VERTICAL DISTRIBUTION OF BIRDS MIST-NETTED IN A MIXED LOWLAND FOREST IN NEW ZEALAND

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ABSTRACT

Birds in forest in the Orongorongo Valley near Wellington were caught over a 7-year period (1969-76) in mist-net rigs consisting of six nets one above another, forming a continuous curtain of nets from near ground level to the forest canopy. We recorded which net in the rigs each bird was caught in, and described the vertical distribution of 14 species of bird. Hedgesparrows, Fantails, Tomtits and Blackbirds were caught more often in the lower nets, Kingfishers, Silvereyes and Bellbirds were caught more often in the upper nets, and Moreporks, Riflemen, Whiteheads, Grey Warblers, Song Thrushes, Tuis and Chaffinches were caught more or less evenly at both levels. The vertical profiles differed between rigs. For the three species caught most commonly (Silvereye, Blackbird and Bellbird), the mean height of capture varied with time of day and with season. The vertical distribution is a useful characteristic in helping to define the niches of these birds.

INTRODUCTION

The partitioning of food resources within a bird community may result, in part, from the segregation of species vertically into different feeding zones (Cody 1974, Dickson & Noble 1978). Several studies have related the spatial distribution of birds within habitats to that of the vegetation, and concluded that birds select habitats largely on the basis of vegetation structure (e.g. James 1971, Pearson 1971, Anderson *et al.* 1979, Terborgh 1980). The vertical segregation of forest birds in New Zealand into feeding zones has been studied by recording heights above ground of feeding individuals of single species (e.g. Atkinson 1966, Merton 1966, Powlesland 1981) and of assemblages of species (Gibb 1961, Gravatt 1971, Gill 1980, O'Donnell & Dilks 1986, H.A. Robertson unpubl.). Each species occupied a more or less distinct feeding niche, with feeding height an important characteristic in segregating the various species.

Although the vertical distribution of birds is usually described from systematic observations of foraging birds, we have described the vertical distribution of birds in forest from the height at which birds were caught in mist-nets on rigs carrying a continuous curtain of six nets from near ground level to the forest canopy (Whitaker 1972). Using this system, Ecology Division staff studied many aspects of the ecology of birds in lowland forest for 7 years (1969-76) in the Orongorongo Valley, near Wellington. This was the first study in New Zealand in which large numbers of forest birds were caught during a long and intensive mist-netting programme. Morphometric data and information on the foods of the insectivorous birds obtained from this study have been published (Robertson *et al.* 1983, Moeed & Fitzgerald 1982).

By recording the height of capture of each bird, we were able to investigate the vertical distribution of captures within the forest for the 14 species (9 native, 1 recently self-introduced and 4 introduced) caught more than 30 times. Variations in vertical distributions between nets, between seasons and through the day were investigated for the three species caught more than 300 times – Silvereye, Blackbird and Bellbird. Scientific names of birds are given in Table 1.

STUDY AREA

The study area was about 4 ha of mixed rata/podocarp/hardwood forest on a raised river terrace (130 m a.s.l.) near the research station of Ecology Division, Department of Scientific and Industrial Research, in the Orongorongo Valley (41° 21'S, 174 °58'E) in the southern Rimutaka Range, 18 km east of Wellington.

The forest structure has been described by Daniel (1972), Fitzgerald (1976) and Moeed & Fitzgerald (1982). The vegetation has emergent trees up to 40 m tall, mainly *Metrosideros robusta, Dacrydium cupressinum, Prumnopitys ferruginea* and *P. taxifolia*. The canopy, between 6 and 20 m, is composed of *Elaeocarpus dentatus, Laurelia novae-zelandiae, Melicytus ramiflorus, Hedycarya arborea, Knightia excelsa, Weinmannia racemosa, Schefflera digitata* and *Pseudowintera axillaris* and many tree ferns (*Cyathea* spp. and *Dicksonia squarrosa*). The dense subcanopy and shrub layer consists of young canopy trees and shrubs such as *Coprosma* spp., *Carpodetus serratus, Geniostoma rupestre* var. *ligustrifolium, Macropiper excelsum, Myrsine australis,* and *Olearia rani*. The large trees support epiphytes, including *Astelia solandri, Collospermum hastatum* and *Griselinia lucida*, and lianes such as *Ripogonum scandens, Metrosideros* spp. and *Freycinetia baueriana* ssp. *banksii*. The forest floor is open, with ferns and seedlings covering about 40% of the area.

