

COMPOSITION AND SEASONALITY OF MIXED-SPECIES FLOCKS OF INSECTIVOROUS BIRDS

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ABSTRACT

Mixed-species flocks of insectivorous birds were investigated at Kowhai Bush, Kaikoura, in monthly transect counts between July 1986 and June 1988. Four native species (Brown Creeper, Silvereye, Grey Warbler and Fantail) and two introduced species (Chaffinch and Redpoll) foraged in mixed flocks. Brown Creepers and Silvereyes appeared to behave as nuclear species by determining the direction of movement of mixed flocks. Mixed flocks were found throughout the day. The mean number of species per flock was 2.5 and the mean number of birds in flocks was 8.5. Mixed flocks were seasonal with none encountered during the main breeding period (Sep-Dec).

INTRODUCTION

Groupings of small insectivorous birds of more than one species are well known in temperate and tropical areas worldwide (Rand 1954). Mixed-species flocks (mixed flocks) occur in practically every habitat type (Powell 1985), from deciduous woodland (Morse 1970) to deserts (Cody 1971). They are common in north temperate regions during the non-breeding season (Morse 1970) but are generally largest and most diverse in the tropics, where they exist almost year round (Winterbottom 1943, Moynihan 1962, Greig-Smith 1978, Powell 1985).

Possible advantages to birds in mixed flocks are less risk of predation and greater feeding efficiency (reviews in Moriarty 1976, Morse 1980, Krebs & Davies 1981, Powell 1985).

Although mixed flocks are known in New Zealand, little attention has been paid to them. Whiteheads (*Mohoua albigilla*) and Yellowheads (*M. ochrocephala*) commonly form flocks with species such as Brown Creepers (*Finschia (Mohoua) novaeseelandiae*), Saddlebacks (*Philesturnus carunculatus*), parakeets (*Cyanoramphus* spp.), Silvereyes (*Zosterops lateralis*), Bellbirds (*Anthornis melanura*), Fantails (*Rhipidura fuliginosa*), Tomtits (*Petroica macrocephala*), and Grey Warblers (*Gerygone igata*) (M'Lean 1907, quoted in Oliver 1955: 470, Henderson 1977, Read & McClelland 1984, Calder & Deuss 1985, and Read 1987). Greene (1988) examined the seasonal occurrence of mixed parakeet flocks and McLean *et al.* (1987) described the structure of mixed flocks on Little Barrier Island. Both found that Whiteheads were the nuclear species and associated strongly with parakeets. Greene (1988) found that Yellow-crowned Parakeets (*C. auriceps*) preferred to forage in mixed flocks whereas Red-crowned Parakeets (*C. novaezealandiae*) foraged mainly in single-species flocks. Yellow-crowned Parakeets were in mixed flocks in autumn and winter.

I studied mixed flocks of insectivorous birds in Kowhai Bush, Kaikoura, to investigate (1) what species are commonly in the flocks, (2) the relative frequency of each species, and (3) whether mixed-species flocking is seasonal.

STUDY AREA

The study site was an area of kanuka (*Kunzia ericoides*) forest in Kowhai Bush (42° 23'S, 173° 37'E), 8 km northwest of Kaikoura on the east coast of the South Island (Fig. 1).

