PART II

SOCIAL ORGANISATION OF THORNBILLS

CHAPTER 5

SOCIAL AND TERRITORIAL ORGANISATION

INTRODUCTION

68. Interactions between closely-related species do not involve only competition for food. For instance, species may also compete for nest-sites, although in this study it was already well-known that thornbill species nested preferentially, Brown Thornbills in low foliage, Buff-rumped Thornbills on the ground or on trunks and in hollows, and Striated Thornbills in high foliage (Campbell 1900, North 1906, McGill 1970, Frith 1976). Some species of birds hold intraspecific territories or may join mixed-species flocks. A species' spatial organisation is influenced by, and may itself influence, the species' use of resources. Therefore I studied each species' social organisation, including: territorial behaviour, flocking, home ranges and density. For this I individually marked birds of each species. Additional data were obtained from the Royal Australasian Ornithologists Union (RAOU) Nest Record Scheme (NRS).

MATERIALS AND METHODS

69. From July to September 1979 (before collecting foraging data) I attempted to net and band all thornbills in the study area. I used ten 13 × 2 m mist-nets, of 30 mm mesh, and all net-sites were numbered and mapped. All birds caught were banded with numbered metal bands, supplied by the CSIRO Division of Wildlife Research. All thornbills, and any other species thought to be resident, were also banded with a combination of coloured plastic bands. Recorded data for each capture, and recapture, were: species, band number, colour combination, net-site, date and time

of capture, presence of brood-patch (*vide* Bailey 1952) and where time permitted measurement of the right wing from the shoulder to the tip of the longest primaries.

70. Subsequent netting was aimed at those individuals remaining unbanded and young of the year, particularly while still with their parents. Throughout the recording of foraging data all colour-banded birds were recorded, note being taken of locality and the proximity to other thornbills both marked and unmarked. Once each week a patrol was made outside the study area, around its perimeter, to a distance of about one kilometre, except where gorges adjoined, where I could only effectively patrol to a distance of one hundred metres. The patrols were aimed at identifying home ranges of marked birds, and observing possible emigration into adjacent areas. Searches were made for nests within the study area but it was not always possible to find them, even when the behaviour of the birds indicated that one was present. The subsequent history and fate of all nests was followed.

71. The death-rate was computed as deaths of thornbills as a percentage of all thornbills known to be present at the beginning of a period. A 'death' was the disappearance of a colour-banded thornbill known to have been an adult member of a pair or breeding group in at least the previous breeding season. Given the cohesive social organisation of the three species (see Results) and my frequent searches for banded birds in areas adjacent to the study area, I believe it unlikely that disappearances of adults were caused by other than death. Values for numbers of thornbills were based on marked individuals and numbers of unmarked birds seen with adults following the breeding season. These unmarked birds, probably mostly young, were usually caught and marked by late autumn following the breeding season.

72. I could not devise any way of measuring interference competition for resources between thornbills but recorded anecdotal evidence as it was observed.

73. Overall, my aims were to clarify:

a. social groupings,

b. territorial behaviour,

c. breeding patterns, particularly individual participation in breeding, and breeding success,

d. dispersal and survival of young,

e. the annual cycle of social groupings and behaviour,

f. mortality; and,

g. interference competition.

74. Hereafter the word 'group' will mean a party of birds, in excess of a single pair, that has a definite membership over an extended period of time, and in which all members attend the nest (Rowley *et al.* 1979). A 'clan' will mean a party of birds, consisting of more than one pair or group, which has also a definite membership over an extended period (Hegner *et al.* 1982). A 'flock' will apply to any aggregation of birds that appears to be of a temporary nature. A mixed-species feeding flock (MSF) of insectivorous birds is a flock composed of more than one species feeding in association (see next chapter).

75. Where the identity of colour-banded birds is shown by letters the colours are referred to as follows: B: black, Bu: blue, D: dark green, L: light green, M: magenta, met: metal band only, O: orange, R: red, W: white, Y: yellow. All colour combinations are on right legs, except where indicated otherwise.

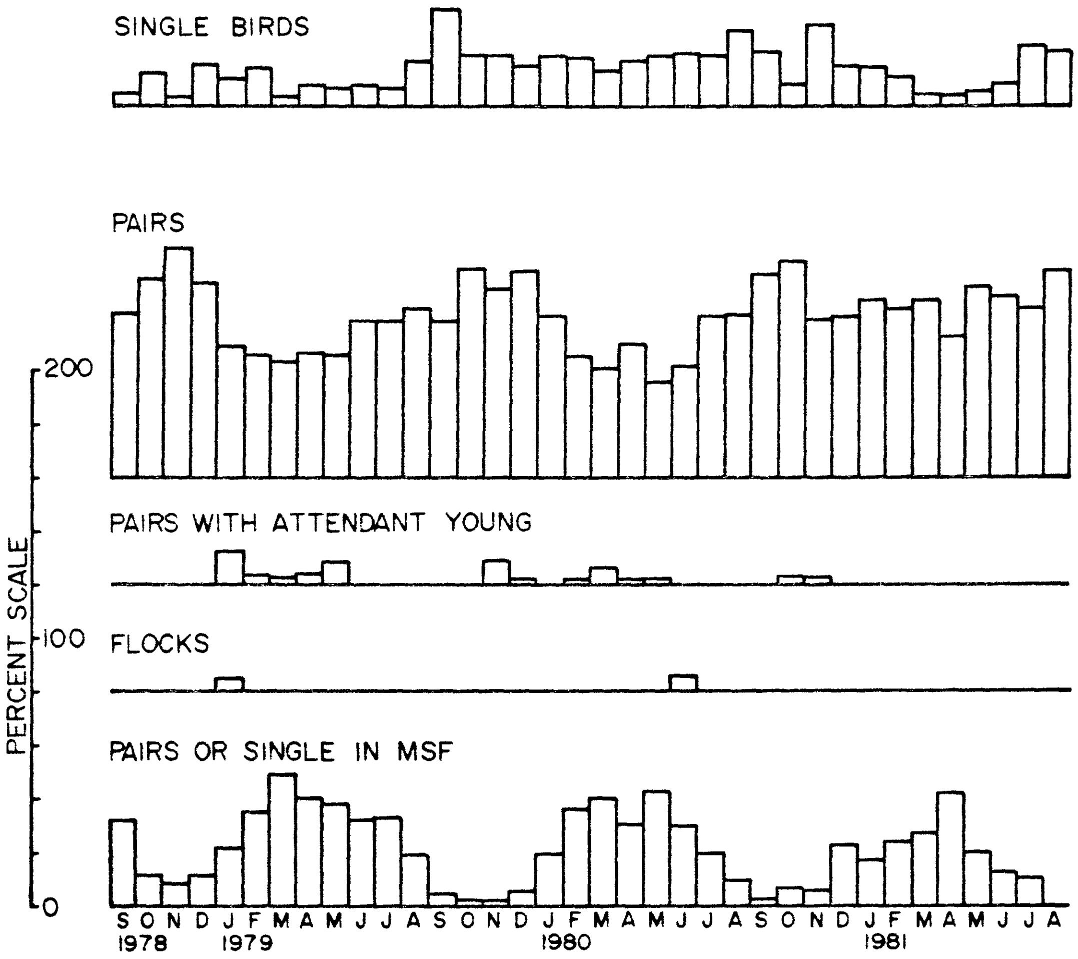
RESULTS

Brown Thornbill *Acanthiza pusilla*

76. As Figure 14 shows Brown Thornbills virtually never formed flocks of their own species. A major exception was on 4 January 1979 when eight unbanded birds were seen perched facing each other in a rough circle about ten metres across, and calling vigorously. The resident pair was about 20 m distant but took no part. The behaviour of the flock seemed to be a display similar to that reported for another Acanthizid, *Hylacola pyrrhopygia* (Eddy 1959, Bell 1966), but was not seen again. Also in June 1980 several parties of four or five birds were seen at a time when they were unlikely to be pairs with attendant young. All other Brown Thornbills seen, other than with attendant young, were seen singly or in pairs.

Figure 14

Percentage occurrences, by months (September 1978-August 1981), of Brown Thornbills by size of party (total n: 4656 individuals, monthly sample sizes 63-112.


SINGLE BIRDS
PAIRS
PAIRS WITH ATTENDANT YOUNG
FLOCKS
PAIRS OR SINGLE IN MSF
PERCENT SCALE
0
100
200
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

77. Each pair had a territory which it defended and rarely left. The limits of a territory were defined as those areas in which sightings of the resident pair outnumbered those of other pairs. During 1978/79 I made 57 observations of resident Brown Thornbills that seemed to be well outside their territories, at a mean distance of 32 ± (S.D.) 15 m from their usual home boundaries, distances ranging from ten to 80 m . Nine sightings were in the breeding season (August-December) and 48 were in the non-breeding period (January-July), the latter usually occurring when a pair followed a mixed-species flock. Territorial boundaries, shown in Figure 15, altered only slightly between years, except where a territory fell vacant because a bird had died. The members of a pair usually fed close to each other. Defence consisted of chasing intruders or confronting them on the boundary by scolding and tail-cocking, followed by chase. The frequency of encounters, (Table 6) shows no significant change by time of year (Kolmogorov-Smirnov Goodness of Fit Test, $P > 0.05$). Defence was thus year-round and was directed at both neighbours and unbanded birds which were probably evicted young of the year because they were most numerous in late autumn. Figure 16 shows an inverse correlation (Spearman Rank Correlation, r: 0.855, $P < 0.01$) between the frequency of territorial encounters and the length of the territorial boundary i.e. holders of small territories spent more time defending. (Note that time spent in each territory by me was in proportion to the size of each, thus I would have spent least time in the smallest, where the most encounters were recorded.) There was little aggression towards Buff-rumped and Striated Thornbills except in spring (Table 6). Territories varied between 0.25 and 3.5 ha and Figure 17 shows an inverse correlation between the proportion of understorey and the size of the territory (Spearman Rank Correlation, r: 1.000, $P < 0.01$).

78. Breeding data, shown in Table 6, indicate that Brown Thornbills started nesting in late winter or early spring and continued until the end of spring, which was earlier than for most birds at Wollomombi. The complete cycle from the start of nest-construction to the fledging of young may take as long as 7-11 weeks (Courtney and Marchant 1971, pers. obs.). I have found no evidence of further broods if the first is successful nor is there any in the literature (e.g. North 1906, McGill

Figure 15

Territories of Brown Thornbills at Wollomombi, 1978/79, 1979/80, 1980/81 (September/August) and 1981/82 (September-February). Letters denote colour-banded birds. Top bird of each pair is female. (Note: BuR daughter of YY, BuW son of LB)

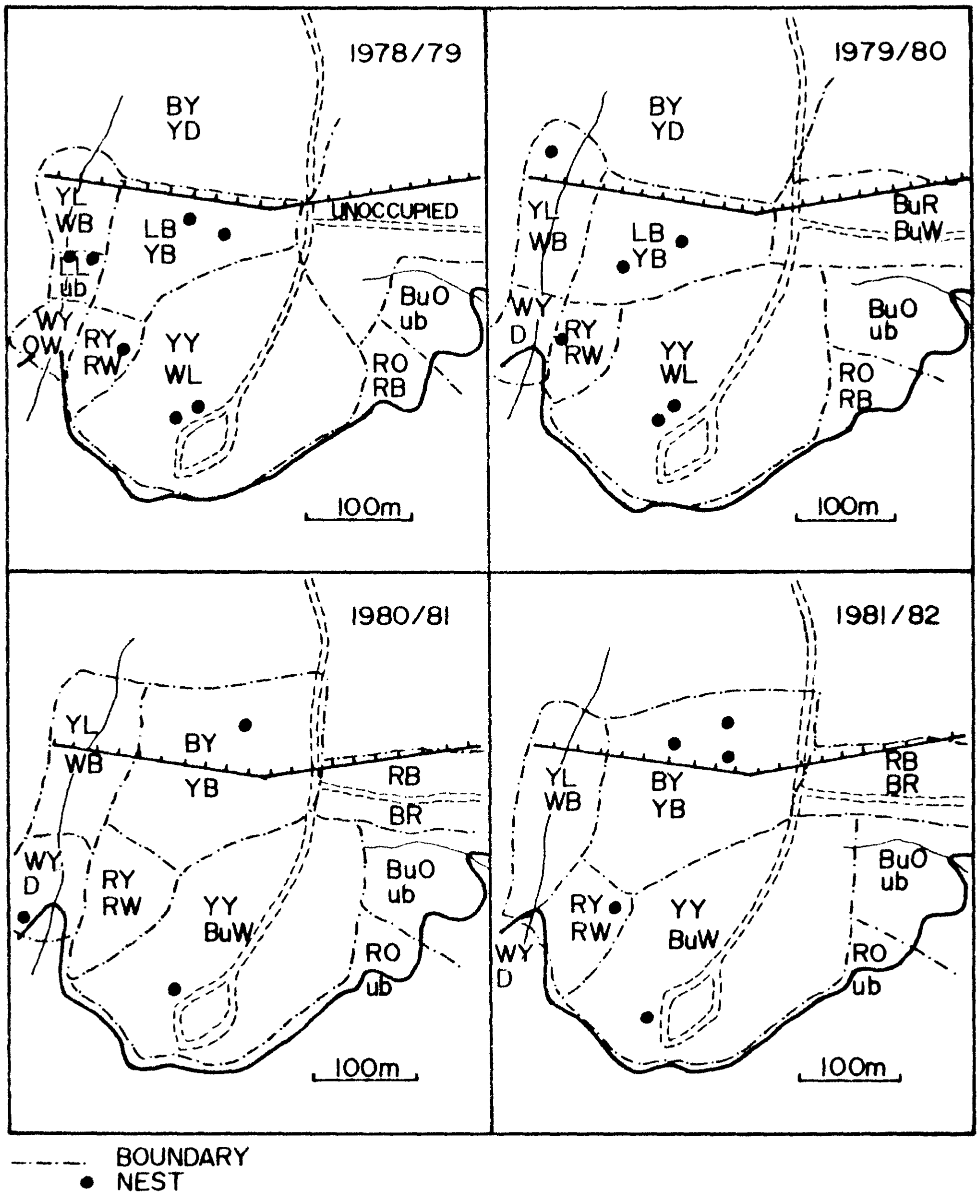

1978/79
BY YD
YL WB
LB YB
UNOCCUPIED
LL ub
WY OW
RY RW
YY WL
BuO ub
RO RB
100m
1979/80
BY YD
YL WB
LB YB
BuR BuW
WY D
RY RW
YY WL
BuO ub
RO RB
100m
1980/81
YL WB
BY YB
RB BR
WY D
RY RW
YY BuW
BuO ub
RO ub
100m
1981/82
YL WB
BY YB
RB BR
BuO ub
RY RW
YY BuW
WY D
RO ub
100m
BOUNDARY
NEST

Figure 16

Inverse correlation (r: 0.855, P: < 0.01) between frequency of observed agonistic encounters by Brown Thornbills against colour-banded neighbours and length of territorial boundary Letters identify females, number in brackets: number of breeding seasons

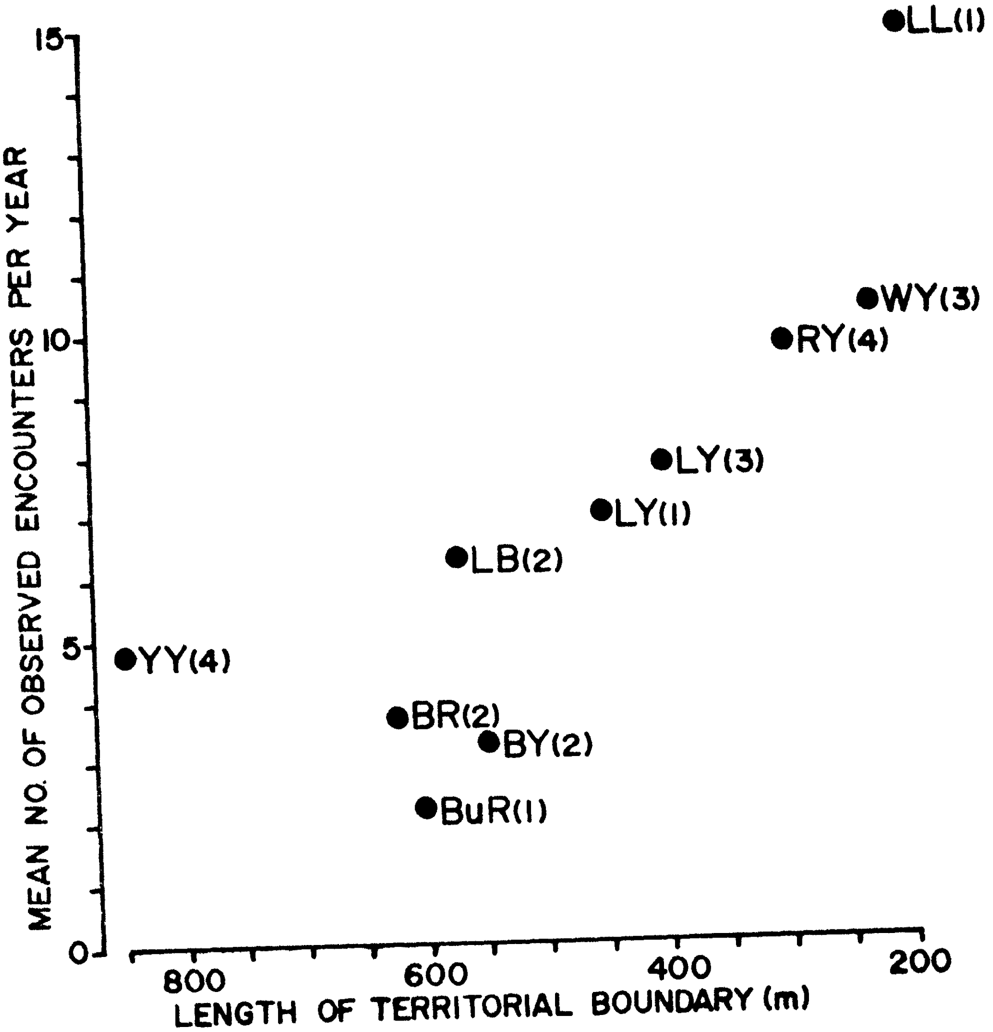

MEAN NO. OF OBSERVED ENCOUNTERS PER YEAR
15
10
5
0
LENGTH OF TERRITORIAL BOUNDARY (m)
800
600
400
200
LL(1)
WY(3)
RY(4)
LY(3)
LY(1)
LB(2)
YY(4)
BR(2)
BY(2)
BuR(1)

Figure 17

Sizes of Brown Thornbills' territories at Wollomombi, and the proportion of each covered by understorey (Spearman Rank Correlation, smallness of territory with proportion covered in understorey, r: 1.000, P: $<$ 0.01).

