EFFECT OF TOPOGRAPHY ON SEASONAL DISTRIBUTION OF FOREST BIRDS IN THE OHIKANUI, LOWER BULLER AND INANGAHUA VALLEYS, NORTH WESTLAND

By P. R. WILSON, R. H. TAYLOR and B. W. THOMAS

ABSTRACT

Birds were counted in the montane Ohikanui Valley and nearby at the mouth of the Buller Gorge in all four seasons of the year. Counts from these areas are compared with those from three sites previously studied in the much larger and broader Inangahua Valley in the same region. The effect of topographic temperature inversion on the deep and glaciated Ohikanui Valley is reflected in the pattern of vegetation and also in the altitudinal and spatial distribution of the birds. Large differences between the seasonal patterns of occurrence of some species of birds in the Ohikanui and Inangahua Valleys are demonstrated. Reasons for these differences are examined, such as seasonal migration in and out of the Ohikanui Valley for species such as Tui *(Prosthemadera novaeseelandiae)*, Bellbird *(Anthornis melanura)*, and Silvereye *(Zosterops lateralis)* and altitudinal movement by species such as Rifleman *(Acanthisitta chloris)* and Grey Warbler *(Gerygone igata)*.

The study emphasises the importance of warm, floristically rich, lowland forest for the winter maintenance of honeyeater populations which breed in the montane valleys.

INTRODUCTION

This study of the seasonal distribution of birds in a large forested montane valley was undertaken to test the hypothesis that lowland forest provides essential resources for birds inhabiting higher-altitude forests for much of the year (Falla 1939, 1955; Taylor 1977). The Ohikanui Valley was chosen because the forest-type mapping (NZ Forest Service 1974) showed that the floor and terraces of the central part of the valley contained significant amounts of podocarp/beech forest of the "P.B.1" type (Naylor 1955, Masters *et al.* 1957), a forest type found to be a favoured bird habitat in the neighbouring Inangahua Valley (Dawson *et al.* 1978). In fact, although for 18 km the altitude of the valley floor is between 30 and 300 m a.s.l., lowland floristic elements are rare. Topographic inversion of temperature has created a climate where the forest composition of the valley floor resembles that of montane slopes elsewhere in the region. Although the lack of type P.B.1 forests was unexpected, the study proceeded as the valley was clearly an excellent area for studying the habitat preferences and seasonal movements of birds. It also provided an opportunity to compare the results from the glaciated montane Ohikanui Valley with those from the much larger, broader Inangahua Valley approximately 15 km to the east (Fig. 1).

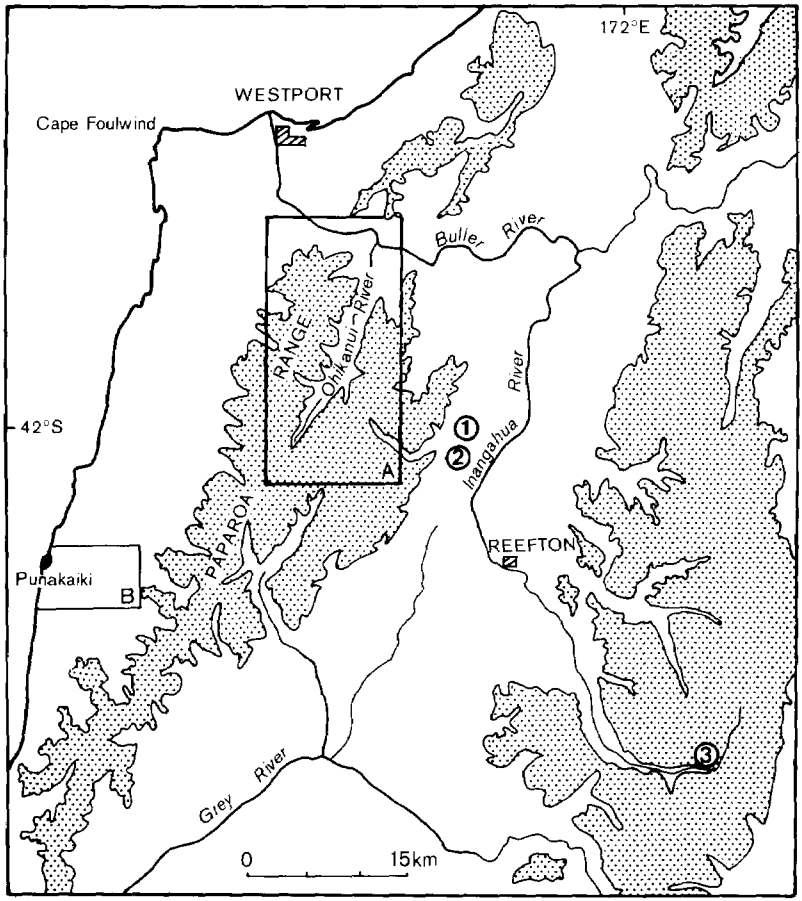

FIGURE 1 — The Ohikanui Valley, Paparoa Range, in relation to previous bird-count study areas in the Inangahua Valley (Dawson *et al.* 1978) and in the Western Paparoas (Onley 1980). Study areas: Ohikanui A. Western Paparoa B. Inangahua Valley (1) Fletcher Creek, (2) Te Wharau, (3) Rahu Saddle. Land over 600 m a.s.l. is shown stippled.

THE OHIKANUI VALLEY

The glaciated U-shaped Ohikanui Valley is 27 km long and drains the northern end of the Paparoa Range (Fig. 2). It joins the Buller River only 6 km before the Buller leaves its gorge to flow a further 13 km across its floodplain to the sea (Fig. 1). The Paparoa Range is formed from a large horst of hard pre-Tertiary rocks, mainly granite and gneiss, which has been carved by glaciation to form knife-edged ridges and deep cirques (Fig. 3). The mountains are mainly over 1200 m with the highest, Mt Uriah, at 1532 m.

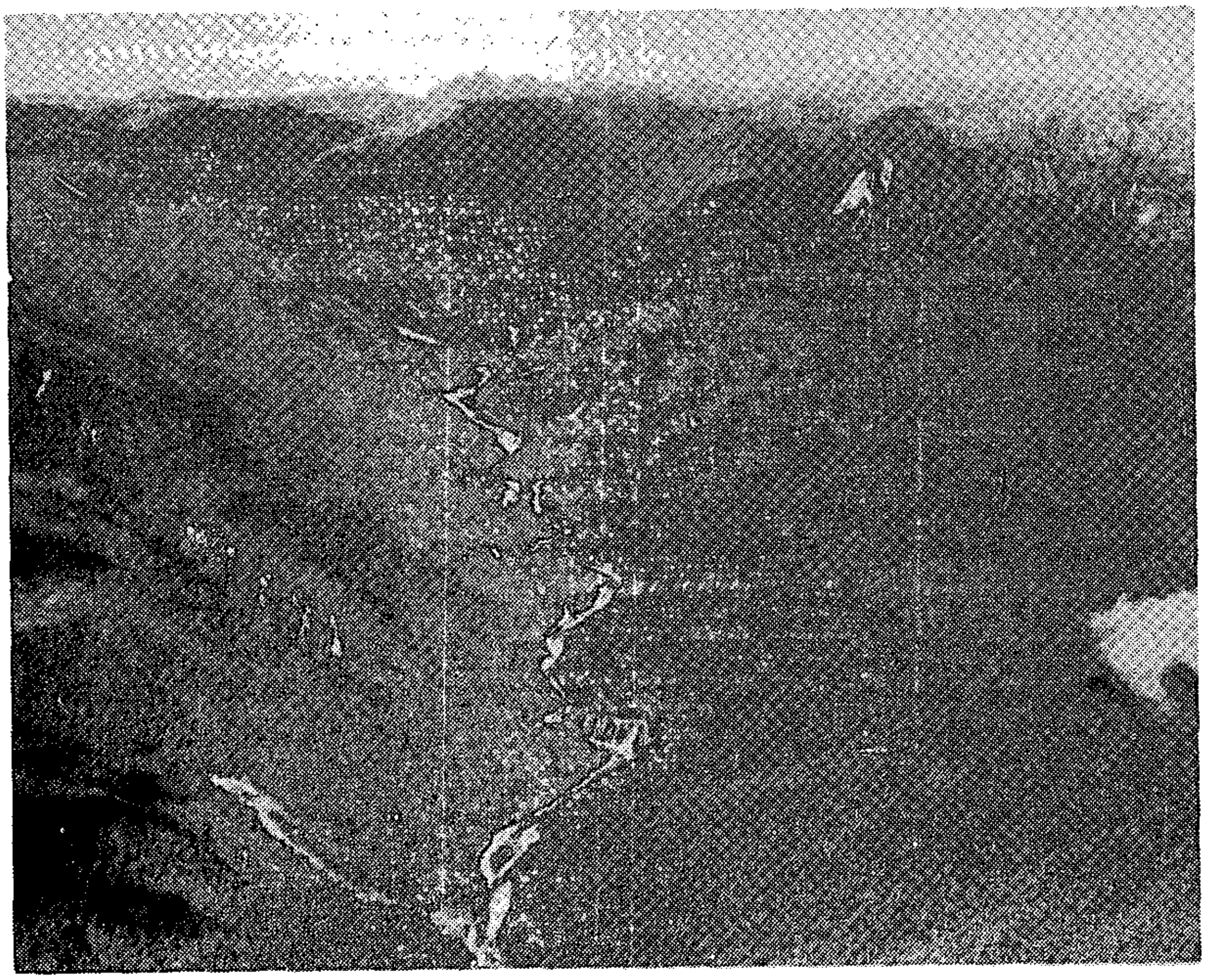

FIGURE 2 — Aerial view of the Ohikanui Valley looking upstream into the heart of the Paparoa Range from a point above the Buckland Creek/Ohikanui River confluence

Photo: Lloyd Homer, NZ Geological Survey

The geology of the Ohikanui River catchment, particularly the south-western portion, consists of undifferentiated schist, gneiss, diorite and granite gneiss, all locally intermingled. Most of the northern and eastern catchment is white muscovite granite. To the west of the mouth of the river a small area of black biotite quartz diorite outcrops (Nathan 1978).