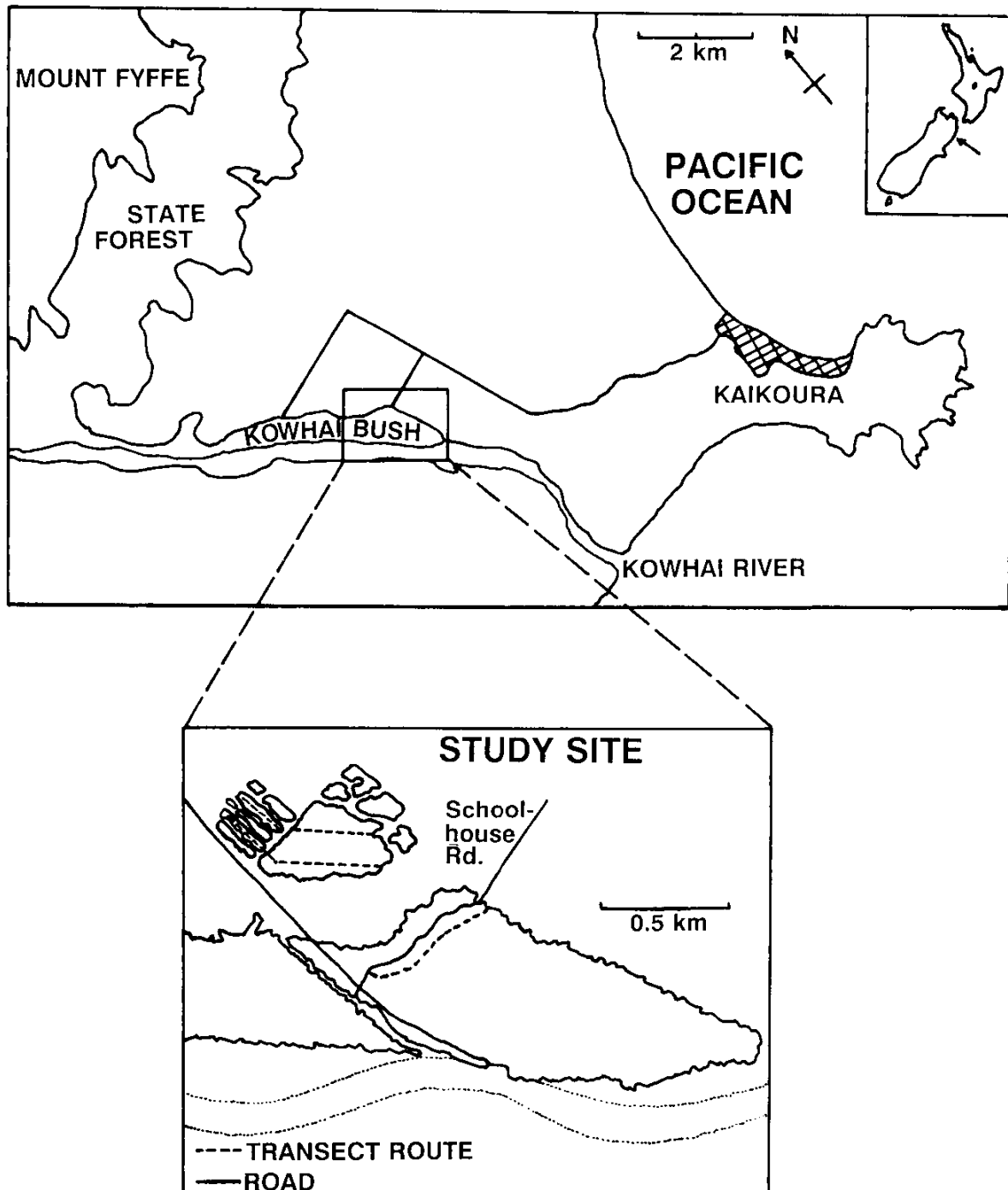


FIGURE 1 — Locality map of Kowhai Bush and study site

The vegetation of Kowhai Bush was a mosaic of successional stages arising mainly from the intermittent flooding of the Kowhai River. Dobson (1979) described the vegetation in detail, recognising 13 habitat types. Two sites of 80 and 20 ha in the southeast portion of Kowhai Bush were selected (see Fig. 1). The forest in both sites was open and flat with kanuka dominant. The trees were 5–7 m high and well spaced, providing excellent visibility and easy access.

The Kaikoura climate is warm temperate but is subject to seasonal extremes of weather (Gill 1980). During winter and early spring, southerly changes may bring sudden showers of rain, hail, sleet and occasionally snow. The summer months are generally mild and dry.

Six native bird species are abundant at Kowhai Bush all year – Rifleman, Brown Creeper, Grey Warbler, Fantail, Silvereye and Bellbird. Eleven introduced species are also common in Kowhai Bush (see Hunt & Gill 1979).

METHODS

I made a transect count twice monthly between 0900 hours and 1130 hours from July 1986 to 1988. No counts were made during rain or high wind. The transect route was 1700 m along three marked lines, two in the southwest to northeast axis of the 20 ha patch and one line alongside Schoolhouse Road, in Kowhai Bush (see Fig. 1). Each month I made two counts, usually one day apart. My path of travel was reversed on the second day. In June 1988, I made an extra 27 transect counts to determine flock changes during the day. Days were divided into three periods (morning 0730–1045 h, middle day 1045–1400 h, and afternoon 1400–1715 h). Nine transects were walked in each time period.

Line transect theory (Emlen 1971) was used to give a relative index of abundance for birds in flocks. I walked along the lines and recorded each bird within 15 m on either side of the line as being in a mixed flock, in a single-species flock, or as paired or solitary. I did not count birds flying overhead, birds more than 15 m ahead, or birds that moved into the transect area after I had passed.

