

ECOLOGY OF THE BIRDS OF KAINGAROA FOREST

JOHN A. GIBB

Animal Ecology Division, Department of Scientific and Industrial Research, Lower Hutt

INTRODUCTION

In common with other pine forests consisting of large blocks of even-aged trees usually of a single species (Voute 1946). Kaingaroa Forest is vulnerable to outbreaks of insect pests. With their low reproductive potential, birds cannot cope with plagues of insects once they have broken out; but at the more prevalent endemic levels of their prey they can eat a significant fraction of their food stocks (Gibb 1958, 1960; Tinbergen 1960), and under certain circumstances their predation can dampen down oscillations in insect numbers which might otherwise develop into serious outbreaks (Tinbergen & Klomp 1960).

It is therefore prudent to know what insectivorous birds live in such forests as Kaingaroa, and to know something of their feeding habits and population ecology. In the natural ranges of the exotic conifers planted in Kaingaroa there are species of birds that have evolved in such forests. As this is not so in New Zealand where the trees lack their natural fauna, it is also intriguing to see which native and introduced birds have managed to colonise them.

The present paper describes the birds' density more precisely than has been done hitherto, and includes a quantitative description of the feeding habits of the four commonest insectivores — pied tit, whitehead, grey warbler and white-eye.* It also reports the use of nest-boxes by pied tits. I am indebted to Dr. K. Wodzicki, Director, and Mr. P. C. Bull, Animal Ecology Division, D.S.I.R., for constructive criticism of this paper.

KAINGAROA FOREST

Kaingaroa Forest extends over some 350,000 acres of the central volcanic plateau

of the North Island of New Zealand, and is centred about 30 miles north-east of Lake Taupo and the same distance south-east of Lake Rotorua. It lies mostly at about 2000 ft. above sea level and has an average annual rainfall of about 55 in. The soils are formed from porous rhyolitic or basaltic scoria, and ash showers occurred in about A.D. 250 and 1200 and in 1886.

To a newcomer Kaingaroa is an astonishing hotchpotch. About 250,000 acres have so far been planted in exotic conifers: *Pinus radiata*, *P. ponderosa*, *P. contorta* and *Pseudotsuga taxifolia* from North America, and *Pinus nigra* from southern Europe. The northern half of the forest was mostly planted in the mid to late 1920's and the southern half in the early 1930's. Native plants intermingle with the exotic conifers, and both support populations of native and introduced birds and insects. Introduced red deer (*Cervus elaphus*), pig (*Sus scrofa*) and feral horses (*Equus caballus*) roam the forest; while rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), stoats (*Mustela erminea*) and ferrets (*Putorius putorius*) frequent the forest edge and open spaces.

METHODS

Six visits were made to Kaingaroa — in July and October 1958, and in January, April, July-August and October-November 1959. Each visit lasted about a week, except in July 1958 and January 1959 when only two or three days were available.

The same procedure was adopted at each visit, whereby the observer walked slowly back and forth through selected compartments counting the number of birds of each species seen or heard per hour (see Gibb 1960). Several approximately straight transects were made through each compartment, and all birds met within about 50 yd. either side were included. Short pauses and slight deviations were allowed in order to check

* Specific names of birds are in Table 1.

the composition of flocks. Singing or calling birds were not especially sought, but were included whether actually seen or not if they were within the 50 yd. range. Simultaneously with these counts, for birds that were feeding, records were made of the species, numbers, heights above ground and the parts of the trees being examined. Repeated observations of this kind can be treated statistically to describe the birds' feeding habits (Gibb 1954, 1960).

In addition, in October-November 1959, about twelve hours were spent making a census of the birds breeding in about 50 acres of *P. nigra*, planted in 1933. During the same period routine counts recorded the number of birds per hour in the *P. nigra* and elsewhere. The density of birds breeding in *P. radiata*, *P. ponderosa* and *Ps. taxifolia* was then estimated on the assumption that the relationship between density and birds counted per hour was the same in these plantations as in the *P. nigra*.

TABLE 1. Mean number of birds counted per hour, by date and tree species.