Letters refer to female of each pair

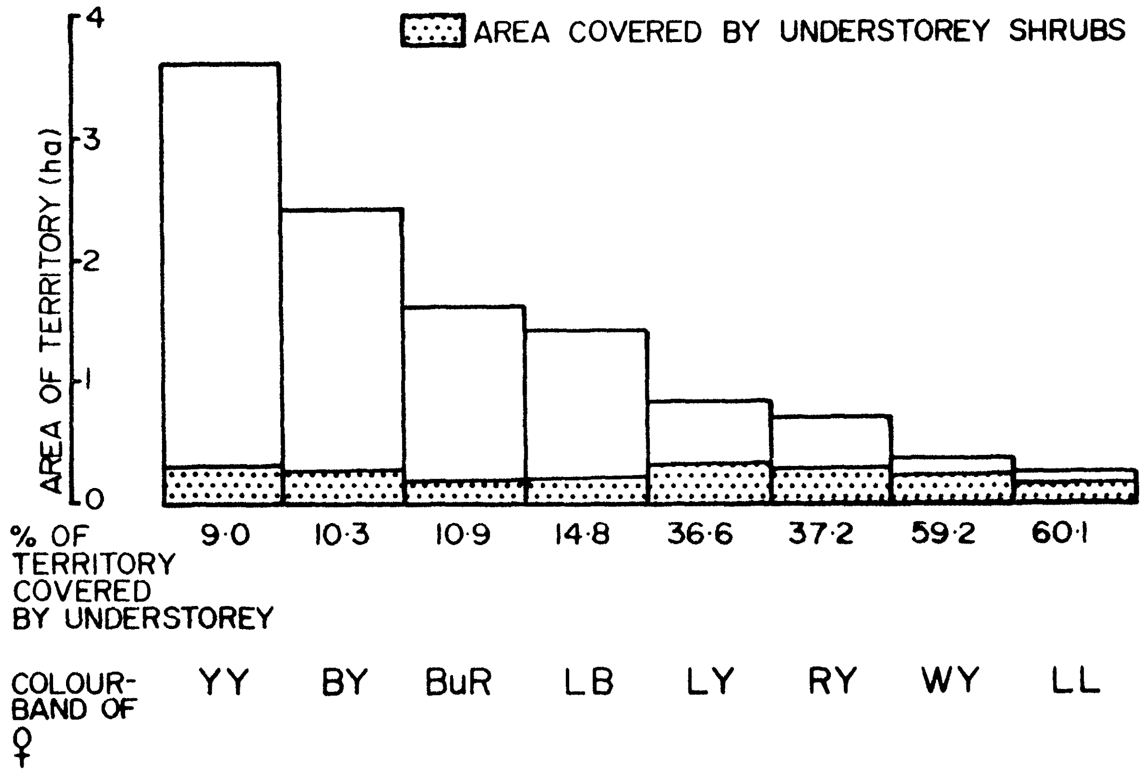

AREA COVERED BY UNDERSTOREY SHRUBS
AREA OF TERRITORY (ha)
0
1
2
3
4
% OF TERRITORY COVERED BY UNDERSTOREY
9·0
10·3
10·9
14·8
36·6
37·2
59·2
60·1
COLOUR-BAND OF ♀
YY
BY
BuR
LB
LY
RY
WY
LL

Table 6

Distribution, by Months, of Agonistic Displays and Breeding Records of Brown Thornbills at Wollomombi, and Division of Labour at the Nest

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Occurrence of agonistic displays by time of year

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Against other Brown Thornbills	17	11	5	10	7	11	12	2	8	4	8	11	106
Against Buff-rumpeds				1									1
Against Striateds	2	1		1		3		2	3	1	3		16

Participants in displays against other Brown Thornbills

Single birds vs. single birds	90	Pairs vs. pairs	13
Single birds vs. pairs	6		

Distribution of breeding records	J	F	M	A	M	J	J	A	S	O	N	D	
Nests of Brown Thornbills							1	8	5	3	1		18
Nests of all bird species	20	1		1			3	34	60	81	69	52	321

(one record: one next at month in which first egg laid)

Division of labour at nest

Sex	Nest-building	Incubation	Feeding of young
♀	118(11)	43(7)	61(8)
♂	1(11)	none(7)	60(8)

(One record: one visit to a nest when building or feeding young; one bird flushed from a nest while sitting on eggs; numbers in brackets: number of nests observed; N.B. the one record of male that carried material was of a bird that carried a feather to near the nest and then dropped it.)

1970, Frith 1976) or in the RAOU Nest Record Scheme. Loss of a clutch, or of young newly out of the nest, resulted in renewed attempts. At least four pairs lost three nests each in one season but successfully reared a fourth clutch. From my observations of marked parents and young, of four families, the young remained with the parents until late summer or early autumn, when they were driven out by the adults. Young presumably dispersed widely because from November until July a regular stream of unmarked individuals were encountered, many of which were later banded. Almost all of these 'new' birds quickly disappeared. During the post-breeding period Brown Thornbills appear in unlikely habitats, such as urban gardens and isolated clumps of trees, far from their breeding habitats (Frith 1976, pers. obs.). Twice, a lone individual maintained itself throughout the breeding season in a patch of marginal habitat adjacent to the study area, one occupying a vacated territory in the following season. One 'new' pair, the young of two pairs under study (see Figure 15) established a territory in previously unoccupied marginal habitat.

79. The breeding unit of Brown Thornbills was invariably a single pair. Only one bird of each pair was ever found to have a brood-patch, to incubate the eggs or build the nest, and this was invariably the bird with the smaller wing-length. Eleven female specimens examined had a mean wing-length of 48.3 ± S.D. 1.4 mm, significantly smaller by Students T-test ($P < 0.05$) than the mean of 22 specimens of all sexes (51.8 ± S.D. 1.2 mm). Copulation was seen only twice but in both cases the presumed female was the passive partner. Thus, presumption of sex seems soundly-based. Both sexes shared equally in the feeding of young, both in the nest and after fledging. Data from the RAOU Nest Record Scheme (NRS) appear to accord with mine, but few of the NRS data are of marked individuals.

80. Breeding success was very low; only three out of sixteen (19%) nests in which eggs were laid produced fledged young. Failures were caused by abandonment of eggs (three) and predation (ten), identified by damage to the nest. However, during the three seasons of the study plus the year following, out of 25 pairs that bred, at least eleven successfully

reared at least one independent young which was observed in association with the parents. Of three nests which fledged young colour-banded in the nest, all nine young disappeared one by one within ten days. Because other young remained with their parents for several months and because seldom was more than one young bird seen with its parents, despite three eggs being a normal clutch, I believe it likely that Brown Thornbill young are vulnerable to predation just after fledging, in contrast to the other thornbill species (to be discussed later).

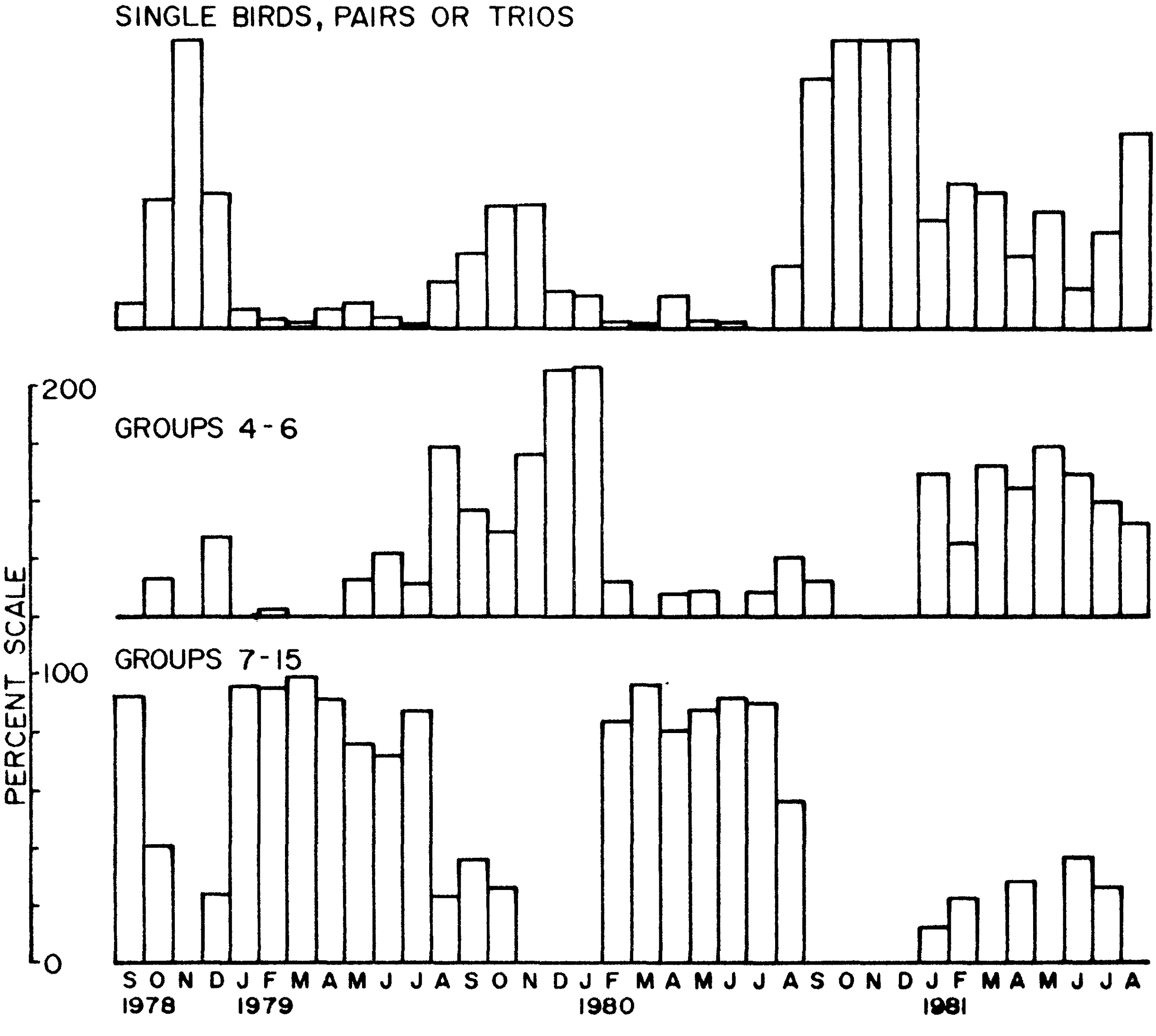
Buff Rumped Thornbill *Acanthiza reguloides*

81. As shown by Figure 18 forthe first two years, 1978/79 and 1979/80, the pattern was of flocks (usually of 10-15 birds) during late summer, autumn and winter, which broke up into pairs or groups of two, three or four birds in spring, increasing to larger parties of four to six birds in summer. This pattern was not repeated in 1980/81 because high mortality in the drought-stricken winter of 1980 and breeding-failure in spring left insufficient birds to form large flocks. As will be shown the pattern was of a permanent flock (clan) during the non-breeding season, breaking-up into breeding groups of two to four birds in spring, which were later accompanied by their young of the season, after which they re-formed into the large clan.

82. Sex of birds was inferred only. Only one bird of a pair, trio or quartet ever built the nest, incubated or had a brood-patch. Of specimens, eleven females had a mean wing-length of 50.0 ± S.D. 1.4 mm, significantly smaller by Students T-test ($P < 0.05$) than the mean of 26 specimens of both sexes (mean 51.6 ± S.D. 0.8 mm). In each breeding group the presumed female always had the shortest wing-length. Copulation was observed five times with the presumed female, in each case, as the passive partner. I did once see a presumed male helper (i.e. an additional young male added to a pair following a breeding season) copulating. However a breeding group of three collected near Wollomombi in September 1979 comprised one female with enlarged ovaries and brood-patch, and two males, one with enlarged gonads and one without, suggesting that perhaps male helpers do not normally come into breeding condition.

Figure 18

Percentage occurrences, by months (September 1978-August 1981), of Buff-rumped Thornbills by size of party (total n: 4674 individuals, Monthly Range 30-232)


SINGLE BIRDS, PAIRS OR TRIOS
GROUPS 4-6
GROUPS 7-15
PERCENT SCALE
200
100
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

83. Each clan had a territory, as shown in Figure 19, and I believe that the clan defends this territory against other clans. Only three encounters between clans were observed. However, because only a small part of the territory of Clan A (where I spent most time) adjoined another territory, and because the clan foraged as a tight unit in only one small part of its territory at any one time, likelihood of encounters was probably rare. In the three encounters all members of both clans participated in aggression. Another behaviour observed also indicates territoriality. On three occasions Clan A was observed foraging 100 m inside the territory of Clan C, when Clan C was absent from that area. Clan A was observed to suddenly fly upwards, as a tight group, and then fly 300 m over the top of the canopy back into the centre of its own territory. Similar behaviour was observed of a strange flock (probably Clan D, then unbanded) that ventured into Clan A's territory when the owners had concentrated their feeding in the south-west corner of their territory for two weeks. These four occasions were the only ones where I saw Buff-rumped Thornbills fly as a tight group or fly high over the canopy. I presume that a clan will not tolerate the presence of another and that the clan territory is defended at all times.

84. The clan territory was divided into group territories during each breeding season and, as shown in Table 7, group territories were defended against other groups of the same clan. All members of a group defended. Figure 20 shows the delineation of group territories in Clan A, based on spot-mapping of colour-banded birds. As shown, a group territory was held by a pair or a group of one female and two or more males. The considerable differences in Figure 20 between 1979/80 and 1980/81 was because of high mortality in the winter of 1980 and the incursion of a group from Flock D, who neither joined Clan A nor returned to Clan D.

85. Figure 21 depicts the fortunes of all members of Clan A during the study (September 1978 to August 1981) and for six months afterwards. Additional members added to two trios were their own young male offspring. In two cases old females that died were replaced in the group by their own daughters. Only one bird transferred within the clan, a nine-months old male that started his own territory. All other transfers were outside the clan, not between groups within it. Three birds immigrated into Clan A, all females. At least four young emigrated to other clans, three females and one male (who a year later returned to his parental clan).