Three or more birds comprised a flock. The criterion for membership in a flock was that a bird I saw had to be within 5 m of another bird for 2 minutes and move in the same direction for at least 10 m (Bell 1980).

Whenever I encountered a flock I stopped to record the number of birds. Bias occurred when observing flocks, as the longer I spent recording the number of birds, the more likely I was to detect more birds. To reduce this error, 5 minutes after leaving a flock, I stopped and recorded all birds seen or heard for the same time period that I had spent watching the previous flock of birds.

Single birds are less conspicuous than flocks and species vary in conspicuousness. To compensate for variation in detectability, two observers assisted with one census by walking behind and to each side of me towards the outer edge of the 30 m wide transect line. The observers noted whether I detected each bird species they encountered. A coefficient of detectability (CD) was calculated for each species (total number of birds undetected over

total number of birds I recorded). Monthly totals for each species were then adjusted according to their detectability values. Solitary Grey Warblers (CD = 0.2), Chaffinches (CD = 0.2) and Brown Creepers (CD = 0.1) were less likely to be observed during transect counts.

Notes were made on intra and interspecific behaviour. I used the terminology of Moynihan (1962) for 'nuclear', 'regular', and 'occasional' species. Nuclear species are those which seem to influence the formation and cohesion of mixed flocks. Regular species follow the nuclear species rather than lead flocks. Occasionals associate only temporarily with a flock as it moves on.

Seasons referred to in this paper are spring (Sep–Nov), summer (Dec–Feb), autumn (Mar–May), and winter (Jun–Aug).

RESULTS

Composition and size of flocks

Table 1 gives the composition of the 76 mixed flocks encountered during transect counts. Table 2 gives the number of species and birds per flock. The number of species per flock ranged from 2 to 6, mean 2.6 ± 0.8 species. The mean number of birds per flock was 8.8 ± 5.8 with the largest flock containing 30 birds and the smallest 3. Of 19 species, 4 native insectivores (Brown Creeper, Silvereye, Grey Warbler, and Fantail) and 2 introduced granivores (Chaffinch and Redpoll) foraged in mixed flocks during the non-breeding season. Of these 6 species, 5 breed in the study area and Silvereyes migrate into it for the autumn and winter.

TABLE 1 — The composition of 76 mixed-species flocks encountered during transects from July 1986 to June 1988.

Species	% of Flocks	Mean No. Birds $\pm$ SD	Min No.	Max No.	Breed in Study Area
Brown Creeper	81.6	4.6 ± 2.1	1	12	yes
Grey Warbler	86.8	2.6 ± 2.1	1	12	yes
Fantail	39.5	1.7 ± 1.0	1	6	yes
Silvereye	34.2	4.2 ± 1.8	2	8	no
Chaffinch	10.5	2.0 ± 1.3	1	5	yes
Redpoll	14.5	3.6 ± 0.9	2	5	yes

TABLE 2 — The number of species and birds in 76 mixed-species flocks encountered during transects from July 1986 to June 1988

Species per flock					
No. of species	2	3	4	5	6
No. of birds	43	24	7	1	1
% of flocks	56.6	31.6	9.2	1.3	1.3
Mean no. of species and SD, 2.59 ± 0.8					
Birds per flock					
Size of flocks	<5	6–10	11–15	16–20	>21
No. of flocks	27	31	9	5	4
% of flocks	35.5	40.8	11.8	6.6	5.3
Mean no. of birds and SD, 8.8 ± 5.5					
Min. value 3					
Max. value 30					

Brown Creepers and sometimes Silvereyes were the nuclear species leading flock direction. Both species also formed monospecific groups in the non-breeding season. My observations of colour-banded Brown Creepers indicated that they were usually residents, forming flocks of 3–7 birds which could be found daily in the same general area. I encountered flocks of up to 12 Brown Creepers, probably consisting of several family groups and/or immigrant birds.

Only when Brown Creepers were absent did Silvereyes become the nuclear species, and these flocks seemed less stable than flocks led by Brown Creepers (often disbanding within 15 minutes).

Regular species were the Grey Warbler and Fantail, which foraged in pairs or as small flocks. Grey Warblers and Fantails followed foraging Brown Creepers, with Fantails often “shadowing” flock members, staying less than 1 m behind a bird to catch insects flushed by it.

