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RESPONSES OF HARRIERS IN THE MACKENZIE BASIN TO THE ABUNDANCE OF RABBITS

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ABSTRACT

Harrier diet and population dynamics were studied at Tekapo River in 1985 and 1986, and stomach contents were analysed from 239 specimens collected in the Cass Valley in 1983-85. Harriers in both study areas fed mainly on rabbits, including young live rabbits and carrion. Local changes in rabbit abundance led to changes in the distribution and numbers of harriers. Immature harriers were mainly transients and responded to changes in rabbit numbers more than adults did. When rabbits were scarce, the resident harriers fed more on alternative prey, such as skinks, but there was no corresponding increase in the numbers of birds eaten. Males fed on alternative prey more than females did. Males were outnumbered by females in the study area with lower prey diversity.

INTRODUCTION

In New Zealand, Australasian Harriers *(Circus approximans)* are flexible in the habitats they frequent and the food they eat (Baker-Gabb 1986). They are particularly common in the MacKenzie Basin and in other tussocklands east of the Southern Alps, where there are high numbers of rabbits *(Oryctolagus cuniculus)*. In Otago in 1949, before large-scale rabbit control was under way, Gurr (1968) found rabbit remains in the stomachs of 90% of 331 harriers. Since then there have been few studies of high country harriers: Douglas (1970) found mainly remains of hare *(Lepus europaeus)* in regurgitated pellets cast at one nest, and Pierce (1986) found infrequent evidence of harrier predation at nests of stilts (*Himantopus* spp.).

The present study was supplementary to research on feral cats *(Felis catus)* and ferrets *(Mustela furo)*, designed to help understand patterns of predation intensity on riverbed birds. The main goal was to establish the responses of predators to fluctuating densities of rabbits, their staple food. For harriers, we examined whether depleted rabbit numbers would cause the birds to hunt elsewhere (numerical response) or to vary their diets and remain within the original area (functional response).

