collected, three contained remains of rabbit and three of possum.

Four of the six juveniles and two of the seven adults contained stomach nematodes, sometimes in substantial numbers. Most were *Toxocara cati* (arrowheaded worm), which is very common in feral cats throughout New Zealand (Fitzgerald, 1990); but one juvenile male was carrying a single large *Mastophorus muris*, a spiruroid common in rats and mice and with an arthropod intermediate host (W.A.G. Charleston, *pers. comm.* and see Charleston and Innes, 1980), together with the remains of a mouse. This cat was caught in the young plantation in April 1985, when mice were still at high density (13 captures per 100 trapnights in May) after the irruption over the preceding autumn and winter (King *et al.,* 1996a).

Reproduction

None of the five adult females was pregnant, but one, trapped in one of the older South Block plantations in April 1985, was lactating from four large nipples. It was in medium condition and had a gut full of assorted prey (mouse, rat, rabbit, possum and bird remains plus insect fragments). Two more females had bred in the current or previous season; a thin cat collected in April had two visible nipples, and another in July had four large nipples. A fourth female caught in the same area as the first only a month later (May 1985) was small (1.8 kg), in medium condition, carried a heavy infestation of *T. cati*, and showed no sign of ever having bred.

The fifth adult female, a black tortoiseshell shot near the Ngaherenga camping area (near the Park headquarters) in March 1985, had been speyed, so had obviously once been (or perhaps still was) a domestic pet. Not all apparently feral cats are truly independent, since even well-fed domestic cats go hunting. She weighed 2.95 kg, was in "medium" condition (i.e., not especially thin) and had recently eaten a rabbit. Pureora village is less than 1 km away from the camping area, and she may have wandered from a home there since at that time there were no regulations preventing people from keeping domestic cats in the village. The two adult males caught in March and April 1985 weighed 3.9 kg and 2.7 kg, and both were sexually mature.

The seven juveniles came from all forest types and all three years in which any cats were caught, which suggests that none of the areas or years we sampled was especially favourable for breeding. Their body weights indicate that most were born in late spring or early summer. Three caught in January weighed 0.70, 0.81 and 0.96 kg, and three in April 1.3, 1.4 and 1.6 kg. One found recently dead in May weighed 0.45 kg.

Discussion

This study complements earlier work using the same monitoring methods in South Island beech forests (King, 1983). The species compositions and relative densities of mammals we collected in the two kinds of forest were remarkably different. In beech, we collected large numbers of stoats (maximum quarterly density index 9.3 C/100TN) and a few ship rats (to 1.7 C/100TN), but no ferrets, weasels or Norway rats. At Pureora the same field techniques produced vastly more ship rats (to 9.2 C/100TN) but fewer stoats (to 0.37 C/100TN), plus at least some ferrets, weasels and Norway rats. Mice were usually uncommon in all forests, but we recorded temporary irruptions in both studies, which reached 73.3 C/100TN in beech forest (in the Grebe Valley in 1979: King, 1983) and 41.1 C/100TN in the young exotic plantation at Pureora in 1984 (King *et al.*, 1996a).

Sampling bias

All four species were collected in the same traplines, which will certainly have introduced some sampling bias because the differences between the four species in body size, hunting methods, sensory acuity and general biology make some more susceptible than others to capture in Fenn traps set in the particular configuration we used. The Fenn was designed to replace the gin trap on British game estates during the 1950s, when legislation required game keepers to kill "ground vermin" (stoats, weasels, hedgehogs and rats) more humanely (Tapper, 1992). Ferrets and feral cats were not included in the design specifications because they were considered to be less important as predators at the time.

Hence, bias by sex, age and species is visible in these data. Firstly, all the weasels were males, as is usual in collections made in widely spaced traps (King *et al.*, 1994). The smaller female weasels (40-60 g) are often too light to set off the trap, and have smaller home ranges than males, likely to include fewer traps or none (Buskirk and Lindstedt, 1989). Conversely, the only stoat caught in a rat trap was a female. In the Orongorongo Valley, six stoats have been caught along the rodent trapline which was the model for ours, of which four were female, one (in February) a male and one unknown (B.M. Fitzgerald, *unpubl. data*). Secondly, few adult cats were collected in the Fenn traps; only two of seven adult cats were trapped, whereas five of seven juveniles were trapped. We cannot tell whether the adult cats were deterred by the horizontal wires across the tunnel entrances, or were more cautious about approaching a trap or more able to escape if caught, or were removed by an intensive control campaign (by shooting as well as trapping) conducted in various parts of the park by the rangers in 1985.