Flock cohesion was variable, with birds ranging from 0.25 m to 10 m apart. Flocks were noisy when the birds were spread out because the Brown Creepers kept in contact by calling. Other species followed the flight calls of the Brown Creepers.

Agonistic behaviour between flock members was rare. Groups of Brown Creepers and Silvereyes foraging with mixed flocks were aggressive among themselves but not towards other species. I twice saw Brown Creepers, with no obvious provocation, briefly chase a Grey Warbler to the ground.

Chaffinches and Redpolls bred in Kowhai Bush, but in the non-breeding season most joined large mixed finch flocks in pasture lands nearby. Large numbers of Silvereyes and sometimes small groups of Grey Warblers joined these finch flocks to feed in the open. In the bush, finches were only in the larger mixed flocks ($\bar{x} = 15.6 \pm 4$) at forest margins and often flew off when they saw me.

Despite their high density in Kowhai Bush, Riflemen did not join mixed flocks, preferring to forage in pairs or family groups. Bellbirds and Robins, present in low density, were not seen in mixed flocks. The Shining Cuckoo is migratory, arriving during the breeding season and leaving in late February/early March. When mixed flocks started forming in late January, cuckoos were present in the area but were not seen in any of the autumn flocks.

Table 3 shows the association between flocking species. All species occurred in flocks together, and no species significantly avoided or preferred flocks containing any other species. The darker numbers on the diagonal in the table are numbers of flocks in which the species occurred. The horizontal row for each species shows the number of flocks that the species occurred in with each of the other species. The X^2 values were calculated by comparing the number of flocks in which both species could occur (i.e. the lowest dark number of the two species on the diagonal) with the number of flocks in which species A was found with species B.

TABLE 3 — The degree of association between the species in mixed-species flocks

Species	BC	GW	FT	SE	CH	RP	X ²	P
Brown Creeper	62	53	22	17	6	9	2.592	0.628
Grey Warbler		66	21	21	7	10	2.898	0.570
Fantail			30	11	5	7	6.772	0.148
Silvereye				26	4	7	8.781	0.067
Chaffinch					8	5	4.576	0.334
Redpoll						11	6.471	0.167

df = 4

Seasonal and diurnal changes

Flocks were found throughout the day with no significant variation in the frequency of flocks ($X^2 = 0.284$, $df = 2$, $p > 0.05$) or the number of birds present (Kruskal-Wallis test, $H = 0.8336$, NS).

Mixed flocks were seasonal, none being encountered during the main breeding period (Sep–Dec). Once, in November 1986, I saw a group form briefly to mob a stoat (*Mustela nivalis*). Figure 2 shows the frequency of mixed flocks and the percentage of all birds seen, of all species, that were in mixed flocks. The percentages of all birds seen that were in mixed flocks ranged from nil to 46% and were related to the occurrence of mixed flocks. Mixed flocks formed in late summer and were most frequent during autumn and winter.

Drought conditions prevailed in the study area during the summer and autumn of 1987, which was followed by a mild winter. Mixed flocks formed in January 1987, but by February many birds had left the area or died, and I saw no mixed flocks. The number of birds and the frequency of flocks remained low during the autumn and winter of 1987 compared with 1986 and 1988.

There was no significant seasonal variation in the number of birds per flock (Kruskal-Wallis test, $H = 2.97$, NS), but there was significant seasonal variation in the proportion of birds of all species taking part in mixed flocks (Table 4).

TABLE 4 — The number of birds of each species in mixed-species flocks and the number found outside mixed flocks, compared by season

Species	Spring		Summer		Autumn		Winter		X ²
	F	NF	F	NF	F	NF	F	NF	
Brown Creeper	6	155	50	133	131	29	81	71	233.30
Grey Warbler	1	126	18	75	68	109	78	105	106.20
Fantail	0	41	13	47	31	48	3	23	31.09
Silvereye	0	25	12	51	22	29	58	51	40.66
Chaffinch	1	191	7	182	4	16	2	97	35.89
Redpoll	0	50	6	52	8	16	0	7	37.99

df = 3

For all species, $P < 0.001$

F = mixed-species flocks

NF = not in mixed-species flocks, including monospecific flocks

Table 5 gives the seasonal occurrence of the six species that were in mixed flocks. Brown Creepers, Fantails, Chaffinches and Redpolls were most likely to be in mixed flocks in autumn. Silvereye numbers in flocks were highest in winter, whereas the percentage of Grey Warblers in mixed flocks remained similar during autumn and winter.