Figure 19

Territories of clans of Buff-rumped Thornbills at Wollomombi 1978-1981. Area to North cleared grazing land, to South gorge country, unoccupied by species

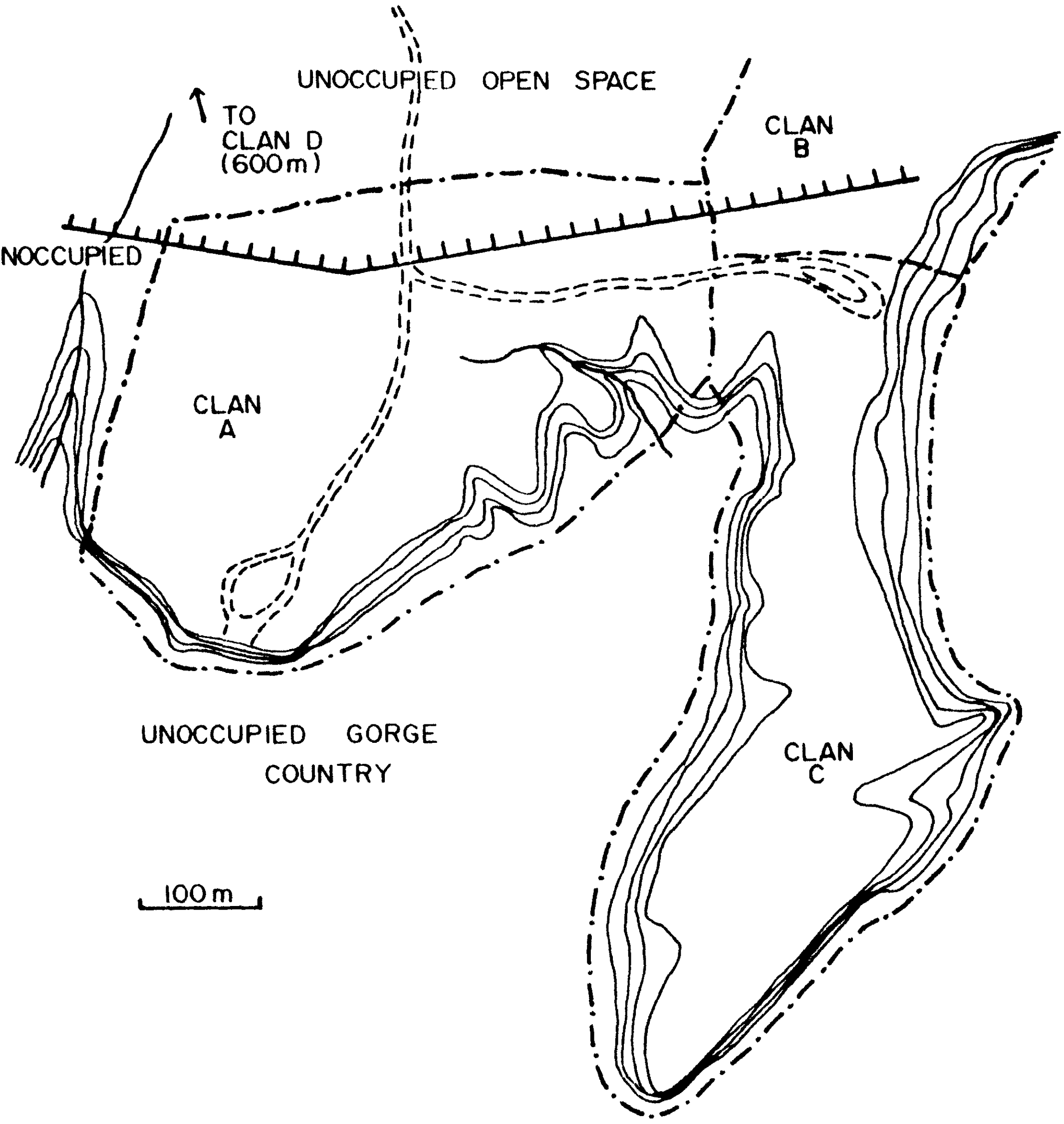

UNOCCUPIED OPEN SPACE
TO
CLAN D
(600m)
CLAN
B
UNOCCUPIED
CLAN
A
UNOCCUPIED GORGE
COUNTRY
CLAN
C
100 m

Figure 20

Clan and group territories of Buff-rumped Thornbill at Wollomombi 1978/79, 1979/80, 1980/81 (September-August) and 1981/82 (September-February). Letters refer to banded birds (paragraph 75); top bird is female

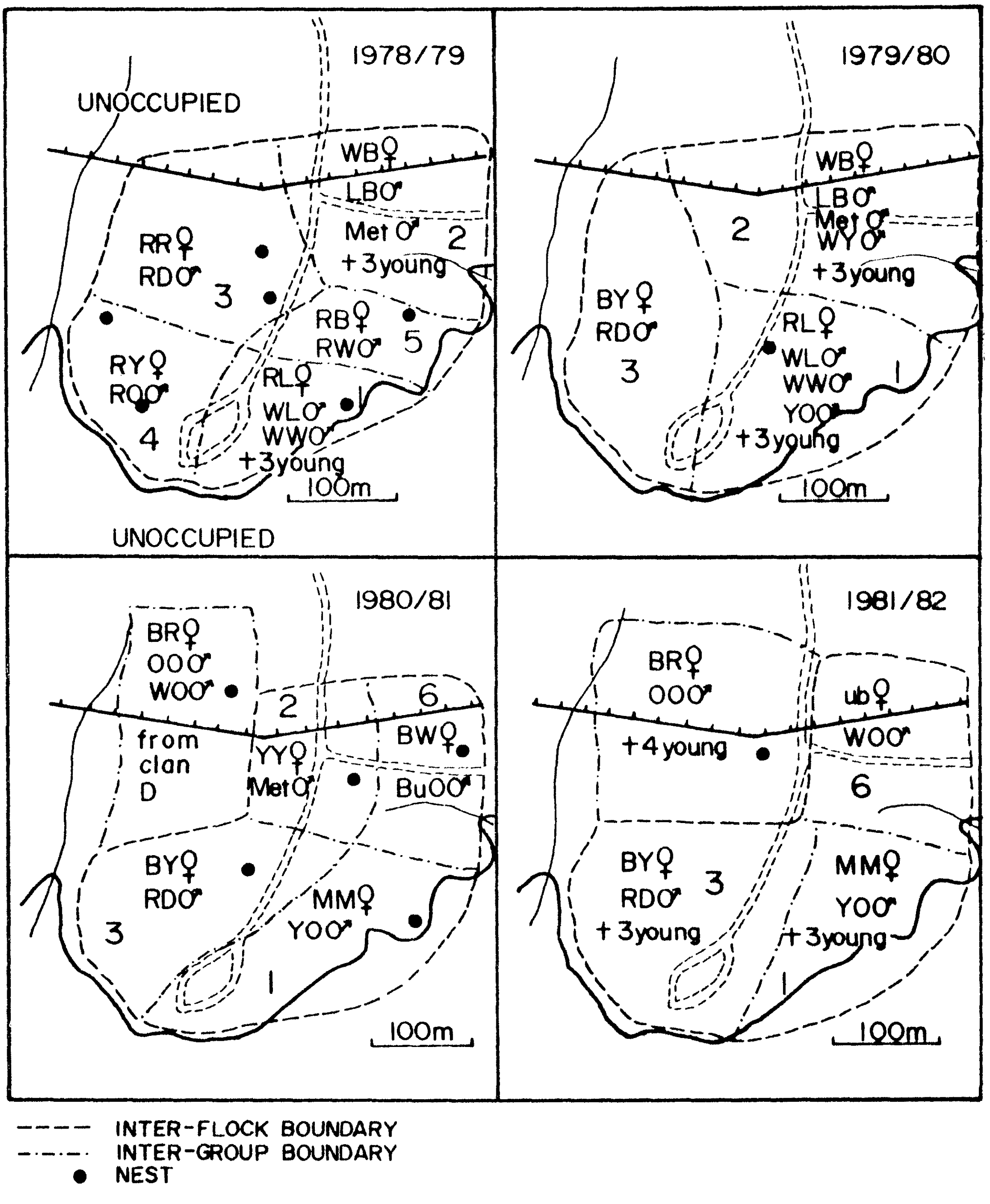

1978/79
UNOCCUPIED
WB♀
LB♂
Met ♂
+3young
2
RR♀
RD♂
3
RB♀
RW♂
5
RY♀
RO♂
RL♀
WL♂
WW♂
+3young
1
4
100m
UNOCCUPIED
1979/80
WB♀
LB♂
Met ♂
WY♂
+3young
2
BY♀
RD♂
3
RL♀
WL♂
WW♂
YO♂
+3young
1
100m
1980/81
BR♀
OO♂
WO♂
2
6
from
clan
D
YY♀
Met ♂
BW♀
BuO♂
BY♀
RD♂
3
MM♀
YO♂
1
100m
1981/82
BR♀
OO♂
+4young
ub♀
WO♂
6
BY♀
RD♂
+3young
3
MM♀
YO♂
+3young
1
100m
INTER-FLOCK BOUNDARY
INTER-GROUP BOUNDARY
NEST

Figure 21

History of individual Buff-rumped Thornbills of Clan A, at Wollomombi 1978/82. Broken edge at left of bar indicates age unknown at banding, at right indicates known to be alive after leaving

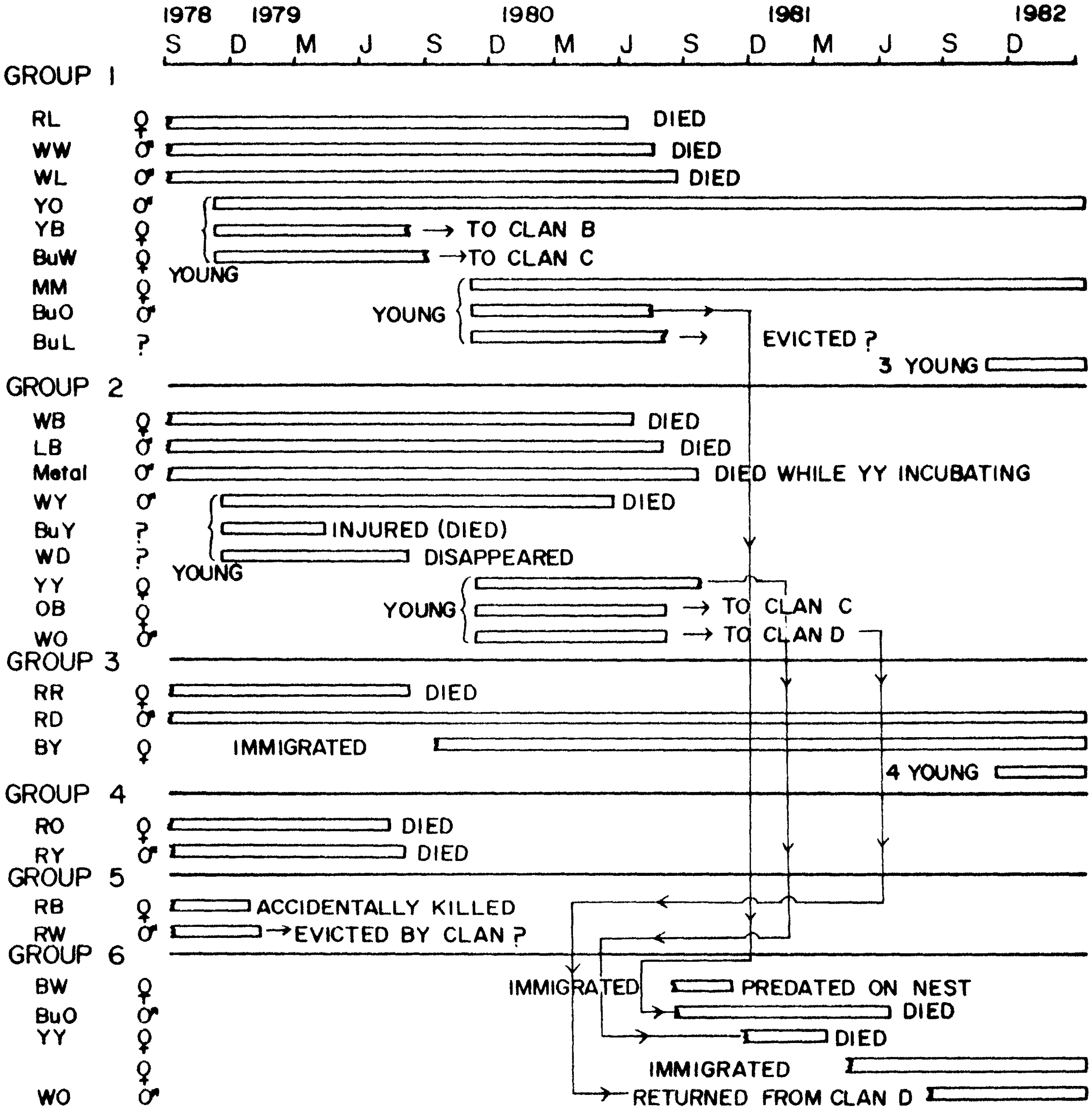

1978
1979
1980
1981
1982
S
D
M
J
S
D
M
J
S
D
M
J
S
D
GROUP 1
RL ♀
DIED
WW ♂
DIED
WL ♂
DIED
YO ♂
YB ♀
→ TO CLAN B
BuW ♀
→TO CLAN C
YOUNG
MM ♀
BuO ♂
YOUNG
BuL ?
EVICTED ?
3 YOUNG
GROUP 2
WB ♀
DIED
LB ♂
DIED
Metal ♂
DIED WHILE YY INCUBATING
WY ♂
DIED
BuY ?
INJURED (DIED)
WD ?
DISAPPEARED
YOUNG
YY ♀
OB ♀
YOUNG
→ TO CLAN C
WO ♂
→ TO CLAN D
GROUP 3
RR ♀
DIED
RD ♂
BY ♀
IMMIGRATED
4 YOUNG
GROUP 4
RO ♀
DIED
RY ♂
DIED
GROUP 5
RB ♀
ACCIDENTALLY KILLED
RW ♂
→EVICTED BY CLAN ?
GROUP 6
BW ♀
IMMIGRATED
PREDATED ON NEST
BuO ♂
DIED
YY ♀
DIED
♀
IMMIGRATED
WO ♂
RETURNED FROM CLAN D

Table 7

Distribution, by Months, of Agonistic Displays and Breeding Records of Buff-rumped Thornbills at Wollomombi, and Division of Labour at the Nest

Occurrence of agonistic displays by time of year

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Against others in same group					3								3
Aginst other groups	3					2	2	5	4	3	3	1	23
Against other clans			1		1	1							3
Against Striated Thornbills		1		1					1	1		2	6

Participants in displays against other Buff-rumped Thornbills

Clans vs. clans	3	Males vs. pairs	1
Paris vs. pairs	2	Males vs. unknown individuals	1
Males vs. males	10	Unknown vs. unknown	5
Males vs. females	2		

Distribution of breeding records

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Nests of Buff-rumped Thornbills									1	6	2	3	12
Nests of all bird species	20	1		1			3	34	60	81	69	52	321

(one record: one nest at month in which first egg laid)

Division of labour at nest

Sex	Nest-building	Incubation	Feeding of young
♀	72(9)	59(8)	65(3)
♂	none(9)	none(8)	72(3)
helper ♂	none(2)	none(2)	30(1)

(one record: one visit to a nest when building or feeding young; one bird flushed from a next while sitting on eggs; numbers in brackets: number of nests observed.)

86. Table 7 gives the breeding data for Buff-rumped Thornbills at Wollomombi, and indicates that the species nested later than most birds at Wollomombi and later than the Brown Thornbill. Nesting was mainly from mid-spring to late summer. The complete nesting cycle appears, from my data, to take from six to ten weeks, depending on how soon the female lays after completing her nest. From my observations and data from the RAOU Nest-record Scheme I do not believe that a second clutch is started after a previous one is successfully fledged. However, repeated attempts were made again when clutches were lost.

87. Breeding success was very low; only three out of thirteen nests with eggs fledged young. Failures were caused by abandonment of eggs (two) and predation (ten). During the four seasons of the study, out of 19 breeding groups (Clan A and two individual.groups in other clans) three out of 13 pairs, two out of four trios and two out of two quartets successfully reared young -- seven out of 19 groups (23 young from 46 adults). Success seemed related to nest-site because out of six nests inside hollow limbs three fledged young (two lost an adult each and were abandoned), but none of the seven nests under bark on the sides of trunks succeeded. Of 152 nests in the RAOU Nest Record Scheme only 27 (ca. 11%) were on the sides of trunks but 55% were on the ground underneath tussocks of grass, a site not used at Wollomombi where there were few tussocks. Nest success, in the RAOU sample, of 58 nests of which the history was followed, was 64%, much better than the 22% of my sample or even the annual success of breeding groups, counting all attempts in a season as one (36%). Unlike Brown Thornbills, the fledged young of Buff-rumped Thornbills stayed with their parental groups throughout the remainder of summer, autumn and winter. They were very successful in keeping their fledged young alive because out of twelve young observed only two failed to survive until the following spring and one of those was accidently killed. Of eleven young produced by Clan A and a pair from Clan D in 1981 at least nine survived for six months. Table 7 shows that only the females ever built the nest or incubated eggs. However all birds in a group, including helper males, seem to share in the feeding of young.