The Ohikanui Valley floor is characterised by a high glacial aggradation terrace and lower degradation terraces; it has a complete forest cover and no grassy flats. The altitude at which tall forest is replaced by stunted forest merging to alpine scrub varies considerably within the Ohikanui catchment. Aspect, geomorphology and the effect of cold air drainage are more important than geology in determining the upper limit of tall forest, which varies from 800 to 1200 m a.s.l.

The Ohikanui area has on average over 2540 mm of rain and more than 200 raindays per annum. It was described by Garnier (1958) – along with much of Fiordland, the West Coast of the South Island and North-west Nelson – as having a cool superhumid climate with a low mean annual range of temperature. The whole Ohikanui catchment has been less modified than many other forested areas of New Zealand. No timber has been extracted; at the time of our survey, red deer *(Cervus elaphus)*, goats *(Capra hircus)*

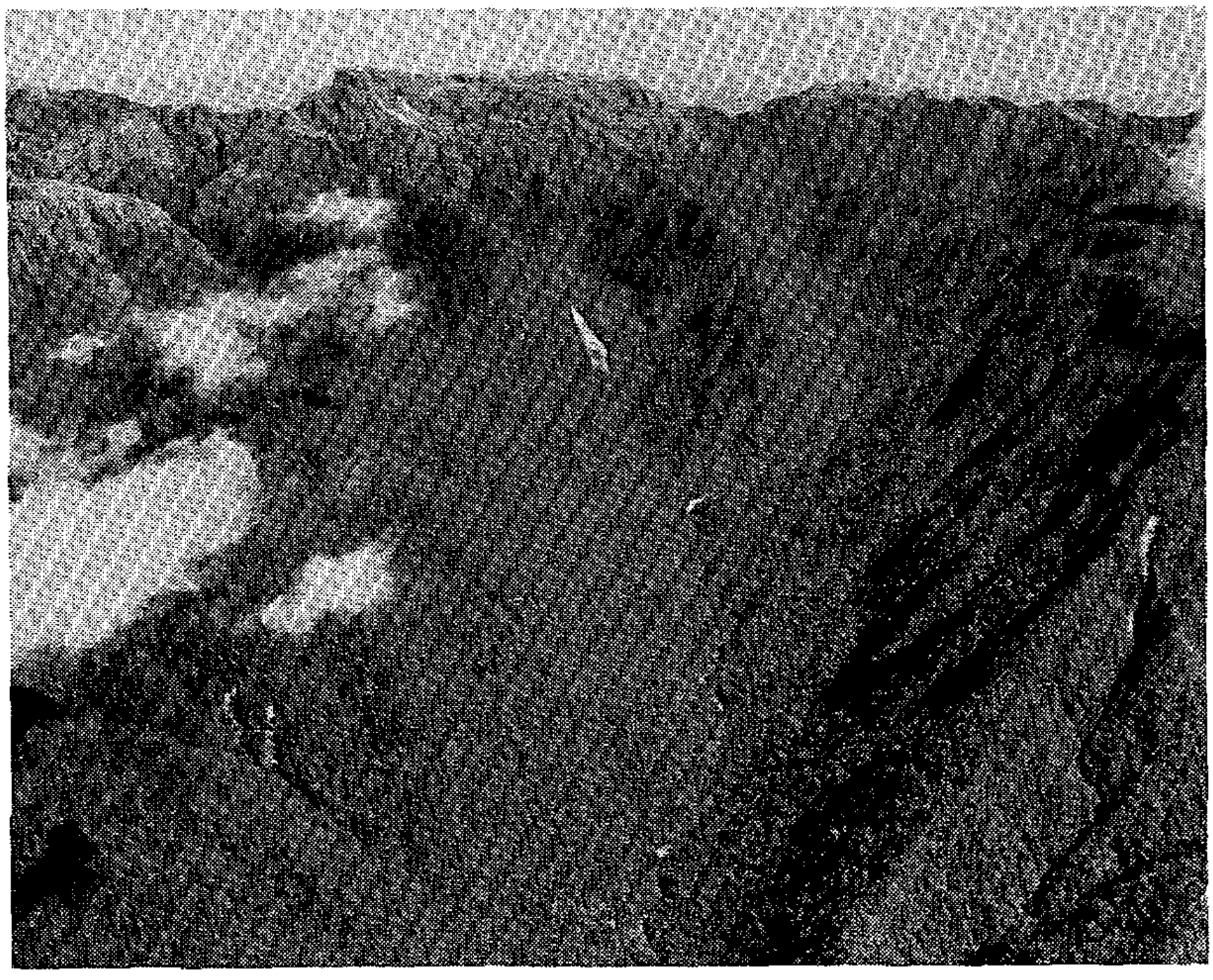

FIGURE 3 — Aerial view of Buckland Creek, a major tributary of the Ohikanui River, showing glacial features and exposed granite tops
Photo: Lloyd Homer, NZ Geological Survey

and rodents *(Rattus* spp. and *Mus musculus)* were scarce throughout most of the area, and possums *(Trichosurus vulpecula)* were in moderate numbers. Stoats *(Mustela erminea)* were present throughout.

FIELD SITES AND METHODS

Field work

The birds of the Ohikanui Valley were studied between June 1975 and December 1977. During this period, four major and three minor field trips to the area involved up to nine ornithologists for a total of 213 man-days. A total of 1920 standard 5- minute bird counts, as described by Dawson & Bull (1975), was made to assess the relative abundance of the various species in different habitats. All bird counts were carried out by observers drawn from a pool of six experienced bird-counters. Numerous incidental observations were also recorded on birds and other wildlife. The base camp was 11 km up the Ohikanui, 1 km below Bartrum Stream (Fig. 4).

As the aim was to compare seasonal and altitudinal changes in bird distribution, study areas and bird-count lines (Fig. 4) were sited to sample valley floor habitats at varying distances up-river from the coastal plain and to sample different altitudinal zones within the Ohikanui Valley. In siting bird-count lines, we attempted to cover the range of vegetation types and land forms in the valley. Each line comprised 10 bird-count stations about

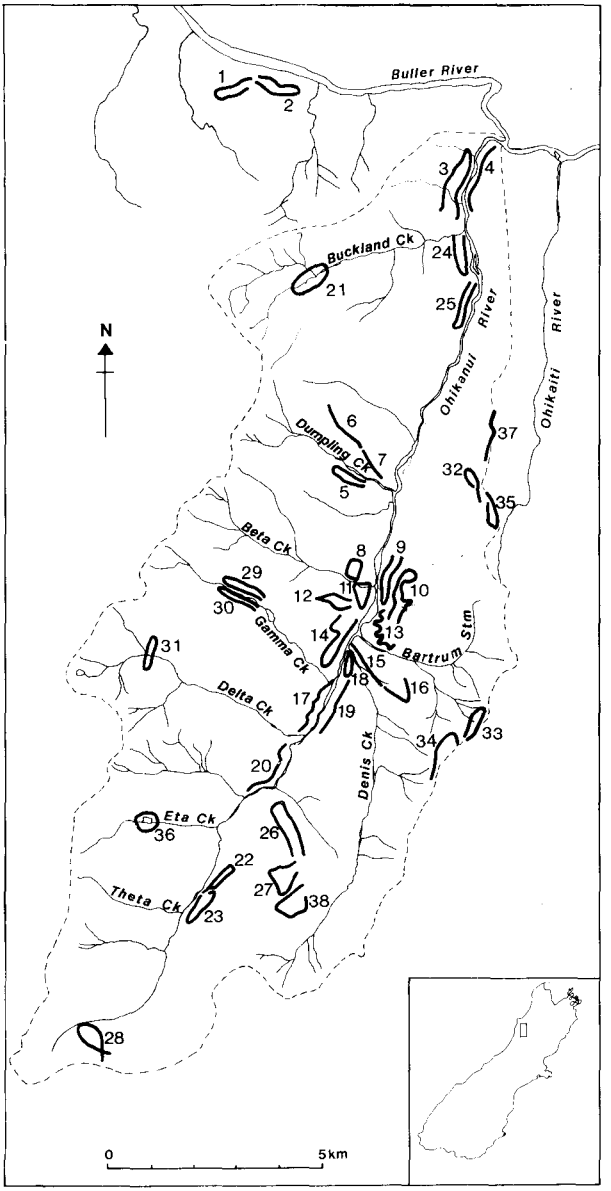

FIGURE 4 — The bird-counting lines (numbered) in the Ohikanui River catchment (dotted line) and at the mouth of the Buller Gorge (lines 1 and 2)

200 m apart. Each line was defined on field maps, but the individual stations were not permanently marked.