TABLE 5 — Percentage, by months, of birds that were in mixed-species flocks

Species	Winter		Spring		Summer		Autumn	
	1986	1987	1986	1987	1987	1988	1987	1988
Brown Creeper	56.8	45.5	6.5	0.0	25.3	29.3	84.8	79.8
Grey Warbler	54.4	16.9	1.5	0.0	16.3	22.0	51.8	34.5
Silvereye	51.8	47.6	0.0	0.0	18.6	20.0	37.5	48.1
Fantail	5.0	9.5	0.0	0.0	20.0	6.1	43.5	37.5
Chaffinch	0.0	0.0	0.0	0.0	0.0	12.8	16.7	25.0
Redpoll	0.0	0.0	0.0	0.0	0.0	0.0	0.0	57.1

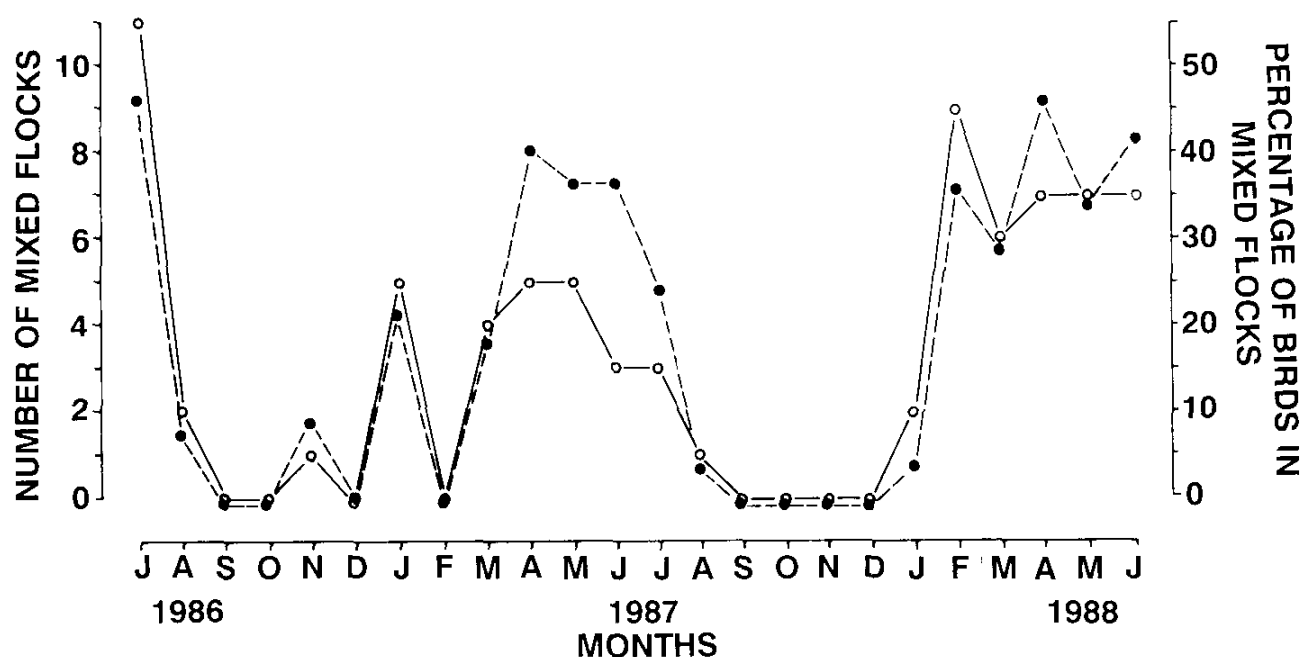


FIGURE 2 — Numbers of mixed-species flocks encountered during transects (denoted by open circles), and percentage of all birds seen in transects (denoted by closed circles) that were in mixed flocks (July 1986 – June 1988)

DISCUSSION

The endemic genus *Mohoua* appears to be the nuclear species in mixed flocks of small insectivores in New Zealand. Greig-Smith (1978) described a nuclear species as the species around which a flock organises its activity; recognised because it is in front of the flock or followed by other species. Winterbottom

(1943, 1949) stated that the nuclear species is "always found in parties, either mixed or pure". Brown Creepers (this study), Whiteheads (McLean *et al.* 1987) and Yellowheads (Read 1987) are the only flocking species that are regularly in both single-species and mixed-species flocks of more than four birds. They are in a high percentage of mixed flocks, keep in almost constant vocal contact with one another and are followed by other species. Nuclear species use contact calls elsewhere (e.g. Chile, Vuilleumier 1970; New Guinea, Bell 1983a), and 'homing in' by various species on the call of a nuclear species, as in this study, has been observed previously (McDonald & Henderson 1977, Bell 1983a).