Date and tree spp.	No. of hours counted	Fantail <i>Rhipidura fuliginosa</i>	Pied tit <i>Petroica macrocephala</i>	Robin <i>Petroica australis</i>	Whitehead <i>Mohoua ochrocephala</i>	Grey warbler <i>Gerygone igata</i>	Song thrush <i>Turdus ericetorum</i>	Blackbird <i>Turdus merula</i>	Duncock <i>Prunella modularis</i>	White-eye <i>Zosterops lateralis</i>	Chaffinch <i>Fringilla coelebs</i>	Others	Total
JULY 1958													
<i>P. radiata</i>	7	—	2.4	0.1	22.7	7.3	0.1	0.7	2.0	18.0	2.4	—	55.7
<i>P. ponderosa</i>	2	—	1.0	—	—	0.5	—	2.0	2.5	1.0	1.5	—	8.5
<i>Ps. taxifolia</i>	4	—	2.7	0.3	13.5	4.2	—	1.5	2.3	44.5	2.5	0.5	72.0
OCTOBER 1958													
<i>P. radiata</i>	8	0.2	5.3	0.1	9.7	5.1	0.2	2.8	1.2	2.8	9.6	1.4	38.5
<i>P. nigra</i>	2	—	3.0	—	5.0	1.5	2.0	8.0	2.5	—	1.5	—	23.5
<i>P. ponderosa</i>	4	—	2.5	—	0.5	2.2	1.5	5.0	2.5	1.0	5.0	2.0	22.2
<i>P. contorta</i>	2	1.0	1.5	—	5.0	5.0	0.5	4.0	1.0	7.0	6.5	7.0	38.5
<i>Ps. taxifolia</i>	2	2.0	6.0	—	5.5	4.5	0.5	2.0	2.0	2.5	4.5	0.5	30.0
JANUARY 1959													
<i>P. radiata</i>	6	—	6.8	—	14.1	2.8	0.7	7.3	1.3	6.5	18.0	1.8	59.3
<i>Ps. taxifolia</i>	1	—	7.0	—	2.0	3.0	—	1.0	—	4.0	10.0	2.0	29.0
APRIL 1959													
<i>P. radiata</i>	9	1.1	3.2	—	26.1	3.2	0.1	1.3	0.3	10.7	3.7	0.1	49.8
<i>P. nigra</i>	5	0.8	2.0	0.8	6.6	5.2	0.2	4.8	0.2	6.6	1.2	—	28.4
<i>P. ponderosa</i>	5	1.0	3.2	—	0.6	2.8	0.2	1.4	1.8	0.8	9.2	3.6	24.6
<i>P. contorta</i>	1	—	3.0	—	12.0	6.0	—	3.0	2.0	3.0	4.0	1.0	34.0
<i>P. strobus</i>	1	—	4.0	—	9.0	2.0	—	3.0	4.0	13.0	8.0	—	43.0
<i>Ps. taxifolia</i>	4	0.2	4.5	1.0	6.5	5.0	—	2.0	1.3	16.7	5.5	4.5	47.2
JULY/AUG. 1959													
<i>P. radiata</i>	11	—	3.3	0.2	15.6	4.1	0.2	2.7	0.8	3.5	1.6	0.2	32.2
<i>P. nigra</i>	5	—	2.4	0.6	4.0	2.8	1.0	3.8	0.2	1.4	—	—	16.2
<i>P. ponderosa</i>	3	1.0	2.3	—	1.3	2.3	4.0	8.0	1.0	0.7	1.7	1.3	23.6
<i>P. contorta</i>	2	—	1.5	—	4.5	2.5	0.5	0.5	1.0	1.0	1.0	—	12.5
<i>Ps. taxifolia</i>	4	1.0	2.5	0.5	4.8	4.5	0.2	3.0	0.5	3.5	1.0	—	21.5
OCT./NOV. 1959													
<i>P. radiata</i>	14	0.2	3.8	0.1	10.3	3.4	0.4	3.5	1.2	2.4	9.8	0.6	35.7
<i>P. nigra</i>	11	0.2	1.7	0.3	3.9	1.8	0.4	4.6	0.4	—	4.3	3.2	20.8
<i>P. ponderosa</i>	4	0.2	1.5	—	0.5	3.5	0.8	4.2	0.8	1.0	8.5	2.5	23.5
<i>P. strobus</i>	2	—	3.5	—	2.5	8.5	—	4.0	4.5	6.0	9.0	0.5	38.5
<i>Ps. taxifolia</i>	3	0.3	3.0	0.3	5.3	5.0	—	—	0.3	2.0	2.3	0.7	19.4

NOTE.

In addition, the following species were recorded irregularly within the plantations: harrier *Circus approximans*, falcon *Falco novaeseelandiae*, pheasant *Phasianus colchicus*, Californian quail *Lophortyx californica*, shining cuckoo *Chalcites lucidus*, long-tailed cuckoo *Eudynamis taitensis*, morepork *Ninox novaeseelandiae*, skylark *Alauda arvensis*, pipit *Anthus novaeseelandiae*, bellbird *Anthornis melanura*, tui *Prothemadera novaeseelandiae*, greenfinch *Chloris chloris*, goldfinch *Carduelis carduelis*, redpoll *Carduelis flammea*, and yellowhammer *Emberiza citrinella*.

DENSITY OF BIRDS

Ryder (1948) and Weeks (1949) listed the birds of Kaingaroa Forest and commented briefly on their status. Though both authors agreed that many species were then increasing in numbers, there have evidently been no dramatic changes in the past decade. Caughley (1960) has recently reported the rifleman (*Acanthisitta chloris*) in Matea Forest, just east of Kaingaroa, in winter.

Table 1 gives the birds encountered inside the pine plantations, together with the numbers of each species counted per hour. Broadly speaking, the same species of birds occur throughout Kaingaroa; but the proportions of each vary with the tree species and with the appearance of the plantations, as well as to a lesser extent seasonally.

TREE SPECIES	<u>P.radiata</u>	<u>P.ponderosa</u>	<u>P.nigra</u>	<u>Ps.taxifolia</u>
AGE IN YEARS	28	26	26	25
STOCK DENSITY	80%	60%	100%	90%
UNDERGROWTH	Sparse	Dense	Absent	Absent

