Genetic variability, distribution and abundance of great spotted kiwi (*Apteryx haastii*)

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ABSTRACT

Recent information on the genetic composition, morphological features, distribution and abundance of great spotted kiwi is collated, analysed and used to evaluate the species' conservation status.

The species exhibits high levels of genetic variability but with no consistent geographical patterns. Some morphological variability is present along latitudinal and altitudinal gradients. Further study is warranted to determine if genetically and/or morphologically distinct populations are present.

There are currently about 22 000 great spotted kiwi spread over 6000 km^2 in the northwest of the South Island. Most great spotted kiwi now live in high rainfall mountainous regions. There are three principal populations: in Northwest Nelson, the Paparoa Range, and the Arthur's Pass–Hurunui district. Since European settlement, the species has become extirpated in eastern Nelson, part of North Westland, and the central Westland mountain valleys. Overall, the species' range has contracted by at least 30%. The principal cause of decline is probably predation by stoats (*Mustela erminea*).

Conservation of the intra-specific genetic and morphological diversity of great spotted kiwi is best achieved by protecting the range of extant populations, although this may be logistically difficult. The focus will probably settle on the three main population groups. We expect further declines to take place, particularly in southern Northwest Nelson and in Arthur's Pass–Hurunui. The large populations in upland areas of Northwest Nelson and the Paparoa Range are probably stable but this needs to be monitored. The species should be classified as 'vulnerable' according to IUCN threat definitions.

1. INTRODUCTION

Great spotted kiwi, *Apteryx haastii*, live only in the South Island, mainly in mountainous regions of Northwest Nelson and the West Coast. There are several separate populations. The largest inhabits some 2600 km^2 of mountains and coastal foothills in Northwest Nelson, between Whanganui Inlet (in the north) and the Buller River (in the south). A second population lives immediately to the south of the Buller River, in the Paparoa Range and its coastal foothills. This population formerly extended into the Inangahua and Grey River valleys, but may no longer do so. A third and smaller group lives within the Southern Alps, in the Arthur's Pass–Hurunui district, some 30–75 km south-west of the Paparoa population. Its distribution extends westwards into the Taramakau watershed and eastwards into the Waimakariri, Poulter and Hurunui catchments. A fourth group formerly lived in some of the large mountain valleys of Westland, south of Hokitika. The type specimen was collected from this area in 1871, but there are no recent records (Jolly 1992).

The present report examines genetic variation between and within populations of great spotted kiwi, and assesses whether there are regional differences in morphology and coloration. We use this information to determine whether conservation management should focus on the species as one unit or on two or more of its constituent populations. The report also provides an account of the past distribution and the current distribution and relative abundance of great spotted kiwi. We relate these to environmental variables, and discuss the likely cause of decline in great spotted kiwi populations since European settlement. Finally, we assess the conservation status and future prospects of great spotted kiwi.

2. METHODS

2.1 Surveys

Surveys, involving call counts at night, were undertaken between 1983 and 1994 on 617 occasions throughout the known and suspected range of great spotted kiwi. Table 1 shows the distribution of survey sites by region and altitude.

Kiwi presence was established by searching for their feathers, faeces and probe holes during the day, and by listening for calls at night. Their relative abundance was determined by measuring call rates, which correlate with density (McLennan & McCann 1991). Most call counts were made in summer, so it was not necessary to correct for season when comparing counts from different areas. We also obtained rough estimates of absolute density by relating the minimum number of different birds heard calling to the size of the area being surveyed.

Most of the surveys (513) were undertaken by volunteers. The records they submitted to the Kiwi Call Scheme (administered by the Department of Conservation) form the basis of this report. The remaining surveys (104) were undertaken by staff of Landcare Research.

TABLE 1. DISTRIBUTION OF SURVEY SITES IN RELATION TO REGION AND ALTITUDE.

REGION	NUMBER OF COUNTS	TOTAL HOURS	< 200 m	% COUNTS AT 200–500 m	> 500 m
Northwest Nelson (North)	153	225	29	16	55
Northwest Nelson (South)	85	159	24	47	29
Paparoa Range	106	240	48	24	28
Arthur's Pass–Hurunui	151	285	2	19	79
Brunner–Victoria–Maruia	110	219	3	29	68
Elsewhere (Reefton–Ahaura)	12	24	0	17	83
Total counts/Average %	617	1152	19.8	24.7	55.5

2.2 Measurements and blood samples

In 1991 and 1992, 15 sites were each visited for 6–10 days specifically to capture, measure and obtain blood samples from great spotted kiwi. Seven of these sites were in Northwest Nelson, three were in the Paparoa Range, two were in the Brunner Range, and three were in the Arthur's Pass–Hurunui area. The sites therefore provided coverage of each of the three populations, and included birds from both lowland and upland forests. No birds were found on the Brunner Range.

We caught kiwi either by attracting them with taped calls at night or by using a trained dog to locate them during the day. Each individual was weighed and measured, as described in McLennan and McCann (1991), and a 1 ml blood sample was taken from a leg vein. The blood was centrifuged in the field to separate the plasma from the cells, then stored in liquid nitrogen. Herbert and Daugherty (this volume) describe the laboratory procedures used to identify the genetic profiles of individuals.

3. RESULTS

3.1 Genetic analyses

Herbert and Daugherty (this volume) have reported the full results of the genetic analyses. In summary, their allozyme data (and mitochondrial cytochrome b analyses, Baker et al. 1995) confirm *A. haastii* as a full species, about as closely related to the little spotted kiwi as northern brown kiwi and tokoeka are to each other.

All species of kiwi have unusually high levels of genetic structuring, similar to that in mammals, presumably because their flightlessness inhibits gene flow between populations. There were, however, no consistent differences between the Northwest Nelson, Paparoa and Arthur's Pass–Hurunui populations of great spotted kiwi, suggesting that separation of these populations is recent. There seems to be no gene flow between lowland (at Kahurangi Point) and upland populations in Northwest Nelson, although they are connected by continuous forest occupied by kiwi. The differences between lowland and upland birds are not, however, large enough to justify splitting them into distinct races or subspecies.

3.2 Morphometrics

3.2.1 Sexual dimorphism

On average, male great spotted kiwi were much smaller and lighter than females (Table 2), a feature common to all species of kiwi. Some great spotted kiwi females weighed nearly twice as much as their mates, but the average difference between them was about 900 g, or 38% of the male's weight. Female body lengths and bill lengths were, respectively, 15% and 26% larger than those of males; and females also had stouter legs, toes and claws than did males.

There was considerable variation within each sex, so that small females overlapped in size with large males. None of our measurements provided an infallible indication of sex (Table 2), but bill length came close to it (Fig. 1). The

TABLE 2. DIMENSIONS OF FEMALE AND MALE GREAT SPOTTED KIWI.