88. The annual sequence of events (see Figure 18) started with the formation of the clan in late January. Those groups that had finished

breeding came together, with any young produced, and all adult birds, regardless of breeding group, fed the young for about six weeks. For example Group 1 (see Figures 20 and 21) fledged three young on 6 December 1978. On 19 December Group 4 (a pair) whose two breeding attempts had failed, joined Group 1 and helped to feed their young. On 1 January Group 3 (also a pair) who had failed to breed, joined and helped to feed the young. Thus seven adults were feeding the young before the young reached independence (about 28 January).

89. Those groups still breeding continued to defend their territories, the non-breeding clan foraging only in those territories of groups that had given up breeding. By February all feeding groups had united in a single clan which then foraged over the whole clan territory. Occasionally the non-breeding clan ventured into unoccupied areas of unsuitable habitat such as dense gullies or grazing pasture. At most times the clan was followed by other species of birds, to be discussed later. During this non-breeding season the members of a breeding group did not appear to associate particularly with fellow members. Of 102 records taken of 'nearest neighbours' within a clan only 15 were of two members of the same breeding group. Around July much chasing occurred within the clan, coupled with occasional aggression between members of different breeding groups. Some groups detached themselves from the clan in July and August, only to re-join a few days later, but by September all breeding groups were back in their old territories and defending them vigorously. During July and August all young of the previous season, unless added to the parental group as an additional male or a replacement for the mother, disappeared, some to turn up in neighbouring flocks. Immigration into the clan, from other clans, also occurred at this time.

Striated Thornbill *Acanthiza lineata*

90. Figure 22 shows the social groupings, by months, of all Striated Thornbills seen foraging. The pattern was similar to the Buff-rumped Thornbill, with flocks (clans) of 7-15 birds in late summer, autumn and early winter, breaking up into pairs, trios or quartets in late winter and spring. These pairs and trios increased to parties of 4-6 birds in late spring and early summer, presumably breeding groups with young.

The social organisation of Striated Thornbills was difficult to discern because of problems in the identification of individuals. The large number banded necessitated the use of many indistinct colour combinations. The species foraged mainly in the canopy of trees and was silhouetted against the sky. Often the birds foraged while hanging upside down. Most importantly, the individuals and flocks moved so quickly that it was often not possible to identify more than one bird, and rarely more than two, before a flock disappeared. I therefore made up a matrix which included all colour-banded birds. The matrix included the percentage of each bird's occurrences with other birds, that were with each of all the other Striated Thornbills. From the matrix I drew a dendrogram, according to Sokal and Sneath (1963) and Cody (1974), which showed the degree of association between individual birds. The dendrogram for 1978/79 shown in Figure 23 showed that there were three distinct flocks, one with 17 banded birds (probably the entire flock), one with 16 and another, on the fringe of the study area, with 11. Mapped sightings of colour-banded birds were then collated on the map, results which are shown in Figure 24 showing that the flocks occupied well-defined home ranges. Mistaken identification may have caused some of the discrepancies shown in Figure 24 but Clan A was seen to bathe at pools in the territories of both Clans B and C. The cliff was a well-defined boundary because all birds seen in tree-tops below the cliff were unbanded. The territories were maintained from year to year except that in 1980 Clan A, which seemed to have lost many birds, retreated before Clan B, which in its turn retreated before another Clan (D) from outside the study area.

91. As Figure 22 shows, the large non-breeding clans broke up in late winter into smaller groups, in similar fashion to the Buff-rumped Thornbill. Because of the difficulties in identifying individuals, and because Striated Thornbills were very secretive during the breeding season, I was unable to define all breeding territories. That the species holds breeding territories is indicated by the data on agonistic displays given in Table 8. Figure 25 shows mapped occurrences of known breeding groups (four pairs and one trio) from 1 August 1979 to 30 November 1979. The vacant spaces in Figure 25 were occupied by others of the species whose nests could not be found. Figure 25 indicates that breeding territories

Figure 22

Percentage occurrences, by months (September 1978-August 1981) of Striated Thornbills by size of parties (total n: 5933, monthly range (120-404)

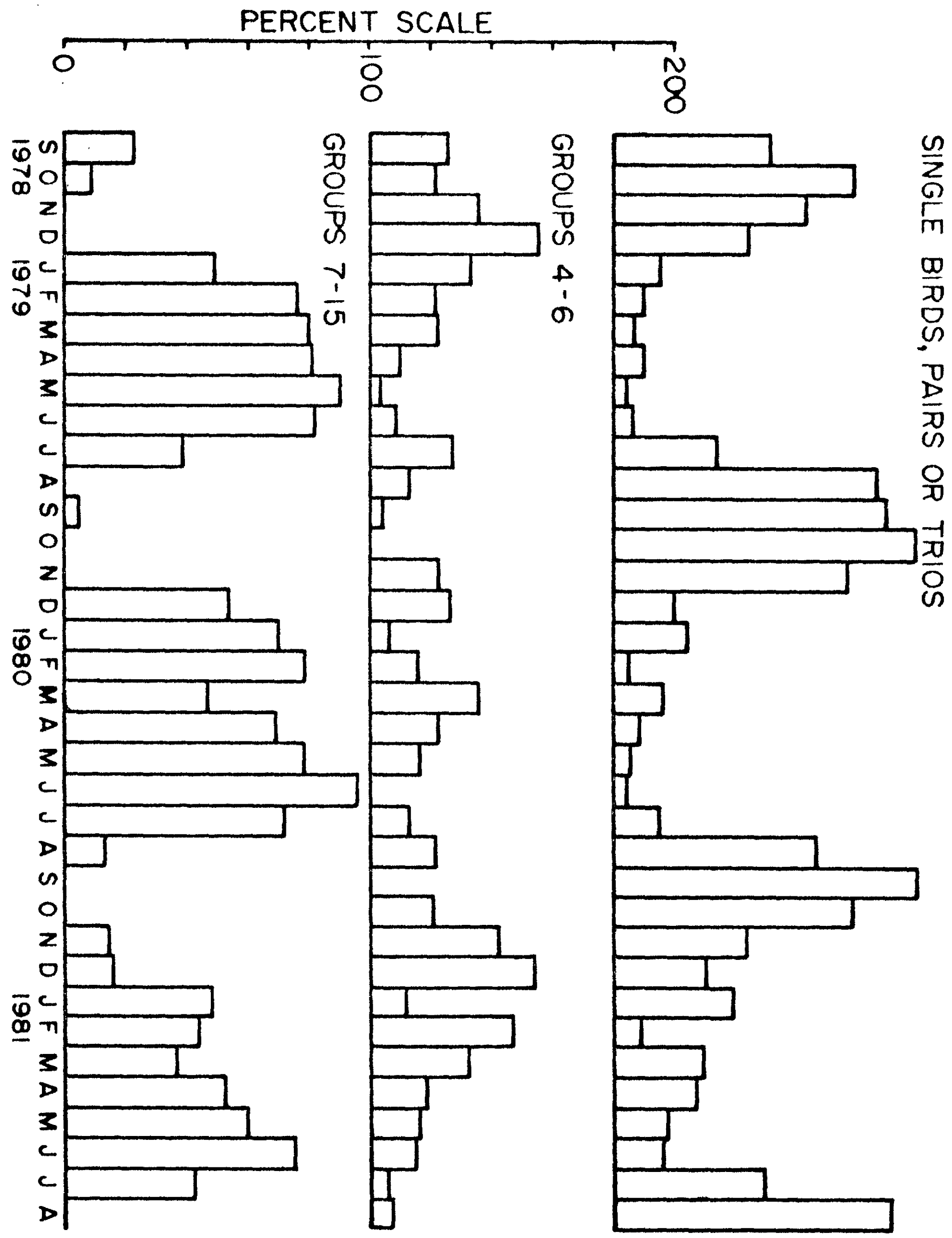

PERCENT SCALE
0
100
200
SINGLE BIRDS, PAIRS OR TRIOS
GROUPS 4-6
GROUPS 7-15
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

Figure 23

Dendrogram showing degree of association between Striated Thornbills

observed at Wollomombi during 1978/79 and

probable membership of clans

(see para 90)

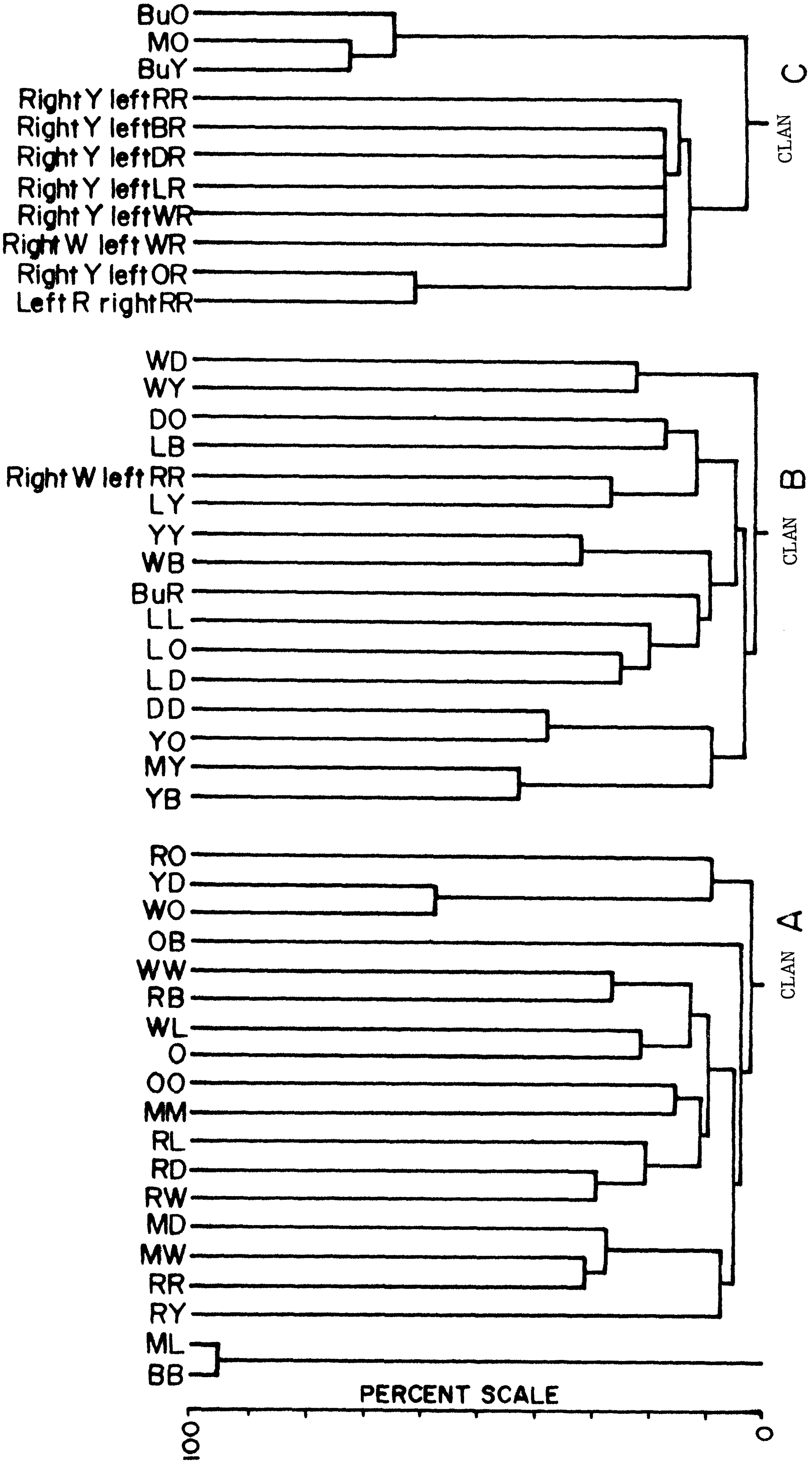

BuO
MO
BuY
Right Y left RR
Right Y left BR
Right Y left DR
Right Y left LR
Right Y left WR
Right W left WR
Right Y left OR
Left R right RR
CLAN C
WD
WY
DO
LB
Right W left RR
LY
YY
WB
BuR
LL
LO
LD
DD
YO
MY
YB
CLAN B
RO
YD
WO
OB
WW
RB
WL
O
OO
MM
RL
RD
RW
MD
MW
RR
RY
ML
BB
CLAN A
PERCENT SCALE
100
0

Figure 24

Observed sightings of clans and presumed clan territories of Striated Thornbills at Wollomombi 1978/79, 1979/80, 1980/81 (September-August) and 1981/82 (September-February). (Closed circles: Clan A, open circles: Clan B, upright crosses: Clan C, diagonal crosses Clan D)

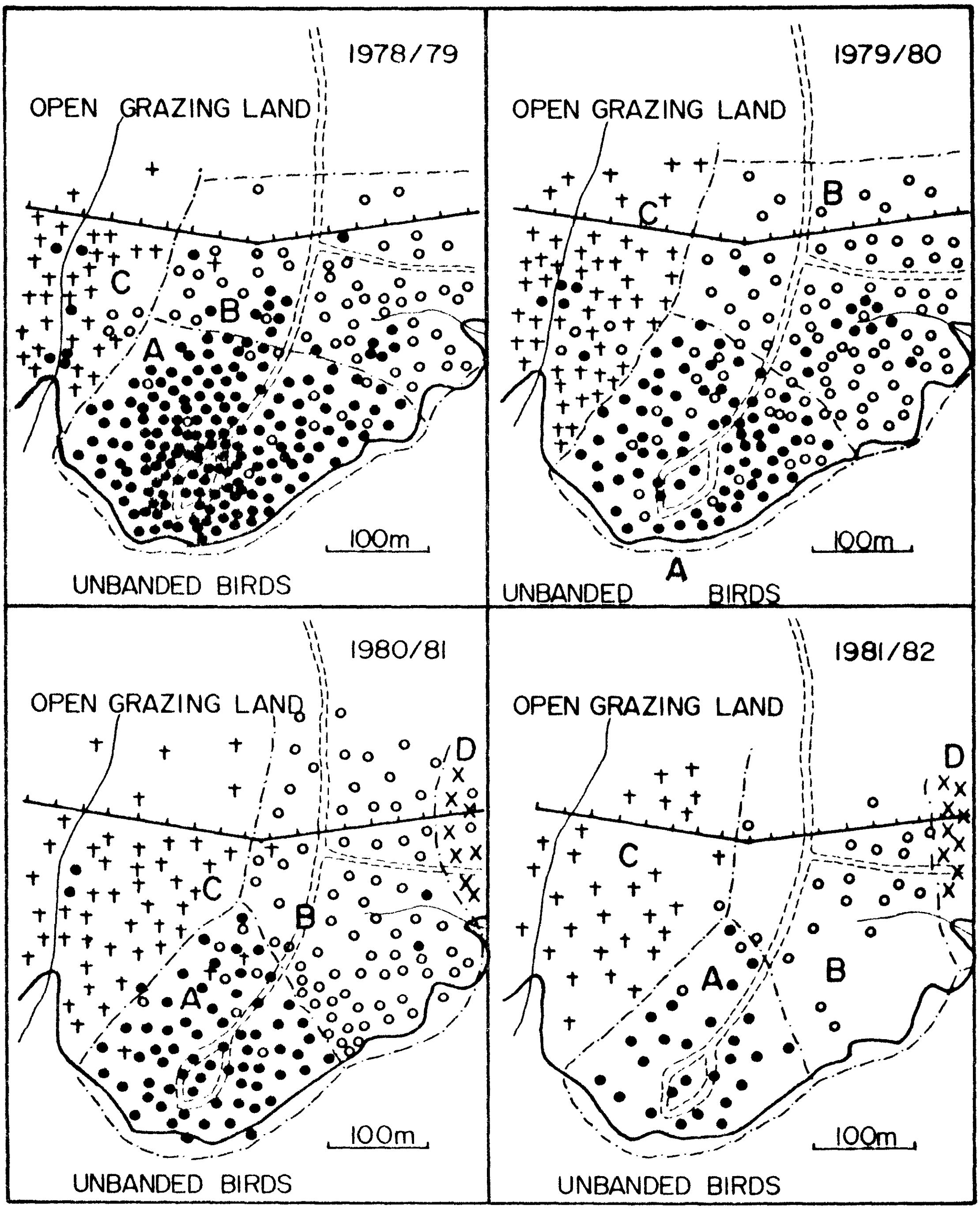

1978/79
OPEN GRAZING LAND
A
B
C
100m
UNBANDED BIRDS
1979/80
OPEN GRAZING LAND
A
B
C
100m
UNBANDED BIRDS
1980/81
OPEN GRAZING LAND
A
B
C
D
100m
UNBANDED BIRDS
1981/82
OPEN GRAZING LAND
A
B
C
D
100m
UNBANDED BIRDS

Figure 25

Sightings during breeding season (1 August-30 November) of 1979 of individuals of five groups of Striated Thornbills at Wollomombi, and location of nests (N). (Note that vacant areas were occupied, by unidentified groups)