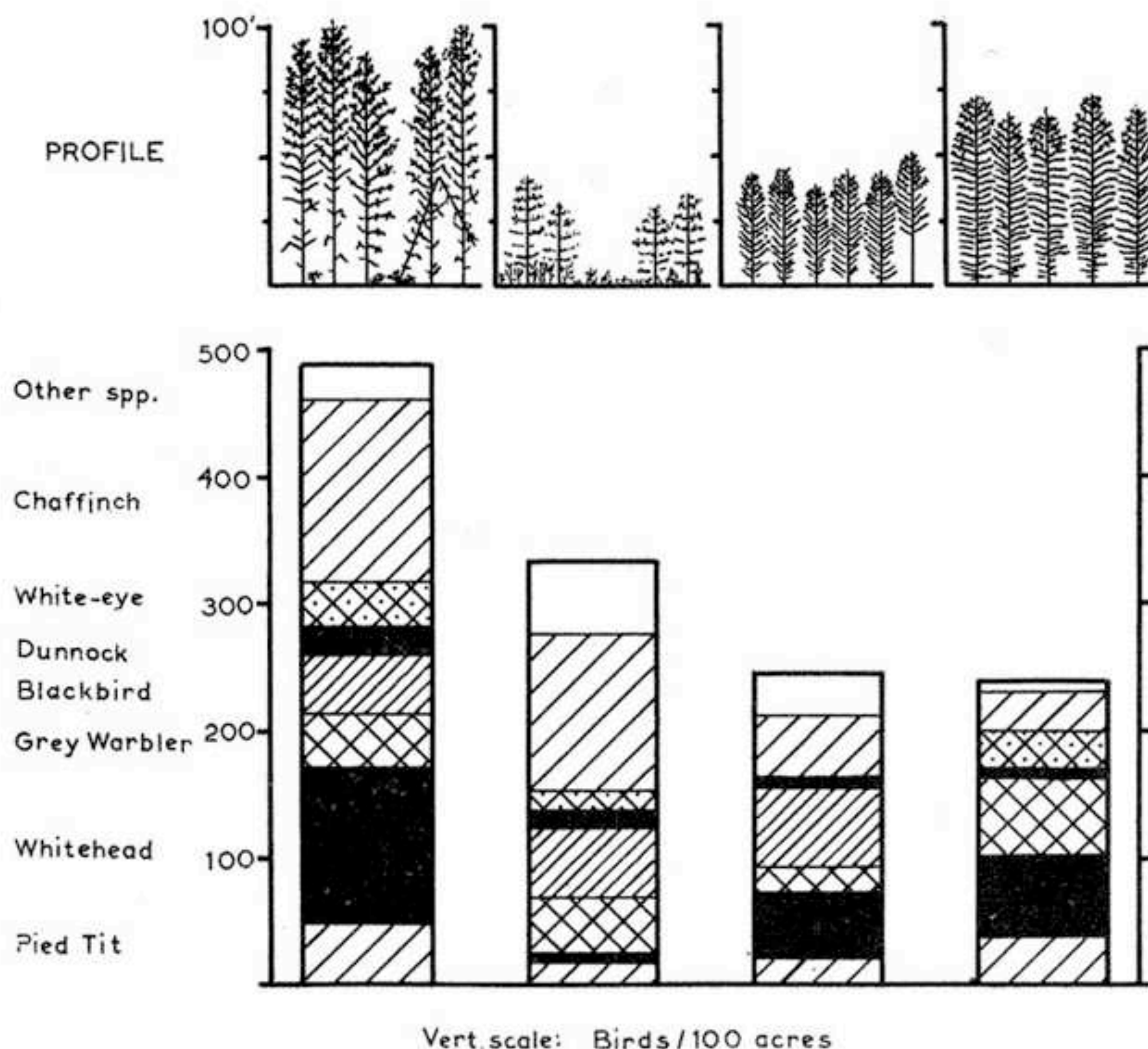


FIGURE 1. Estimated density of adult birds breeding in compartments of *Pinus radiata*, *P. ponderosa*, *P. nigra* and *Pseudotsuga taxifolia* of similar age: October-November 1959.

TABLE 2. Density of adult birds in October-November 1959.

Species	Approx. number of birds per 100 acres			
	<i>P. nigra</i>	<i>P. radiata</i>	<i>P. ponderosa</i>	<i>Ps. taxifolia</i>
Shining cuckoo	6	12	22	0
Fantail	2	2	3	3
Pied tit	21	47	19	37
Robin	4	1	0	4
Whitehead	51	125	6	64
Grey warbler	21	42	43	62
Song thrush	10	10	19	0
Blackbird	63	45	55	0
Dunnock	8	24	15	6
White-eye	0	35	15	3
Greenfinch	0	1	2	0
Goldfinch	4	0	0	0
Redpoll	8	0	10	0
Chaffinch	48	143	124	33

NOTES.

1. Estimates for *P. nigra* are based on a census of c. 50 acres. Other estimates are based on counts of birds per hour (*P. radiata* 14 hrs., *P. ponderosa* 4 hrs., *Ps. taxifolia* 3 hrs.) compared with similar counts in *P. nigra*, and are therefore less accurate.

2. In the census area in *Pi. nigra* most birds were about twice as numerous in an edge strip 100 yards wide bordering a firebreak as in the interior of the compartment.

In the breeding season

Table 2 and Figure 1 show the most frequent breeding species in different types of plantations. Pied tits, whiteheads, dunnocks (hedge sparrows), white-eyes and chaffinches are all more numerous in *P. radiata* than in less well-grown plantations. The figure illustrates how very different are the plantations of *P. radiata* and *P. ponderosa*, for instance, though of similar age. Whiteheads are plentiful in *P. radiata* but almost absent from the scrub-like *P. ponderosa*; but grey warblers are equally common in both habitats. Grey warblers are surprisingly numerous in *Ps. taxifolia*, possibly because their light weight and special feeding habits (see below) enable them to feed successfully in the rather flimsy foliage. In Europe, goldcrests (*Regulus regulus*), whose feeding habits are rather similar to those of the grey warbler, are also especially numerous in *Ps. taxifolia*. Blackbirds are most numerous in *P. nigra*, probably because they can feed in the wake of the many pigs which disturb the top soil in their search for the roots of *P. nigra*, a favourite food. Likewise robins are more frequent in 25-year-old *P. nigra* than in other plantations of the same age, and they too wait on rooting pigs for disturbed food. Finches and shining cuckoos (the latter not surprisingly with the many grey warblers, their principal hosts) make up most of the other species which are more numerous in *P. ponderosa* than elsewhere.