METHODS

From June 1969 to August 1976, seven permanent mist-net rigs (Whitaker 1972) were operated for four days each month except during rain. Six of these rigs consisted of six standard (9 m x 2 m) 38-mm-mesh mist-nets set one above the other, forming a continuous curtain from 1.5 m above the ground to 13.5 m in the canopy layer; the remaining rig held five, or sometimes six mist-nets. Being placed between large trees that could support them, the net rigs varied in aspect, exposure to sunlight, and amount of surrounding vegetation. The rigs were 57 m to 76 m apart.

We recorded in which of the six nets (but not which shelf within the net) each bird was captured (net 1 = 1.5-3.5 m, net 2 = 3.5-5.5 m, etc.), so records are accurate only to within 1 m. Data are presented from only the six-net rigs in the main analysis, but additional data from the other rig are included in the analysis of seasonal and diurnal patterns for the three most commonly caught species because the bias due to the missing net should be constant.

For all the analyses of diurnal patterns, daylight hours were divided into 12 equal periods. In June (shortest days) these periods were of 46 minutes and in December (longest days) they were of 76 minutes. For comparative purposes these periods were assigned to the 'standard times' 0600 to 1800 h irrespective of the time of year.

RESULTS

Differences between species

For seven species the observed vertical distribution in the nets differed significantly (i.e. $p < 0.05$) from an equal chance of capture in each tier (Kolmogorov-Smirnov one-sample test). Hedgesparrows, Fantails, Tomtits and Blackbirds were caught more often in the lower nets, and Kingfishers, Silvereyes and Bellbirds more often in the higher nets (Figure 1, Table 1). No species was caught significantly more often in the middle nets.

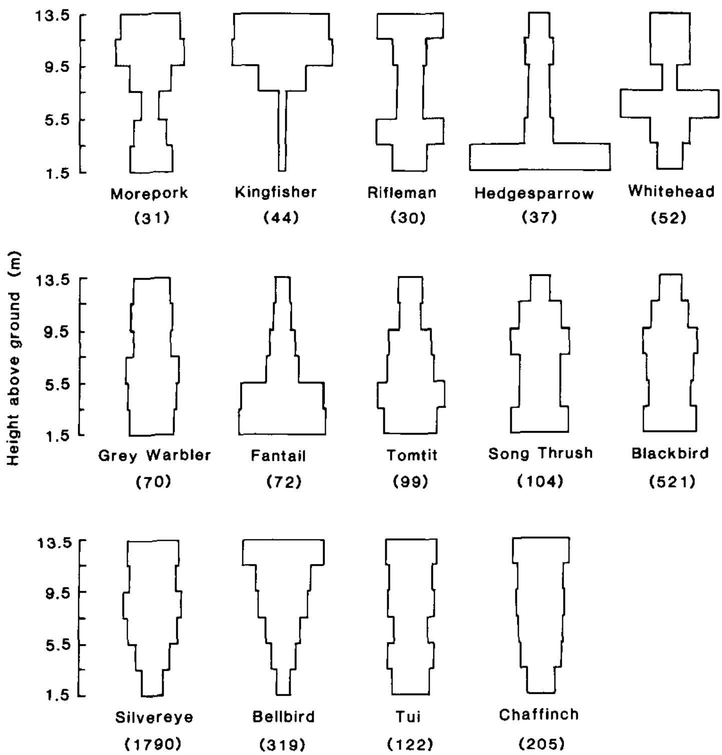

FIGURE 1 —Vertical distribution of captures of the 14 most commonly caught species, in 2 m intervals from 1.5 m above the ground. Sample size is given in brackets