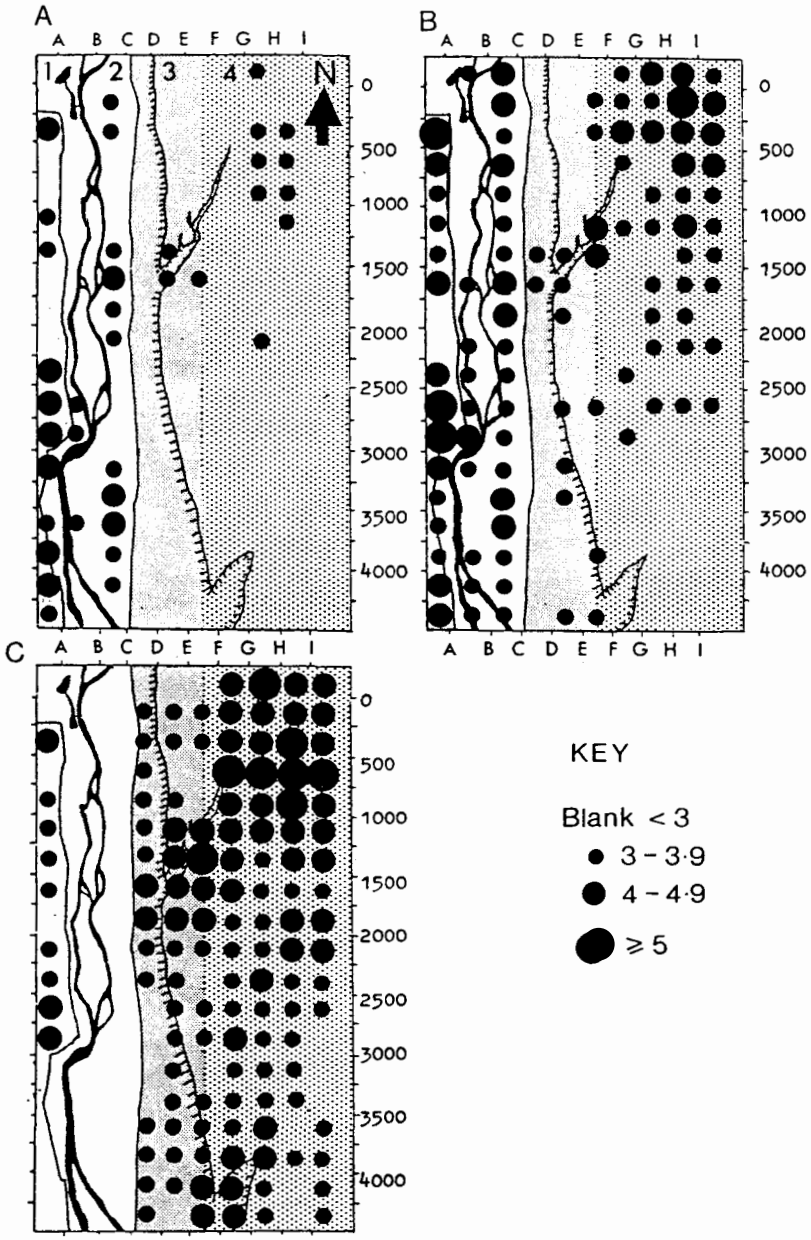

FIGURE 1 — Zones 1-4 of the Tekapo study area and indices of rabbit abundance in three years. Size of dot denotes scale of rabbit sign (see key) and follows Anon (1968). A. March - May 1985; B. March - April 1986; C. February 1987

Like most raptors, harriers are sexually dimorphic in reverse, females being larger than males (Carroll 1970). Overseas studies have revealed dietary differences between the sexes in several raptor species (Newton 1979). In the Manawatu, Baker-Gabb (1981 and unpub.) found that harriers preyed on a variety of animals and that females fed on larger prey than males. We were interested in finding out whether there were sex- or age-related differences in diet in the MacKenzie Basin, or whether rabbits were of equal importance to all cohorts.

STUDY AREAS

The main study area, 8.5 km^2, comprised mainly tussock grassland, flanking the bed of the Tekapo River (44°05' S, 170°25' E) at 590-700 m a.s.l. We divided the study area into 250 m grid-squares bordered by lines A-I and rows 0-4250 (Fig. 1). Within this area we recognised four zones. Zone 1 on the western side of the river (grid-line A of Fig. 1) comprised a well-vegetated terrace edge, bordering extensive tussock *(Festuca)* grassland. Zone 2 comprised the bed of the Tekapo River (grid-lines B and C), which had diverse vegetation ranging from herbfields and rank grass to thick matagouri *(Discaria toumatou)* and patches of willows (*Salix* spp.). Zones 3 and 4 (grid-lines D-I) comprised a plateau of tussock grassland and a 25-30 m high terrace slope between grid-lines D and E. Rabbit-netting fences ran parallel to grid-lines A and C, thus separating the rabbits into three groups – zone 1, zone 2 and zones 3-4.

North of the study area was a cluster of artificial ponds (Patterson's Ponds) surrounded by tall grass. The study area has warm summers and cold winters. The 1986 winter was colder than usual with about eight weeks of snow cover, compared with about two weeks of snow cover in 1985.

Supplementary data were collected along the south-west bank of Cass River (43°50' S, 170°25' E), 25 km north of Tekapo River. The Cass River is in a deep valley, 710 m a.s.l. at the base, rising to 2000 m on the flanking Joseph Ridge. Like the Tekapo study area, the Cass Valley was mainly tussockland: it was more fully described by Pierce (1983).

METHODS

In the Tekapo study area, we captured harriers in wire cages (mammal traps) located at the grid points. The cages, 610 mm long, 340 mm wide and 300 mm high, were baited with rabbit meat from which all hair, claws and teeth had been removed. We aged harriers from the presence (adult) or absence (immature) of underwing barring (Baker-Gabb 1981), sexed them from the size of the feet and talons, which are larger in females (Carroll 1970), and banded them. About every 10 days, we checked for vehicle-killed harriers along 33 km of main road (all 3-9 km away) to the east, north and west of the study area. We searched for harrier nests along about 10 km of the Tekapo River bed (including the study area) and on the adjacent plateau.