With about 487 adult birds (not pairs) per 100 acres, the well-grown compartments of *P. radiata* had an appreciably higher density than had the other habitats sampled. Compartments of *P. ponderosa* had the next highest density with about 333 birds per 100 acres. Although the *P. ponderosa* was poorly grown and thinly stocked, it usually had a dense undergrowth of *Leptospermum* and *Dracophyllum* with some grasses in places. Compartments of *P. nigra* and *Ps. taxifolia* are usually very dense so that little light penetrates the canopy; and they have relatively few breeding birds — about 240 birds per 100 acres in each.

At other seasons

As in the breeding season, the greatest density of birds is still to be found in *P. radiata* (Table 1). Finches, notably chaf-

finches, which breed inside the plantations, leave them in autumn to feed along the fire-breaks and in clearings. Hence, out of the breeding season they are no longer the commonest birds inside the plantations, and native insectivorous birds predominate: in order of frequency, whiteheads, white-eyes, grey warblers and pied tits. All but the last of these four species, and most especially white-eyes, were seen more often in the winter of 1958 than in 1959; whereas more blackbirds were seen in 1959 than in 1958.

Interpretation of the bird counts

Although the number of birds counted per hour is a reasonably good measure for comparing different (but not too different) habitats at the same season, or one habitat at the same season in different years, it is a misleading measure for comparing seasonal changes in density because of concomitant changes in the birds' individual conspicuousness. Thus of the most extensively sampled species only whiteheads, which are individually perhaps the most evenly conspicuous species through the year, show a seasonal rise and fall in the numbers counted hourly that can possibly correspond to actual population changes; and even so, the greater numbers counted hourly in April than in January 1959 are best explained by their probably increased conspicuousness rather than by supposing a real increase in their numbers.

TABLE 3. Influence of time of day on numbers of birds counted per hour: all seasons grouped.

Time of day, hours	08-10.00	11-13.00	14-16.00
No. of hours observation	56	34	32
Mean birds counted per hour: all tree spp.			
Pied tit	3.1	3.8	2.9
Whitehead	11.3	12.6	7.9
Grey warbler	4.3	3.4	2.9
Blackbird	3.0	3.7	3.2
Dunnock	0.8	1.4	1.7
White-eye	5.8	8.3	2.1
Chaffinch:			
Autumn	3.4	5.3	8.5
Winter	1.7	1.5	1.3
Spring	8.1	6.6	6.2
Mean	4.5	4.9	4.9
Mean birds counted per hour: <i>P. radiata</i> only, all species grouped	42.2	47.2	34.4
No. of hours observation	27	20	8

Birds are commonly regarded as being individually least conspicuous in the middle of the day, yet Table 3 shows that in *P. radiata* (the most sampled habitat) rather fewer birds were counted hourly in late afternoon than early in the afternoon. Pied tits and blackbirds were counted about equally often throughout the day; grey warblers decreasingly and dunnocks increasingly often from morning to late afternoon; and whiteheads and white-eyes distinctly least often in late afternoon.

Song and the conspicuousness of pied tits

The numbers of pied tits counted hourly varied closely with the numbers heard singing. Most were counted and most heard in October 1958 and January 1959; and likewise more in the middle of the day than at other times (Table 4). I have the impression that pied tits normally sing much less in January

elsewhere than in Kaingaroa in January 1959: the 1958-59 breeding season may have been unsuccessful in Kaingaroa (no young were seen in January 1959), which could account for their prolonged singing late in the summer.

Male pied tits are much more conspicuous than the females because of their loud song and striking plumage. The intensity of the male's song is often impressive: from 0900-1000 hours on a mild morning in a steady drizzle in late October 1959, for instance, one sang an average of 8.3 song phrases per minute over the full hour, and sang in all but seven of the 60 minutes. Surprisingly, although the time that males spend singing varies seasonally and to a lesser extent with the time of day, the mean number of phrases delivered per minute does not vary much (Table 4).

TABLE 4. *Intensity of song of male pied tits*

		AUTUMN <i>April</i> 1959	WINTER <i>July-Aug.</i> 1959	SPRING <i>Oct. 1958 & Oct.-Nov. 1959</i>	SUMMER <i>January</i> 1959
No. of hours observation	08-10.00	14	15	20	2
	11-13.00	7	5	14	6
	14-16.00	5	7	20	0
	Totals	26	27	54	8
Mean singing males/hour	08-10.00	0.9	1.1	1.3	(2.0)
	11-13.00	1.6	2.4	1.7	4.5
	14-16.00	0.2	0.7	1.7	—
	Mean	1.0	1.2	1.6	(3.9)
Mean song phrases/minute	08-10.00	7.5	8.3	9.2	(7.0)
	11-13.00	7.8	7.8	8.8	8.4
	14-16.00	(10.0)	(8.2)	9.1	—
	Mean	7.7	8.1	9.0	8.1

NOTE.

In singing males/hour, the few summer figures are placed in parentheses; likewise figures for mean song phrases/minute if based on fewer than 10 observations.