	WEIGHT (g)	BODY LENGTH (mm)	BILL LENGTH (mm)	TARSUS DEPTH (mm)	TARSUS WIDTH (mm)	MID-TOE LENGTH (mm)	MID-TOE DEPTH (mm)	MID-TOE WIDTH (mm)	MIDDLE CLAW LENGTH (mm)
Females									
Number	29	15	29	25	25	29	15	19	25
Mean ± S.D.	3189 ± 421	93.3 ± 4.2	121.6 ± 7.1	21.2 ± 1.3	14.3 ± 1.1	60.8 ± 3.4	19.7 ± 1.5	13.0 ± 0.6	27.3 ± 3.2
Range	2300–4300	84–100	103–135	18–24	13–16	54–68	17–22	12–14	23–38
Males									
Number	39	25	41	37	37	37	23	24	35
Mean ± S.D.	2309 ± 331	81.2 ± 3.4	96.5 ± 4.9	18.9 ± 1.4	12.3 ± 0.9	57.7 ± 2.9	17.0 ± 0.9	11.7 ± 0.6	25.5 ± 2.3
Range	1750–3000	74–88	83–108	16–21	10–15	50–63	15–18	11–13	20–34
Significance									
T	-9.3	-9.9	-16.5	-6.6	-7.9	-3.9	7	7	-2.63
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.01

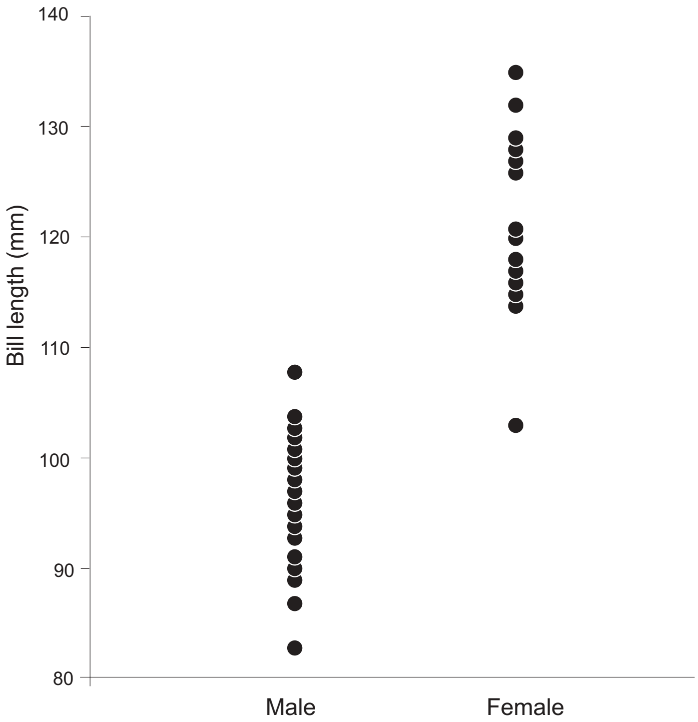


Figure 1. Bill lengths in male and female great spotted kiwi.

shortest-billed female (103 mm) overlapped with the longest-billed males (108 mm), but the two samples were otherwise discrete.

We accurately predicted the sex of all 70 adults in our samples using the product of bill length (cm), weight (kg), tarsus depth (cm), tarsus width (cm), mid-toe depth (cm) and mid-toe width (cm). These six measurements differed most between males and females. Our choice of units means that bill length has a disproportionately large influence on the final value, consistent with its importance. The six measurements are not highly correlated with each other, so exceptionally high and low values can occur within the same individual.

TABLE 3. REGIONAL DIFFERENCES IN MEASUREMENTS OF GREAT SPOTTED KIWI. THE TOE MEASUREMENT IS THE PRODUCT OF TOE LENGTH × TOE WIDTH × TOE DEPTH. STATISTICAL DIFFERENCES BETWEEN REGIONS WERE TESTED BY ANOVA: F VALUES AND SIGNIFICANCE VALUES ARE SHOWN.

	WEIGHT (g)	BODY LENGTH (cm)	BILL LENGTH (mm)	TOE (mm)	MIDDLE CLAW (mm)
Females					
Northwest Nelson					
Number	23	10	23	9	20
Mean ± S.D.	3255 ± 416	92 ± 4	121 ± 7	150 ± 23	26 ± 2
Paparoa Range					
Number	1	1	1	1	1
Mean ± S.D.	2900	95	132	164	30
Arthur's Pass–Hurunui					
Number	5	4	5	5	4
Mean ± S.D.	2940 ± 405	97 ± 2	125 ± 6	172 ± 17	32.2 ± 5
F	1.4	3.0	1.9	1.7	12.9
P	< 0.25	< 0.087	< 0.165	< 0.220	< 0.0001
Males					
Northwest Nelson					
Number	32	19	33	14	29
Mean ± S.D.	2330 ± 342	80 ± 3.0	96 ± 4	114 ± 9.0	25 ± 2
Paparoa Range					
Number	3	2	4	2	2
Mean ± S.D.	2200 ± 230	86 ± 2	100 ± 6	112 ± 15.0	27 ± 1
Arthur's Pass–Hurunui					
Number	4	4	4	4	4
Mean ± S.D.	2225 ± 340	83 ± 4	95 ± 8	130 ± 11	29 ± 4
F	0.34	3.9	1.7	4.4	7.2
P	< 0.712	< 0.033	< 0.18	< 0.028	< 0.003

TABLE 4. DIMENSIONS OF GREAT SPOTTED KIWI IN RELATION TO ALTITUDE, NORTHWEST NELSON.

	WEIGHT (g)	BODY LENGTH (cm)	BILL LENGTH (mm)
Females			
< 200 m			
Number	7	4	7
Mean ± S.D.	3017 ± 136	90 ± 5	116 ± 6
200-500 m			
Number	3	1	3
Mean ± S.D.	2933 ± 431	94	126 ± 8
> 500 m			
Number	13	5	13
Mean ± S.D.	3458 ± 420	93 ± 4	122 ± 6
F	4.8	0.6	2.9
P	< 0.02	0.6	0.075
Males			
< 200 m			
Number	7	5	8
Mean ± S.D.	2088 ± 244	79 ± 4	95 ± 6
200-500 m			
Number	9	6	9
Mean ± S.D.	2137 ± 303	81 ± 1	96 ± 3
> 500 m			
Number	16	8	16
Mean ± S.D.	2544 ± 266	81 ± 3	97 ± 4
F	9.9	0.8	1.1
P	< 0.001	0.45	0.33

The values ranged from 67 to 177 in males and from 195 to 597 in females. Adult females in exceptionally poor condition (say less than 2.2 kg) could produce values typical of males, as could juvenile females less than two years old. Ratios such as (weight × bill length)/body length might enable small and/or light females to be distinguished from males, but this remains to be tested.

3.2.2 Regional differences in body size

Our samples are too small to detect anything other than large regional differences in body size: the tentative conclusions presented here may change with additional measurements.

The body length of great spotted kiwi appeared to increase with increasing latitude (Table 3). This trend was significant for males, but not for females, perhaps because fewer of them were measured. Southern males also had significantly larger toes than those further north, but again the trend was not significant for females (Table 3). Claw length increased with latitude in both sexes.

Average weight did not differ significantly between regions, nor did tarsal diameter (not shown in Table 3). Kiwi in the Paparoa Range appeared to have longer bills than those elsewhere, but more measurements are needed to confirm this.

3.2.3 *Altitudinal differences in body size*

Overall, there were few significant correlations between body size and altitude when data from all regions were combined (data not presented). Bill length tended to increase with altitude, but only in females ($F = 4.7$, $N = 29$, $p = 0.018$).

Within Northwest Nelson, however, body weight increased significantly with altitude in both sexes (Table 4). Males in coastal forests, less than 200 m above sea level (a.s.l.), were on average 18% lighter than their counterparts in alpine and subalpine areas, 500 m or more asl. The equivalent difference for females was 13%. These weight changes were not associated with significant differences in body length, although the smallest birds in our samples were from coastal forest. Upland birds possibly have more fat than lowland ones, for insulation against the cold.

3.2.4 *Other altitudinal and regional variations*

Leghold trap injuries

Seven of the 70 birds in our sample had lost toes, presumably in leghold traps set for possums (*Trichosurus vulpecula*). One bird had injuries on both feet, indicating that it had been caught on two separate occasions. Birds with foot injuries were significantly more common in lowland forests of Northwest Nelson than elsewhere. Six (40%) of 15 birds at Kahurangi Point and Karamea had missing and/or broken toes, compared with none out of 40 in upland regions of Northwest Nelson, and none out of five in the Paparoa Range. One of eight in the Taramakau catchment had foot injuries.