Harriers regurgitate pellets of undigested parts of prey such as bones, hair and feathers. Birds often disgorged pellets while perched on fence posts in the study area. At the end of each month, we collected these pellets and soaked them in water before analysing them. We could not always distinguish remains of rabbit from remains of hare. However, all of the lagomorph hard parts that we could identify were of rabbit, and so in the results and discussion

sections we refer to "lagomorphs" as "rabbits". We could often estimate the approximate size of rabbits eaten by measuring claw lengths and comparing them with claw lengths of rabbits of known weight.

The main limitation of analysing pellets of harriers is that some prey, such as nestling birds, leave few or no remains (Schipper 1973), giving rise to biased results. Nevertheless, pellets can show general patterns of feeding behaviour between seasons and between habitats. Except for some captured harriers which regurgitated while they were in the cages, we did not know the age and sex of the birds which deposited the Tekapo River pellets. These pellets may have been biased towards the adult harriers that defended territories over both of the fence lines. One sample of 80 pellets collected at a harrier roost at Patterson's Ponds (where up to 30 birds were seen at once) may have been biased towards immatures.

In the Cass Valley, many harriers were trapped and killed by staff of the Department of Conservation in and around nesting areas of Black Silts *(Himantopus novaezelandiae)* during September-December in 1983, 1984 and 1985. The sex of these birds was first estimated externally. Subsequent autopsy and gonadal inspection showed that external sexing gave 95% accuracy. For all analyses of pellets and stomach contents, data are presented as percent occurrence. Volumetric or biomass assessments were unnecessary, owing to the very high proportion of one prey type: rabbits.

THE PREY

Rabbits were very common in both study areas, but there were seasonal and annual variations within each area. In the Cass Valley, rabbits were at a high density during spring 1983, but extensive poisoning (carrots impregnated with compound 1080) by the Tekapo Pest Board in autumn 1984 resulted in low rabbit densities in 1984 and 1985. MacLean Scale indices of rabbit abundance (on a 1-10 scale and based on frequency of rabbit droppings, Anon 1968) were 4-6 during the 1983 season (D. May, pers comm.), but averaged only about 2 in 1984 and 2-3 in 1985 (pers. obs.).

In the Tekapo study area, two poisoning operations dominated rabbit numbers. Zones 3 and 4 had been poisoned in August 1984, and rabbit indices increased markedly throughout the study (Fig. 1, A-C). In zone 2, rabbits were moderate to common until they were poisoned in May 1986 and few rabbits survived there in winter and spring 1986 (Fig. 1C). In zone 1 and the tussockland to the west, rabbits were common throughout the study.

Rabbits were born in all months in the Tekapo study area, but mostly from August to November. Young rabbits were commonly seen from October to March. The 1984 breeding season was a very poor one for rabbits in zones 3 and 4, apparently because ground predators were feeding heavily on nestling and juvenile rabbits (unpub. data). Thus, during autumn and winter 1985 juvenile rabbits were relatively scarce in zones 3-4, compared with the following 18 months, when they were common.

In both study areas, the avifauna was dominated by charadriiforms (e.g. Pierce 1983) and especially introduced passerines, both groups being more common in the Cass Valley. Of the lizards, common skinks *(Leiolopisma nigriplantare macanni)* were widespread and common in both areas, while zones 1-3 of the Tekapo study area also had localised populations of long-toed skinks (undescribed species), *L. chloronoton* and/or *l. lineoocellatum* and

Heteropholis gemmeus. The nocturnal common gecko *(Hoplodactylus maculatus)* also was in zones 1-3 and in the Cass Valley. Large diurnal terrestrial insects were few, mainly grasshoppers (e.g. *Sigaus australis*), which were very common in the Cass Valley but rare in the Tekapo study area. Small numbers of hares *(Lepus europaeus)* were in both study areas, but they became very rare on zones 3 and 4 of the Tekapo study area during the study, none being seen there from autumn 1985 to winter 1986.