In June 1975, birds were counted by five observers on 15 lines (6-20). Each line was counted twice, usually by two different observers who made ten 5-minute counts at each. With one minor variation, these same lines were counted similarly in December 1975, September 1976 and March 1977. Because of a misunderstanding, line 5 was counted instead of line 8 in September 1976. However, as the two lines are at similar altitudes and have comparable bird habitats, this variation should not have affected the overall results. Another four lines were counted similarly in September 1976, and in March, June and December 1977: two at the mouth of the Buller Gorge (1 and 2) and two near the mouth of the Ohikanui (3 and 4). Consequently, birds were counted during four seasons (winter, spring, summer and autumn), on each of 19 lines over a 2.5 year period; no season was replicated at any site.

In March 1977 two additional lines (24 and 25) were counted twice in the lower Ohikanui Valley about 4 km up from the Buller confluence. Helicopters were used in September 1976 and March 1977 to gain access to some of the more remote areas of the Ohikanui catchment, and ten 5-minute bird counts were made at each (lines 26-34 in September 1976; 21-23 and 35-38 in March 1977). These lines were not revisited.

Study areas

"Buller" (lines 1 & 2): Tall emergent northern rata* over a dense canopy of mahoe, pigeonwood, toro, and kamahi, with much supplejack, kiekie, epiphytic ferns, and climbing ratas. This forest has been selectively logged in the past, probably to remove large podocarps (rimu, kahikatea) (G. N. Park and G. Y. Walls, pers. comm.; pers. obs.).

"Lower Ohikanui" (lines 3 & 4): The effect of temperature inversion continues the entire length of the Ohikanui Valley, and it is only here, within the lowermost 2 km at the confluence with the Buller River, that matai and kahikatea occur in the canopy and lowland species such as mahoe, *Coprosma australis, C. robusta*, supplejack, *Coriaria arborea, Cordyline banksii* and kowhai are present on the valley floor and terraces. There is much rimu, with yellow-silver pine, mountain toatoa and mountain beech at the mouth.

"Central Ohikanui" (lines 5-20): The majority of seasonally repeated bird-counting sites were in the central portion of the Ohikanui Valley (Fig. 2 & 4). Nine forest types were recognised in this area. They were distributed altitudinally as in Fig. 5, and they are described as follows.

1. Tall forest on the lowest terraces with a canopy of silver beech, red beech and occasional rimu. There is a dense understorey of horopito and crown fern, and bush rice grass and moss are abundant on the ground.

2. Tall red beech forest on fans and the base of the main slope. More open beneath with some horopito and crown fern, and less moss than the terrace forests.

* Common and scientific names of plants in the text and glossary (Appendix 1) follow Allan (1961), Moore & Edgar (1970) and recent changes listed in Edgar & Connor (1983).

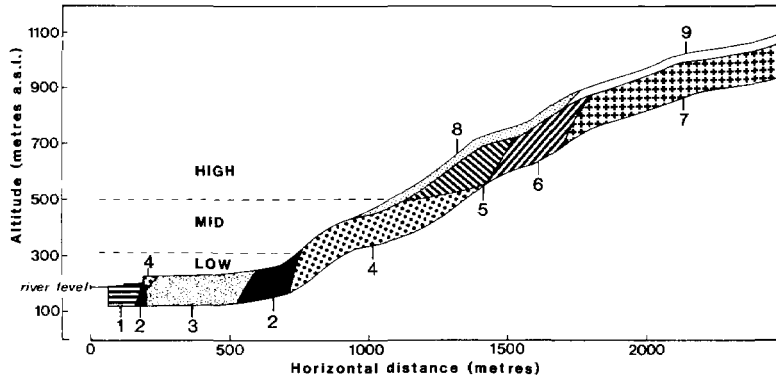

FIGURE 5 — Typical altitudinal profile of the central Ohikanui River valley near count lines 15 and 16 (after G.N. Park, unpublished). The relationships of "low", "mid" and "high" altitudinal bird counting zones to the valley profile and broad vegetation categories (numbered and described in the text) are indicated.

3. Forest on the upper terraces with a fairly open canopy of rimu, cedar and Hall's totara; a subcanopy of yellow-silver pine and mountain beech; and an understorey of mountain toatoa, Westland quintinia, *Myrsine divaricata*, and other species. The ground is very mossy and poorly drained. In some places where this forest is stunted, yellow-silver pine is dominant.

4. Hard beech/silver beech/Hall's totara forest on the main slopes to about 500 m a.s.l., and on the tread of upper terrace, with a dense understorey of Westland quintinia, kamahi and much crown fern.

5. Forest on the middle slopes at about 500-700 m a.s.l. in which silver beech dominates, with some hard beech, red beech and Hall's totara. Some Westland quintinia, kamahi and crown fern, but less than lower down. Mosses increase with altitude.

6. Above 700 m, to about 850 m a.s.l., silver beech dominates, with occasional kamahi, southern rata and Westland quintinia. The understorey is mostly silver beech and the ground is very mossy.

7. Above 850 m to the timberline, silver beech and mountain beech dominate with *Archeria traversil* and *Dracophyllum traversii* common in the understorey, and much moss is on the ground and trees.

8. On ridges of the valley sides between 400 and 900 m a.s.l., low forest of yellow-silver pine/mountain beech/southern rata is common.

9. On ridges between 900 m and the bushline, a low forest of bog pine, yellow-silver pine, and mountain beech is characteristic.

Lower valley terraces and fan slopes south of Buckland Creek (lines 24 & 25): Broadly similar to forest types 1 and 2 of the Central Ohikanui.

Remote areas (lines 21,26-38): High-altitude sites fall mainly in forest types 7-9 as described for the Central Ohikanui.

Upper Valley (lines 22 & 23): Similar in composition to valley bottom forests of the Central Ohikanui.

Analysis

Bird counts from Buller (lines 1 & 2), Lower Ohikanui (lines 3 & 4) and Central Ohikanui (lines 5-20) were analysed and compared. In the Central Ohikanui, the bird-count stations of the 15 counting lines which were repeated during four seasons were analysed according to which altitudinal zone they fell in, as follows: low (0-315 m a.s.l.), mid (316-500 m a.s.l.) and high (501-999 + m a.s.l.). The counting sites in "Lower Ohikanui" and "Buller" were all classed as low altitude.

Bird counts from the present study are compared with those from three areas studied in the Inangahua Valley (Dawson *et al.* 1978). The Inangahua Valley areas (Fig. 1) were Fletcher Creek (230 m a.s.l.), a remnant of the forest type once common on alluvial flats and terraces; Te Wharau (300-420 m a.s.l.), representing the main hill-country forest type; and Rahu Saddle (820-1070 m a.s.l.), a high-altitude "protection forest".

Data from the "low" altitude zone of Central Ohikanui are compared with data from Fletcher Creek; data from the "mid" altitude zone of Central Ohikanui are compared with data from Te Wharau and data from the "high" altitude zone of Central Ohikanui are compared with data from Rahu Saddle.

Ohikanui birds were counted in March, June, September and December, whereas Inangahua birds were counted in April, June, August, October, December and February. To compare the results of the two studies, we took the mean number of each species of bird counted in February and April in each of the Inangahua study areas to represent March, and took the mean of the August and October counts to represent September. The seasonal trends of most species studied at Inangahua and Ohikanui suggest that this procedure was valid.

Data for the more frequently recorded species were analysed by both non-parametric analysis (Kruskal-Wallis) and analysis of variance on transformed data. The transformation used was $\sqrt{x} + \sqrt{x+1}$, which Snedecor & Cochran (1967) reported to be slightly better at stabilising variances for low counts than a simple square-root transformation. This transformation was sometimes still inadequate, but as the conclusions were all corroborated by the Kruskal-Wallis test, we considered the results to be valid. All mean values presented in the paper are back-transformed.

Data from remote sites, and for infrequently recorded birds, were categorised into present/absent and analysed as contingency tables by the chi-square test.

To compare the frequently recorded species from remote sites with those in Central Ohikanui and in Lower Ohikanui, we used the Kruskal-Wallis test. The data did not allow seasonal effect to be separated from annual effect. In making these comparisons we have assumed that the patterns observed relate to altitude and season and are not caused by major differences between years.

All statistical differences stated to be significant are at the 1% probability level or less. We chose this level of significance, rather than the usual 5%

level, to increase confidence in differences detected because the study design was not completely balanced. For example, the seasonal counts did not all fall in the same year and the bird-count stations were not fixed exactly.

RESULTS

Broad habitat preferences

As was to be expected, bird species were not distributed evenly throughout the Ohikanui Valley, and most displayed obvious habitat preferences. Two aspects of these preferences are illustrated in Fig. 6, which is based on yearly averages of counts at seasonally repeated sites.