These figures under-rate actual capture rates in leghold traps because they exclude those kiwi (an unknown proportion) that receive fatal injuries. Furthermore, our survey was preceded by several years of poor prices for pelts, when few people trapped possums: our records of leg injuries might therefore be at a cyclic low. Even so, they show clearly that incorrectly set leghold traps are a significant hazard for kiwi, especially in areas accessible to weekend hunters.

Eye injuries

Two kiwi (3%) were blind in one eye. These birds were otherwise in good health, judging from their weight and overall appearance. This incidence of partial blindness is much lower than that among brown kiwi at Okarito (20%; J. Lyall, pers. comm.) but similar to that in brown kiwi in the North Island (1%; J. McLennan, pers. obs.).

Colour

Some kiwi had a sprinkling of white feathers on their nape and flanks: the frequency of such partial albinism did not vary noticeably between regions. Kiwi with pigmented claws were more numerous in Northwest Nelson than elsewhere (McLennan & McCann 1993), and kiwi with entirely dark claws were recorded only in Northwest Nelson. Claw pigmentation levels did not change within individuals over time, so regional differences in claw colour did not reflect differences in the age structure of populations. Pigmentation levels also varied in leg and foot scales, from pale brown to dark brown. One bird in the lower Ohikanui Valley in the Paparoa Range had pinkish-white legs and feet, similar to those of little spotted kiwi.

Vocalisation

We did not notice any marked differences in the calls of great spotted kiwi between regions.

3.3 Distribution and abundance

3.3.1 *Distribution of samples*

Night-time counts of calls were undertaken throughout the known and suspected range of great spotted kiwi in five districts in the northwest of the South Island. We split Northwest Nelson into northern and southern parts ('northern Northwest Nelson' and 'southern Northwest Nelson'), differentiated by climate and landform and demarcated from each other by the Karamea River. A large area in inland North Westland was surveyed, including the Brunner and Victoria Ranges, and the Maruia and upper Grey valleys. Most surveys in the Arthur's Pass–Hurunui district were undertaken within 30 km of the Arthur's Pass township. This district has no clear boundaries that delineate it from the mountains to the north and south, but the remaining districts are all clearly defined by roads and rivers.

At least 85 listening watches were undertaken in each district (Table 1). Some sites were sampled up to three times on different nights, but most were surveyed just once. There were fewer samples from remote areas, especially the Paparoa Range and southern Northwest Nelson. Coverage in northern Northwest Nelson and in Arthur's Pass–Hurunui was exceptionally good. Overall, the combined sample from all districts comprised 617 listening watches and 1152 hours of listening.

3.3.2 *Distribution of great spotted kiwi*

Total study area

The populations in each district, and in the total study area, are summarised in Table 5.

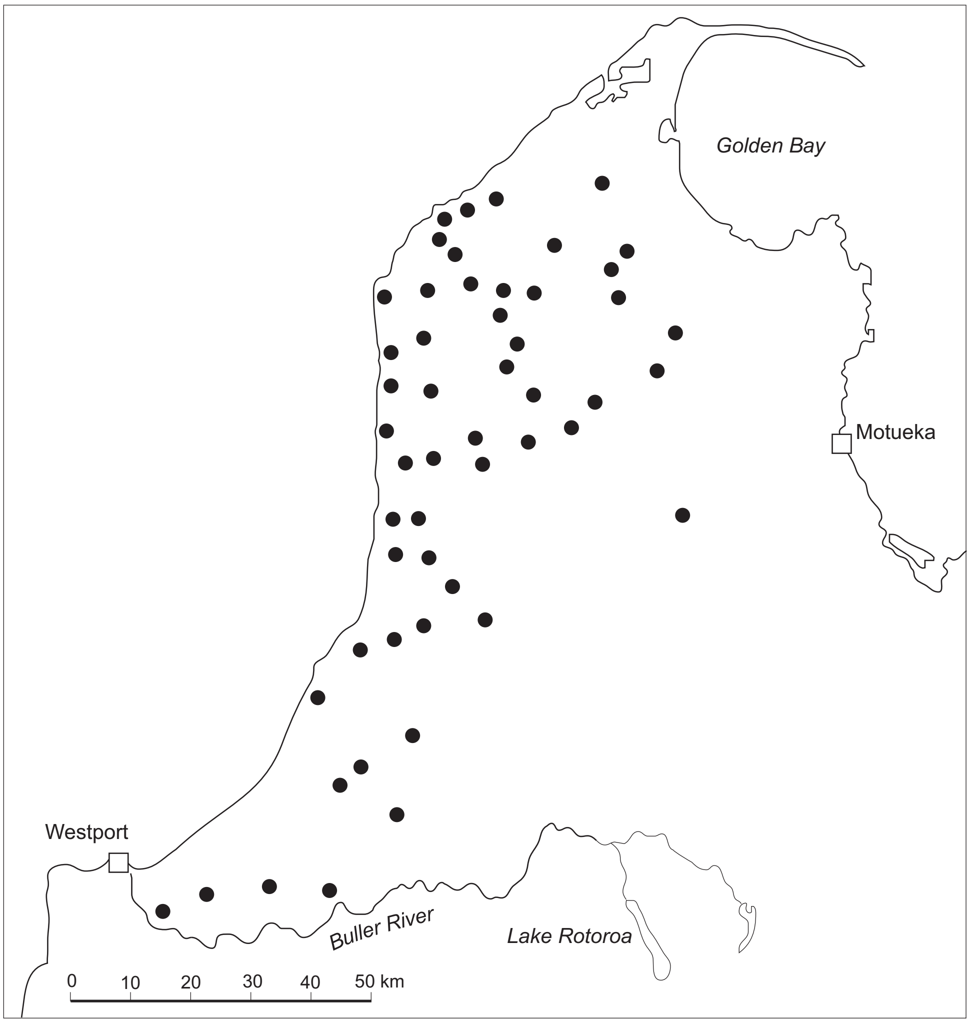
Northern Northwest Nelson

Great spotted kiwi were detected during 96 (63%) of 153 listening watches in northern Northwest Nelson, in a diverse range of habitats, from sea level to alpine scrub and grasslands (Fig. 2). Most records were from the mountains inland and south of Golden Bay. The Aorere River, flowing into Golden Bay, supports kiwi on both banks, at least in its middle and upper reaches. The ranges along its eastern bank contain scattered populations, but these peter out

TABLE 5. APPROXIMATE DISTRIBUTION AREA, AND SIZES OF EXTANT GREAT SPOTTED KIWI POPULATIONS.

DISTRICT	AREA (km^2)	ESTIMATEI
Northwest Nelson (North)	1550	10 0(
Northwest Nelson (South)	1050	
Paparoa Range	2100	
Arthur's Pass-Hurunui	1260	
Total	5960	2

Figure 2. Distribution of great spotted kiwi (dots) in Northwest Nelson.