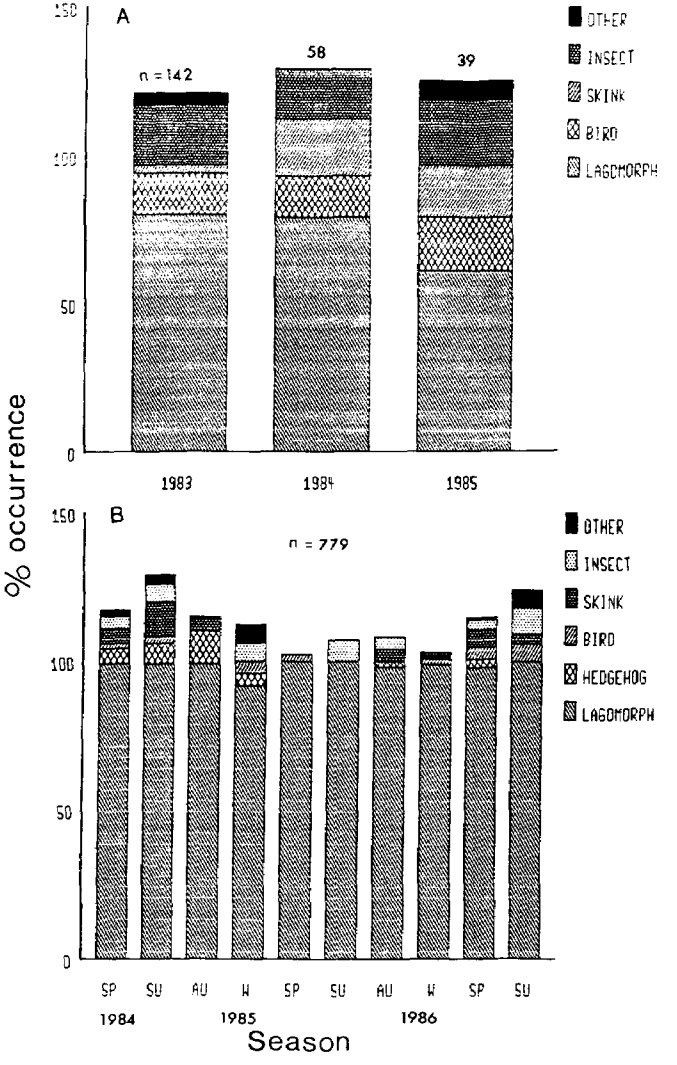

FIGURE 2 — Diet of harriers. A. Contents of harrier stomachs, Cass Valley, September - December 1983-85. B. Contents of pellets collected monthly at Tekapo River

RESULTS

Changes in diet

In the Tekapo study area rabbit remains occurred in 98.5% of pellets. After rabbit poisoning there in 1984, many pellets also contained hedgehog and skink remains (Fig. 2B). Few young rabbits (< 500 g) were recorded in pellets in 1984, but they were recorded much more frequently in 1985 and especially in 1986 (Table 1).

TABLE 1 — Estimated weights of lagomorphs eaten or partly eatan by harriers at Tekapo River

Season	N	Lagomorph weight (g)			
		< 100	100-500	> 500	Unknown
Spring 1984	116	3	9	9	80
Summer 1984-85	104	3	24	5	68
Autumn 1985	74	0	8	7	85
Winter 1985	46	4	22	15	59
Spring 1985	55	8	36	2	55
Summer 1985-86	55	20	20	2	58
Autumn 1986	43	0	21	9	70
Winter 1986	80	5	16	18	61
Spring 1986	155	30	32	5	34

Note: 1. Data presented as % occurrence.
2. Lagomorphs of "unknown weight" are all over 100 g.
3. "Spring" = Sep-Nov, "Summer" = Dec-Feb, etc.