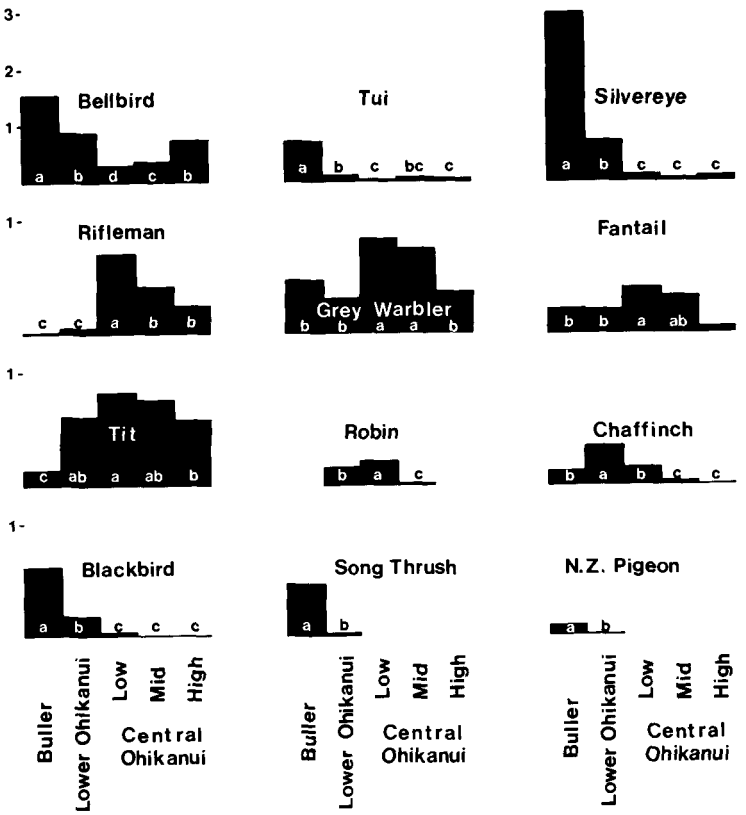

FIGURE 6 — The mean number of each species counted in 5 minutes in low-altitude forest at Buller (n = 160 counts), Lower Ohikanui (n = 160), and in each of the low, mid and high altitudinal zones in the Central Ohikanui (n = 705 low atlitude; 295 mid; 250 high) averaged over the whole year. Note differing scales. Means with the same letter do not differ significantly ($P<0.01$).

The figure shows the effect of distance up-river from the coastal plain for low-altitude forest and the effect of increasing altitude in the Central Ohikanui. Bellbirds, Tuis, Silvereyes, Blackbirds, Song Thrushes, and New Zealand Pigeons were most common at Buller, less so in Lower Ohikanui, and least common in Central Ohikanui. The converse was true for Riflemen, Fantails, Tits and Robins, which increased in abundance with distance up the valley. The preferences of certain species for the three altitudinal zones up the sides of the valley in Central Ohikanui are also illustrated. Numbers of Riflemen, Grey Warblers, Fantails, Tits, Robins and Chaffinches decreased significantly with increasing altitude. Blackbirds, Shining Cuckoos and Wekas (Table 1) had a similar trend. In contrast, Bellbirds and Redpolls (Table 1) showed a significant preference for the higher-altitude zones.

Lines counted over four seasons

The average 5-minute counts for the 12 most common forest birds from the Ohikanui and Buller study areas are given by altitudinal zone and season in Fig 7. Less frequently encountered species are listed in Tables 1-3. Each species is discussed below, and its seasonal and altitudinal habitat preferences in the montane Ohikanui Valley are compared with those found in the Inangahua Valley. It is well known that many birds vary in conspicuousness seasonally (Dawson 1981). As most birds counted are located by sound rather than sight, a greater proportion of the population is indexed by counts during their song period. Where known, seasonal changes in conspicuousness have been considered in the interpretation of our counts.

Bellbird *(Anthornis melanura):* Bellbirds were few in the Central Ohikanui at all times of the year. On average, low-altitude counts were one-fifth of those at Fletcher Creek, and mid-altitude counts one-sixth of those at Te Wharau; only high-altitude counts compared in magnitude with those from Rahu Saddle, though with an entirely different seasonal pattern (Fig. 7A). Bellbirds in the Central Ohikanui clearly favoured the high altitude zone, and significantly more were found there than at mid or low altitude in all seasons except September.

The Lower Ohikanui area exhibited a marked and significant reduction in the number of Bellbirds in June, as in all three altitudinal zones of the Central Ohikanui. The increase in numbers counted between June and September was much more marked in the Lower Ohikanui than in the Central Ohikanui; numbers fell in the Lower Ohikanui between September and December while they rose (significantly in low and high altitudes) in the same period at all altitudes in the Central Ohikanui.

Large numbers of Bellbirds were found in Buller during June. The whole pattern of seasonal abundance demonstrated at Buller, with its lowest count in December, is virtually the converse of that for all Central Ohikanui Valley sites. The Buller area, with its more diverse and warmer forest type, could have been acting as wintering-over quarters for many Bellbirds coming out of the Ohikanui. The significant decrease in numbers of Bellbirds at Buller from June to December, and the corresponding significant increase between June and September in the Lower Ohikanui, followed by a decline there in December (though not significant), is entirely consistent with a return

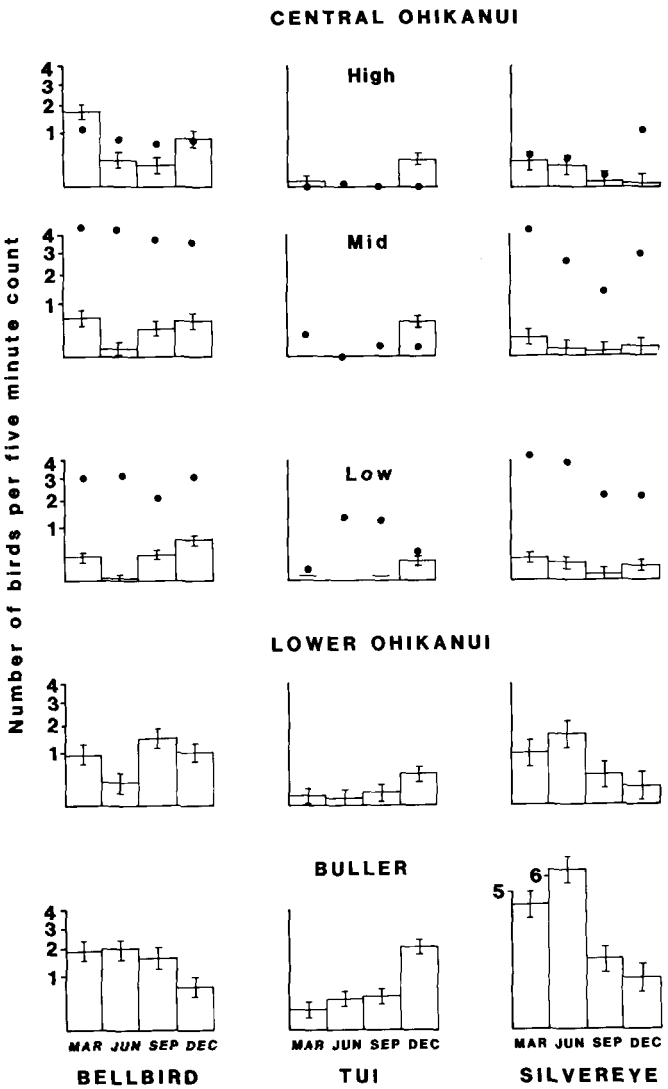

FIGURE 7A — Seasonal and altitudinal distribution of 12 species of birds indexed by standard 5-minute counts in and near the Ohikanui Valley. Seasonally repeated lines for each area were: "Central Ohikanui", lines 6-20 inclusive; "Lower Ohikanui", 3 & 4; "Buller", 1 & 2 (Fig. 4). For the "Central Ohikanui", "high", "mid" and "low" indicate counts from above 500 m a.s.l., 316-500 m a.s.l. and 315 m a.s.l. and below, respectively. Both "Lower Ohikanui" and "Buller" are low-altitude areas. Histograms show mean values (with their 99% confidence limits) from the Ohikanui study. Values too small to plot are indicated by a horizontal bar. Black dots show means from the Inangahua Valley study areas (see analysis section).

flow of Bellbirds through forests at the mouth of the Ohikanui en route to summer quarters higher up the valley.

In contrast, Bellbirds in the Inangahua Valley preferred hill country forests and only rarely exhibited statistically significant variation in apparent numbers in any of the four areas counted throughout the year. The small changes observed there can probably be explained by seasonal conspicuousness.

Tui *(Prosthemadera novaeseelandiae):* Only during December were Tuis distributed throughout the altitudinal range in the Central Ohikanui. Almost none was detected during the months of June or September (Fig. 7A), although a very few were counted in March, almost all at high altitude. Tuis are generally common, noisy and hence conspicuous during winter in low-altitude mixed beech/podocarp forest (Dawson *et al.* 1978; pers. obs.). A feature of the Central Ohikanui was that no Tuis were found in the beech/podocarp forests during winter (at any altitude) and those that did migrate into the valley for summer were significantly more common at mid altitude than at low or high altitude. This was the converse of Tui distribution found in beech and beech/podocarp forests in the Inangahua Valley (Fig. 7A). Similarly, there was no winter peak in numbers of Tuis in either the Lower Ohikanui or the Buller study areas (Fig. 7A). In fact, although on an annual basis significantly more were counted in Lower Ohikanui, and particularly Buller, than in the Central Ohikanui, the seasonal pattern of a significant increase in December is the same in all areas (2% level, Lower Ohikanui) and altitudes.

Although Tuis were fairly numerous at Buller during the winter (0.5 per count), over three times as many were counted there during December. By comparison, numbers at Fletcher Creek had halved from winter to December. Clearly, Buller is not a prime wintering area for Tuis but does attract them in large numbers in summer, presumably from overwintering areas not sampled during this study.