TABLE 5. *Relative conspicuousness of male and female pied tits*

	July 1958	October 1958	January 1959	April 1959	August 1959	October 1959
Total birds counted	31	77	49	74	72	96
Percent males	65	91	96	85	81	93
Percent of males, heard only	0	60	66	43	43	67
Total birds sighted	31	20	18	47	47	36
Percent males	65	85	89	77	70	81
Total females counted	11	7	2	11	14	7
Percent with males	82	(not recorded)		36	86	71

Table 5 shows that on the average about three-quarters of all the tits counted were males, and that up to two-thirds of all the males counted were heard and not seen. But even in July 1958 when none were singing, two-thirds of all the tits counted were males. Similarly at other seasons more than three-quarters of all the tits first seen rather than heard were males.

Of the few females counted, more were closely attended by males in July 1958 and in August and October 1959 than in April 1959. This suggests that pied tits are unpaired or that the pair bond is loose in autumn, but is well established by mid-winter.

pied tits and chaffinches forage together in mixed flocks. At first sight the feeding habits of the whiteheads, white-eyes and grey warblers appear rather alike; but analysis of the routine observations reveals marked differences between them.

It is as immediately obvious in the field as from Figure 2 that pied tits feed chiefly on or close to the ground. Their normal habit is to perch on a look-out, usually not more than ten feet up, and to scan the ground beneath for invertebrates moving on the surface. I have never seen them turning over the litter like blackbirds often do. Besides feeding close to the ground, pied tits also examine the foliage of the trees but seldom penetrate high into the canopy except when singing. When perched on swaying twigs pied tits keep their heads stationary in relation to the ground, the better to detect movements of their prey. A bird can accommodate small movements of its perch by flexing its neck

FEEDING STATIONS

Out of the breeding season, whiteheads, white-eyes, grey warblers and occasional

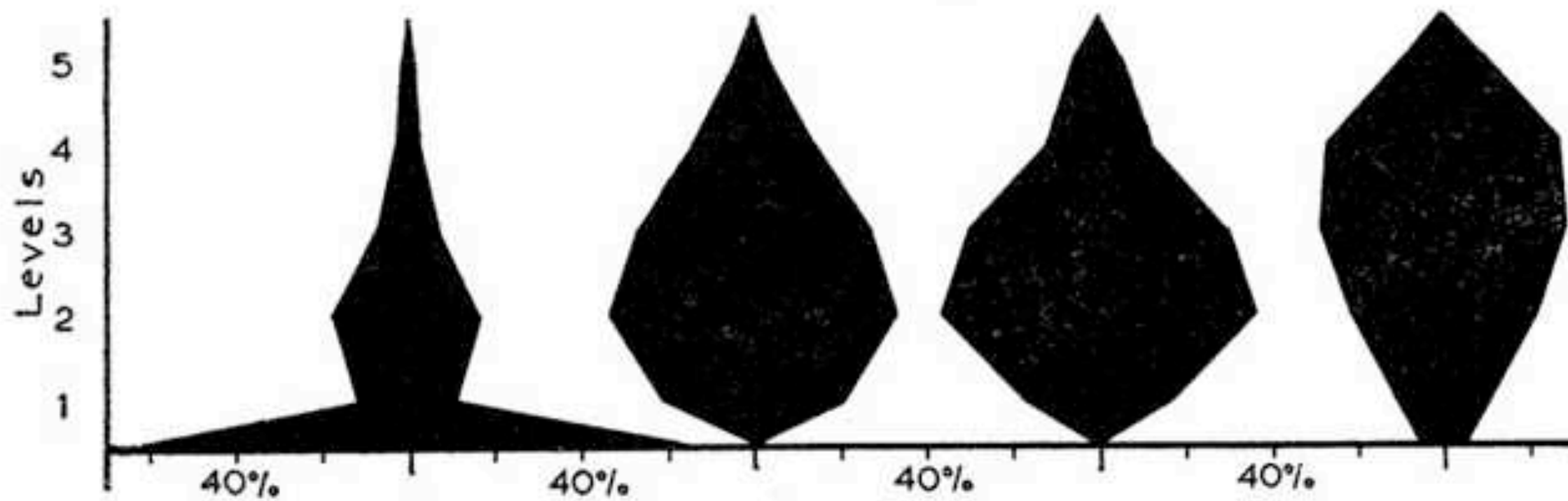
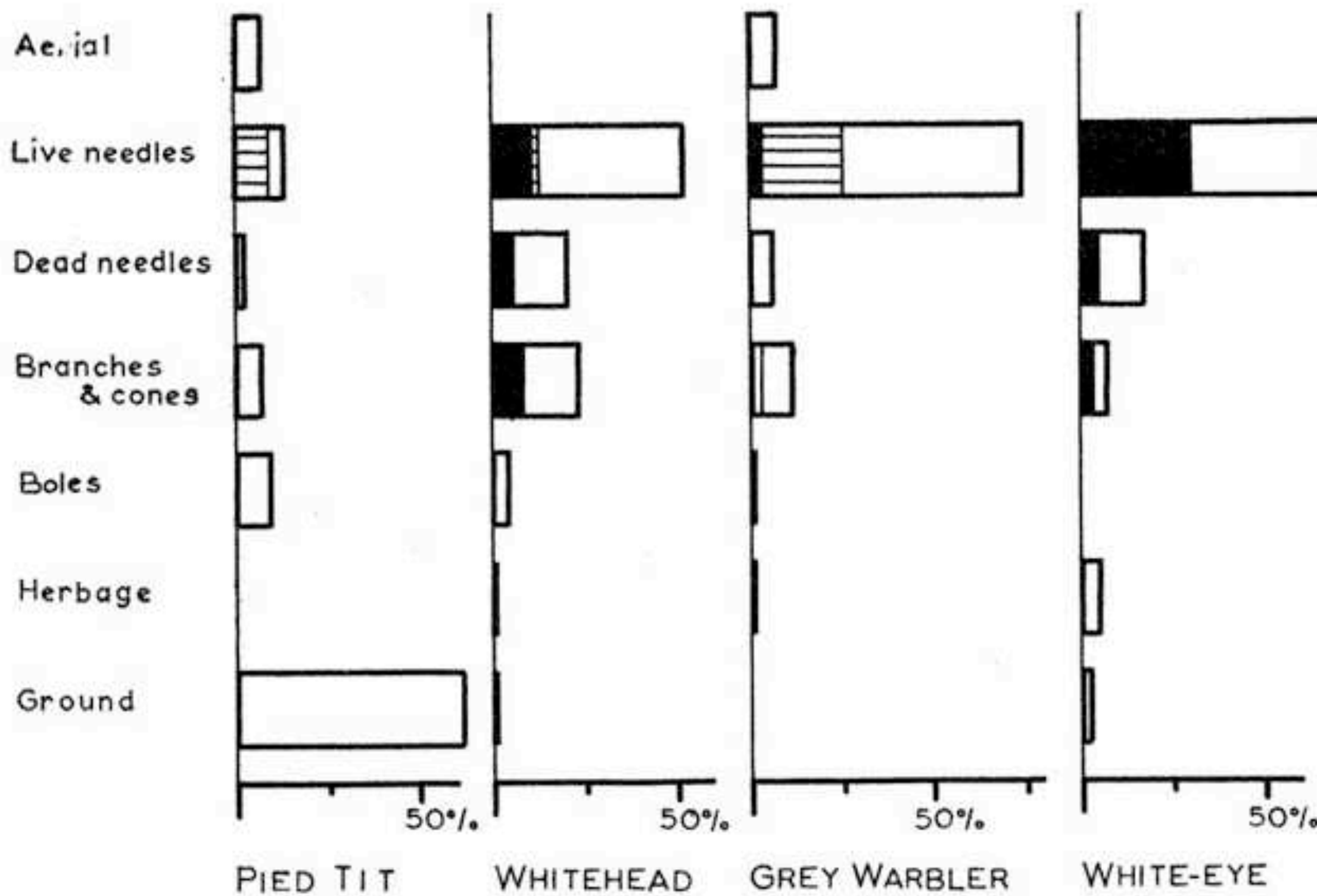