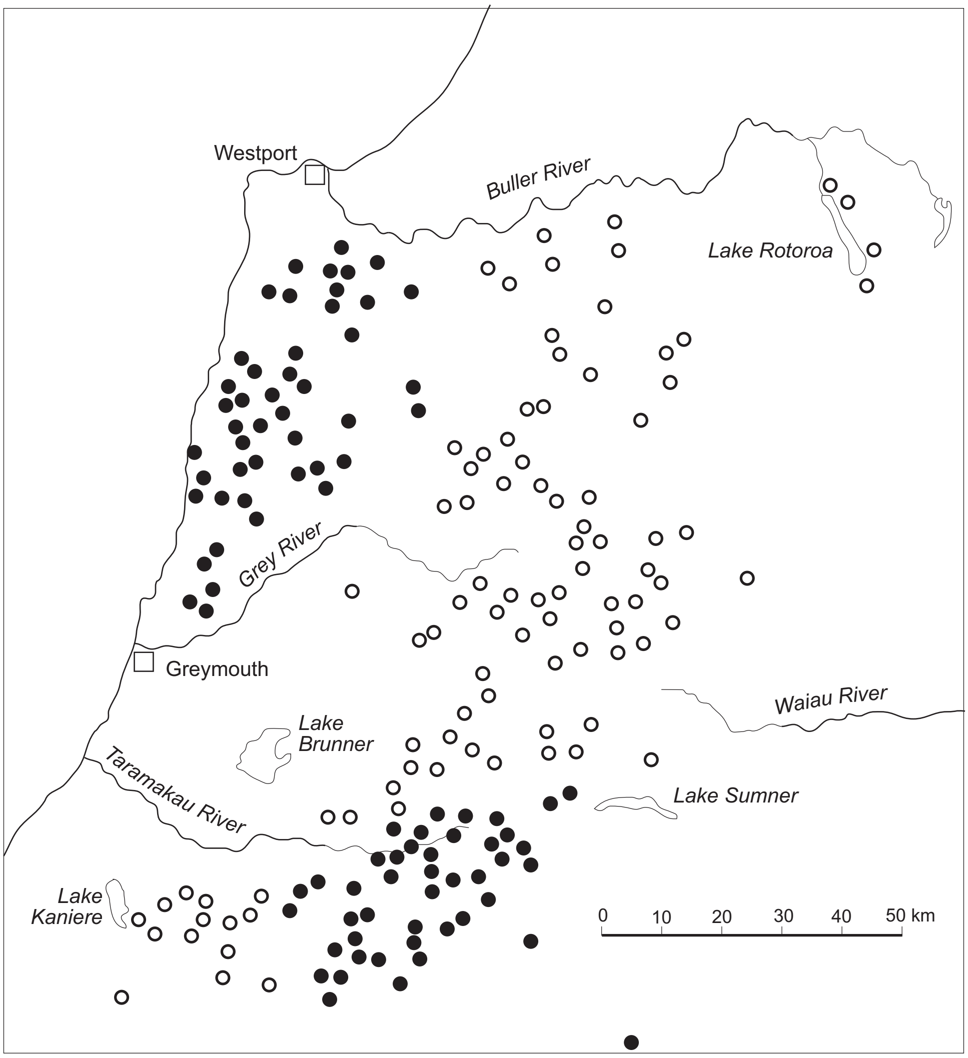
a few kilometres north of Boulder Lake. Kiwi are widespread in the Wakamarama Range to the west of the Aorere River, at least as far north as the Kaituna River. Forested catchments draining the western flanks of the Wakamarama Range support great spotted kiwi, from the summit of the range to the tidal estuaries. Kiwi are also widespread in coastal vegetation from Kahurangi Point south to the Kohaihai River.

Great spotted kiwi range as far east as the Waingaro River (a tributary of the Takaka River). There appear to be no great spotted kiwi in the Takaka River catchment itself, in Abel Tasman National Park, on the Takaka Hill, in the Peel Range, in the Cobb River catchment, or at the northern end of the Arthur Range. A female great spotted kiwi was seen on Mt Arthur in 1980 and again in 1990 at two sites, some 6.5 kilometres apart. The 1980 observation almost certainly involved a bird that had been caught by a toe in a leghold trap set for possums. According to local rumour it had been flown out from the Karamea River, rehabilitated in 'town', then released on Mt Arthur. The 1990 observation may have been of the same bird. There are no other records of kiwi from the Arthur Range, so it is questionable whether the 'population' there is natural or introduced.

Nearly all listening watches from the headwaters of the Aorere River, the Gouland Downs, the Tasman Mountains, the Oparara River and the northern tributaries of the Karamea River recorded kiwi, indicating that the birds are

Figure 3. Distribution of great spotted kiwi in the Paparoa, Brunner–Victoria–Maruia and Arthur's Pass–Hurunui districts: dots indicate presence, circles show sites where no kiwi were recorded.

Notes: (1) Records shown in the Lewis Pass and Nelson Lake areas are not included in Table 1. (2) Sites in the Paparoa and Arthur's Pass–Hurunui districts at which kiwi were not recorded are not shown.



distributed both widely and continuously through some 1550 km^2 of upland and subalpine vegetation.

Assuming an average density of 3–4 pairs per km^2, as measured by McLennan and McCann (1991) in the forests of Kahurangi Point and the Saxon River, northern Northwest Nelson probably contains about 10 000–11 000 kiwi.

Southern Northwest Nelson

Great spotted kiwi were detected during 34 (40%) of 85 listening watches in southern Northwest Nelson. The results of 159 hours of listening indicate that great spotted kiwi are present in the northern and southern sections of the district, but are rare and sometimes absent altogether within its central regions (Fig. 2). The birds appear to be widespread in the mountains between the Karamea River and Little Wanganui River, and may extend as far east as the southern tip of the Arthur Range. Trampers often hear them near the Wangapeka track, in the headwaters of the Karamea and Little Wanganui rivers. Numbers decline immediately to the south of the Little Wanganui River. One kiwi was heard (and seen) in the Mokihinui River near the junction of the North and South branches; another male was recorded during 6 nights of listening in the middle reaches of the South Branch.

Kiwi were heard in the lowland forests on the north bank of the Buller River and in the foothills of the Mount William Range, on the edge of regenerating farmland. The birds are probably also scattered throughout the Orikaka State Forest and upper reaches of the Ngakawau River, but these areas were not sampled[1]. A juvenile great spotted kiwi was hit by a car in the Buller Gorge in 1994, near Lyell Creek on the edge of Orikaka State Forest. This is the easternmost record of kiwi in the Buller region.

Southern Northwest Nelson probably contains about 2000 kiwi, assuming an average density of one pair per km^2 and an occupied area of 1050 km^2. This estimate is little more than a guess and could well change after further sampling.

Paparoa Range

Kiwi were detected during 77 (73%) of 106 listening watches in the Paparoa district. The birds are scattered throughout the main range, on both the eastern and western sides (Fig. 3). They are also present in the catchments of the Ohikanui and Blackwater rivers, which drain northwards into the Buller River. The birds extend westwards into the coastal forests and pakihi in the lower reaches of the Nile, Fox and Punakaiki rivers, and are present in some remnant patches of vegetation on the coastal plain south of Westport. They are also present in the cutover forests in the Nile River, in regenerating scrub and gorse on gold workings near Charleston, and in lowland pakihi vegetation a few kilometres south-west of Reefton.

The Paparoa population is spread more-or-less continuously over some 2100 km^2. It probably comprises some 6300 kiwi, assuming a mean density of 1.5 pairs/km^2, about half that in northern Northwest Nelson.

Brunner and Victoria ranges and Maruia and Grey Valleys

Kiwi were not recorded in the Brunner and Victoria Ranges, in the catchments of the Maruia and upper Grey Rivers, or at Lewis Pass (Fig. 3).

Arthur's Pass–Hurunui

Great spotted kiwi were recorded in the Arthur's Pass–Hurunui district in catchments draining both sides of the Main Divide (Fig. 3). On the western side, the birds were found in the upper reaches of the Taipo River, the middle and upper reaches of the Taramakau River, and the Otira River. They extend north of the Taramakau River into the headwaters of the Trent and Haupiri Rivers, but not beyond this. They appear to be absent in the Arahura and Styx Rivers, even though the headwaters of these valleys are close to those of the Taipo River.

Great spotted kiwi have a more extensive range on the eastern side of the Divide. They are present around Arthur's Pass township and its neighbouring catchments. They extend northwards to Lake Sumner and possibly as far as the upper reaches of the Hope River. They do not however generally extend more than 12–14 km from the central mountain chain; the easternmost records are from the North Esk, the South Branch of the Hurunui River, and the Puketeraki Range.

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1 Later surveys indicate great spotted kiwi are widespread and abundant in the catchments of Orikaka and Ngakawau rivers. The population in Northwest Nelson (South) is now estimated to be 3000 birds, and the total great spotted kiwi population to be 23 000 birds.