Silvereye *(Zosterops lateralis):* Silvereyes displayed a significant preference for high and low altitudes in the Central Ohikanui and were found there at all altitudes and in all seasons. Like Bellbirds, they were surprisingly few at lower altitudes in Central Ohikanui compared with their numbers at Lower Ohikanui and Buller, and in the Inangahua Valley (Fig. 7A).

Kikkawa (1962) suggested that some Silvereyes leave the montane forests in winter. Figure 7A tends to support this suggestion. A significant decrease in Silvereyes counted occurred at low and high altitudes in the Central Ohikanui from March to September, but increases were recorded in June in the Lower Ohikanui (not significant) and Buller forests (significant), before numbers dropped there also in September (significant at both Buller and Lower Ohikanui). The very large number of Silvereyes recorded in the Buller area in March and June may reflect the result of breeding followed by possible migration down from the montane environment to a richer winter food supply, such as the abundant autumn-flowering *Metrosideros fulgens* in these forests.

South Island Rifleman *(Acanthisitta chloris chloris):* The distribution of the Rifleman in the Ohikanui is perhaps the best illustration of the effect of temperature inversion on habitat in such a montane valley. In the Central Ohikanui they were more common in low-altitude forests than at mid or high altitudes (Fig. 7B), which is the converse of the pattern recorded in

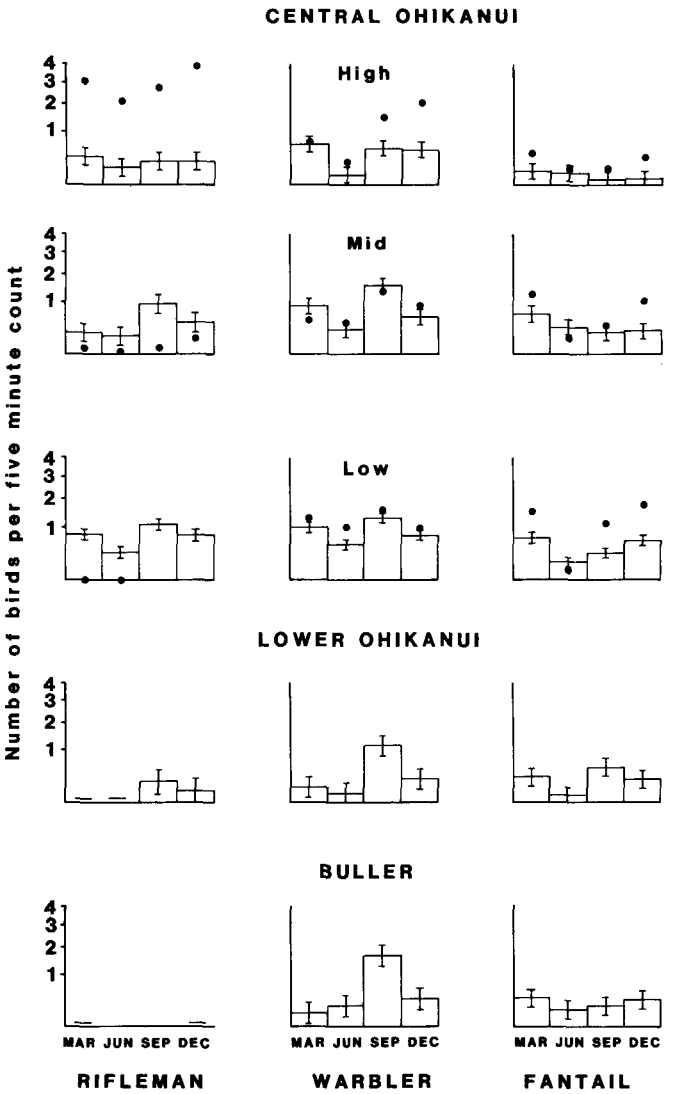

FIGURE 7B — Seasonal and altitudinal distribution of 12 species of birds indexed by standard 5-minute counts (continued)

the Inangahua Valley (Dawson *et al.* 1978). However, although some Riflemen were counted at all altitudes in the Ohikanui, nowhere were their numbers as high as those recorded at Rahu Saddle, where over twice as many Riflemen as anywhere else were counted in any season (Fig 7B). At Rahu Saddle, Rifleman numbers rose from a low in winter to a peak in summer and remained high in autumn. The closest approximation to this pattern is illustrated by the low-altitude Central Ohikanui counts, but without a peak in December. The mid-altitude counts are less similar, with a pronounced peak in September, while Rifleman numbers at high altitudes were relatively constant throughout the year.

Our data suggest that, in the Ohikanui, some birds may move down to breed in September. Significantly more Riflemen were counted in September than in June in the mid- and low-altitude Central Ohikanui and the Lower Ohikanui. This pattern was not repeated at high altitude.

Grey Warbler *(Gerygone igata):* Grey Warblers were spread throughout the altitudinal range in the Central Ohikanui, being a little more numerous at low and mid altitudes than at high altitudes (Fig. 7B). Numbers of warblers counted seasonally at low and mid altitudes in the Central Ohikanui correspond very closely to those at Fletcher Creek and Te Wharau in the Inangahua Valley. In all these areas the numbers counted between June and September increased by 2-3 times because of increased conspicuousness, warblers being most vocal from August until October.

The number of Grey Warblers counted in the Lower Ohikanui and Buller in September was significantly larger than in March and June. In March, significantly more warblers were recorded at all altitudes in the Central Ohikanui than in either Lower Ohikanui or Buller. A possible explanation is that some birds move down the valley to breed in September but that breeding is more successful further up the valley.

South Island Fantail *(Rhipidura fuliginosa fuliginosa):* Significantly more Fantails preferred low- and mid-altitude forests in both the Ohikanui and Inangahua studies. The seasonal pattern recorded in the Ohikanui was similar to, but less accentuated than, that in the Inangahua (Fig. 7B).

Yellow-breasted Tit *(Petroica macrocephala macrocephala):* The altitudinal and seasonal distributions and the numbers of Tits counted were very similar in both the Central Ohikanui and Inangahua Valley (Fig. 7C). This pattern is mainly due to seasonal conspicuousness, but the comparatively high numbers counted in the low-altitude area of Central Ohikanui in June suggest that some Tits may migrate there in winter.

The significant reduction from September to December in the numbers of Tits counted in the Lower Ohikanui and at Buller is inconsistent with the seasonal pattern recorded in the Central Ohikanui and at all study sites in the Inangahua Valley. Either some Tits in the Lower Ohikanui and Buller areas move higher up the valley sides in December or, more likely, they breed much earlier in these low-altitude areas and territorial singing finishes sooner.

South Island Robin *(Petroica australis australis):* In the Central Ohikanui, Robins were most abundant at low altitudes where, in fact, they were in almost identical numbers and exhibited the same seasonal pattern as Robins at Fletcher Creek. A few Robins were recorded at mid altitude, as at Te Wharau, but none was recorded in the high-altitude counting zone in the

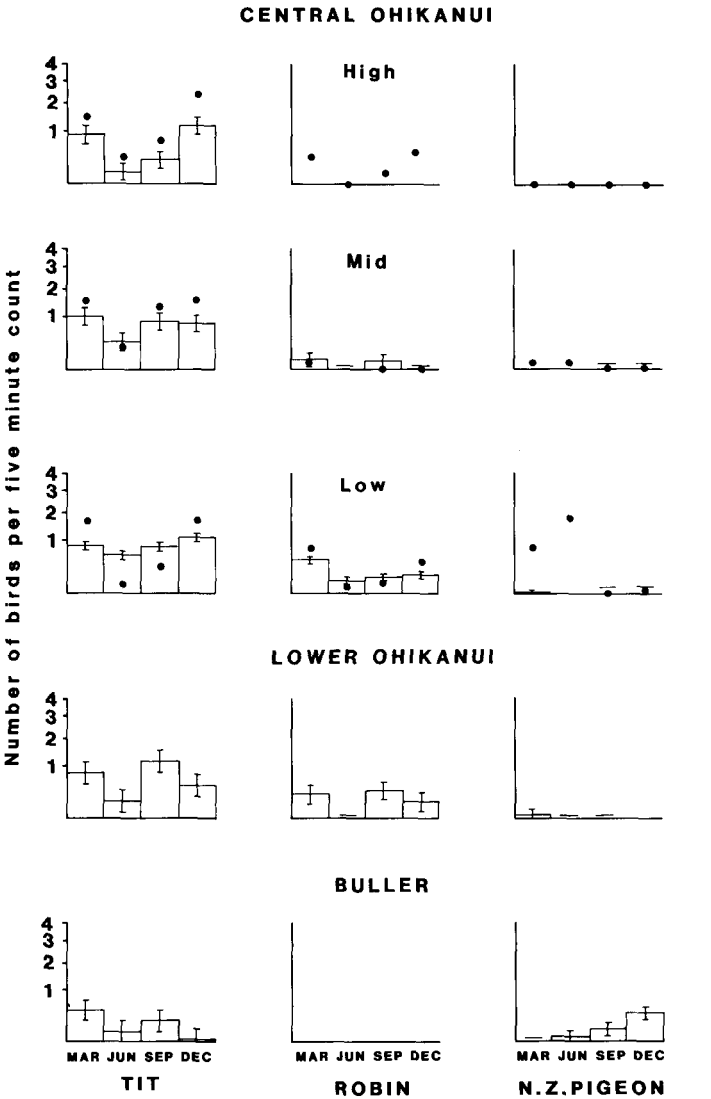

FIGURE 7C — Seasonal and altitudinal distribution of 12 species of birds indexed by standard 5-minute counts (continued)

Central Ohikanui, whereas at Rahu Saddle they were quite common (Fig. 7C). On average, similar numbers of Robins were recorded in Lower Ohikanui as in the low-altitude zone of Central Ohikanui. None was recorded at Buller, however.