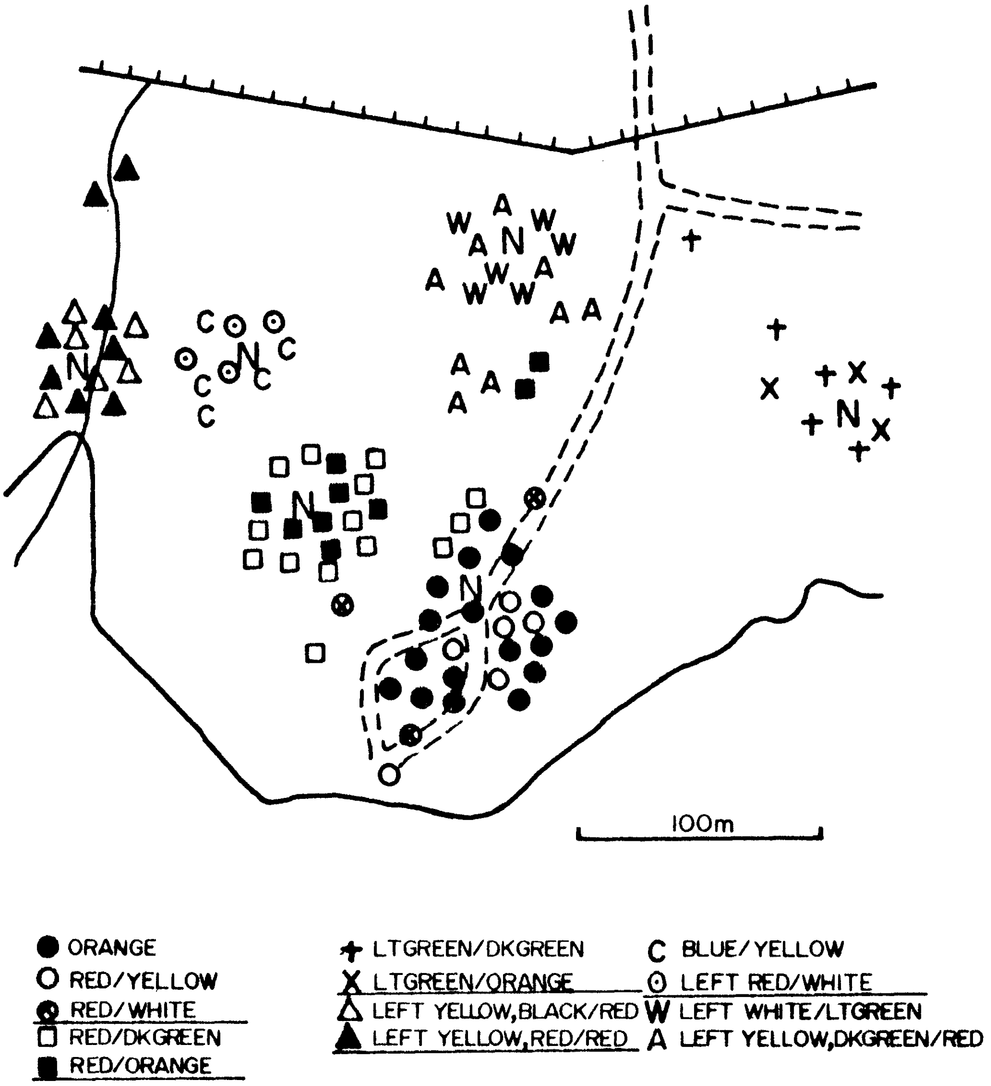

100m
● ORANGE
O RED/YELLOW
⊗ RED/WHITE
□ RED/DKGREEN
■ RED/ORANGE
+ LTGREEN/DKGREEN
X LTGREEN/ORANGE
△ LEFT YELLOW,BLACK/RED
▲ LEFT YELLOW,RED/RED
C BLUE/YELLOW
⊙ LEFT RED/WHITE
W LEFT WHITE/LTGREEN
A LEFT YELLOW,DKGREEN/RED

Table 8

Distribution, by Months, of Agonistic Displays and Breeding Records of Striated Thornbills at Wollomombi, and Division of Labour at the Nest

Occurrence of agonistic displays by time of year

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Against Striated in other groups							1	3	2	2	1	1	10
Against Striated in other clans		1	1	1	1								4
Against Brown Thornbills			1			1		1	2	3			8
Against Buff-rumped Thornbills		1							5			1	7

Participants in displays against other Striated Thornbills

Clans vs. clans	4	Pairs vs. single birds	1
Trios vs. single birds	1	Single birds vs. single birds	6
Trios vs. pairs	1		

Distribution of breeding records

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Nests of Striated Thornbills							1	5	9	5	1		21
Nests of all bird species	20	1		1			3	34	60	81	69	52	321

(one record: one nest atmonth in which first egg laid)

Division of labour at nest

Group		Nest-building		Incubation		Feeding young
Identified pairs	♀	27(3)		31(4)		7(1)
	♂	19(3) *		none(4)		9(1)
Unidentified pairs	o	4(2)			o	9(2)
	o	3(2)			o	9(2)
Identified trio			♀	12(1)	♀	8(1)
			♂	none(1)	♂	10(1)
			♂	none(1)	♂	8(1)
Unidentified trio	o	5(1)			o	5(1)
	o	7(1)			o	7(1)
	o	none(1) *			o	7(1)

*: one took no part inbuilding (one record: one visit to nest when building or feeding young; one bird flushed from nest while sitting on eggs; numbers in brackets; number of nests).

were less than one hectare. The result in Figure 25 was not influenced by observer bias towards known nesting sites. I covered all areas equally and only found the nests because of repeated sightings of banded birds in the same area, not the other way round. One breeding group used the same territory four years in succession, and two others at least twice, so it seems likely that breeding territories were permanent. In those cases where I could positively identify birds at a nest, the numbers were eight pairs, five trios and one quartet. Sexes of birds in trios or quartets could not be determined but of two breeding trios collected outside the study area there were one female and two males in each.

92. Table 8 shows that breeding groups defended their territories against other groups. With non-breeding clans only four inter-clan encounters were seen but these were violent, and involved ten birds or more on either side. Clan A was twice driven from the waterhole in Clan B's territory, and similarly it was evicted from the creek in Clan C's territory. Importantly, on 26 July 1978, eleven birds of Clan B were netted and placed in a cage for two hours, when six birds of Clan A were also caught in the same net, one hundred metres inside Clan B's territory. Similarly on 12 August 1980 I captured ten birds of Clan B on the eastern boundary of their area, placed them in a cage, and two hours later found five of Clan D in the same net. Thus it would appear that maintenance of territorial integrity, by a non-breeding clan, is a continual process.

93. Breeding is shown in Table 8 and the Striated Thornbill completed breeding before the other two species. My calculation of the nesting cycle is 7-9 weeks. Many nests were started in July but were blown down by the strong winds prevailing at that time. The species at Wollomombi, as elsewhere (RAOU Nest Record Scheme), usually builds a nest suspended from leaves in a tall eucalypt. As for other thornbills in this study I do not believe that a second clutch is started if the first is successful, but in at least one case, repeated attempts were made after failure. Breeding success was very low, only four out of 22 (18%) nests fledging young compared to 44% for the 108 records of the RAOU Nest Record Scheme. I could not assess how many young joined each flock when breeding finished but in all seasons, except that of 1980, unbanded birds were always seen

in flocks at that time. Like Buff-rumped Thornbills these 'new' birds, presumably young of the year, remained with the flock until the following season. Of the clutches lost one was parasitized by a cuckoo, four were blown down by wind, fourteen were torn apart by an unidentified predator, three (one with eggs, two with young) were actually seen being predated by a Pied Currawong *Strepera graculina* and one with young was seen predated by an Olive-backed Oriole *Oriolus sagittatus.*

94. Table 8 shows that, unlike the other two species, both sexes build the nest, but it is unknown whether helpers assist. Only the female incubated and all birds, including helpers, feed the young. Presumption of sex was based upon the netting of birds that were currently nesting. All four incubating birds had brood patches but none of their five spouses or helpers did. My sample of wing measurements shows no significant difference between sexes (T-test, $P > 0.05$).

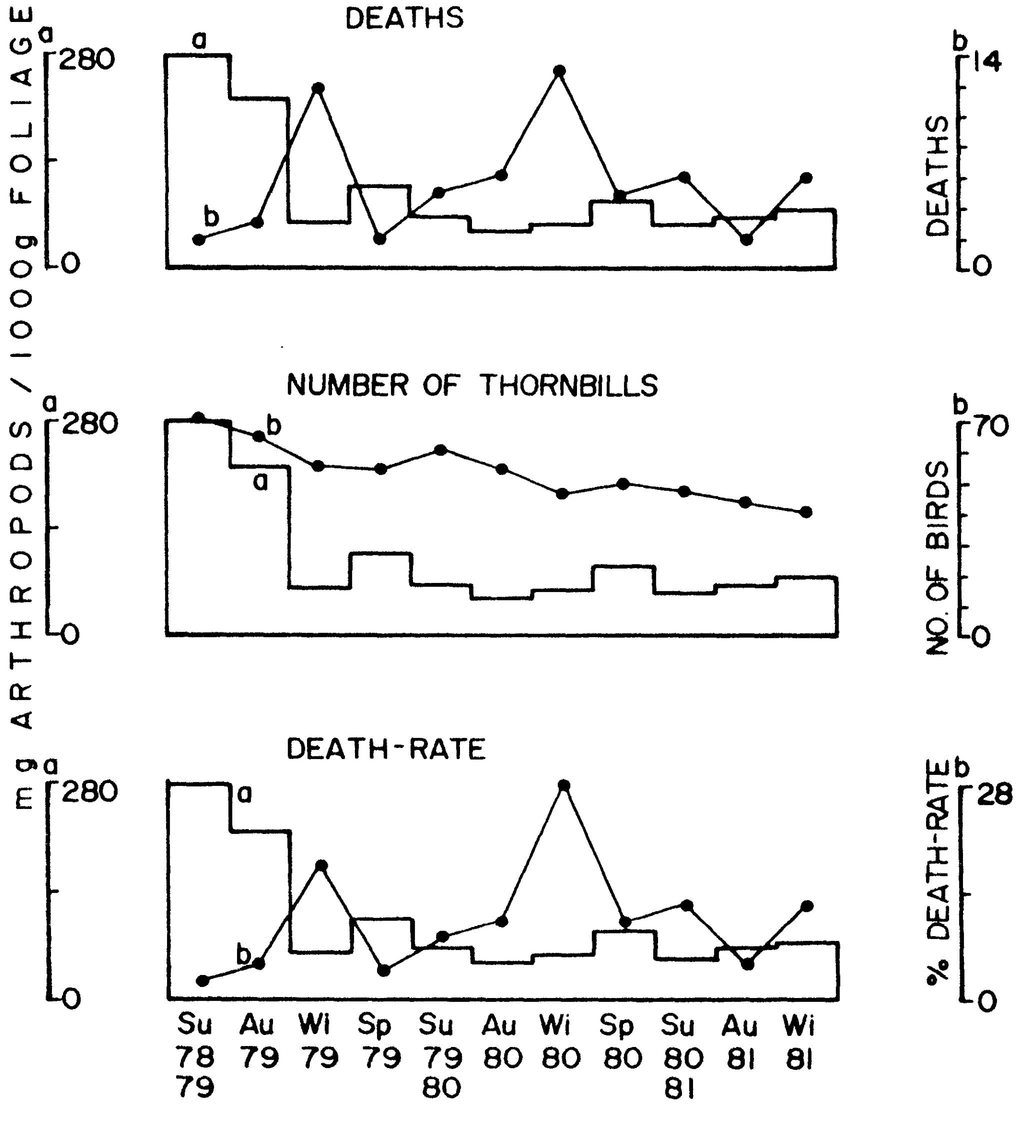
95. The annual cycle (see Figure 22) resembled that of the Buff-rumped Thornbill. The non-breeding clan re-formed in mid-summer and thereafter foraged in its own territory, usually accompanied by other species. In June breeding groups started to detach themselves from the clan and by late July all groups were holding their breeding territories. Because of difficulties in identification it was not possible to closely follow the fortunes of individual birds. However several birds changed clans between breeding seasons, these all being 'new' birds banded in the preceding summer, suggesting that they were young of the year. At least one adult bird changed its breeding group within the clan, being one of a trio that left and established (or inherited) a territory with an adult female that had presumably lost its mate.

Mortality

96. Figure 26 shows, by seasons, deaths of colour-banded thornbills compared to the abundance of arthropods. I have little doubt that the birds did die; in all cases they were seen regularly but then suddenly vanished. All had been adult members of pairs or breeding groups that had bred during the previous season. No data for spring 1978 are given because at that stage it was not clear as to which individuals were

Figure 26

Abundance (mg/100 g of foliage) of arthropods in foliage samples, by seasons compared to (a) deaths of thornbills, (b) numbers of thornbills present, and (c) death-rate of thornbills (deaths as % of numbers), at Wollomombi



DEATHS
NUMBER OF THORNBILLS
DEATH-RATE
mg ARTHROPODS / 1000g FOLIAGE
a
280
0
b
14
DEATHS
70
NO. OF BIRDS
28
% DEATH-RATE
Su 78 79
Au 79
Wi 79
Sp 79
Su 79 80
Au 80
Wi 80
Sp 80
Su 80 81
Au 81
Wi 81

adults. Figure 26a shows a strong correlation between deaths of thornbills and the scarcity of arthropods (Spearman Rank Correlation, r: 0.800, $P < 0.01$). Numbers of thornbills present throughout the study are compared to abundance of arthropods in Figure 26b. These do not correlate ($P > 0.1$) but a continuous downward trend in numbers is evident for the two years of drought (1979/80 and 1980/81) in which even the summer peaks of arthropods were depressed far below the levels seen in the first year. The slight upward trend in numbers shown each spring would be caused by attendant young of the season. Figure 26c gives the death-rate i.e. deaths as a percentage of individuals present. The correlation between the death-rate and scarcity of arthropods is strong (Spearman Rank Correlation, r: 0.796, $P < 0.01$).

Interference Competition

97. Little evidence was seen for interference competition between species except for a clear case of defence of a resource in August 1980, when the drought conditions were very severe. By that time scale insects, both psyllids and coccids, had almost disappeared, whereas during the first year of the study they usually contributed most of the arthropod numbers and a major part of the biomass on almost every sample taken from foliage. However one small bush of *Acacia irrorata* was heavily infested with coccids. The Brown Thornbill YELLOW/BLACK, in whose territory the bush was located, stayed close to the bush from about 2 to 14 August, and was seen feeding on either the scale-insects or their secretions. On 6 August he drove off two Striated Thornbills that perched on the bush and later that day twice drove off a Buff-rumped Thornbill. On 10 August three Buff-rumped Thornbills alighted on the bush but the Brown Thornbill immediately appeared and drove them off. Later that day he drove off a Striated Thornbill. On 12 August the Brown Thornbill drove off one Striated Thornbill and two Buff-rumped Thornbills. There seems little doubt that the Brown Thornbill was defending a food resource rather than showing aggression related to other activity. At that time Brown Thornbills, including YELLOW/BLACK, were freely associating with the other two species in mixed-species flocks elsewhere including some of the very same individuals driven away from the *Acacia*.

98. Indirect evidence of interference competition within species were the fights between three pairs of Brown Thornbills over a single *Exocarpos* tree which in 1979/80 had become the junction between the territories of LIGHT GREEN/BLACK, RED/YELLOW and YELLOW/YELLOW (see Figure 15b). Although *Exocarpos* was a minor component of the vegetation (Chapter 3) it was, as will be shown later, highly favoured as a foraging site by Brown Thornbills. Of agonistic encounters by pairs of Brown Thornbills, eight of 40 by RED/YELLOW's pair, four out of 20 by YELLOW/YELLOW's pair and five out of 12 by LIGHT GREEN/BLACK's pair were either in or around this particular tree. Another *Exocarpos* on the boundary between LIGHT GREEN/BLACK and YELLOW/YELLOW was the scene of seven encounters. Of the eight *Exocarpos* in the study area seven were on territorial boundaries between Brown Thornbills.

DISCUSSION

99. What are usually considered to be three common and well-known birds (e.g. McGill 1970, MacDonald 1973, Frith 1969, 1976) turn out to be poorly-known if the birds at Wollomombi are typical of their species. Some authors refer to flocking by Brown Thornbills in winter (e.g. Clark *et al.* 1972, MacDonald 1973) while others mention pairs or small flocks (e.g. Cayley 1959, Frith 1969, McGill 1970). The true situation, that of either pairs or family parties (i.e. a pair with dependent young) is, however recognized by Frith (1976), Kloot and McCulloch (1980) and Pizzey (1980) i.e. by recent authorities. The impression of flocks is probably conveyed by Brown Thornbills in mixed-species flocks of other species of thornbills, in which the Brown is often the noisiest member. Fidelity to territory of Brown Thornbills does not seem to have been generally recognised, in spite of several very long-term (> ten years) recoveries of banded birds at their original netting-site (Anon. 1977).