The population in the Arthur's Pass–Hurunui district inhabits an elongated strip of the Southern Alps, some 60 km long and 18–23 km wide. Much of this land is above the tree line, unstable, and exceptionally steep; it is unsuitable for great spotted kiwi except, perhaps, in the height of summer when the land is largely free of snow and ice. The birds live almost entirely in the forested valleys between the various mountain ranges and in the alpine shrublands along their margins. This means the overall density of kiwi throughout the district is relatively low—about 2-3 per square kilometre. The total population is probably about 3000 kiwi.

No great spotted kiwi were found during recent extensive surveys in the large river catchments south of the Waimakariri and Taipo Rivers (Jolly 1992).

3.3.3 *Mean call rates*

Regional differences

There is undoubtedly some correlation between mean call rates and kiwi density, although the form and closeness of the relationship are largely unknown. Mean call rates were 2–3 times higher in northern Northwest Nelson (3.3/h) than in the Paparoa Range (1.8/h), Arthur's Pass–Hurunui (1.1/h) and southern Northwest Nelson (0.9/h, Table 6). The same results emerged when zero counts were omitted from the analyses, suggesting that regional differences in mean call rate reflect real changes in kiwi density within occupied habitats. Call counts from such areas sometimes exceeded 15 per hour in northern Northwest Nelson, but seldom reached 6 per hour in the southern districts.

Mean call rates in relation to altitude

In parts of Northwest Nelson and the Paparoa Range, great spotted kiwi inhabit forests that extend continuously from the coast to the tree-line (1100–1300 m a.s.l.). The forests themselves change in composition with increasing altitude, as do a range of other environmental factors such as mean temperature and rainfall. One or more of these variables appear to influence great spotted kiwi

TABLE 6. MEAN CALL RATE OF KIWI IN VARIOUS DISTRICTS IN THE NORTH-WEST OF THE SOUTH ISLAND. STATISTICAL CONVENTIONS AS IN TABLE 3.

POPULATION	NUMBER OF LISTENING WATCHES	MEAN CALL RATE/HOUR ± S.D.
Northwest Nelson (North)	153	3.3 ± 4.8
Northwest Nelson (South)	85	0.9 ± 1.8
Paparoa Range	106	1.8 ± 2.3
Arthur's Pass–Hurunui	151	1.1 ± 1.7
Brunner–Victoria–Maruia	110	0 ± 0
Elsewhere (Reefton–Ahaura)	12	0.15 ± 0.34

Significance (Anova)	F	P
Overall	22.1	< 0.0001
Northwest Nelson (South) vs Paparoa	96	< 0.002
Northwest Nelson (South) vs Arthur's Pass–Hurunui	1.5	< 0.229
Paparoa Range vs Arthur's Pass–Hurunui	7.8	< 0.006

TABLE 7. MEAN CALL RATE OF KIWI IN RELATION TO ALTITUDE IN NORTH-WEST NELSON AND THE PAPAROA RANGE. CONVENTIONS AS IN TABLE 3.

ALTITUDE (m)	NUMBER OF OBSERVATIONS	MEAN CALL RATE/HOUR ± S.D.
Northwest Nelson (North)		
< 200 m	46	1.9 ± 2.4
200-500 m	20	2.0 ± 2.1
501-800 m	36	4.9 ± 5.1
> 800 m	49	4.0 ± 6.3
	F = 3.8, P = 0.012	
Paparoa Range	50	
< 200 m	50	1.3 ± 1.8
200-500 m	25	2.2 ± 3.0
501-800 m	8	1.9 ± 1.3
> 800 m	22	2.5 ± 2.6
	F = 1.9, P = 0.144	

density: in both districts, the birds increased in abundance at higher altitudes (>500 m), although the trend was significant only in Northwest Nelson (Table 7). Few kiwi in the Arthur's Pass–Hurunui district were recorded at altitudes below 500 m a.s.l.

Mean call rates in relation to distance from the Tasman Sea

On the west coast of the South Island, temperature and rainfall change markedly over relatively short distances. The mountain ranges parallel and adjacent to the coast intercept moist westerly winds sweeping in from the Tasman Sea, and so are both wetter and have more equable climates than otherwise similar ranges a few kilometres further inland. There are significant vegetation changes along these environmental gradients.

In Northwest Nelson and the Paparoa Range, great spotted kiwi penetrate up to 38 km inland from the coast. Their densities, as indicated by mean call rates, follow a bell-shaped curve with increasing densities inland: numbers initially rise to a peak 10–25 km from the coast, then decline to zero at about 40 km (Table 8). The birds, then, are not distributed evenly in these two adjoining mountain ranges. The Arthur's Pass–Hurunui population, by comparison, is situated much further inland, some 41–88 km from the coast.

TABLE 8. MEAN CALL RATE OF KIWI IN RELATION TO DISTANCE FROM THE TASMAN SEA. DATA FROM NORTHWEST NELSON AND THE PAPAROA RANGE.

	DISTANCE FROM THE TASMAN SEA (km)					
	0–5	5.1–10	10.1–15	15.1–20	20.1–25	> 25
Number	66	54	23	24	28	64
Mean calls/h ± SE	1.9 ± 0.3	3.0 ± 0.5	5.0 ± 0.9	4.3 ± 1.1	4.7 ± 1.3	0.9 ± 0.2

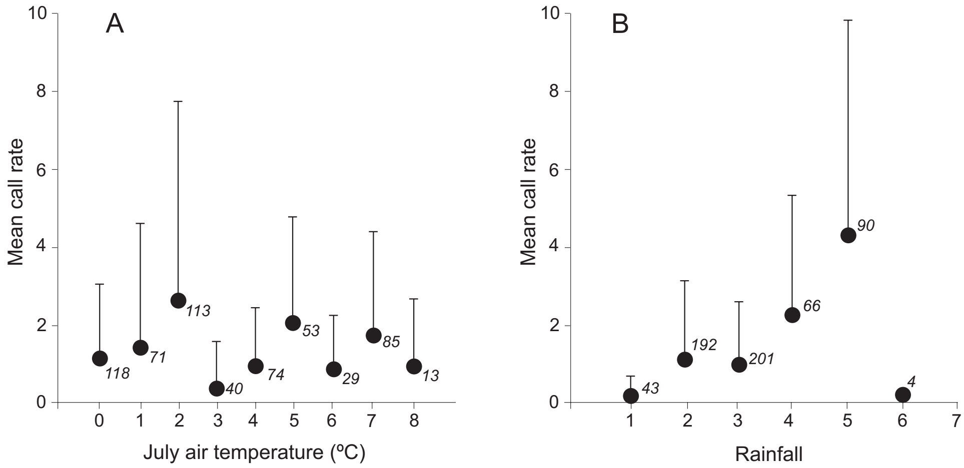

Figure 4. Relationship between mean call rates (calls/h) of great spotted kiwi and mean July air temperatures (A) and rainfall (B). Rainfall codes: 1, 1600–2400 mm; 2, 2401–3200 mm; 3, 3201–4800 mm; 4, 4801–6400; 5, 6401–9600 mm; 6, >9600 mm.

Mean call rates in relation to temperature and rainfall

Great spotted kiwi live in a wide range of environments spread along two principal climatic gradients. Mean winter (July) air temperatures in their present range vary by about 8ºC, and annual rainfall varies by about 7000 mm.

Mean call rates were not correlated with winter temperatures, but they increased significantly with rainfall (Fig. 4), peaking in areas receiving 6400–9600 mm per year. No parts of the northwest of the South Island receive more than 9600 mm a year, other than a narrow alpine zone immediately to the south-west of Arthur's Pass: no kiwi were recorded there.

Partial correlation coefficients indicate that rainfall has a much stronger relationship with kiwi abundance than either altitude or distance inland. The latter variables ceased to be significant when the effect of rainfall was held constant. This suggests that the birds have no strong associations with particular vegetation types, landforms or temperature zones. Overall, annual rainfall (based on partial coefficients) accounted for 12% of the variation in mean call rates throughout the range of great spotted kiwi, and 19% of the variation within Northwest Nelson.