New Zealand Pigeon *(Hemiphaga novaeseelandiae):* Very few New Zealand Pigeons were counted in the Ohikanui (Fig. 7C). They were absent in June, except for a few in the Lower Ohikanui; they were rarely recorded at other times of the year and then only at low and mid altitudes. By comparison, their numbers peaked in June at Fletcher Creek in the Inangahua Valley (Fig. 7C). In fact, the seasonal use of the Buller forest by pigeons is the converse of that recorded at Fletcher Creek. Pigeons were present in very low numbers at Fletcher Creek during counts in August, October and December, whereas there were peak numbers at Buller during the September and December counts.

Chaffinch *(Fringilla coelebs):* Significantly more Chaffinches were recorded in low-altitude forest than in mid- and high-altitude forests in the Ohikanui Valley. During September and December fewer were in the mid- and high-altitude zones of the Central Ohikanui than in the hill and protection forests of the Inangahua. During March surprisingly few were recorded in Central Ohikanui, the Lower Ohikanui, or Buller, compared with other times of year. This and the large differences between Buller and Lower Ohikanui in June, September and December (Fig. 7D) are best explained by seasonal migrations out of the valley in autumn and winter.

Blackbird *(Turdus merula):* Blackbirds were evenly spread throughout the altitudinal range in both the Central Ohikanui and Inangahua study areas. The seasonal pattern of change in the number of Blackbirds recorded throughout the year was identical in both the Ohikanui and Inangahua Valleys. At all times of year significantly more Blackbirds were recorded at Buller than in the Ohikanui study areas, probably because of their preference for more modified habitats. The highest numbers were recorded at Lower Ohikanui and Buller in December (Fig. 7D), when Blackbirds were still in full song and there were large numbers of fledged young.

Song Thrush *(Turdus philomelos):* Song Thrushes were rare in the Central Ohikanui. None was counted there in March, and only in December were they recorded at all altitudes (Fig. 7D). However, the counts were higher during September and December in the Lower Ohikanui, and were significantly higher at Buller, particularly in spring and summer.

Brown Creeper *(Finschia novaeseelandiae):* Brown Creepers were only rarely recorded during bird counts in the Central Ohikanui but were significantly more common at high altitudes (Tables 1 & 4). They were recorded only once at Lower Ohikanui and never at Buller. In the Inangahua Valley, Brown Creepers were recorded only at high-altitude Rahu Saddle.

Lines counted in one season only

September 1976: The bird-counting team was positioned in nine remote areas of high-altitude forest (counting lines 26-31, 33 and 34, Fig. 4). The results from these nine lines (Table 4) were compared with the September high-altitude counts from the Central Ohikanui counting area. Very few differences were detected. Brown Creepers and Rifleman were significantly

more common in the remote counts. Tuis and Robins were recorded in low numbers, whereas they were not recorded during the Central Ohikanui high-altitude counts. Of the introduced birds, only the Chaffinch was significantly more common in the remote counts. Otherwise, for all other species, the

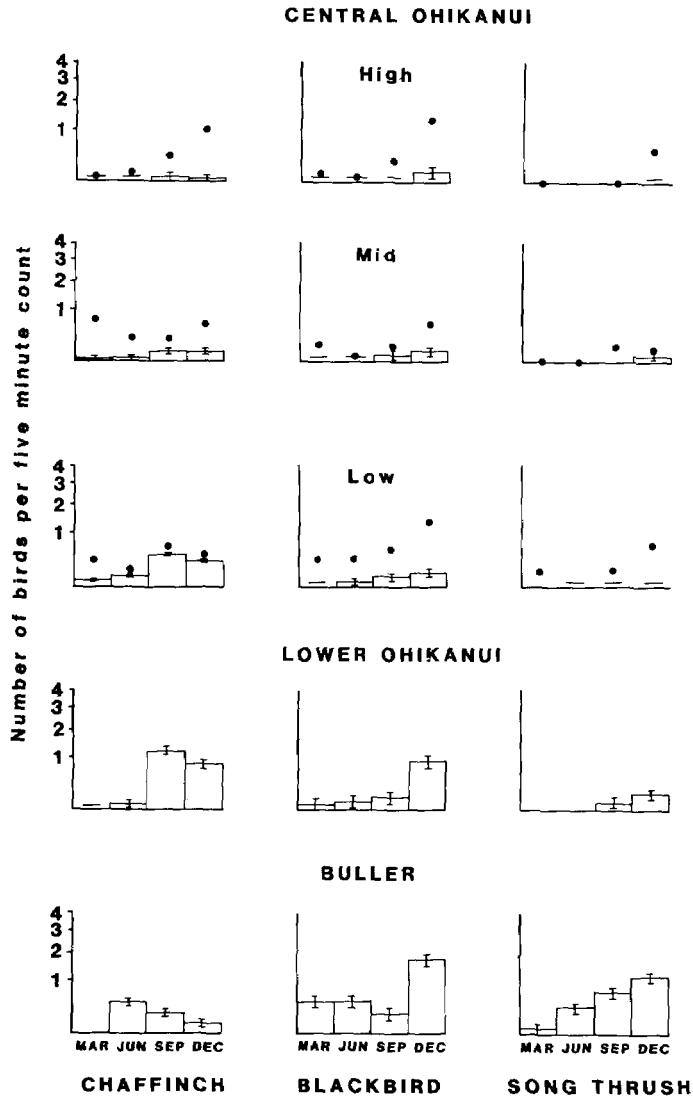

FIGURE 7D — Seasonal and altitudinal distribution of 12 species of birds indexed by standard 5-minute counts (continued)

TABLE 1 — Species in the "Central Ohikanui" area not included in Fig. 7. Percentage of 5-minute counts in which each species is represented

	Altitude	Mar 1977	Jun 1975	Sep 1976	Dec 1975	Significance of chi-squared
Number of observations	high	67	62	59	62	*** P<0.001
	middle	69	69	78	77	** P<0.01
	low	184	179	173	171	
SPECIES:						
Brown Creeper	high	5	0	0	7	***
	middle	0	0	0	3	
	low	0	1	1	1	
Parakeet	high	9	3	5	13	n.s.
	middle	7	13	8	9	
	low	12	3	12	11	
Kaka	high	2	0	0	5	n.s.
	middle	1	1	1	3	
	low	0	1	2	2	
Kea	high	0	0	2	0	n.s.
	middle	0	4	4	1	
	low	1	0	2	1	
Shining Cuckoo	high	0	0	0	5	***
	middle	0	0	0	8	
	low	0	0	0	11	
Pipit	high	0	0	2	3	***
	middle	0	0	0	0	
	low	0	0	0	0	
Weka	high	0	0	2	0	n.s.
	middle	3	0	1	1	
	low	1	2	4	2	
Kingfisher	high	2	0	0	0	n.s.
	middle	0	0	1	0	
	low	1	0	0	0	
Redpoll	high	10	3	22	10	***
	middle	0	0	9	3	
	low	2	3	2	7	
Goldfinch	high	0	0	0	0	n.s.
	middle	0	3	0	0	
	low	0	1	1	0	
Greenfinch	high	0	3	0	0	n.s.
	middle	0	0	1	0	
	low	0	1	0	1	
Hedgesparrow	high	0	0	0	0	n.s.
	middle	0	0	0	0	
	low	0	0	1	0	

TABLE 2 — Species in the "Lower Ohikanui" area not included in Fig. 7. Percentage of 5-minute counts in which each species is represented

	Mar 1977	Jun 1977	Sep 1976	Dec 1977	Significance of chi-squared
Number of observations	40	40	40	40	** P<0.01
SPECIES:					
Brown Creeper	3	0	0	0	n.s.
Parakeet	0	5	5	13	n.s.
Kea	0	0	8	0	n.s.
Shining Cuckoo	0	0	0	10	**
Weka	0	3	3	0	n.s.
Kingfisher	3	0	5	10	n.s.
Redpoll	0	0	8	0	n.s.
Greenfinch	0	0	0	3	n.s.
Hedgesparrow	0	0	5	0	n.s.

TABLE 3 — Species in the "Buller" area not included in Fig. 7. Percentage of 5-minute counts in which each species is represented

	Mar 1977	Jun 1977	Sep 1976	Dec 1977	Significance of chi-squared
Number of observations	40	40	40	40	*** P<0.001
SPECIES:					
Kea	0	0	0	3	n.s.
Shining Cuckoo	0	0	3	8	n.s.
Skylark	0	0	13	0	***
Weka	3	0	3	3	n.s.
Harrier	0	5	5	0	n.s.
Redpoll	5	3	5	3	n.s.
Goldfinch	3	0	0	0	n.s.
Hedgesparrow	0	0	3	0	n.s.

mean number counted in the remote sites compared remarkably well with the Central Ohikanui high-altitude zone.