100. References to Buff-rumped Thornbills describe 'small parties' (MacDonald 1973), 'flocks of 5-15' (Frith 1976), or 'pairs and flocks' and 'parties' (Cayley 1959, Frith 1969, Pizzey 1980). McGill (1970) and Clark *et al.* (1972) did recognise that seasonal change occurs from pairs in the breeding season to flocks during the non-breeding season.

However, communal breeding seems not to have been identified before (Dow 1980) despite the species having been frequently photographed, and thus intensively observed, at the nest.

101. Similarly the Striated Thornbill is described as occurring in 'pairs or flocks' (Cayley 1959), 'small flocks' (MacDonald 1973), and 'flocks of twelve or more' (McGill 1970) with some recognition that flocks are more numerous in winter (Frith 1969). Communal breeding was recorded, on two occasions, by Dow (1980), who overlooked an earlier report of four or five birds feeding the one clutch, by Gwynne (1935). The long-term association of Striated Thornbills in flocks has been deduced from recaptures of banded birds, in some cases after a lapse of several years (Wilson 1965, Reilly 1967, Morris 1971) but, as for Buff-rumped Thornbills, a two-tiered permanent organisation has not been recognised.

102. There seems little information on the sharing of nesting labour, although Ford (1963) found with *A.chrysorrhoa* that both sexes built the nest but only the female incubated, and both Ford, and Immelman (1960) found that both sexes, and helpers, fed the young. In the three species studied by me only the female incubated, but both sexes, and helpers, where present, fed the young. With Brown and Buff-rumped Thornbills only the female built the nest but with Striated Thornbills both sexes did, possibly because there is strong selection for speedy construction i.e. with both sexes working. The Striated Thornbill habitually builds its nests among the outer leaves in the canopy of eucalypts and it also breeds very early, in July-August, when the south-west winds at Armidale reach their greatest intensity (George *et al.* 1977). I counted at least seventeen nests, mostly uncompleted, on the ground, but otherwise undamaged, suggesting that high winds were responsible.

103. Breeding success at Wollomombi, based on small samples, appears about the same for all three species (18-23%) and in each is less than half of that for the much larger samples in the NRS. Ultimate breeding success, based on clutches reared per season per breeding unit (i.e. pair, trio or quartet), between Brown and Buff-rumped Thornbills, is much the same, 44% and 40% respectively. However, in the rearing of young to independence (i.e. when they cease to be fed by adults) the

success rate is greater with the communally breeding Buff-rumped Thornbill. Whereas 46 adult Buff-rumped Thornbills reared 23 young to independence, 50 Brown Thornbills reared 11-16 young. Moreover, Buff-rumped Thornbills, which, unlike the Brown, keep their young in the territory until the following breeding season, lose very few of them. Out of nine colour-banded fledglings of the Brown Thornbill, all had disappeared in a few days, long before they could possibly have become independent. However of 23 Buff-rumped fledglings 19 were alive six months later, one of the missing being accidentally killed. This suggests that the flocking habit of the Buff-rumped Thornbill reduced the risk of predation, a fact already known with other species, from experimental testing e.g. Lazarus (1979) with *Quelea* spp., Caraco et al. (1980) and Goldman (1980) with juncos, *Junco* spp., and field studies by Murton *et al.* (1971) on Wood Pigeons *Columba palumbus* and Kenward (1978) on goshawks. It could be argued that a large clan territory of Buff-rumped Thornbills facilitates more versatile feeding than that possible in the small pair territory of the Brown Thornbill. However in the winter of 1980 when insects were very scarce (see Chapter 3) only four out of 14 adult Brown Thornbills, but six out of ten adult Buff-rumpeds disappeared. Flocks of Buff-rumped Thornbills may also minimise predation by the 'flashing' of rump-patches as a deterrent to predators, similar to other species, e.g. the Purple Gallinule *Porphyrio porphyrio* (Woodland *et al.* 1980).

104. The multi-tiered organisationof Buff-rumped and Striated Thornbills, i.e. permanent breeding groups that are part of a permanent clan, is paralleled by only three other species, as far as is known. The White-fronted Bee-eater *Merops bullockoides* of Africa has a three-tiered organisationof communally-breeding groups that make up a territorial clan that in turn is part of a large nesting colony (Hegner *et al.* 1982). The colonial nesting is possibly dictated by availability of nest-sites. The Mexican Jay *Aphelocoma ultramarina* has a two-tiered organisation of simple pairs making up a territorial clan (Brown 1963). The Long-tailed Tit *Aegithalos caudatus* of Eurasia has an organisation seemingly identical to that of the Buff-rumped and Striated Thornbills, except that inter-group transfer is frequent and groups larger than pairs are uncommon,

probably because of high winter mortalities (Gaston 1973). The organisation of the actual breeding group of thornbills, of one female and one or more males, is, however, well-known in many species of birds (Brown 1978, Emlen 1978). Such groups may range from merely the young of the previous brood or season helping at their parents' nests (the 'opportunistic communal breeders' of Dow 1980) to extremely complex groups where all members share in all or any of nest-construction, incubation, feeding of the sitting bird, or feeding of young; e.g. Grey-crowned Babbler *Pomatostomus temporalis* (King 1980) and Noisy Miner *Manorina melanocephala* (Dow 1978). The breeding groups of Buff-rumped and Striated Thornbills fit into an intermediate category, of relatively simple organisation, but of permanent duration. This is very similar to that of the Malurids (Rowley 1965, 1981) but differs in that the thornbills are not double-brooded and have breeding groups which themselves are part of a higher organisation. The major difference with thornbills is that after a clan re-forms, members of breeding groups other than the parents will assist in feeding young.

105. Although Zahavi (1976) claimed that helpers at the nest may inhibit successful breeding most workers agree that, within a species, those nests that have helpers produce more young than those without (see summary in Emlen 1978). More recently Koenig (1981) re-analysed the data of the studies usually referred to in discussion on communal breeding. Koenig concluded that in most cases the PER CAPITA production of young by pairs was greater than that of groups, and that in cases where group breeding was more productive the per capita production of young fell off when group-size exceeded certain limits. With my small sample, groups of Buff-rumped Thornbills appear more productive, both per breeding unit and per capita, than pairs of either their own species or of Brown Thornbills (0.75 young per capita for groups of 4, (n:2); 0.50 for groups of 3, (n:4); 0.35 for pairs, (n:14); 0.22-0.44 per capita for pairs of Brown Thornbills, (n:25).

106. Despite the above, I postulate that in the case of Buff-rumped Thornbills success is causally unrelated to group breeding or the size of the group that breeds, but depends upon freedom from predation of the nest.

My nesting data indicated that individual females of thornbills had a predilection for the same type of nest site, regardless of repeated failure in such sites. Of those female Buff-rumped Thornbills whose nests were found, one bird, (RED/LIGHT GREEN, see Figure 20) that twice nested in hollows reared two clutches but four others that nested on the sides of trunks, six times, all had their nests predated. Failure was not caused by failure to feed the young. Whereas, in the first two years of the study twelve young were reared by two trios (that became quartets in the second year), in 1981 three simple pairs reared ten young suggesting that contributions by helpers, while no doubt important (see Table 7), were not vital to success. I suggest that in the case of the Buff-rumped Thornbill, successful breeding units may not have succeeded because they had helpers at the nest; rather they had helpers at the nest because they had been successful breeders.

107. Perhaps the two-tiered organisation of the Buff-rumped and Striated Thornbills is a response to the benefits of both a large (i.e. > 10 birds) flock size, to minimise predation, and a communal breeding group. It may be noteworthy that communal breeders whose groups are much larger than the three or four of thornbills, are usually large aggressive birds which have a good chance of defending their nests against predators. Typical such species are babblers *Pomatostomus* spp., jays *Aphelocoma* spp., White-winged Choughs *Corcorax melanorhamphus*, kookaburras *Dacelo* spp., bee-eaters *Merops* spp. and Woodpeckers *Melanerpes* spp. It is debatable, for reasons given earlier, whether the breeding group is more productive than a pair. However the retention of young males in the parental breeding group for over a year and the retention of all young, until the start of the following breeding season, ensures ready replacement, particularly after winter mortality, by a close relative. Moreover, the replacements will already be familiar with the group and clan territory. This ready replacement was seen after the winter and drought of 1980. Despite the loss of more than half of all adult Buff-rumped Thornbills in Clan A, all breeding groups held their territories, with at least one breeder related to theprevious breeders, and attempted breeding. Helper males took over their group and young females replaced

their mothers. Thus the habits of communal breeding and retention of young until the next breeding season virtually ensures that parents' genes are likely to be retained in the breeding group. Of course, a major disadvantage of retaining young through winter is increased pressure on resources, possibly reflected in the high mortality in the winter of 1980.

108. The reasons why Brown Thornbills should differ from the other two species (and probably from most other species of thornbills, judging from their gregariousness); may relate to preferred habitat. Wollomombi is possibly sub-optimal habitat for Brown Thornbills. Throughout their wide range they prefer rain forest, wet sclerophyll forests and, as shown in this study, the denser parts of dry sclerophyll forests and woddlands, places where they cannot see far but where neither can their predators. Even those communal breeders that prefer dense habitats, such as the White-browed Scrub-wren *Sericornis frontalis* (Bell in press) and Brown Gerygones *Gerygone mouki* (Mackaness 1976), do not occur in social groups that exceed a single breeding unit. It is reasonable to assume that flock cohesion is easier to maintain in more open habitats where vulnerability to predation, particularly by accipiters, is greater. One selective advantage however, of monogamy combined with expulsion of young in autumn, may be that dispersal, and therefore the ability to colonise, is greater. There are no quantified data but Brown Thornbills are known, in the post-breeding period, to appear in areas distant from their breeding habitat. They are the only species of the three thornbills to colonise exotic *Pinus* plantations (see Chapter 7). Furthermore, of the three species, which all occur on the Northern shores of Bass Strait, only the Brown Thornbill has colonised Tasmania (Keast 1961).

109. From Figure 26 the deaths of thornbills seem related to the abundance of food. However, the peak periods of deaths were in winter, and it could be argued that long nights and below-freezing temperatures may have been more important than mere scarcity of food, particularly for such small birds (*ca.* 7 g). Probably a combination of factors was responsible. Numbers of thornbills (Figure 26b), although not correlated with arthropod abundance, mainly because of annual increments of young birds

each spring, suggest that the cumulative effects of the drought steadily reduced numbers as time progressed. In the case of the monogamous Brown Thornbill (see Figure 15) when adults died during the drought, the survivors mated with other survivors in adjacent territories. Thus territories were combined, suggesting that perhaps the original ones were no longer sufficient to sustain one breeding pair. The death-rate (Figure 26c), an outcome of deaths and total numbers, shows a higher rate in the winter of 1980 than in 1979, and a fairly low rate in that of 1981. The fact that the winter of 1980 followed what appeared to be a collapse of insect reproduction in summer, and that the winter of 1981 followed good rains in Autumn suggests that the food supply may have been more important to the survival of thornbills than night-length and temperature.

110. The anecdotal evidence for direct competition between species is based on one resource, a single bush covered in scale insects. Yet there can be little doubt that all three species tried to feed at that resource and that one of them defended it, successfully, against the other two. The indirect evidence for intra-specific competition of Brown Thornbills appearing to fight over *Exocarpos* bushes, suggests that this tree species, the only one, possibly because of its root parasitism, to produce fresh shoots throughout the drought (Chapters 3 and 8), was a resource worth fighting for. Not only did *Exocarpos* trees harbour more arthropods than most other plant species (see Figure 8), they provided dense cover at a time when many plants of all other species were defoliated. It may be more than a coincidence that seven of the eight *Exocarpos* trees were on territorial boundaries. That no other evidence was found was probably because the food of the thornbills appears not to be clumped or readily renewable in such a way to be economically defensible.

CHAPTER 6

MIXED-SPECIES FLOCKS OF INSECTIVOROUS BIRDS

INTRODUCTION

111. The importance of mixed-species feeding flocks of insectivorous birds (hereafter called MSF) is already known world-wide (see Stresemann 1917 and Rand 1954 for summaries). MSF have been studied little in Australia (Bell 1980a, Hermes 1981). Bell (1980a) showed that of the species in this study, Buff-rumped and Striated Thornbills were the nuclear species of MSF at Canberra. This role for thornbills had long been suggested of the two species, but without any quantified evidence (Roberts and Jarvis 1922, Gannon 1934, Sedgwick 1949). 'Nuclear' species are those whose behaviour contributes appreciably to stimulate formation and cohesion of MSF (Winterbottom 1949, Greig-Smith 1978b). Nuclear species usually form flocks themselves. 'Attendant' species are those that contribute little to flock formation but are usually followers of nuclear species (Moynihan 1962). As will be shown the Brown Thornbill is very much an attendant species of MSF. Data on MSF presented here are only a small part of that collected during the study. I have therefore dealt only with aspects that are related to the ecology of the three species of thornbills.

MATERIALS AND METHODS

112. For all mixed-species flocks including insectivorous birds (which included two non-insectivores) I recorded date, time, locality, species present and number of individuals for each, identities of marked individuals and the height range frequented by each species. In addition, when recording foraging data I kept separate those observations that were made on individuals in MSF, and noted the composition of the flock. The extent of mixed-species flocking was quantified by comparing numbers of flocks seen with hours of observation (noted daily) and, after July 1979, in the regular census counts by noting which birds were in MSF.

The criteria for membership of a MSF were that all members had to be within twenty-five metres of individuals of another species, that a flock stayed together for at least five minutes and that all members moved at least thirty metres in the same general direction.

113. To ascertain which species were leaders or followers within the MSF I opportunistically took data of two types. One I called 'individual following' where an individual of one species followed one of another species. The criterion for 'individual following' was that within twenty seconds of a bird of one species alighting on a perch, a bird of another would perch within one metre of it. The second I called 'species following', where two or more birds of one species followed a group of another without necessarily having any interaction with individuals of that group. The criterion was that the following party, after the leading party had moved at least thirty metres, flew at least thirty metres to perch within ten metres of the leaders. For 'species following' I recorded the number of individuals of each species involved.

114. I aimed to find out:

a. if participation in MSF was related to social organisation;
b. if temporal patterns of participation were related to the availability of food;
c. whether and how one species influenced another's behaviour when in MSF; and
d. why each species joined MSF.

The data obtained would facilitate comparison of seasonal patterns in MSFs, foraging habits, the abundance of food and social organisation; show changes in niche overlap consequent upon joining MSF; and give clues as to the relative importance of defence against predators, social factors and optimal foraging.

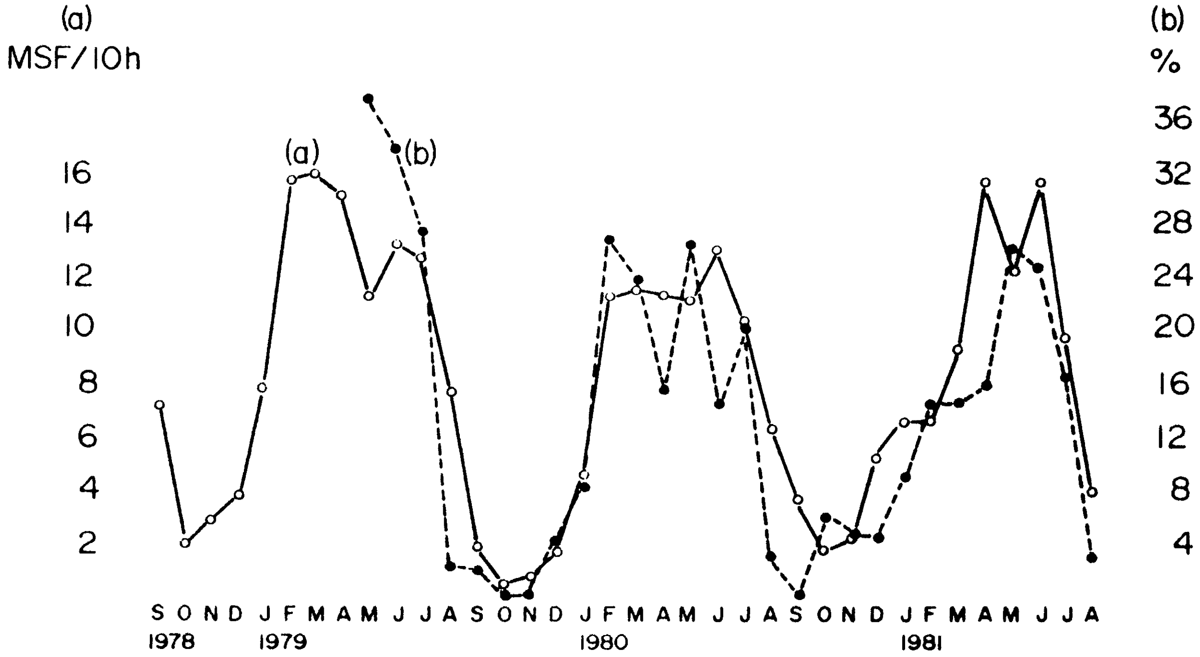
115. Scientific names of species mentioned in this and following chapters are given in Appendix R.