Comparisons with other New Zealand populations

Stoats

Exotic forest has not been sampled for stoats before anywhere in New Zealand. However, the Pureora plantations are surrounded by, and interspersed with, remnants of mixed podocarp/broadleaf forest, which was well represented in the survey of New Zealand forest stoats made by King and Moody (1982). The diet of Pureora stoats was broadly similar to that of the stoats from comparable podocarp and mixed forests, such as Egmont and Westland, sampled in that study (Table 3). Rats were a prominent item, as was expected in view of the abundance of rats in all habitats except the young plantation. Few mice were eaten at Pureora, which confirms our previous conclusion (King *et al.,* 1996a) that the Pureora stoats got little benefit from the 1984 irruption of mice in the young plantation; only one stoat was caught there, in 1983. The proportion of birds in the Pureora sample is similar to that in the earlier survey; the species of insects eaten by stoats is unknown but they probably took much the same selection as did cats (see below).

The Pureora sample is the only one we have seen from a non-beech forest for which the ages of adult stoats have been determined. It is very small, but consistent with other, much larger samples from beech forests in two respects. Firstly, the field data showed that, despite the abundance of rats in the indigenous forests of Pureora, the general density of stoats there, always <1/100TN, was about the same as or lower than in a beech forest in a non-seed year (range of seasonal indices from two valleys in Fiordland National Park during non-seed years 0-1.63 C/100TN: King, 1983). In beech forests, many females failed to produce young in non-seed years (King, 1981); these few records are consistent with the suggestion that at Pureora, low density may also be linked with poor survival of pre-independent juveniles. Secondly, the Pureora figure for mean age at death (15 months) is similar to the figures calculated from beech forests in Fiordland (Eglinton Valley 14.0 ± 1.22 months, n=231; Hollyford Valley 15.1 ± 1.42 months, n=218) and in Canterbury (Craigieburn 12.3 ± 1.14 months, n=237: R.A. Powell and C.M. King, *unpubl. data*). The annual mortality from independence to one year old (about 0.76) was similar to that estimated from the very much more extensive data from the two Fiordland valleys (0.78, 0.64) and Craigieburn (0.73). The mortality rates of adults between their second and fourth years at Pureora (0.38-0.42) tended to be somewhat lower than in Fiordland (0.40-0.68) or Craigieburn (0.48-0.67), though the distributions of survival data did not differ significantly between the four areas. The decline in the proportion of older stoats as trapping proceeded was even more pronounced in the three beech forest study areas (P <0.001) than it was at Pureora (R.A. Powell and C.M. King, *unpubl. data*).

Weasels and ferrets

Practically the only thing that can be said about these species is that our data confirm the general observation that ferrets tend to concentrate on larger prey (possums, rats and lagomorphs), and weasels on small prey (mice and insects). The dominance of mice and insects in the weasels' guts is also consistent with our field data showing substantially higher densities of weasels in the weedy habitats that support most mice and insects, especially during an irruption of mice in winter 1984 (peak capture rate, 41.1 C/100TN in May 1984) in the young plantation. The density index for weasels reached a temporary peak of 1.15 C/100TN in the plantation and surrounding exotic forest over the following summer, October 1984 to April 1985 inclusive (King *et al*., 1996a).

Weasels grow rapidly and reach full size within six months, and (unlike stoats) males may be fertile and females may produce young in the season of their birth, so all those captured were nominal adults. By contrast, five of the nine ferrets that could be classified were juveniles, and none was a breeding adult.

Cats

The Pureora cats differed little from other mainland populations of feral cats. A sample of 42 adult feral cats collected in the Orongorongo Valley averaged larger in size, but they were caught in large cage traps that must have been more effective in sampling larger animals than Fenn traps set in tunnels with restricted entrances. The Orongorongo population also included fewer blacks and more striped tabbies (Fitzgerald, 1990).

Competition and co-existence

Pureora Forest Park seems to have a greater diversity of resident carnivores compared with the beech forests which we have sampled before with the same methods. Why should that be so? We suggest the main reason is that the original extensive forest has been converted to a mosaic of different vegetation types, providing for a range of habitat requirements.