4. DISCUSSION AND CONCLUSIONS

4.1 Present distribution of great spotted kiwi

The surveys indicate that there are currently about 22 000 great spotted kiwi distributed over some 6000 km^2 in the north-west of the South Island. Northern Northwest Nelson, from Karamea to Golden Bay, is the stronghold of the species. It comprises about 25% of the known range of great spotted kiwi, yet it supports about 55% of the total population. The birds here occupy some 1500 km^2 of predominantly mountainous landscape, largely untouched by humans. The area has little farmland, no commercial forestry plantations, and few roads. The habitat has a high area-to-edge ratio and few exposed margins, where the birds border on modified rather than natural landscapes.

Numbers diminish rapidly in southern Northwest Nelson, between the Karamea and Buller Rivers. This landscape is generally less mountainous and more modified. The coastal plains have been cleared for farming, and many of the native forests in the coastal foothills have been burnt or logged. The less modified habitats further inland support kiwi, but populations are sparse, fragmented and apparently declining.

The Paparoa population, with some 6000 birds (c.30% of the total population) is second in size to that in northern Northwest Nelson. The large size of the Buller River in its middle and lower reaches, and the loss of merging populations from its headwaters, probably now severely restrict gene flow between the Paparoa and Northwest Nelson populations. Densities throughout the Paparoa Range appear to be fairly uniform: call rates in disturbed habitats near the coast were often similar to those in the mountain valleys within the range itself. The habitat has a relatively high area-to-edge ratio and a continuous distribution, but is flanked on all margins by modified habitats.

The Arthur's Pass–Hurunui population differs from the northern ones in that it is much further inland and its habitat is almost entirely upland vegetation ($\geq$500 m a.s.l.). Here kiwi occupy a relatively narrow, elongated strip of approximately 1260 km^2: the habitat therefore has no core as such, diffuse boundaries, and a very high edge-to-area ratio. There are no obvious features that confine the birds to certain areas, and in some instances kiwi abundance differs markedly in neighbouring and apparently similar catchments (e.g. upper Taramakau and Crooked River valleys).

Several general points emerge from the surveys. Most great spotted kiwi now live in mountainous regions; densities are generally higher above 500 m a.s.l. than below; the birds are habitat generalists rather than specialists; and, although ground feeders, they are capable of surviving in areas where soils are sometimes frozen or covered in snow for days at a time. For all that, their distribution is patchy: factors other than geographical ones appear to limit populations in some areas, and birds are sometimes absent altogether from areas with apparently suitable habitat.

The present distribution of great spotted kiwi appears to be linked primarily to high rainfall: this is the single factor common to all three populations. Rainfalls of $\geq$6000 mm/year are typically associated with mountainous areas, but altitude *per se* appears to have no direct effect on kiwi abundance, irrespective of its influence on mean temperature and vegetation. Rainfall is also unlikely to have a direct effect on kiwi abundance. We suspect, however, that it influences the abundance and composition of predator communities (chiefly stoats, *Mustela erminea* and possums, *Trichosurus vulpecula*), which in turn impact on kiwi productivity and abundance. It appears that the present distribution of great spotted kiwi is a remnant one, that the species' range is still retreating to regions of high rainfall, and that introduced predators are driving these changes. This view is expanded in the following sections.

4.2 Historical distribution of great spotted kiwi

Great spotted kiwi are no longer as widespread as they used to be. Subfossil remains indicate the species extended into coastal regions of Canterbury before Polynesian settlement (Reid & Williams 1975). Other subfossil bones in eastern Marlborough, South Canterbury and Southland hint at an even wider distribution, although these remains could be of brown kiwi.

The recent distribution of great spotted kiwi in South Westland and Fiordland is uncertain. Oliver (1955) reported that great spotted kiwi extended south to Foveaux Strait, but J. Jolly (pers. comm.) believes that the species did not extend beyond the Karangarua River in Westland. Some specimens in the Canterbury Museum were supposedly collected in South Westland and Fiordland (Oliver 1955) but neither Charles Douglas (Pascoe 1957) nor Richard Henry (Hill & Hill 1987) recorded the birds during their early expeditions into these areas. Jolly's view, that the museum specimens have been mislabelled, might therefore be valid.

Recent changes in distribution elsewhere in Westland and Nelson are better documented, especially those occurring in the last few decades. Jolly (1992) and Stilwell and Barnett (1993) consider that great spotted kiwi have disappeared from the large mountain valleys of Westland, the type locality of the species. The birds, though, have been rare in central Westland for at least a century: Charles Douglas found just one pair of 'mountain kiwi' (between the Karangarua and Cook Rivers) during his extensive travels in the region (Pascoe 1957). Nevertheless, kiwi (presumably great spotted) were still present in the headwaters of the upper Wanganui and Waitaha Rivers as recently as 1978 (C. Roderick, unpubl. data); and a carcass of a spotted kiwi (now in the Canterbury Museum) was recovered from the Smyth River in 1978 (Jolly 1992). Jolly (1992) believes this specimen is a great spotted kiwi; R. Colbourne (pers. comm.) thinks it is a little spotted kiwi. DNA tests are currently underway to reveal its true identity.

Views differ on the extent to which the Arthur's Pass–Hurunui population has contracted in the last 50 years. A local farmer reports kiwi were numerous in the catchment of the Haupiri River in the 1940s; other locals, whose visits to the Haupiri also span 50 years, have never encountered kiwi there (Barker 1993). The last confirmed record of great spotted kiwi in the lower catchment of the Crooked River (a bird caught by a possum trapper) dates to the mid-1970s (Barker 1993). Kiwi appear to be holding on elsewhere on the western side of the Southern Alps. The distribution of the highly localised population in the upper Taipo River has changed little since 1966 (C. Roderick, unpubl. data); and the same is true of the Taramakau population, except that it may have contracted slightly upstream.

Little historical information exists for the population of great spotted kiwi on the eastern side of the Alps. C. Roderick (unpubl. data) lists various locality records, some dating back to 1949, from the Poulter, Cox and Hurunui Rivers, in the same areas where the birds are present today.

Few, if any, kiwi survive in the catchments of the Ahaura, Grey and Inangahua Rivers, or in the Spenser, Victoria and Brunner Ranges. These populations disappeared within living memory, some within the last 20 years (see Barnett & Stilwell (1993) for details of interviews with local residents). Kiwi were plentiful around Springs Junction in 1905, and present in the Brunner Range in 1928. Locals note that kiwi disappeared when stoats arrived. Residual pockets of kiwi survived in the Robinson River (a tributary of the Grey) at least until the mid-1970s (C. Roderick, unpubl. data); and a few may still survive at Big River, some 18 km south of Reefton (Barnett & Stilwell 1993). These accounts indicate that the now disjunct populations in the Arthur's Pass–Hurunui area and Paparoa Range were linked together at the turn of the century.

The pattern of kiwi decline is much the same in the Nelson district. Kiwi were widespread in the Nelson Lakes Region in the mid-1800s, though the species involved is unknown. This population is now almost certainly extinct, although kiwi-like calls (all unconfirmed) are still reported almost every year from within the National Park. The populations of brown and little spotted kiwi in Abel Tasman National Park and the Marlborough Sounds disappeared in the early 1900s (Oliver 1955). Subfossil remains indicate the recent presence of great spotted and/or brown kiwi in the Arthur Range (T. Worthy, pers. comm.). More recently, great spotted kiwi have declined noticeably in lowland coastal forests, at least in the vicinity of Kahurangi Point (comments from a daughter of one of the lighthouse keepers, who spent her childhood there in the 1940s).