FIGURE 2. Feeding stations of pied tit, white-head, grey warbler and white-eye: all tree species and all seasons combined, 1958-59.



NOTE. Upper row of figures: percentage distribution of birds feeding in ascending levels 1-5 in the trees. Lower histograms: percentage distribution of birds feeding from different sources; black parts represent birds hanging upside-down, and striped parts represent birds hovering. Percentages are based on 187 observations on pied tits, 451 on whiteheads, 180 on grey warblers, and 173 on white-eyes.

and legs; but it is amusing to watch one trying to keep its head still when perched on a twig that is swaying just too much to allow it to do so without overbalancing.

As Figure 2 shows, the living pine foliage is the most frequent feeding station for whiteheads, warblers and white-eyes alike, all of which also feed chiefly in the middle levels of the trees. However, white-eyes and warblers feed significantly ($P = <0.01$) more often from the living foliage than do whiteheads; and white-eyes significantly ($P = <0.01$) higher in the canopy than either warblers or whiteheads. Both whiteheads and white-eyes, but not warblers, occasionally feed also on the ground.

Whiteheads probably weigh about 25g., white-eyes about 15g. and grey warblers perhaps about 8-10g. Accordingly, whiteheads feed mostly on stouter parts of the trees which will support them upright; they are rather inept at taking food from the tips of flimsy foliage; they seldom hang upside-down from slender twigs, and rarely hover or catch flying insects. White-eyes feed generally farther out towards the tips of the foliage than do whiteheads, and they spend much time hanging upside-down to get food close to the tips; but they too rarely hover or catch flying insects. Grey warblers, which are much the lightest of the trio, specialise in taking food from the tips of the foliage by hovering, and seldom feed on the stouter branches; and they frequently catch flying insects. Though pied tits feed only a little in the foliage, when doing so they often hover round the tips and catch flying insects; but they rarely feed hanging upside-down.

Whiteheads are versatile in their feeding and possess some of the special skills often associated with titmice (Paridae) of the genus *Parus* of the Northern Hemisphere. They frequently use their feet to clamp large morsels of food to a branch for dismemberment with the bill, instead of holding them less efficiently in the bill and battering them against a branch—as do most small passerines. Though whiteheads, like tits of the genus *Parus*, sometimes use the latter method too, it is the only method used by pied tits (only distantly related to *Parus*), grey warblers, white-eyes and chaffinches, for instance. Also, to facilitate extraction with the bill, both whiteheads and *Parus* tits

commonly use their feet to grasp foliage in which food is hidden; and both use their rather stout bills to hack soft dead wood and to flake off fragments of bark. Thus in New Zealand the whitehead occupies a rather generalised feeding niche comparable to that of *Parus* spp.; and in size, build and feeding habits, it most closely resembles the great tit (*Parus major*).