TABLE 1 — Mean net of capture, for all records from 6-net rigs (1 = lowest, 6 = highest)

Species	$\bar{x}$	*sd*	*n*
Kingfisher (*Halcyon sancta*)	5.05	1.03	56
Bellbird (*Anthornis melanura*)	4.45	1.50	374
Silvereye (*Zosterops lateralis*)	4.03	1.54	2093
Morepork (*Ninox novaeseelandiae*)	3.94	1.77	36
Chaffinch (*Fringilla coelebs*)	3.88	1.66	230
Tui (*Prosthemadera novaeseelandiae*)	3.83	1.69	155
Whitehead (*Mohoua albicilla*)	3.68	1.57	59
Rifleman (*Acanthisitta chloris*)	3.68	1.88	31
Grey Warbler (*Gerygone igata*)	3.49	1.68	84
Blackbird (*Turdus merula*)	3.24	1.63	609
Song Thrush (*Turdus philomelos*)	3.15	1.61	121
Tomtit (*Petroica macrocephala*)	3.07	1.56	119
Fantail (*Rhipidura fuliginosa*)	2.67	1.58	94
Hedgesparrow (*Prunella modularis*)	2.33	1.72	42

Of the six small insectivorous species, Hedgesparrows, Fantails and Tomtits were caught significantly more often in the lower nets, and Riflemen, Whiteheads and Grey Warblers were caught at all levels. Of the two larger insectivorous species (that also take some small vertebrates), Kingfishers were caught almost exclusively in the top three nets (above 7.5 m); Moreporks were caught rarely, but at all levels.

TABLE 2 — Mean nets of capture of males and females of the sexually dimorphic species

	Males			*Females*			χ^2
	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	
Rifleman	3.61	1.69	18	3.81	2.09	11	3.4
Whitehead*	3.38	1.71	16	3.59	1.56	32	1.7
Tomtit	3.04	1.64	70	3.10	1.45	49	7.6
Blackbird	3.27	1.63	295	3.30	1.59	263	3.2
Bellbird	4.43	1.50	231	4.47	1.52	139	1.3
Tui	3.68	1.68	92	4.07	1.71	58	5.7
Chaffinch	3.80	1.63	126	3.96	1.71	102	1.6

* Whitehead sex based on plumage

Although two of the nectar-feeders (Silvereye and Bellbird) were caught significantly more often in the upper nets, Tuis were distributed fairly evenly. Of birds with a mixed diet of invertebrates and fruit, Song Thrushes and Blackbirds had similar height distributions (Spearman rank correlation $r_s = 0.81$, $0.05 < p < 0.10$), although the vertical stratification was significant for only the Blackbird. Chaffinches were caught fairly evenly at all heights.

The vertical distributions of captures of males and females of the seven commonly caught species that are sexually dimorphic were not significantly different (Table 2).