March 1977: Five remote high-altitude lines (21, 35-38) were counted – three in alpine scrub and two predominantly in high-altitude forest (Table 4) – and the results were compared with those from the Central Ohikanui high-altitude zone.

Significantly fewer Bellbirds, Tits and Warblers were encountered in the remote sites. Robins and Pipits were also recorded in low numbers, whereas they were not found in the high-altitude zone in the Central Ohikanui. Conversely, Parakeets were not found in the remote sites, but were recorded in all altitudinal zones of Central Ohikanui. There were no significant differences for any other species counted.

Another two remote lines (22 and 23) in the upper reaches of the Ohikanui River between Eta and Theta Streams were counted in March 1977. Although these two sites were in the bottom of the Ohikanui Valley they fell on the boundary of the mid- and high-altitude zones. Significantly fewer Bellbirds and significantly more Riflemen, Robins and Warblers were counted on lines 22 and 23 (Table 4) than in the Central Ohikanui mid- and high-altitude zones. There were no other significant differences.

Two lines (24 and 25) in the Ohikanui Valley above Buckland Creek were also counted in March 1977 (Table 4) and compared with Lower Ohikanui lines 3 and 4. Bellbirds and Silvereyes were fewer above Buckland Creek

TABLE 4 — Lines counted in one season only, giving the percentage of 5-minute counts in which each species is represented and mean values per 5-minute count for frequently recorded species

	Lower Valley Lines 24, 25 Mar 1977		Upper Valley Lines 22, 23 Mar 1977		High altitude Lines 21,35-38 Mar 1977		High altitude Lines 26-34 Sep 1976	
Number of observations	40		20		70		180	
SPECIES:								
	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Bellbird	55	(0.45)	25	(0.11)	43	(0.36)	44	(0.35)
Tui	8	(0.01)	0	(0.00)	1	(0.00)	5	(0.01)
Silvereye	25	(0.26)	5	(0.02)	14	(0.06)	8	(0.03)
Rifleman	18	(0.08)	95	(2.56)	31	(0.25)	56	(0.81)
Grey Warbler	45	(0.29)	95	(1.56)	21	(0.07)	47	(0.40)
Fantail	33	(0.25)	40	(0.42)	17	(0.07)	16	(0.05)
Tit	70	(0.82)	75	(0.99)	40	(0.25)	55	(0.53)
Robin	40	(0.31)	70	(1.04)	9	(0.01)	8	(0.02)
NZ Pigeon	3	(0.00)	0	(0.00)	0	(0.00)	0	(0.00)
Chaffinch	8	(0.01)	5	(0.00)	3	(0.00)	27	(0.17)
Blackbird	0	(0.00)	5	(0.00)	3	(0.00)	12	(0.03)
Song Thrush	0		0		0		3	
Brown Creeper	0		0		6		14	
Parakeet	3		15		0		1	
Kaka	0		0		0		1	
Kea	0		0		0		1	
Pipit	0		0		10		5	
Fernbird	0		0		1		1	
Weka	0		0		0		1	
Harrier	0		0		0		1	
Falcon	0		0		1		0	
Redpoll	0		0		0		18	
Hedgesparrow	0		0		0		3	

than at Lower Ohikanui (significant at 5% level). This is to be expected because the vegetation changes abruptly about Buckland Creek. Lines 24 and 25 sampled forests similar to other low-altitude sites in the Central Ohikanui area, whereas lines 3 and 4 were in warmer lowland forests at the mouth of the Ohikanui.

Nocturnal and infrequently recorded species

Great Spotted Kiwi or Roa *(Apteryx haastii):* Roas were common from the valley bottom to above the bushline in all parts of the Ohikanui except near the confluence of the Ohikanui and Buller Rivers. At all times of year, their tracks were frequently found in snow or soft mud and birds were heard calling. Nearly all calls heard were after dark but one bird was calling as early as 1415 h on 16 September 1976. Often three or four were heard at night from the one site, and on 12 March 1977, four pairs of Roa were calling in the hanging valley at Gamma Lake. No sign of kiwis was seen or heard at the Buller counting area, nor did any kiwis respond to tapes played in this area or along the Buller Gorge to the confluence of the Ohikaiti River in March 1977. On this visit a special effort was made to tape kiwi calls, and to attract kiwis by playing tapes of their local dialect at Buller, Lower Ohikanui and in many places from the valley bottom to above the bushline in Central Ohikanui. This exercise clearly indicated the wealth of calls in the Roa repertoire, which had almost convinced us that Little Spotted Kiwi *(A. owenii)* and South Island Brown Kiwi *(A. australis australis)* were also present. However, after closely observing several Roa clearly producing all the calls we heard at night, we concluded that Roas were common and were the only species present.

Morepork *(Ninox novaeseelandiae):* Moreporks were recorded at all altitudes. They were commonly heard at night throughout the valley, at the mouth of the Ohikanui, and in the Buller study area.

Blue Duck *(Hymenolaimus malacorhynchos):* Blue Ducks were recorded on the main Ohikanui River on each of the four visits. Only one was observed in June 1975, just above the Denis Creek confluence. In December 1975, one pair was found between Denis and Delta Creeks and another pair, with four ducklings (probably not more than 2 weeks old), 400 m below the Bartrum Stream confluence. In September 1976, single birds were seen on different days at the Bartrum Stream confluence and on a rock in the river just downstream from Denis Creek. In March 1977, a pair was twice observed flying upstream past the main camp and once at the Bartrum Stream confluence.

Yellow-crowned Parakeet *(Cyanoramphus auriceps):* Parakeets were recorded in small numbers at all altitudes in all seasons in both the Central Ohikanui and the Inangahua study areas. They were recorded in all seasons, except autumn, at Lower Ohikanui but never at Buller. Although most were heard and not seen, all were probably Yellow-crowned Parakeets.

South Island Kaka *(Nestor meridionalis meridionalis):* Small numbers were present in the Central Ohikanui throughout the year. They were not recorded at Lower Ohikanui or at Buller.

Kea *(Nestor notabilis):* A few were present throughout the year at Central Ohikanui. They were recorded only in September at Lower Ohikanui and only in December at Buller.

Shining Cuckoo *(Chrysococcyx lucidus):* Shining Cuckoos were recorded at all altitudes in Central Ohikanui in December, at Lower Ohikanui in December, and at Buller in September and December.

Long-tailed Cuckoo *(Eudynamys taitensis):* Long-tailed Cuckoos were not recorded during 5-minute bird counts in any of the Ohikanui study areas, but they were present in the Ohikanui Valley.

Pipit *(Anthus novaeseelandiae):* Pipits were recorded on the river bed and on open ground on some low fan deposits throughout the Ohikanui Valley, and also occasionally on the tops above the scrub zone.

South Island Fernbird *(Bowdleria punctata punctata):* At 1036 m a.s.l., Fernbirds were seen and heard on the tops between the Ohikanui and Ohikaiti Rivers in scattered scrub (up to 2 m high) of manuka, bog pine, yellow-silver pine, mountain toatoa and stunted mountain and silver beech. This appears to be the highest altitude at which the Fernbird has been recorded anywhere in New Zealand.

Western Weka *(Gallirallus australis australis):* Wekas were widespread but nowhere common in the Ohikanui Valley. Wekas were also present in low numbers at Buller.

Australasian Harrier *(Circus approximans):* The only Harrier recorded in the Ohikanui Valley was at count line 32 on the open tops east of Dumpling Creek. A few were present at Buller.

New Zealand Falcon *(Falco novaeseelandiae):* Falcons were rarely recorded in the Ohikanui. They were not encountered at Lower Ohikanui or at Buller.

New Zealand Kingfisher *(Halcyon sancta):* Kingfishers were recorded in low numbers in the Central Ohikanui during March and September and at Lower Ohikanui during December, March and September. They were not recorded at Buller.

Southern Black-backed Gull *(Larus dominicanus):* Black-backed Gulls were noted in September and December above the open tops in the Central Ohikanui. One was seen in the Ohikanui River bed in December, and single birds were recorded in June and December flying over the Buller study area. There is a breeding colony on the tops just west of the Buckland Peaks (Dennis 1981).

Black Shag *(Phalacrocorax carbo):* Single Black Shags were occasionally seen flying along the Ohikanui River in March, June and September.

Little Shag *(P. melanoleucos):* A Little Shag (pied phase) was seen in the Ohikanui River above the Delta Creek confluence in September 1976.

Other infrequently recorded species were Skylark *(Alauda arvensis)*, Redpoll *(Carduelis flammea)*, Goldfinch *(C. carduelis)*, Greenfinch *(C. chloris)* and Hedgesparrow *(Prunella modularis)* (see Tables 1-3).

GENERAL DISCUSSION AND CONCLUSIONS

The steep glaciated topography of the Northern Paparoa Range has a profound effect on the dispersion of many species of birds in the lower Buller and Ohikanui Valleys. Cold mountain air, draining down these long deep valleys, clearly influences the distribution of forest types and affects species richness in both plant and animal communities. In turn, these environmental factors affect the numbers and movement of birds, both altitudinally and seasonally.