The three mustelids are well separated by body size, and apparently also by diet; weasels ate mostly small items, ferrets mostly large ones and stoats something of everything. The distributions of prey types (Table 3) suggest that weasels concentrated on habitats favouring mice, such as the young plantation and the road verges; ferrets hunted mainly on the ground in the native forest blocks where rats and possums were abundant; and stoats ranged throughout the mosaic of all forest types but especially the older exotic blocks, hunting rabbits on the ground and rats, possums and birds both on the ground and in the trees.

It could be argued that these different diets, and the associated different distributions of the three mustelids in Pureora, are evidence of an evolved mechanism for avoiding competition. That could well be true; but the same result would also follow as the simple consequence of the different hunting strategies of predators which are different sizes for other reasons. For example, Sandell's (1989) model of the factors determining body size in stoats ascribes greater importance to energy conservation and hunting strategy than to competition. The possible effects of competition can be measured only by controlled and reversible field experiments, which have never been done on the suite of predators present in New Zealand. Field observations of linked changes in the behaviour of two species do not prove competition, but suggest what experiments might be done. For example, Gibb, Ward and Ward (1978) saw stoats in the rabbit enclosure at Kourarau only after ferrets and cats had been excluded from it; and Pierce (1987) observed an increase in numbers of stoats in an area of the MacKenzie Basin from which ferrets and cats had departed after a rabbit-poisoning operation. Stoats and weasels may be killed by cats (Fitzgerald and Karl, 1979; King and Moody, 1982), so intraguild predation is possible as well as competition. These various possible explanations cannot be distinguished by simple observation.

Implications for conservation management

Where the natural density and adult mortality of stoats are relatively low, a trapping campaign has some chance of increasing their mortality rate and removing them faster than they can be replaced, thereby temporarily reducing their local density. Managers at Pureora sometimes became concerned about the large effort and apparently poor results of trapping stoats in the park. On the contrary: our observations of the declining density indices and change with time in the age structure of the stoats trapped suggests, with some reservations, that it is possible to exceed the natural mortality of adults at Pureora, and also to remove the relatively small numbers of young produced each year. Both the capture rate of stoats at Pureora, and the proportion of adults caught, declined after the first year of regular trapping and remained low for the rest of the five year study.

Kokako and other birds are potentially at risk from all four carnivore species, although probably much more so from stoats than from weasels, which are rarer and smaller, or from cats and ferrets, which are also rarer and hunt birds less often. The risk or impact due to the various potential predators can be determined only by studying the kokako themselves, and this is extremely difficult with present research tools, especially for the mobile subadults and adults. Most (60-85%) kokako nesting attempts fail due to predation, and the predators identified so far are ship rats, possums, and kahu (Australasian harrier, *Circus approximans*) (Brown *et al.,* 1993; Innes *et al.*, 1994, 1995). On the other hand, the contribution of predators to mortality of kokako away from nests in unknown, let alone the identity of the predators. Large-scale multi-species pest control at Mapara and Kaharoa (central North Island) since 1989 has resulted in significant increases in kokako chick output and adult density (J.G. Innes and J.R. Hay, *unpubl. data*), but mustelids and feral cats were also killed in those areas, so the research has not so far provided good evidence for the relative importance of the various candidate predators of kokako away from nests. This question can now be explored, since mustelid control was dropped at Mapara before the 1995-96 kokako breeding season.

There are also complex interactions between predators. In the Orongorongo Valley, rats were much more important than birds in the diet of cats (Fitzgerald and Karl, 1979), and when the cats were removed the rats became much more abundant. Removing cats may have left bird populations no better off than they were before, and perhaps worse off than when cats were common and rats were scarce (Fitzgerald, 1988). Similarly, after a successful poisoning programme against rats at Mapara (King Country, North Island), stoats then ate more birds (Murphy and Bradfield, 1992). Of the three mustelids at Pureora, stoats had eaten proportionately the most birds, but even they might do less damage to the local bird populations than the vastly more abundant ship rats and possums which destroy many nests. The cats we examined contained as many remains of rats as of birds (three each). We suggest that both the uncertainty about which predator is most damaging, and also the possibilities of diet switching and/or rodent population release, demand that pest control operations to protect threatened birds at Pureora should include all mustelids, rodents, feral cats and possums together, until further research suggests otherwise.

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