RESULTS

116. A total of 1046 mixed-species flocks of insectivorous birds were recorded during the study. Figure 27 shows the frequency of MSF and, from May 1979, the percentages of birds seen of all species that were

Figure 27

Numbers of MSF/10 h of observation; by months, (September 1978-August 1981), and percentage of all birds seen in transect counts, by months, that were in MSF (May 1979-August 1981)


(a)
MSF/10h
(b)
%
(a)
(b)
16
14
12
10
8
6
4
2
36
32
28
24
20
16
12
8
4
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

in MSF. The percentages of all birds seen that were in MSF ranged from nil to 36% and are clearly related to the frequency of the flocks themselves. MSF were most frequent in late summer, autumn and winter and were much less frequent during spring and early summer, the breeding season. There was no significant difference in frequency of MSF at different times of the day (morning, mid-day and afternoon) (x^2 Test, $P > 0.1$).

117. Figure 28 shows the frequency of participation in MSF by Brown, Buff-rumped and Striated Thornbills. Participation generally followed that of all MSF, with little or none in the breeding season. Frequency for the three species is similar with slightly more for the Brown Thornbill and less for Buff-rumped. Within my main study area on Edgars Spur there were usually seven pairs of Brown Thornbills but only one clan of Buff-rumped and three of Striateds. Therefore the Brown Thornbills, unlike the Buff-rumped Thornbills, were able to have several pairs following different MSF at the same time, either with the other two thornbills or with other nuclear species, particularly the Varied Sittella, Superb Fairy-wren and White-browed Scrub-wren.

118. Figure 29 shows the proportion of all foraging observations, by months, that were made of birds in MSF, for the three species. As can be seen, during the non-breeding season 30-60% or more of thornbills seen foraging may be in MSF, indicating that such activity is an important part of foraging.

119. Figure 30 shows the mean number of each species of thornbill each month in each MSF that included the species, and the mean number of species in each MSF including each thornbill species for each month. Mean monthly number of individuals is not given for Brown Thornbills because they occurred almost invariably in pairs (see Figure 14). Just as participation in MSF declined during the breeding season (Figures 27, 28) so the numbers of Buff-rumped and Striated Thornbills per MSF also fell, most likely because both species broke up into pairs, trios and quartets when breeding (see Figures 18, 22). Numbers of Buff-rumped Thornbills per flock remained low in the non-breeding season of 1981,

Figure 28

Number of MSF/10 h in which Brown, Buff-rumped and Striated Thornbills participated (September 1978-August 1981)

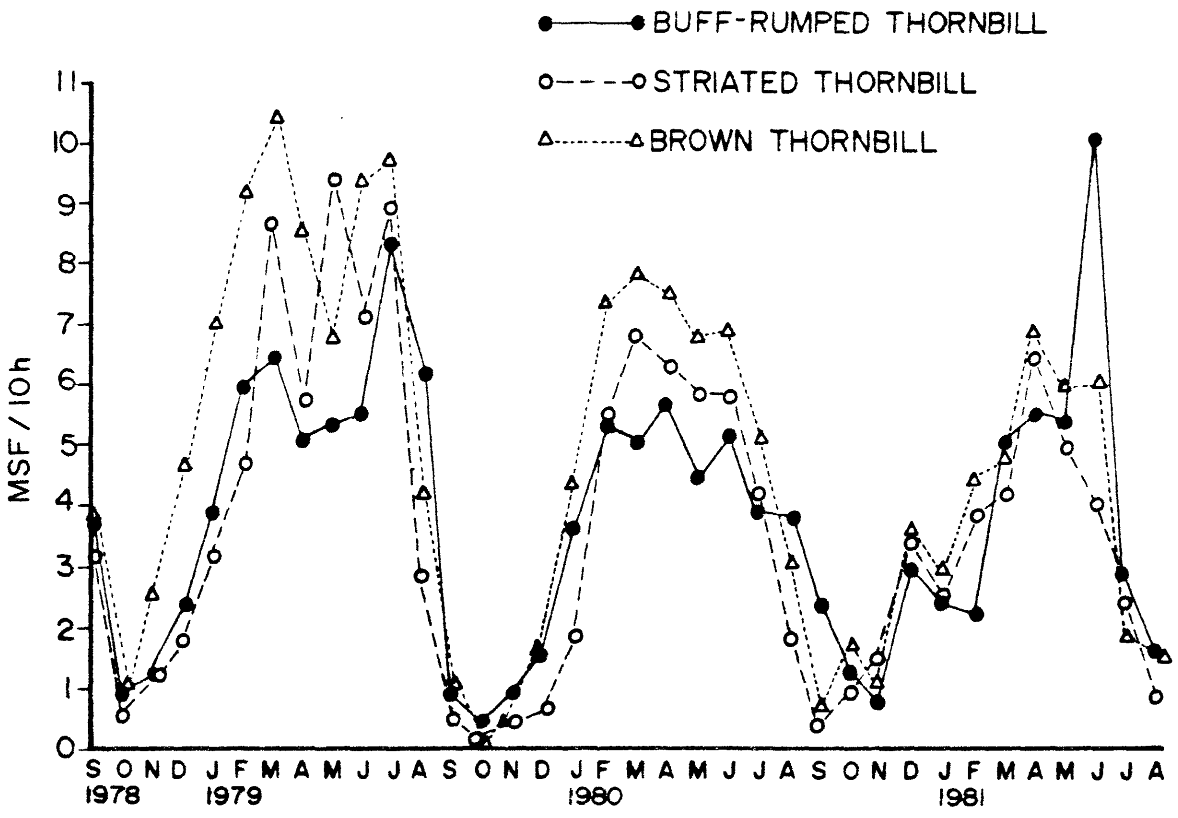

BUFF-RUMPED THORNBILL
STRIATED THORNBILL
BROWN THORNBILL
MSF / 10h
0
1
2
3
4
5
6
7
8
9
10
11
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

Figure 29

Percentage of all thornbills seen that were in MSF, September 1978-August 1981. (n of individuals: Brown 4656, Buff-rumped 4690, Striated 5491)

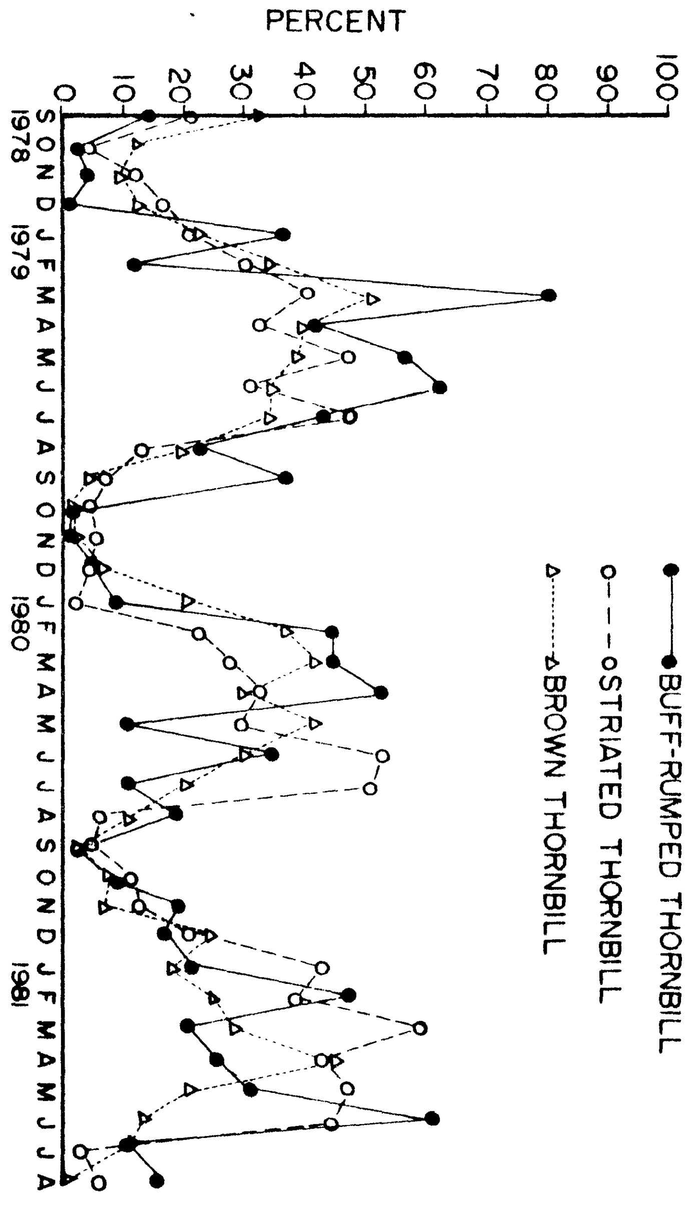
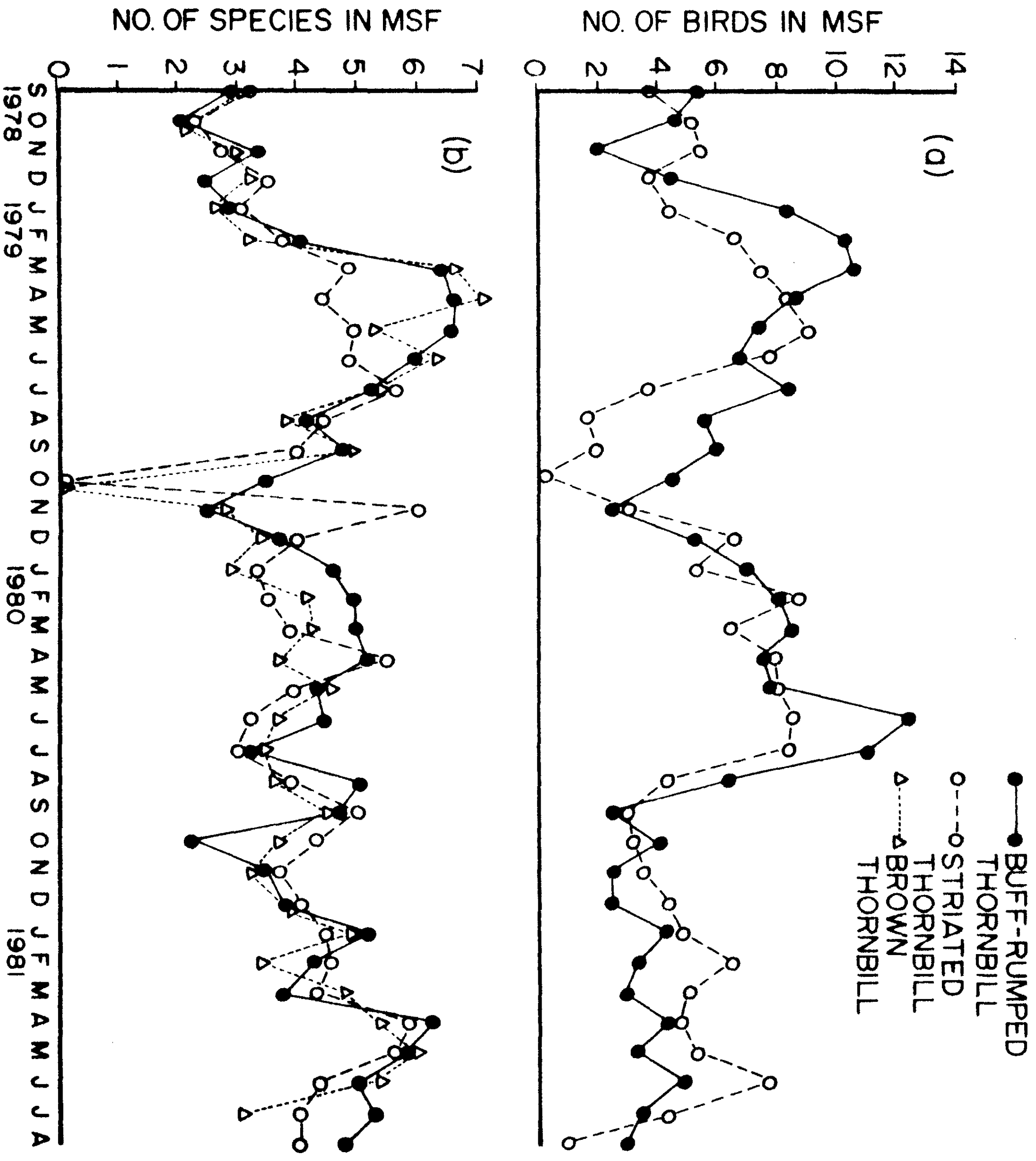

PERCENT
0
10
20
30
40
50
60
70
80
90
100
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981
BUFF-RUMPED THORNBILL
STRIATED THORNBILL
BROWN THORNBILL

Figure 30

Mean monthly number of individual thornbills per MSF (a), and mean monthly number of bird species per MSF of which thornbills were members (b). (n of MSF: Brown 626, Buff-rumped 493, Striated 470)


NO. OF BIRDS IN MSF
NO. OF SPECIES IN MSF
(a)
(b)
0
2
4
6
8
10
12
14
0
1
2
3
4
5
6
7
BUFF-RUMPED THORNBILL
STRIATED THORNBILL
BROWN THORNBILL
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

because of losses during the drought and winter of 1980 and the failure to rear any young in the 1980/81 breeding season. In fact there were only six survivors of a flock that in the previous year had numbered ten adults with six young of the year. Species numbers in MSF tended to be higher in the early part of the non-breeding season i.e. late summer and early autumn, probably because more species were available to join. At this time summer migrants, the first of the winter migrants and passage migrants were all present.

120. Table 9 shows the interactions involving leading and following of the three species. Species differed greatly in the extent to which they related to parties or individuals of other species. For example, White-throated Treecreepers regularly followed flocks of thornbills, but within a flock, rarely did they follow individuals. Individuals of other species, especially the Grey Fantail, often followed individual thornbills of all three species. However, while many parties or individuals of other species often followed Buff-rumped and Striated Thornbills, few other than Grey Fantails followed Brown Thornbills, probably because Brown Thornbills did not form flocks.

121. From the combined data of Table 9 species that themselves formed flocks led significantly more than followed (84% of occurrencies in MSF) but those which did not form flocks followed significantly more (71% of all occurrences).

122. Combining the data of both types of following, the Brown Thornbill was clearly the follower of the three Thornbills. Striated Thornbills mostly led and thus were nuclear species on many occasions; however they in turn often followed Buff-rumped Thornbills and Varied Sittellas. Within a MSF individual Striated Thornbills rarely followed individuals of other species but other species often followed them. Buff-rumped Thornbills were the leading nuclear species, rarely following others either as individuals or as a flock, but being followed by all other species present. Interactions between the three thornbills are illustrated in Figure 31, showing the importance of the Buff-rumped to the activities of the other two, and that of the Striated Thornbill to the Brown.