4.3 Introduced mammalian predators as the cause of great spotted kiwi decline

At a conservative estimate, the distribution of great spotted kiwi has contracted by about 30% since European settlement. The birds have declined most in dry areas (<2500 mm/yr) dominated mainly by beech forest (*Nothofagus*), but have persisted in wet habitats, usually at high altitude. Their pattern of retreat resembles that of other flightless birds (e.g. takahe and Lord Howe woodhen) whereby the survivors have ended up near the tops of mountains, presumably in habitats less favourable to the agent(s) of decline.

The tenuous link between the decline of kiwi (and other birds) and the arrival of predators (chiefly stoats) suggested in some historical accounts may indeed be causal rather than casual. Video surveillance confirms that both stoats and possums attempt to enter kiwi nests, but are usually repelled by the incubating adult(s) (J. Lyall, pers. comm.). Nevertheless, they do eat some eggs (McLennan 1988) and probably cause others to be damaged and abandoned. Stoats also kill juvenile kiwi (J. Lyall, pers. comm.; J. McLennan & L. Dew, unpubl. data) but not adults except, perhaps, those of little spotted kiwi. Indirect measures indicate that mortality of juvenile kiwi is much higher in mainland forests than on Kapiti Island, an offshore island free of stoats and possums (McLennan & Potter 1993).

Evidence of predation is not proof that these mammals have caused the changes in kiwi distribution in the recent past. King (1984) warned that observations made during the irruptive phase of stoat colonisation are unlikely to apply today. Nevertheless, stoats at present-day densities are still sufficiently numerous to cause declines in several endemic bird species, including Okarito brown kiwi (J. Lyall, pers. comm.), yellowhead (Elliot & O'Donnell 1988) and kaka (P. Wilson, pers. comm.).

In beech forests, stoats increase in abundance following mast years, apparently in response to increased numbers of mice (King 1983). Predation on birds increases when stoat numbers increase, and may be particularly severe in the months immediately following the decline of mice. In other mainland forests, stoats eat more birds and fewer rats (*Rattus* spp.) following rodent control (Murphy & Bradfield 1992). Stoats probably do not 'boom and bust' in forests with a diverse composition, although they sometimes reach moderate densities in lowland podocarp forests on the West Coast (J. Lyall, pers. comm.). King (1983) noted that the predictability of the relationship between seedfall and populations of mice decreased with increasing diversity of forest composition.

Most of the forests currently occupied by great spotted kiwi contain beech, and those above the altitudinal limit of rimu are dominated by beech. Although there are no measures of stoat abundance in any of the forests of Northwest Nelson and the Paparoa Range, they (and other mammals) appear to be rare in upland beech forests in high rainfall areas. McLennan and McCann (1991) observed stoat sign just twice in four years in the Saxon River area of Northwest Nelson. Ferrets (*Mustela furo*), feral cats (*Felis catus*), goats (*Capra hircus*) and pigs (*Sus scrofa*) were absent altogether, while red deer (*Cervus elaphus*), possums, rats and mice (*Mus musculus*) were present in low numbers. McLennan and McCann (1991) proposed that the climate was too harsh for most introduced mammals; and that in such areas, the relationships between beech seed, rodents and stoats established elsewhere either do not exist or occur irregularly. This hypothesis remains to be tested.

In summary, stoats probably caused the demise of great spotted kiwi in the relatively dry and uniform beech forests in the central regions of the upper South Island. Other predators may have also contributed to the decline, although historical accounts suggest that the main changes took place before possums arrived. Predators apparently do not have the same impact in high rainfall areas, possibly because of increased forest diversity, and because the harsh climate limits their abundance.

The patterns of decline evident in great spotted kiwi also apply to kiwi elsewhere in the South Island. The localised Haast tokoeka population of 200–300 birds is now mostly found in subalpine and alpine habitats (J. Lyall, pers. comm.). In Fiordland, southern tokoeka have largely disappeared from Preservation and Chalky inlets (J. McLennan, pers. obs.), which receive much lower rainfall than do the fiords further north. The remnant population of northern brown kiwi in lowland forest at Okarito appears at first glance to be an exception. But preliminary studies indicate that stoats kill most of the young produced by these birds, and the population as a whole will not persist unless predation rates are reduced (J. Lyall, pers. comm.).

Finally, the apparent vulnerability of little spotted kiwi to introduced predators may be related to their habitat requirements as well as to their small size. Their preference for relatively dry and warm northern slopes (Richard Henry, quoted by Hill & Hill 1987) was probably also shared by introduced predators, especially in the rain forests of Fiordland. Little spotted kiwi may still survive in the South Island: our results suggest that remnant pockets, if they exist at all, are most likely to be located in subalpine regions.

4.4 Conservation status

4.4.1 Populations and management units

Great spotted kiwi are now split into two discrete populations—possibly three, if the Buller River prevents gene flow between birds in Northwest Nelson and the Paparoa Range. All populations are genetically similar, suggesting separation is recent, but have high variation, indicating restricted gene flow between localised groups (Herbert & Daugherty, this volume). Patterns in genetic variation are paralleled by some variation in morphological characters with latitude and altitude.

The view that populations rather than species are the appropriate management units for conservation (Crozier 1992) is especially relevant to great spotted kiwi where morphological characteristics and genetic profiles sometimes differ over short distances. Indeed, each regional population is clearly a population of populations (a metapopulation as defined by Hanski & Gilpin 1991) with no distinct boundaries between localised groups. For example, the genetic differences between great spotted kiwi at Saxon River and Kahurangi Point exceed those between (a) North Island and Okarito populations of brown kiwi, and (b) Kapiti Island and D'Urville Island populations of little spotted kiwi (Herbert & Daugherty, this volume). The Saxon and Kahurangi populations are separated by 700 m of altitude and 15 km of forest, occupied from the bottom to the top by kiwi. It is not clear what mechanisms prevent gene flow along this altitudinal gradient, how separation is maintained, and where the two populations diverge. Differences in the mean body weight of Kahurangi and Saxon kiwi are probably related to temperature-induced differences in fat storage and metabolism, rather than genetics (Bednekoff et al. 1994).

Conservation managers need to decide whether efforts to conserve great spotted kiwi should focus on the species or population level. In the former case, the species would be treated as a single homogenous group, minor losses of localised populations would be of little consequence, and the success or otherwise of management would be determined solely by a count of total numbers. In the latter case, the emphasis switches to the maintenance of genetic and morphological diversity and localised extinctions become important, even if the species as a whole is not threatened.

Recent molecular genetic and other taxonomic studies have revealed hitherto unappreciated genetic diversity in geographically isolated populations of many species (e.g. Herbert & Daugherty, this volume). Few would dispute that a population focus is the better option—but it is probably unrealistic in a world with limited resources. In reality, the focus will probably settle on the three large kiwi populations, principally for logistic reasons, and this could well be a reasonable compromise.

4.4.2 Persistence and stability of remaining populations

The three remaining populations of great spotted kiwi each contain a minimum of several thousand breeding adults. All of them therefore exceed Frankel & Soulé's (1981) estimate of the minimum effective population size for the maintenance of genetic variance (500 individuals), but only two of the three populations exceed the more stringent criteria (5500 individuals) identifed by Thomas (1990).

The large population in northern Northwest Nelson may be stable in core areas, but is not stable along its edges. McLennan and McCann (1991) recorded a slight decline in adult density over four years at Saxon River; and a repeat survey in 1994 confirmed that 10 territories occupied in 1991 still contained resident pairs (H. Robertson, pers. comm.). These early signs are encouraging, but it would be risky to assume that all core populations are holding their own, and there is an urgent need to monitor more of them.