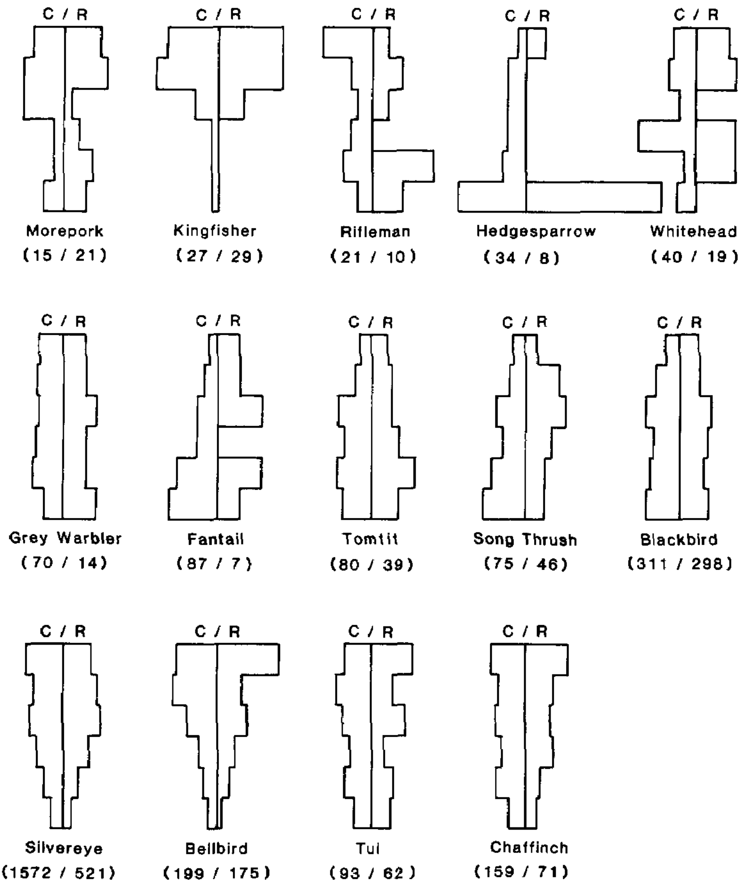

FIGURE 2 —Vertical distribution of first captures (on left) and recaptures (on right) of the 14 most commonly caught species

In some species the vertical distributions of birds caught for the first time differed from the distributions when they were recaptured (Figure 2). Of the three species caught most often, the distributions of first captures and recaptures of Silvereyes and Bellbirds differed significantly ($x^2 = 12.21$, $p < 0.05$, and $x^2 = 12.19$, $p < 0.05$, respectively). Some other species show differences, but the numbers of recaptures were very small. The difference is greatest for Hedgesparrows (only one of the eight recaptures of six individuals was higher than the first net) and the number of captures and recaptures in net 1 compared with the upper five nets is significant (Fisher's exact test $p = 0.03$). This suggests that transient birds may pass through the forest at a different level from that in which resident birds forage or sing.