Rather surprisingly, fantails sometimes clamp large morsels of food between their feet to dismember them with the bill (pers. obs.). So among New Zealand Muscicapidae this ability is shared by whiteheads (sub-fam. Malurinae) and fantails (sub-fam. Muscicapinae), but seems lacking in other members of each sub-family, namely, grey warblers (Malurinae) and pied tits (Muscicapinae).

PIED TITS BREEDING IN NEST-BOXES

In Europe nest-boxes are used extensively to enhance the numbers of hole-nesting insectivorous birds such as tits (*Parus* spp.) and flycatchers (especially *Muscicapa hypoleuca*); and they have proved notably effective in pine plantations where natural nest sites are scarce. Also, a ready supply of accessible nests greatly facilitates the collection of reproductive data concerning the species which use the boxes. Yet nest-boxes have not hitherto been tried out in New Zealand, although there are several native hole-nesting birds which might be attracted to them.

One hundred nest-boxes were therefore put up in Kaingaroa in July 1958 in the hope that pied tits and perhaps robins might use them. The boxes were tied to trees about four feet above ground; and they were sited in groups of five or ten with about 25 yd. between each box, in four different compartments. Originally six out of every ten boxes had circular holes of $1\frac{1}{4}$ - $1\frac{3}{4}$ in. diameter, and the remainder had slit or letter-box entrances; but after the 1958-59 breeding season all were given letter-box entrances as these seemed more closely to resemble the natural sites used by pied tits.

Only pied tits have so far used the nest-boxes: one box was laid in during the 1958-59 season and two others had small amounts of nest material only. In 1959-60, seven boxes

were laid in and two more had some building material. But none had been used by mid-November 1960, when the boxes were last inspected in the 1960-61 season.

These few occupied boxes were in groups. In one compartment with 20 boxes, the single box used in 1958-59 was only 50 yd. from that used in 1959-60. Again, the two boxes with material only in 1958-59 were in the same group of ten which contained three (possibly four) occupied nests in adjacent boxes in 1959-60; and in 1959-60 of four adjacent boxes two held eggs and two had some material only. Only one box in each group held eggs at the end of October 1959, and very likely a single pair of birds was responsible for all the nests within each group.

This grouping of occupied nest-boxes suggests that certain pied tits had come to recognise and look for nest-boxes rather than natural sites in which to breed; and this is consistent with experience in Europe. A further increase in the number of occupied boxes was therefore expected in 1960-61, whereas in fact none was occupied by November 1960.

It has sometimes been found in Europe that pied flycatchers (*Muscicapa hypoleuca*), which are closely related to pied tits, will not use nest-boxes when they are scattered widely as they are in Kaingaroa; but do so when they are concentrated more densely. So it may be better to concentrate all the 100 boxes in Kaingaroa in a single compartment. However, pied tits are not so restricted to

hole-nesting as are pied flycatchers, and they sometimes nest in only partly enclosed cavities: indeed, I found one completely open, cup-shaped nest with eggs in Kaingaroa, nine feet up in a manuka crotch.

From a dozen nests in boxes and other sites in Kaingaroa, it seems that the laying season extends from late September to late December or early January; and of six completed clutches seen, one was of two eggs, two were of three eggs, and three were of four eggs. Each pair probably raises two or three broods in a season.

DISCUSSION

Table 6 compares the densities of birds in Kaingaroa with some other habitats. The Kaingaroa densities slightly exceed those for native beech (*Nothofagus*) forest in the South Island; but are less than those for offshore islands with scrub or low forest, and much less than those for gardens and regenerating bush (refs. in Table 6). There are no comparable measurements for podocarp forest in New Zealand. The Kaingaroa densities lie broadly within the range for natural coniferous forests in North America (Udvardy 1957); but considerably exceed those for 25-year-old East Anglian pine plantations with trees up to about 40 ft. tall (pers. obs.). Chaffinches, blackbirds and dunnocks, present in both Kaingaroa and the East Anglian plantations, are all distinctly more numerous in Kaingaroa.

TABLE 6. *Density of birds in the breeding season in Kaingaroa Forest compared with other habitats*

Locality	Habitat	Approx. no. of birds per 100 acres	Authority
Kaingaroa Forest	<i>P. radiata</i> , aged 28 years	487	This paper
	<i>P. nigra</i> , aged 26 years	246	This paper
East Anglia	<i>P. sylvestris</i> , aged 25 years	75-100	Gibb, unpubl.
	<i>P. nigra</i> , aged 25 years	50-75	Gibb, unpubl.
North America	Coniferous forests	100-300 (500)	Udvardy, 1957
South Is., N.Z.	<i>Nothofagus</i> forest	140-330	Kikkawa, 1960a
	Gardens & regenerating forest	1000	Kikkawa, 1960a
Three Kings Is., Hen & Chicken Is.; both off North Is., N.Z.	<i>Leptospermum</i> & mixed forest	620-720	Turbott & Bull, 1954; Turbott, 1940
Kapiti Is., off North Is., N.Z.	Regenerating mixed forest	830-880	Kikkawa, 1960b

NOTE. Different observers have used different census methods.

In Europe generally, there are many fewer birds in pine plantations than in mixed broad-leaved woodland. Yet the pines of Kaingaroa are heavily populated compared with native beech forest in New Zealand, or with the East Anglian plantations. This is the more remarkable in the absence in New Zealand of bird species that have evolved in such habitats.