In the Cass Valley, harrier stomachs contained fewer rabbits (61-80%; $x^2 = 9.04$, $p < 0.01$) and contained more alternative food than Tekapo pellets (Fig. 2). As at Tekapo, skinks were eaten more after rabbit poisoning. Thus, skinks occurred in 3% of crops in 1983, 19% in 1984 and 18% in 1985 ($x^2 = 13.1$, 2 d.f., $p < 0.01$). In 1985, a reduction of rabbits as prey and an increase in birds were not significant ($x^2 = 1.4$, 2 d.f., $p > 0.1$).

TABLE 2 — Birds identified in harrier pellets (Tekapo River) and in stomachs (Cass River)

	Tekapo	Cass
Number examined	779	239
Duck egg (Anas sp.)		2
Duckling		1
Banded Dotterel chick		2
Black-backed Gull	1	
Black-fronted Tern egg	1	
Black-fronted Tern chick		1
Blackbird	1	
Skylark	4	7
Goldfinch		1
Greenfinch	1	
Redpoll		1
Chaffinch	1	
Yellowhammer	1	4
Unidentified passerine	3	4
Unidentified bird	3	12
Total birds (and % occurrence)	16 (2.1)	35 (14.6)

Birds (mainly passerines, Table 2) and their eggs occurred in 15% of Cass crops and 2% of Tekapo pellets and there were no significant inter-year differences. Fish were not recorded in pellets from either study area, but a sample of 87 pellets collected from a harrier roost at Patterson's Ponds, on 2 August 1985, included three with fish remains. There were two observations of harriers catching trout *(Salmo* sp.), one of 400 g from Patterson's Ponds and one from the hydro canal.

TABLE 3 — Numbers and percent occurrence of food items in harrier stomachs Cass River September-December 1983-86

	Adult males	Adult females	Immature males	Immature females	Total
No. examined	37	36	81	85	239
Lagomorph	26 (70)	30 (83)	57 (70)	71 (84)	184 (77)
Hedgehog	1 (3)	1 (3)	2 (2)	0	4 (2)
Sheep	1 (3)	0	0	3 (4)	4 (2)
Mouse	1 (3)	0	0	0	1 (<1)
Bird	5 (14)	5 (14)	16 (20)	9 (11)	35 (15)
Skink	3 (8)	3 (8)	10 (12)	6 (7)	22 (9)
Insect	6 (16)	3 (8)	27 (33)	12 (14)	48 (20)
Total items	42	41	110	99	292

Note: Figures in parentheses are % occurrence.

Sex- and age-related differences in diet

In the Cass Valley, the diet varied between the sexes (Table 3). Small prey (birds, skinks, insects or mice) occurred in 58% of male crops compared with only 31% of female crops (x^2 = 9.30, 1 d.f., $p < 0.01$). Small prey were most frequent in immature males (65% of crops), followed by adult males (41%), immature females (32%) and adults females (31%). This difference was significant between immature males and immature females (x^2 = 9.81, $p < 0.01$) and between immature males and adult females (x^2 5.55, $p < 0.05$) for the three years combined. (These differences were also significant for the 1983 season alone, the only year in which sample sizes were large enough to permit single-season analysis.)

Rabbit remains tended to occur more frequently in female crops (83-84%) than male crops (70%), but this difference was not significant (x^2 = 1.32, 1 d.f., $p > 0.05$).