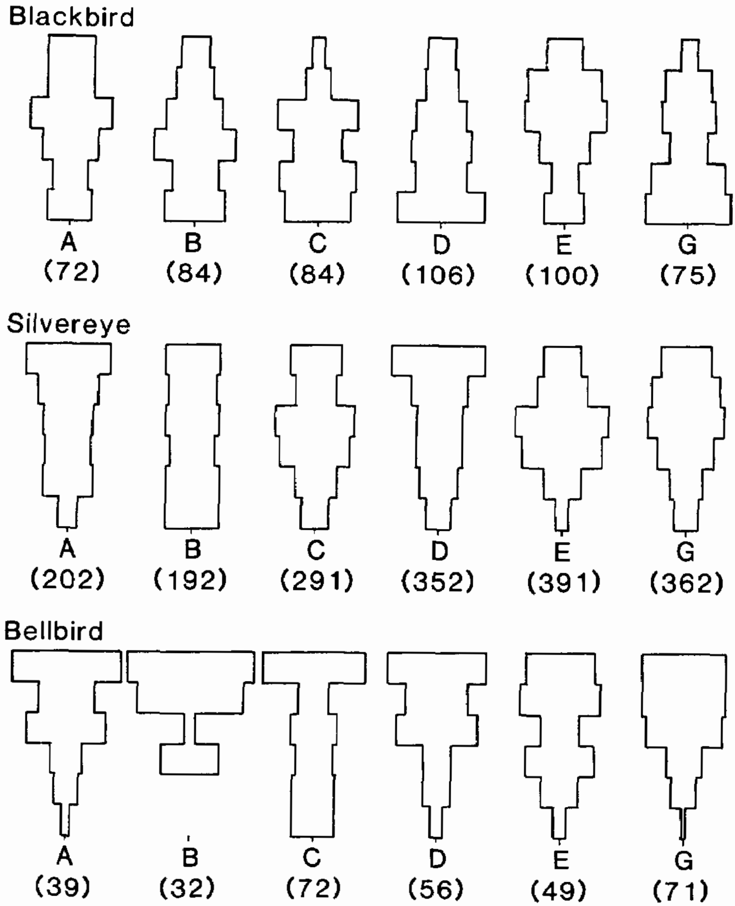

FIGURE 3 — Vertical distribution of the three most commonly caught species (Blackbird, Silvereye, and Bellbird), showing differences in the vertical distribution by net-rig site

Differences between net-sites

The height profiles given in Figure 1 were averaged over six mist-net rigs; however, for some species the shape of the profile differed significantly between rigs. Blackbirds and Silvereyes were captured at heights significantly different between nets (Figure 3) (Kruskal-Wallis $H = 27.1$, $p < 0.001$ and $H = 31.7$, $p < 0.001$ respectively). At net G, for instance, 51% of Blackbirds were caught between 1.5 m and 5.5 m, but in net E only 22% were caught at similar heights.

The differences in the vertical distributions between mist-net rigs are not consistent between species of birds (see Figure 3 for Blackbird, Silvereye and Bellbird), and it is likely that several factors interact to produce these differences between rigs. They may include: 1) differences in the local topography of trees and foliage around the nets, making parts of some rigs remain in sunlight and therefore visible longer than others; 2) differences in height of natural "flight-lines" through the forest that are intercepted by each rig; 3) differences in spatial distribution of important food resources near each rig; and 4) variations in the vegetation profile through the forest, making the top of some rigs nearer to the canopy-subcanopy boundary than others.

Variations with standard time of day

The vertical distribution of the three most commonly caught species varied with the time of day similarly (Kendall coefficient of concordance, $W = 0.65$, $x^2 = 23.4$, $p < 0.05$). Birds were caught highest in the early morning (before 0700 h) and the late afternoon (1600-1800 h) and lowest around midday (1000-1500 h) (Figure 4). The changes in heights through the day were significant for Blackbirds (Kruskal-Wallis $H = 21.1$, $p < 0.05$)

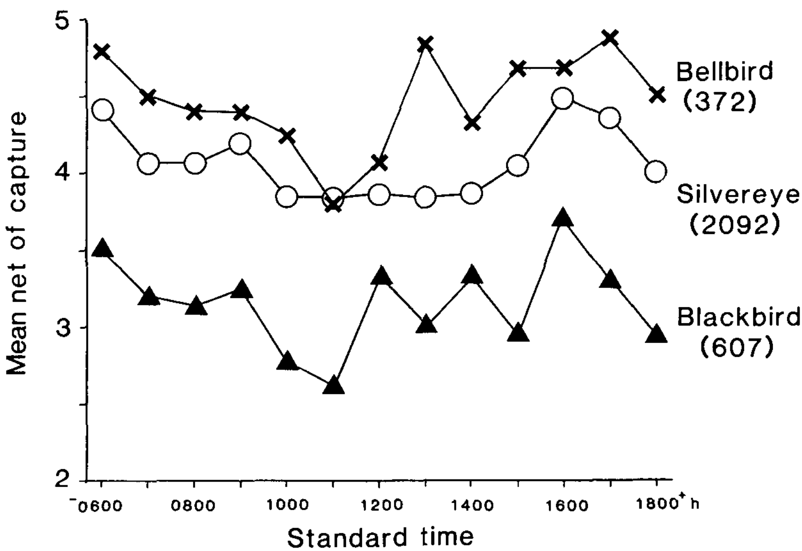

FIGURE 4 —Variation in the mean height of capture of Bellbirds, Silvereyes, and Blackbirds through the day. (Daylight was divided into 12 equal periods of 'standard time' with sunrise at 0600 and sunset at 1800 h.)

and Silvereyes (Kruskal-Wallis H = 36.7, $p<0.001$), but although Bellbirds showed a pattern of change similar to that of the other two species, the differences through the day were not statistically significant when grouped into 2-hour intervals (Kruskal-Wallis H = 11.5, $0.05< p<0.10$).