The ancestors of a few birds introduced to New Zealand will have seen coniferous forest superficially resembling Kaingaroa: chaffinches and redpolls for instance breed commonly in European pine forests. Hence it is not surprising that they and others have colonised Kaingaroa Forest; nor even perhaps that some native New Zealand birds have done so, since the invertebrate fauna consists largely of native species (Rawlings 1960). What is surprising, however, is that some native birds are now as numerous in the Kaingaroa pines as in almost any native forest, and a good deal more numerous than in most of it. This is most striking with the whitehead, and only slightly less so with the pied tit and robin.

The density of insectivorous birds (e.g. *Parus* spp.) breeding in East Anglian pine plantations is determined primarily by the food supply in winter, of which the birds then eat a substantial part (Gibb 1960). If this is so also in Kaingaroa, then the stock and/or production of invertebrates per unit area of forest must be much greater than in the East Anglian pines, to support the denser population of insectivorous birds. Whilst cursory examination of the pine foliage in Kaingaroa does not suggest that the stock of invertebrates is large, their production in New Zealand's more temperate climate may be considerably higher than in the East Anglian pines. However, only proper quantitative measurements can settle this point.

In Kaingaroa Forest there are insectivorous birds exploiting all the obvious niches, on the ground, in the lower parts of the trees, and in the canopy; with the one exception that there are no birds corresponding to woodpeckers (Picidae). In native forest elsewhere in New Zealand the role of woodpeckers is partly taken by kakas (*Nestor meridionalis*): but while there are many dead trees and rotten logs in which kakas might feed in mature stands of *P. radiata*,

their diet normally also includes fruit and nectar which are not available in the pines of Kaingaroa.

Although whiteheads, grey warblers and white-eyes all feed predominantly in the living pine foliage, each species in fact specialises on different parts of the food supply. Such segregation does not necessarily preclude interspecific competition for food, but its existence does imply that intraspecific competition must be stronger than interspecific competition; and if food is important in the natural control of these populations of birds, this may be sufficient to allow the several species to live together in a state of balance.

SUMMARY

1. Standard observations were made on the birds of Kaingaroa Forest in 1958-59, recording their density, frequency of occurrence and feeding habits.

2. The birds' density in the breeding season was estimated at about 487 birds per 100 acres in *P. radiata*, 333 in unthrifty *P. ponderosa*, and 240 each in *P. nigra* and *Ps. taxifolia*. At other seasons the birds' abundance was measured by the numbers of each species seen or heard per hour in transect counts. The greatest density was again in *P. radiata*. The five commonest species were, in order, chaffinch, whitehead, grey warbler, blackbird and pied tit. These densities slightly exceed those in *Nothofagus* forest, but are less than in scrub or low forest on off-shore islands and much less than in gardens and regenerating bush. Native birds are remarkably numerous in Kaingaroa considering that none have evolved in such a habitat.

3. Variations in the birds' individual conspicuousness masked seasonal changes in numbers. On the average fewer birds were counted hourly in late afternoon than at other times of day. The numbers of pied tits counted hourly varied with the intensity of their song; and many more males than females were seen.

4. Insectivorous birds are exploiting all the obvious feeding niches in the pines, except that of woodpeckers. No two species have like feeding habits, and this evidently

allows them to live side by side in a state of balance. Out of the breeding season, whiteheads, white-eyes and grey warblers forage together in mixed flocks. Whiteheads are the most versatile in their feeding habits, which resemble those of *Parus* spp. in the Northern Hemisphere.

5. A few pied tits bred in nest-boxes provided for them for the first time in New Zealand. Their laying season extends from late September to late December, and clutch-size ranges from 2-4 eggs.

REFERENCES

- CAUGHLEY, G., 1960. Riflemen in exotic pine-forests. *Notornis* 9:63.
- GIBB, J., 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* 96:513-543.
- GIBB, J. A., 1958. Predation by tits and squirrels on the eucosmid *Ernarmonia conicolana* (Heyl.). *J. Anim. Ecol.* 27: 375-396.
- GIBB, J. A., 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* 102: 163-208.
- KIKKAWA, J., 1960a. The seasonal change of bird populations in a modified South Island habitat. *Proc. N.Z. Ecol. Soc.* 7: 11-13.
- KIKKAWA, J., 1960b. A bird census on Kapiti Island. *Rec. Dom. Mus. N.Z.* 3: 307-320.
- RAWLINGS, G. B., 1961. Entomological and other factors in the ecology of a *Pinus radiata* plantation. *Proc. N.Z. Ecol. Soc.* 8: 47-51.
- RYDER, H. R., 1948. Birds of Kaingaroa Forest. *N.Z. Bird Notes* 3: 20-22.
- TINBERGEN, L., 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* 13: 265-343.
- TINBERGEN, L. and KLOMP, H., 1960. The natural control of insects in pinewoods. II. Conditions for damping of Nicholson oscillations in parasite-host systems. *Arch. Neerl. Zool.* 13: 344-379.
- TURBOTT, E. G., 1940. A bird census on Taranga (The Hen). *Emu* 40: 158-161.
- TURBOTT, E. G. and BULL, P. C., 1954. A bird census and some recent observations on birds on Great Island, Three Kings Group. *Rec. Auck. Inst. Mus.* 4: 245-262.
- UDVARDY, M. D. F., 1957. An evaluation of quantitative studies in birds. *Cold Spring Harbor Symp. Quant. Biol.* 22: 301-311.
- VOUTE, A. D., 1946. Regulation of the density of insect-populations in virgin-forests and cultivated woods. *Arch. Neerl. Zool.* 7: 435-470.
- WEEKS, M. F., 1949. Bird population of exotic forests. *N.Z. Bird Notes* 3: 83-84.