At Kahurangi Point, on the western edge of Northwest Nelson, adult densities declined significantly between 1987 and 1990, chiefly because of pig hunting and possum trapping (McLennan & McCann 1991). Coastal forests immediately to the south of Kahurangi are less accessible to people, so their kiwi populations may be declining at a slower rate. Genetic evidence (Herbert & Daugherty, this volume) clearly implies that migrants dispersing down from the hills will not rescue failing lowland populations. Overall, a very small proportion of kiwi in northern Northwest Nelson live in lowland areas, so the regional population would decline only slightly if these were lost. The losses in genetic variation, however, could be of much greater significance.

None of the populations in southern Northwest Nelson has been monitored, but it is here that kiwi may decline significantly over the next few decades. The region has four high-rainfall zones centred on mountain ranges, separated from each other by valleys with sparse and apparently declining populations of kiwi. Three of these upland populations (on the Allen, Matiri and Glasgow Ranges) will probably soon become islands in a sea of uninhabited lowland forest, analogous to populations in bush remnants in agricultural landscapes. The fourth population is centred on Garibaldi Ridge and the Herbert Range, rising from the south bank of the Karamea River. It is contiguous with the large population in northern Northwest Nelson, and may be part of it, since kiwi probably cross the Karamea River from time to time.

Small, capped populations face a number of special problems, reviewed by Caughley (1994) and others. Demographic and environmental stochasticity can cause chance extinctions; and for isolated populations, size is the dominant factor influencing the rate of local extinction (Diamond 1984).

Population viability analyses are beyond the scope of this report and we do not have the necessary data to run them. They would nevertheless probably confirm the obvious: the Allen Range remnant has the greatest risk of extinction because it is the smallest, and the Glasgow Range population the lowest risk because it is the largest. All populations could be in trouble if they are subject to significant predation in their upland habitats: this is unknown.

The size, continuous distribution, and area occupied by the Paparoa population suggests that it is not in any immediate danger. The population is centred on a high-rainfall zone of some 840 km^2, about 40% of the total area occupied by this population.

The prospects for the Arthur's Pass–Hurunui population are gloomy. The occupied area is so narrow that a relatively small localised extinction, perhaps in a single valley, could fragment the population. The southern-most birds in this population live in much wetter habitats than those in the north: indeed, the forests above Lake Sumner receive less than 2400 mm a year and are some of the driest still inhabited by great spotted kiwi. Coincidentally, perhaps, the area has one of the few populations of yellowhead (*Mohoua ochrocephala*), a species susceptible to stoat predation, still extant outside of Fiordland (O'Donnell 1996). This suggests that historical predation rates have been lower here than elsewhere, although stoats are causing this population of yellowhead to decline (Elliot & O'Donnell 1988).

We predict that great spotted kiwi in the Arthur's Pass–Hurunui district will gradually 'retreat' southwards and westwards to high rainfall areas. Indeed, the process is probably already well advanced. In the meantime, the eastern side of Arthur's Pass, with its steep rainfall gradient, offers an excellent opportunity for testing how predation rates change with rainfall. Here kiwi a few kilometres apart in the same valley inhabit markedly different rainfall zones that sometimes span the extremes experienced by the species throughout their entire range.

Williams and Given (1981) did not list great spotted kiwi in the New Zealand Red Data Book, partly because they did not have enough information to make an informed judgement. The information presented in this report suggests great spotted kiwi probably fit into the 'vulnerable' IUCN threatened species category.[2] Williams and Given (1981) point out that the critical difference between a 'rare' species and a 'vulnerable' one is that the former has a relatively stable population while the latter is declining. 'Vulnerable' species include those that are still abundant but are under threat from serious adverse factors throughout their range. We expect great spotted kiwi to maintain their numbers in the high-rainfall zones of Northwest Nelson and the Paparoa Range, but to decline elsewhere. Time will tell.

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6. REFERENCES

Baillie, J.; Groombridge, B. (Comps and Eds) 1996: 1996 IUCN red list of threatened animals. IUCN, Gland, Switzerland.

Baker, A.J.; Daugherty, C.H.; Colbourne, R.; McLennan, J.L. 1995: Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. *Proceedings of the National Academy of the USA 92*: 8254–8258.

Barker, D. 1993: North Westland kiwi survey, 1992/93. Department of Conservation, Hokitika (unpublished). 12 p.

Barnett, S.; Stilwell, J. 1993: North Westland kiwi survey. Department of Conservation, Hokitika (unpublished). 12 p.

Bednekoff, P.A.; Biebach, H.; Krebbs, J. 1994: Great tit fat reserves under unpredictable temperatures. *Journal of Avian Biology 25*: 156–160.

Caughley, G. 1994: Directions in conservation biology. *Journal of Animal Ecology 63*: 215–244.

Crozier, R.H. 1992: Genetic diversity and the agony of choice. *Biological Conservation 61*: 11–15.

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[2] The great spotted kiwi is listed as vulnerable in the most recent IUCN listing (Baillie & Groombridge 1996), on account of its restricted and fragmented distribution and continuing decline in its population.

Diamond, J.M. 1984: 'Normal' extinction of isolated populations. Pp. 191–246 in Nitechi, M.H. (Ed.) Extinctions. Chicago University Press, Chicago.

Elliot, G.; O'Donnell, C. 1988: Recent decline in yellowhead populations. *Science and Research Internal Report No. 29*. Department of Conservation, Wellington. 11 p.

Frankel, O.H.; Soulé, M. 1981: Conservation and evolution. Cambridge University Press, Cambridge. 327 p.

Hanski, I.; Gilpin, M. 1991: Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society 42*: 17–38.

Herbert, J.; Daugherty, C.H. 2002: Genetic variation, systematics and management of kiwi. Pp. 11–34 in Overmars, F. (Ed.) Some early 1990s studies in kiwi (*Apteryx* spp.) genetics and management. *Science & Research Internal Report 191*, Department of Conservation, Wellington.

Hill, S.; Hill, J. 1987: Richard Henry of Resolution Island. John McIndoe, Dunedin. 183 p.

Jolly, J.N. 1992: Great spotted kiwi survey, South Westland. Department of Conservation, Hokitika (unpublished). 10 p.

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

King, C.M. 1984: Immigrant killers: Introduced predators and the conservation of birds in New Zealand. Oxford University Press, Auckland. 224 p.

McLennan, J.A. 1988: Breeding of North Island brown kiwi, *Apteryx australis mantelli*, in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology 10*: 97–107.

McLennan, J.A.; McCann, A.J. 1991: Ecology of great spotted kiwi, *Apteryx haastii*. DSIR Land Resources Contract Report No. 91/48 (unpublished). DSIR, Lower Hutt. 36 p.

McLennan, J.A.; McCann, A.J. 1993: Claw colour in great spotted kiwi. *Notornis 40*: 76–78.

McLennan, J.A.; Potter, M.A. 1993: Juveniles in mainland populations of kiwi. *Notornis 40*: 294–299.

Murphy, E.; Bradfield, P. 1992: Change in diet of stoats following poisoning of rats in a New Zealand forest. *New Zealand Journal of Ecology 16*: 137–140.

O'Donnell, C.F.J. 1996: Predators and the decline of New Zealand forest birds: an introduction to the hole-nesting bird and predator programme. *New Zealand Journal of Zoology 23:* 213–219.

Oliver, W.R.B. 1955: New Zealand birds. A.H. & A.W. Reed, Wellington. 661 p.

Pascoe, J. (Ed.) 1957: Mr Explorer Douglas. Reed, Wellington. 331 p.

Reid, B.; Williams, G.R. 1975: The kiwi. Pp. 301–330 in Kuschel, G. (Ed.) Biogeography and ecology in New Zealand. Dr W. Junk B.V., The Hague.

Stilwell, J.; Barnett, S. 1993: South Westland kiwi survey. Department of Conservation, Hokitika (unpublished). 6 p.

Thomas, C.D. 1990: What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology 4*: 324–327.

Williams, G.R.; Given, D.R. 1981: The Red Data Book of New Zealand. Nature Conservation Council, Wellington. 175 p.