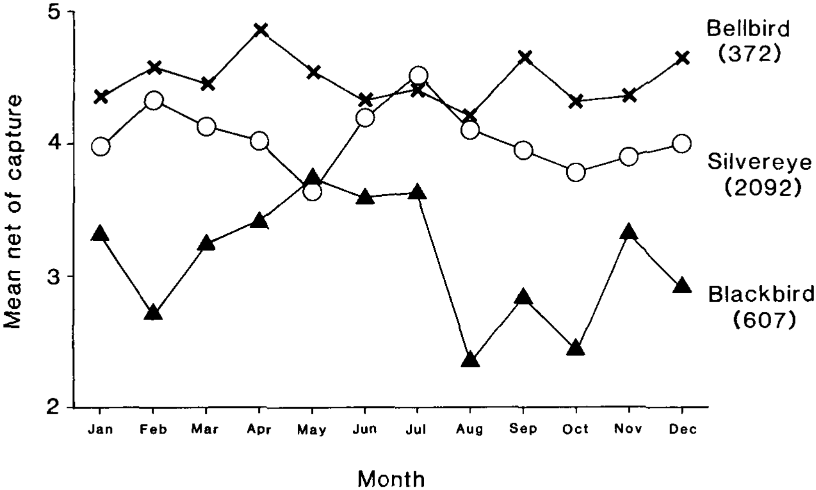

FIGURE 5 — Seasonal variation in the mean height of capture of Bellbirds, Silvereyes, and Blackbirds

Seasonal variations

Heights of mean monthly captures are shown in Figure 5 for the three most commonly caught species. The overall patterns of the three species were not similar (Kendall coefficient of concordance W = 0.41, x^2 = 13.7, n.s.). Blackbirds and Silvereyes showed highly significant changes in their height distribution throughout the year (Kruskal-Wallis H = 42.5, $p<0.001$ and H = 55.6, $p<0.001$ respectively), whereas Bellbirds did not (H = 5.6, $p>0.05$). Blackbirds were caught more often in high nets from April to July inclusive, and in low nets from August to October inclusive. The mean 'net of capture' in each mist-net rig dropped very sharply between July [$\bar{x}$ = 3.64 (= 6.8 m), n = 42] and August [$\bar{x}$ = 2.37 (= 4.2 m), n = 30]. Silvereyes were caught higher in the forest in February and from June to August inclusive, but low down in May and from September to January inclusive. The mean capture height increased sharply between May [$\bar{x}$ = 3.64 (= 6.8 m), n = 460] and June [$\bar{x}$ = 4.20 (= 7.9 m), n = 269], with the mean height increasing at six of the seven mist-net rigs.

DISCUSSION

The 14 species for which vertical distributions are presented here include most of the species that we mist-netted in the forest in the Orongorongo Valley. Half of them had vertical distributions that differed significantly from even distributions. A few native species (New Zealand Pigeon, Shining

Cuckoo and Long-tailed Cuckoo), and some introduced species that mainly frequented grass and scrublands (Robertson *et al.* 1983), were caught infrequently and were not included in the analysis.