Bellbirds (Andersen 1926, Calder & Deuss 1985) and Riflemen (Read 1987) have been reported in mixed-species flocks, but they did not do so in my study, or on Little Barrier Island despite their abundance (McLean *et al.* 1987).

Shining Cuckoos did not join mixed flocks in Kowhai Bush. Bell (1986) recorded cuckoos (*Chrysococcyx*) in mixed flocks in Wollomombi, Australia, but little evidence is in the literature of parasitic cuckoos joining mixed-species flocks.

Introduced European finches have been observed in mixed flocks in Australia (Bell 1983b) and New Zealand (Henderson 1977). Finches are gregarious in the non-breeding season and feed in large groups on pasture land near Kowhai Bush. A large mixed flock of native birds may attract Chaffinches and Redpolls because it is a large moving body of feeding birds.

Winter flocks of insectivorous birds in temperate forests are similar in size regardless of habitat. Northern Hemisphere flocks average 10–17 birds (Austin & Smith 1972) and Australian flocks average 10–18 birds (Bell 1980, 1983b). Such factors as crowding, cohesion, level of interaction, food availability and foraging efficiency can place an upper limit on the size of flocks (Austin & Smith 1972). In this study the flocks averaged only 9 birds. The flocks in Kowhai Bush may be rather small because usually only one nuclear species is present (Silvereyes were not in 66% of flocks). In Australia two group-forming species were in 91% of flocks (*Acanthiza pusilla* and *Malurus cyaneus*; Bell 1980). Northern Hemisphere flocks are dominated in numbers by two genera, *Parus* and *Regulus* (Austin and Smith 1972). Tropical flocks appear more variable in size, flocks in Brazil averaging about 9 birds (Davis 1946) and Malayan flocks more than 35 birds (McClure 1967).

The seasonal pattern of mixed-species flocking at Kowhai Bush resembled that found by Bell (1980, 1983b) at Canberra and Wollomombi, Australia, the percentage of all birds seen in mixed flocks varying from 0 to 46% and the frequency of mixed flocks being lowest from September to December. A low frequency of mixed flocks during the breeding season is also typical for other regions (e.g. Nearctic, Morse 1970; Palaetropical, McClure 1967), presumably because birds are constrained to live near their nests.

It is difficult to test the advantages of mixed-species flocking behaviour. Enhanced feeding efficiency and protection from predators are commonly cited advantages (Powell 1985). Fantails obviously gain food flushed by flock

members (McLean 1984), but the benefits to other species of foraging together are not known. A mixed flock may detect, mob, or distract predators better than single-species flocks (Page & Whitakre 1975, Caraco *et al.* 1980). The Morepork (*Ninox novaeseelandiae*), Little Owl (*Athene noctua*), Australasian Harrier (*Circus approximans*), New Zealand Falcon (*Falco novaeseelandiae*) and introduced mammals (stoat *Mustela erminea*, ferret *M. putorius*, weasel *M. nivalis*, cat *Felis catus*) are in the Kowhai Bush area (Hunt & Gill 1979).

A flock may find food better than birds would when foraging on their own, by finding places of high prey density and avoiding places that are less profitable (Morse 1970) or sites already searched by the flock (Moynihan 1962, Cody 1971, Croxall 1976, Greig-Smith 1978). In a flock an individual may gain access to habitats or territories otherwise unavailable to it (Greig-Smith 1978, Paton 1980, Diamond 1987).

Mixed-species flocking by New Zealand birds may increase foraging efficiency or offer protection from predation. Probably both factors interplay and confer advantages to the species.

ACKNOWLEDGEMENTS

I thank my supervisor Ian McLean for his enthusiastic interest and critical comments, and S & P Wood and J. van Berkel for logistic support. I. McLean and R. de Hamel were the additional observers who assisted during one transect count. S. Mackle allowed access to her farm and the Marlborough Catchment Board allowed access to Kowhai Bush reserve. The manuscript has been reviewed by J. Waas, B. Rebergen, B. Gill, and an anonymous referee. This research was conducted under permit from the Dept. of Conservation. Funding was provided by the Dept. of Conservation and the University of Canterbury.

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