TABLE 4 — Monthly occurrence of dead harriers on roadsides in the Tekapo area

	1985						1986									
Age/sex	J	J	A	S	O	N	F	M	A	M	J	J	A	S	O	Total
Adult male												3				3
Adult female								1		1		3	1			6
Immature male			1									3	1			5
Immature female			1					4				2	2		1	10
Unknown	4	3	3	1			1	5	2			2		1		22
Total	4	3	5	1			1	10	2	1	0	13	4	1	1	46

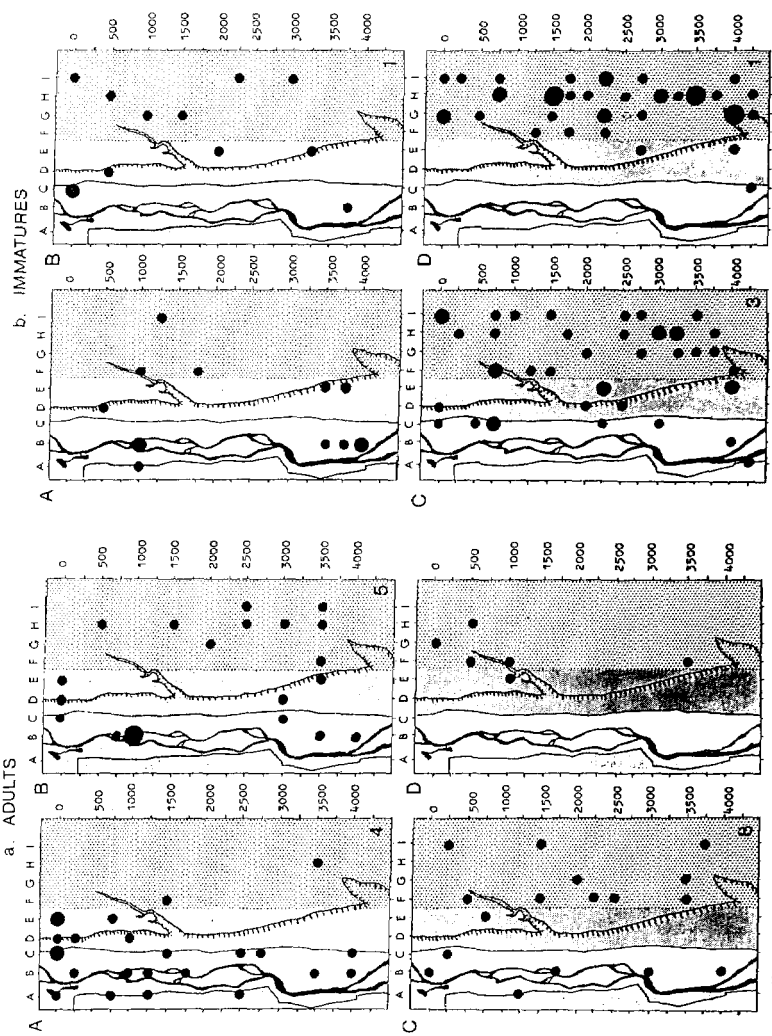

FIGURE 3 — Distribution and number of captures of (a) adult and (b) immature harriers Tekapo River. Time periods are A. February - August 1985; B. September 1985 - January 1986; C. February - August 1986; D. September - December 1986. The numbers in the lower right-hand corners denote number of recaptures.

Scavenging

Not all rabbit food was initially killed by harriers. An unknown proportion of food was scavenged from roadside carcasses over 4 km from the Tekapo study area. From June 1985 to October 1986, we found dead a total of 46 harriers (including four adults banded in the study area) along 33 km of road east, north and west of the study area. Half of these dead birds were found in two months only – March 1986 (mostly juvenile birds) and July 1986 (the only month with continuous snow-cover). Because the Cass Valley is 12-20 km from the main road, resident harriers there had little access to roadside carcasses.

Harriers also scavenged on remains of rabbits which cats had killed and left in the open or in areas of matagouri scrub, where they would have been visible to flying harriers. After rabbit poisoning in the riverbed in May 1986, harriers were conspicuous as they ate carrion for up to 6 weeks after the poisoning. We found no evidence of secondary poisoning of harriers.