The vertical distributions of birds in New Zealand forests have been described previously, by recording either the structural level in the forest in which they feed (canopy, understorey, floor, etc.) or the site at which they feed (leaves, twigs, branches, trunk, floor, etc.) (Gibb 1961, Gravatt 1971, Gill 1980, O'Donnell & Dilks 1986). Results from mist-netting cannot be compared directly with those from observations of feeding height but the patterns are broadly similar. One exception is that we caught Bellbirds mostly in the upper nets and Tuis fairly evenly at all levels, whereas Gravatt (1971) and O'Donnell & Dilks (1986) recorded Bellbirds more often at lower levels and Tuis more often at higher levels in the forest. Moeed & Fitzgerald (1982) noted that individuals of several species of birds living in pine forest (Gibb 1961), mixed native forest (Gravatt 1971), and kanuka forest (Gill 1980) fed to about the same extent on different substrates (trunk, branch, leaf, ground, etc.), despite the differences in the structure of the forests. This suggests that the feeding niches are well-defined, being little affected by habitat differences, and that the height distributions of forest birds are a useful coarse measure of differences in the niches that they occupy.

Oceanic islands generally have fewer species of landbird than mainland areas of equivalent size, and island birds tend to have wider niches than their mainland counterparts (Van Valen 1965, Lack 1976). Bull & Whitaker (1975) stated that the landbirds of New Zealand lack diversity and occupy broad niches. They used the Fantail as an example; it was, until recently, the only bird species feeding mainly on flying insects and it occupies a wide range of habitats throughout the country. It is also one of the few New Zealand birds that is common in farmland habitats created after European settlement last century (Turbott 1961). The species is widespread, being found also in Tasmania, mainland Australia, New Guinea, New Caledonia, and Vanuatu (Ford 1981), and in some places it occupies a narrower range of habitats than in New Zealand. Diamond & Marshall (1977) reported that in Vanuatu a second species of fantail (*R. spilodera*) is also present on some islands, where *R. fuliginosa* is confined to forest edge and open habitats and *R. spilodera* occupies closed forest. However, on islands where *R. fuliginosa* alone is present it is found in forest as well as more open habitats – a pattern similar to that in New Zealand where the Fantail has no congeneric competitors and occupies a wide range of habitats, including forest. If the Fantail is primarily a bird of open habitat and forest edge, and only secondarily occupies forest, this may explain why it adapted so readily to farmland habitat.

The niche of a species, as defined by Hutchinson (1957), is based on measurement of the range of values within which a species can survive and reproduce, for any number of independent biotic and abiotic characteristics. Usually the niches of two species can be separated on just two or three of the many characteristics (Hutchinson 1978). Do the New Zealand forest birds occupy niches that are broad in all characteristics, or only in some, and is vertical distribution an important characteristic of their niches?

In southeastern Australia, guilds of forest birds (groups of species with similar foraging habits) separate firstly by differences in foraging height and bird weight and secondly by foraging methods and food substrate (Holmes & Recher 1986). This implies that the heights at which birds forage, and therefore the heights at which they are caught in mist-nets, are useful, measurable dimensions of the niches of birds in forest. The study of Holmes & Recher included two species, the Grey Fantail and the Silvereye, that are also in New Zealand and *Petroica multicolor*, the closest relation of the Tomtit (Fleming 1950). A comparison of the proportion of foraging sites used by these species in Australia (Recher *et al.* 1985) with the proportion used by the New Zealand forms (Gibb 1961, Gravatt 1971, O'Donnell & Dilks 1986) does not suggest that this aspect of their niches is narrower in Australia than in New Zealand. Detailed comparative work on Fantails or Silvereyes in similar habitats in Australia and New Zealand is needed.

Our study shows that the species of forest birds in the Orongorongo Valley differ significantly in the height at which they are active and are caught in the mist-nets. It also shows that the height of capture varies with the time of day, time of year, and with capture or recapture. Because of the differences in the vertical distributions of birds caught in different net-rigs, we emphasise that it is important to use several rigs to obtain representative average profiles of the captures. Also, because of the differences between distributions of first captures and recaptures, analyses should use all captures, not just first captures, to describe the height distribution of the whole population.

Future studies should attempt to identify the factors that are most important in influencing the height of capture of forest birds. These might include the vegetation profile within the forest, seasonal changes in the distribution of food, changes in the incidence of sunlight, temperature profile and wind velocity through the forest, and the proportions of residents and transients in the populations.

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