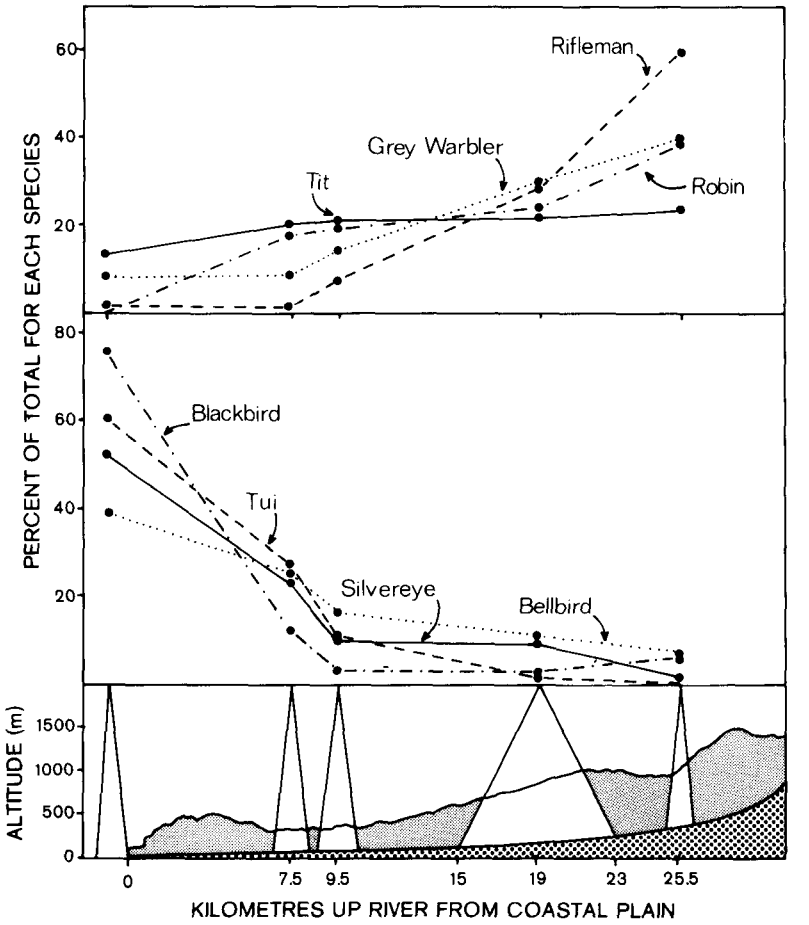

FIGURE 8 — Distribution of eight selected species of birds in valley bottom forests in March, in relation to the topographic position of 5 counting areas. The mouth of the Ohikanui Valley is 6 km up-river from the coastal plain.

Differences between counts in a complex of forest types, grading from modified warm forest at Buller through progressively less modified and colder forests to the headwaters of the Ohikanui (Fig. 6 & 8), illustrate the contrast between the habitat reqirements of the Tui, Bellbird and Silvereye (significantly more counted in more diverse, warm forest types) and the habitat requirements of some less mobile specialist insectivores, the Rifleman, Warbler, Robin and Tit (significantly more counted in less modified colder forests). Resources for nectar- and fruit-eating birds such as the Tui and Bellbird are severely reduced in the cold valley bottom. The variation in abundance of these two species at different distances into the valley in March (Fig. 8) reflects the effect on numbers of the rapid environmental changes that occur inside the mouth of the Ohikanui Valley.

Modification of natural habitat also affects the distribution of birds in the Ohikanui Valley (cf. Diamond & Veitch 1981). Blackbirds, which are very common in the modified forests of Buller, rapidly declined in numbers up the valley, reflecting their partly frugivorous food habits and their preference for modified habitat. Song Thrushes, Hedgesparrows and Harriers were also most abundant towards the edges of the forest, whereas Parakeets and Kaka and the native insectivores (Rifleman, Fantail, Tit, Robin and Brown Creeper) were most plentiful in the remoter, less modified forests.

The differences found between counts in remote sites and those in the high-altitude counting zone in the Central Ohikanui are not unexpected. The forests sampled at remote sites were on average at higher altitudes, and most were above the steep glaciated sides of the main valley and in forest with a more even canopy. Brown Creepers favour simple, even-canopy forests, apparently irrespective of altitude, as has been found elsewhere (pers. obs.; Clout & Gaze 1984). Robins tend not to favour steep land, but in the Ohikanui were found on the slopes above and below glacially truncated spurs.

Upper valley lines 22 and 23, which sampled beech forest in the bottom of the Ohikanui Valley, illustrate how spurious conclusions can be made if altitude alone is used to categorise the samples throughout the length of the valley. There, Bellbird numbers were much more like those recorded in low-altitude valley bottom sites affected by cold air drainage, than those in mid- or high-altitude sites in the Central Ohikanui. Robins and Rifleman also clearly preferred this cold valley bottom habitat in both the Upper and Central Ohikanui.

Overall, the Ohikanui remains a relatively unmodified montane valley habitat. In the less disturbed parts are good numbers of Roa, breeding pairs of Blue Duck, and low numbers of introduced bird species, together with few browsing mammals.

The hypothesis that "lowland" forest can provide essential resources for birds inhabiting higher-altitude forests for much of the year is supported by our results, provided that forest is warm, floristically rich, and has abundant flowers, fruit or invertebrates. However, this study has clearly demonstrated that not all low-altitude forest has these characteristics. Our results show that many Bellbirds and most Tuis migrate in winter from the Ohikanui Valley to other forests. For Bellbirds, the lowland forest type in

the Buller study area appears to suit their winter requirements. Tuis in the Ohikanui and Lower Buller catchments apparently overwinter in forests not sampled in our study, but there is evidence to suggest that their winter habitat must contain nectar or honeydew (Gravatt 1970, Onley 1983, pers. obs.). From early September, numbers congregate in areas of flowering kowhai elsewhere in the Buller Gorge (pers. obs.).

The question remains of where the Tuis from montane valleys such as the Ohikanui and from hill forests such as Buller go during winter. In winter they probably favour species-rich, warm, lowland beech-podocarp forests, of a type rapidly becoming rare in central North Westland. It is likely that Tuis have progressively declined along with the decline in lowland forest on the coastal plain during the last 120 years and are now far fewer to disperse into their summer montane range.

During June 1982, Onley (1983) found an average of 1.5 Tuis per count in unlogged low-altitude podocarp-beech-hardwood forest near Karamea, and a very similar average of 1.3 Tuis per count was recorded at Fletcher Creek in the Inangahua Valley in June 1974. In another study of six lowland forest types of the Western Paparoas, Onley (1980) counted birds in November, December and January, and for Tuis there were averages of 0.41 (coastal), 0.79 (old Tertiary), 0.86 (karst), 1.1 (limestone talus), 0.62 (cutover) and 0.83 (cutover near road). Onley's figures for Tuis accord reasonably well with those found in the Ohikanui during December, with the exception of our Buller counts (2.2 Tuis per count). Onley reported, however, that in October before his counts began "Tuis were present in large numbers feeding on nectar in the coastal forest." This suggests that the lowland forests of the Western Paparoas, like those at Karamea, Fletcher Creek and elsewhere, are winter refuges for many Tuis which in summer migrate to and breed in montane areas such as the Ohikanui Valley. Montane forests are apparently suitable for rearing young, but they do not adequately provide the large amounts of nectar or fruit required by Tuis for the rest of the year (see Gravatt 1970).

Suitable wintering habitat for Tuis is not found only at low altitude. The abundant honeydew crop produced on red beech in the forests of the warm north-facing fan-slopes (460-610 m a.s.l.) of Mt Misery, Nelson Lakes National Park, supports twice as many Tuis in winter as in summer (unpublished results).

The results from the Ohikanui and Inangahua Valley studies provide compelling evidence for the seasonal movement of many species of birds, particularly long-distance movements of honeyeaters. Montane forests without attendant warm, floristically rich winter habitat will not by themselves satisfy the annual requirements of the birds. Banding and radio-telemetry studies are now urgently needed to determine more precisely the seasonal movements and habitat use of Tuis and Bellbirds. Managers of indigenous forests must recognise that their management decisions for individual forests affect not only the wildlife values of the particular forest, but also the welfare of wide-ranging species such as the Tui, Bellbird, Pigeon and Kaka, which use the forest resource of the whole region.

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APPENDIX 1

Glossary of plant names

Bog pine	*Halocarpus bidwillii*
Bush rice grass	*Microlaena avenacea*
Cedar	*Libocedrus bidwillii*
Crown fern	*Blechnum discolor*
Hall's totara	*Podocarpus hallii*
Hard beech	*Nothofagus truncata*
Horopito	*Pseudowintera colorata*
Kahikatea	*Dacrycarpus dacrydioides*
Kamahi	*Weinmannia racemosa*
Keikei	*Freycinetia bauriana var. banksii*
Kowhai	*Sophora microphylla*
Mahoe	*Melicytus ramiflorus*
Manuka	*Leptospermum scoparium*
Matai	*Prumnopitys ferruginea*
Mountain beech	*Nothofagus solandri var. cliffortioides*
Mountain toatoa	*Phyllocladus aspleniifolius var. alpinus*
Northern rata	*Metrosideros robusta*
Pigeonwood	*Hedycarya arborea*
Red beech	*Nothofagus fusca*
Rimu	*Dacrydium cupressinum*
Silver beech	*Nothofagus menziesii*
Southern rata	*Metrosideros umbellata*
Supplejack	*Ripogonum scandens*
Toro	*Myrsine salicina*
Westland quintinia	*Quintinia acutifolia*
Yellow-silver pine	*Lepidothamnus intermedius*