Capture sites

There was a marked change in the distribution and numbers of harriers captured during the Tekapo study (Fig. 3). During the early part of 1985, adult and immature harriers were caught mostly on or near the riverbed, but by late 1986 nearly all captures were in zone 4. This difference was significant for adults between trapping sessions A and C ($D = 0.51$, $p < 0.01$) and for immatures between sessions A and C ($D = 0.49$, $p < 0.05$) and A and D ($D = 0.78$, $p < 0.001$ Kolmogorov-Smirnov D+ test).

Overall capture rates increased from about 1.2 per 100 trap days in 1985 to 3.1 per 100 trap days in 1986. This increase in capture rate was a result of more immatures in the area: immatures had comprised only 35% of the captured sample in Feb - Aug 1985 and 36% in Sep 1985 - Jan 1986, but this had increased to 71% in Feb - Aug 1986 and 85% in Sep - Dec 1986. Of the immatures captured, 62% were females ($x^2 = 5.76$, $p < 0.05$; Table 5), but in the Cass Valley 51% of immatures were females (Table 3).

TABLE 5 — Recoveries of Tekapo River harriers 1985-86

	Number banded	Number of recoveries	Number of individuals recovered	Distance between sites (km)		
				Max.	Min.	Average
Adult male	22	12	9	20	0.5	5.7
Adult female	20	10	7	4	0.5	1.1
Immature male	38	4	2	850	2.0	280
Immature female	62	7	7	560	1.7	126
Pullus male	4	0	0			
Pullus female	3	2	2	2	1.8	1.9
Total adults	43	24	17	20	0.5	2.8
Total immatures	105	11	9	850	1.7	159
Total pulli	9	2	2	2	1.8	1.9

Note: Totals include some unsexed birds.

Dispersal of banded birds

All 17 adults recovered (40% of number banded) were on the Tekapo Plain within 20 km of their initial capture sites. Immatures, however, appeared to be mainly transients. Only 10 immature and pullus harriers (9% of number banded) were subsequently recovered, and 5 of these were 80 - 850 km to the north, including three in the North Island (Table 5). No harriers from other parts of New Zealand were captured during the study period. However, a juvenile female harrier which had been banded at Lake Ferry, Wairarapa, on 1 June 1982 (D. M. Sim, pers comm.) was found dead on the Cass Delta on 19 December 1982, 470 km from the banding site.

Nesting

In the Tekapo study area harriers nested only in zones 1-3 and no nests were found on the tussock plateaux on either side of the riverbed. Nest sites were rushes or tall grass (6 nests), matagouri bushes on terrace slopes (3), and riverbed debris (2). Closest nesting neighbours were 370 - 3220 m away (average 1180 m for the two years combined). Laying occurred in October and November each year, and except for one bird which had flown by 26 December 1985, young fledged in January in both years. In the 1985 season usually two young were reared (average 2.25, range 2-3, n = 4), but in the 1986 season five successful pairs each reared three young. Of three nests found in the 1987 season, two each contained two well-grown young and the other contained two well-grown young and a small nestling.

DISCUSSION

Dietary response

Baker-Gabb (1986) found New Zealand harriers to be more diverse and flexible in their diets than Australian harriers, and they also fed more on carrion, especially sheep *(Ovis aries)* and road-killed animals. MacKenzie Basin harriers, however, specialised on rabbits. Even after rabbit poisoning, rabbits were still prominent in the diet of harriers, probably reflecting the large hunting range of individuals. In the Manawatu dune country, Baker-Gabb (1981) found resident harriers ranging over about 900 ha.

Local poisoning of rabbits did, however, result in a slight broadening of the diet of resident harriers, and in the Tekapo study area there was also a reduction in the proportion of young rabbits eaten. In both study areas, the dietary broadening comprised mainly a switch to skinks. All identified skinks were *L. nigriplantare*, which were common even on fairly bare ground (including on the plateaux), where they may have been vulnerable. The larger *L. lineoocellatum/chloronoton* were not recorded, probably because they stayed near boulders, running under them when disturbed.

Lizards (and insects) are important in the diet of several species of palearctic harrier (Schipper 1973, 1980), particularly the smaller two species: Pallid Harrier *(C. macrourus)* and Montagu's Harrier *(C. pygargus)*. Surprisingly few lizards have been recorded in the diet of harriers in other parts of New Zealand, although many birds have been. These differences are probably due to regional and seasonal differences in prey availability, skinks being particularly common in parts of the MacKenzie Basin. Similarly, the contrasting levels of predation on birds in the Tekapo and Cass study

areas probably reflect the more diverse avifauna in the Cass Valley. No evidence was found of harriers preying heavily on eggs or young of native bird species in either study area.

MacKenzie Basin harriers fed little on sheep carrion, and scavenging on roadside animals was of local importance only. Cat-killed rabbits were probably more important carrion in both study areas, as Gibb *et al.* (1978) found for Wairarapa harriers. The relative importance of carrion and live prey to harriers was difficult to determine. If carrion provided the bulk of the food for Tekapo harriers, one might expect that rabbits would be more frequent in the diet when cats were most common and when harriers were least common (the latter thereby reducing competition for carasses). The opposite occurred: rabbit remains were least often found in harrier pellets in 1984-85, when harriers were scarce but cats were common (20 adult cats recorded compared with 11 in spring-summer 1985-86 and 13 in spring-summer 1986-87). In addition, remains of rabbits able to be aged in harrier pellets were mainly of young rabbits (whereas cats killed mainly large rabbits), which suggested that harriers killed most of their food themselves.

Numerical response

In the Tekapo study area, our higher rates of capturing harriers on the plateau in 1986 corresponded with increasing rabbit numbers there in 1985 and 1986. Poisoning of riverbed rabbits in 1986 may have enhanced this trend in capture rates, although our capture rates were already high on the plateau before the poisoning in the riverbed. That raptor numbers change in response to changing prey numbers is known in other species of raptor, particularly those which prey on rodent species whose populations oscillate from year to year (Galushin 1974, Newton 1979, Phelan & Robertson 1980, Hammerstrom 1984).

Galushin (1974) believed that, because raptors are more mobile than mammalian predators, raptors repopulate favourable areas quickly and so have steady reproductive outputs and more stable total populations. The situation in the MacKenzie Basin and other parts of New Zealand is probably similar. By the current means of rabbit control, areas usually only a few thousand hectares each are poisoned to different timetables. Thus, the range of a harrier (especially the more mobile juveniles) is likely to include blocks of land with differing rabbit densities. Whereas harriers responded quickly to Tekapo poisoning, numbers of feral cats and ferrets lagged for up to 6 months after poisoning, and their recolonisation of the plateau was much slower than that of harriers (RJP, unpub. data).

Despite the increase in harrier activity on the plateau in 1986, none were found nesting there. On the Tekapo Plain harriers nested mainly on the riverbed, which may have limited the number of breeding birds but clearly not the transient birds. Some adults appeared to defend territories centred on zones 1 - 3, from which intruding birds (usually immatures) were often seen being "escorted" to about the terrace edge of zone 3. This behaviour may have influenced the distribution of capture sites of immatures.

Reversed sexual dimorphism and diet

That males prey on small animals (as occurred in Cass Valley) is predicted for raptors with strong reversed sexual dimorphism (Newton 1979). Whatever the main role of reversed sexual dimorphism (see e.g. Amadon 1975, Newton 1979, Mueller 1986), it is clearly an important factor in the diets of MacKenzie Basin harriers. Likely ways for this to come about would be for males to be more manoeuvrable (and therefore able to catch small prey) and for females to be able to catch larger rabbits and defend carcasses against other harriers. Perhaps females have a competitive advantage over males in the open tussock country of the MacKenzie Basin, where small prey are scarce. This view is supported by the sex ratios of captured harriers, which favoured females in the rabbit-dominated Tekapo study area whereas in the more diverse Cass Valley, the sex ratio was approximately even. To test these ideas, it would be necessary to colour-mark individuals and make field observations of their hunting behaviour and abilities.

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