Figure 31

Combined total occurrences of 'following' by thornbill species of each other

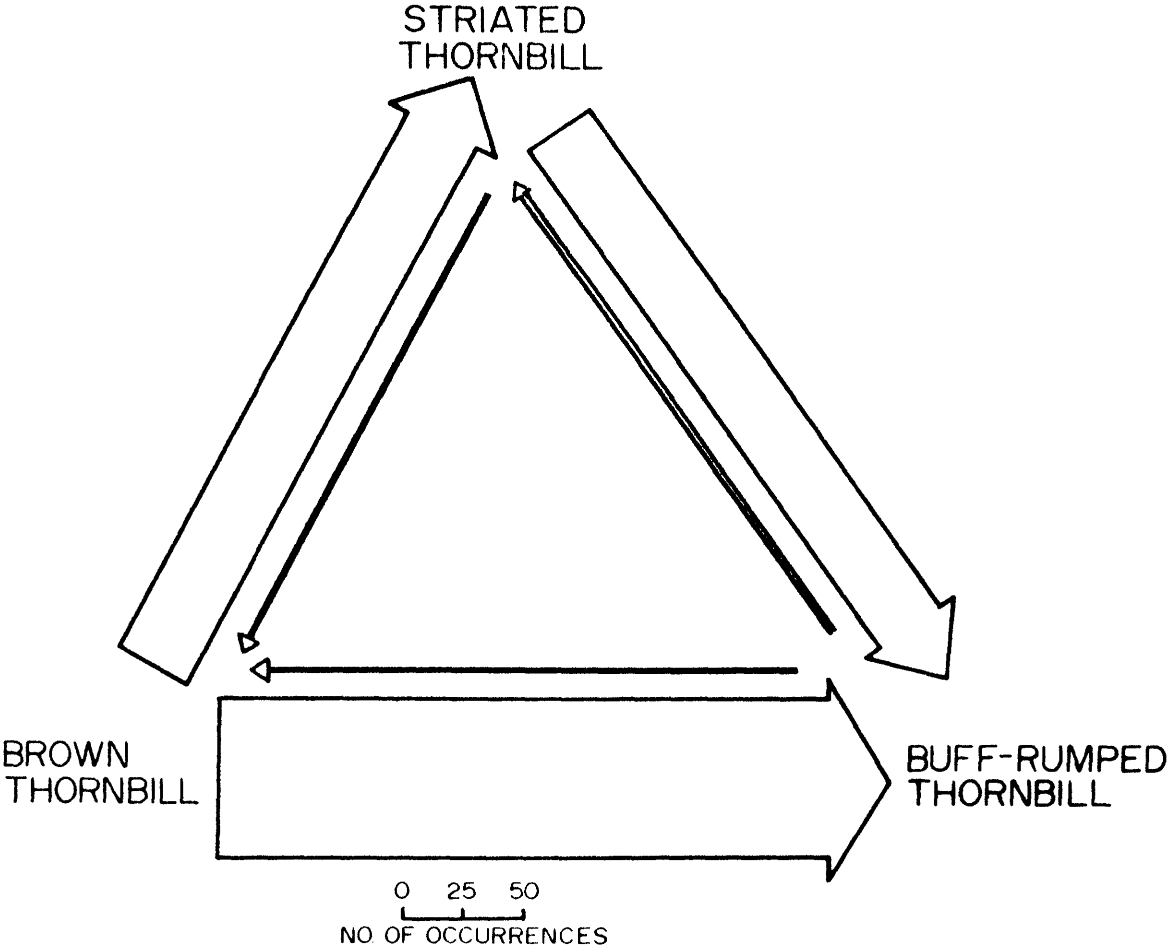

STRIATED THORNBILL
BROWN THORNBILL
BUFF-RUMPED THORNBILL
0 25 50
NO. OF OCCURRENCES

Table 9

Interactions (see paragraph 111) in Mixed-species Feeding Flocks, Between Thornbills and Other Species

	Followed		Followed by		Total	
	Species	Individuals	Species	Individuals	Followed	Followed by
BROWN THORNBILLS						
Buff-rumped Thornbills*†	87	44	2	2	131	4
Striated Thornbills*†	14	19	1	3	33	4
Varied Sittella*†	7	6			13	
Superb Fairy-wren*†	11	7		1	18	1
White-browed Scrub-wren* †	4	9			13	
Speckled Warbler	3	5	1	5	8	6
Red-browed Firetail*	2	1	3	7	3	10
Golden Whistler			3	8		11
Grey Fantail		1	6	85	1	91
Other species (16)	4	4	19	10	8	29
Total	132	96	35	121	228	156
BUFF-RUMPED THORNBILL*†						
Varied Sittella*†	7	6	24	4	13	28
Striated Thornbill*†	7	3	39	3	10	42
Brown Thornbill	2	2	87	44	4	131
Scarlet Robin		3	61	30	3	91
Grey Fantail		1	41		1	41
White-throated Tree-creeper			32	8		40
Speckled Warbler	2		27	9	2	36
Golden Whistler			14	13		27
Red-browed Firetail*			18	6		24
Red-browed Tree-creeper		1	15	4	1	19
Other species (22)	2	3	53	17	5	70
Total	20	19	411	138	39	549
STRIATED THORNBILL*†						
Buff-rumped Thornbill*†	39	3	7	3	42	10
Varied Sittella*†	12	4	6	2	16	8
Brown Thornbill	1	3	14	19	4	33
Grey Fantail			18	81		99
White-eared Honeyeater			2	9		11
Other species (17)	8	12	26	31	20	57
Total	60	22	73	145	82 .	218

*: species that form flocks of their own species.
†: nuclear species of MST.

123. MSF, at least those following Buff-rumped Thornbills, often stayed together for long periods. Those following Striated Thornbills probably were also cohesive but their flocks in the canopy were difficult to observe for long periods. Figure 32 shows the movements of four MSF based on Buff-rumped Thornbills, that were followed for 1½ to 7½ hours. The four MSF moved at an average of 6½, 4½, 3½ and 3 m/min respectively. This was much slower than ten other MSF followed for shorter periods, where the rate was five to thirty m/min. The difference is because MSF often halted, particularly around mid-day, and would preen, sunbathe and feed perfunctorily.

124. I several times saw all three species of thornbills, and other species, particularly Speckled Warblers, preening in the same tree. The MSF following Buff-rumped Thornbills were an elliptical shape, the narrow ends along the axis of movement of the MSF, the mean area covered at one particular time by 26 MSF was 15.5 x 8.3 m. However MSF seemed looser in summer because the eight MSF measured in summer covered a mean area of 27.5 x 15.0 m (Students T-test, for length, $P < 0.002$; for width $P < 0.002$). Comparing Figure 32 to Figure 20 (showing the territory) indicates that the resident clan of Buff-rumped Thornbills may cover their territory several times a day. However there were occasions when it concentrated, apparently for days at a time, in only a small part of the territory, although even then other species would usually be in attendance. Areas covered by MSF led by Striated Thornbills were hard to estimate but three each covered an area of 10 x 10 m.

125. Membership of MSF was fairly constant and Table 10 shows that of the MSF depicted in Figure 32b. Although some species joined and left, the same individuals of at least three followed the Buff-rumped Thornbills for at least seven hours. At Wollomombi the flock territories of Buff-rumped Thornbills are larger than those of pairs of the Brown Thornbills, and of several other attendant species present, tree-creepers and Scarlet Robins (Huddy 1979, Noske 1980), and a 'changeover', often occurred when an MSF crossed a territorial boundary. Sometimes, if an MSF was a large one, a pair of Brown Thornbills would follow it into the territory of another pair, and both pairs would forage, at opposite end of the MSF. Once discovered the intruders would quickly depart.

Figure 32

Routes and timings of movements by four MSF at Wollomombi in which Buff-rumped Thornbills were the nuclear species

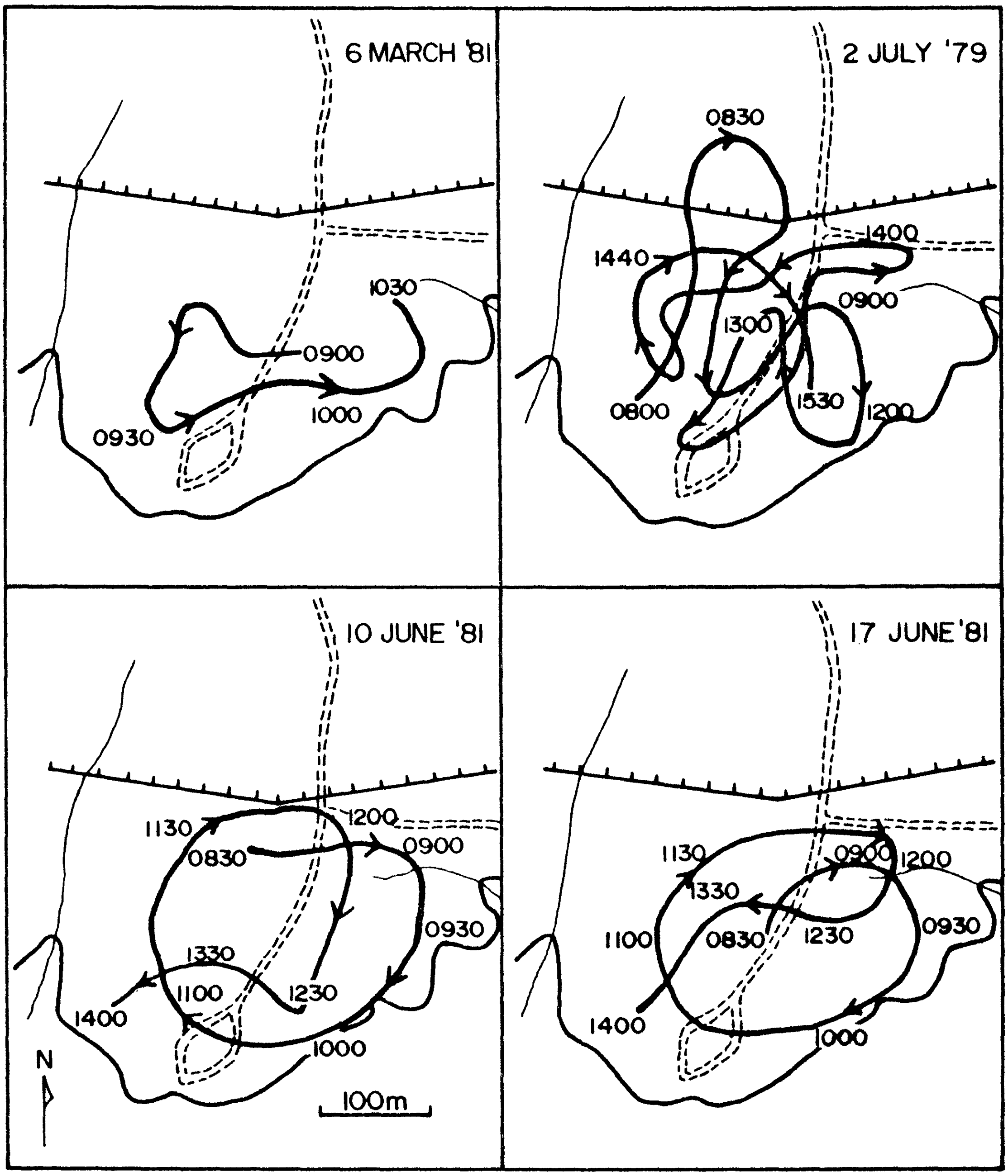

6 MARCH '81
1030
0900
0930
1000
2 JULY '79
0830
1400
1440
0900
1300
0800
1530
1200
10 JUNE '81
1130
1200
0830
0900
0930
1330
1100
1230
1400
1000
N
100m
17 JUNE '81
1130
0900
1200
1330
1100
0830
1230
0930
1400
1000

Table 10

Composition by Time, of a MSF Following Buff-rumped Thornbills 2 July 1979

(see Figure 32b)

	0800	0830	0900	1200	1300	1400	1440	1530	
Buff-rumped Thornbill	10	10	10	10	10	10	10	10	*(10)
Brown Thornbill	2	3	2	2	2	2	2	2	*(2)
Striated Thornbill	3	2		1	3	3	1	2	*(1)†
Golden Whistler ♀	2	1	1	1	1	1	1	1	
Varied Sittella			8	10	8	10	8		
White-throated Treecreeper	1	1	1		1	1		1	
Scarlet Robin	2	2	2	2	2	2	2	2	*(2)
Red-browed Firetail			10						
Grey Fantail				1	1	2	1		
Yellow-faced Honeyeater						2	2		
White-eared Honeyeater					1				
Total individuals	20	19	34	27	29	33	27	18	
Total species	6	6	7	7	9	9	8	6	

*: Same colour-banded individuals seen on each occasion; number in brackets is that of colour-banded birds.

†: The bird seen all day was the male of a sitting bird whose nest was in the centre of the flock's activity for that day.

126. On 21 occasions MSF were seen to take alarm at the approach of a large bird flying overhead, all members of the MSF flying into dense shrubbery and remaining still. Notably, birds on the ground would simultaneously fly up into the foliage and on at least six occasions Striated Thornbills left the canopy and dived for cover in the understorey. Alarm calls could have been used by members of MSF but because of my hearing disability I could not identify them. Of the 21 occasions three occurred when raptors appeared and on all the others the large birds were harmless, chiefly Crimson Rosellas. After the 'false alarms' activity reverted to normal within 30 seconds. Both Peregrine Falcons and Brown Goshawks stooped once at flocks of thornbills.

DISCUSSION

127. The pattern of mixed-species flocking at Wollomombi resembled that found at Canberra (Bell 1980a). At Canberra the percentage of all birds seen that were in MSF varied between 4 and 43%, compared to none and 36% at Wollomombi. However the numbers of MSF seen per unit of time at Wollomombi was twice that for the Canberra study. I believe that this results from observer bias. At Canberra all data were obtained from walking a set transect path from which no deviation occurred (Bell 1980a). At Wollomombi, apart from 4-6 hours per month spent in transect counts, I was free to move over the whole study area and seek out MSF. As for Canberra, frequency of MSF at Wollomombi was lowest from September to December, during the breeding season. This seems usual for other regions (e.g. Nearctic, Morse 1970; Palaeotropical, McClure 1967). Species restricted to the vicinity of their nests cannot easily follow MSF for long periods, but, more importantly, the gregarious nuclear species round which MSF form, have themselves split into smaller groupings in the breeding season. The Canberra data showed that the nuclear species, in the breeding season, dropped out of mixed-species flocking even more than did the attendant species, and my data from Wollomombi supported this.

128. The variation in mean monthly number of individual thornbills per MSF (Figure 30) was to be expected because flocks of Buff-rumped and Striated Thornbills broke up into smaller groups during the breeding

season. Notably mean numbers of Striated Thornbills per MSF dropped earlier than did those of the Buff-rumped Thornbill. This corresponded to the earlier breeding season of the Striated Thornbill (see Table 8).

129. The high incidence of participation by thornbills in MSF at Wollomombi accords with that seen in other areas (e.g. Western Australia, Sedgwick 1949; Sydney, Hindwood 1937; and South Queensland, Roberts and Jarvis 1922). Gannon (1934) correctly described thornbills as 'primary association formers', but did not distinguish between the roles of the various species. Prior to this study no data had been published on the 'leading' and 'following' roles of the species.

130. Of 27 species at Wollomombi that were most frequently seen in MSF, 13 are known to be communal breeders. These are Buff-rumped and Striated Thornbills, Yellow-rumped Thornbills (Ford 1963, Thomas 1974, pers. obs.), Varied Sittella (Noske 1982a), Superb Fairywren (Thomas 1974), White-browed Scrub-wren (Bell, in press), Red-browed and Brown Tree-creepers (Noske 1980), Brown-headed Honeyeater (Noske, in press), White-naped Honeyeater (Dow 1980), Hooded Robin (Rowley 1976), Crested Shrike-tit (Howe and Noske 1980) and the Striated Pardalote (Dow 1980). Nine nuclear species of MSF were communal breeders, more than would be expected by chance (x^2, $P < 0.05$). Only one species the Spotted Pardalote not yet known as a communal breeder was a nuclear species, and then but rarely. Twelve of the 27 species formed large intraspecific (i.e. > 5) flocks, including nine of the communal breeders. Flocking species were not nuclear species more than randomly expected (X^2, $P < 0.05$). Thus it seems that a species role as a nuclear species owes less to the size of the flock formed by that species and more to its cohesiveness, in the case of communal breeders a group of inter-related individuals that are permanently organised and hold territory.

131. The cohesiveness of MSF at Wollomombi, with particular individuals of one species associating for long periods with those of another, was similar to situations described elsewhere e.g. Neotropics, Powell (1979); New Guinea, Bell (1982a). Some interspecific mimicry of calls did occur, namely by Buff-rumped and Brown Thornbills of each other. (Unfortunately I am incapable of detecting the calls of the Striated Thornbill). However

there were no examples of social mimicry, where a 'following' species adopts the colour and call of the 'leading' one, such as occurs in the tropics (e.g. Moynihan 1968, Bell 1982a).

132. The advantages of joining MSFs are usually given as reduced predation and improved foraging efficiency. As stated in Chapter 5, experiments have shown that both alertness towards potential predators, and avoidance and discouragement of them, increases with the size of a flock (e.g. Lazarus 1979, Caraco *et al.* 1980, Goldman 1980). Predation seems a more likely explanation for large parties of granivorous Red-browed and Diamond Firetails in MSFs, of insectivorous species, at Wollomombi. Some workers (e.g. Murton *et al.* 1971, Pulliam 1973, Siegfried and Underhill 1975) have shown that with reduced risk of predation members of MSF are able to forage more efficiently.

133. Early workers writing on MSF (e.g. Swynnerton 1915, [illegible] Stanford 1947) and even later ones (e.g. Brosset 1968) used to stress the benefits to birds of having insects flushed by other species in an MSF. Only one member of MSF at Wollomombi, the Grey Fantail, regularly took insects so flushed. However the records given in Table 9, of individuals of one species following individuals of other, often morphologically unlike, species suggest that some other species could have been taking insects disturbed by other birds. On balance however I believe that the 'beater' hypothesis does not apply to MSF at Wollomombi. Krebs *et al.* (1972) showed experimentally that individuals of a species are capable of learning about new sources of food from other individuals. Krebs (1973) went further to show that individuals of one species could also learn from those of another and there is much circumstancial field evidence to support this (e.g. Austin and Smith 1972, Greig-Smith 1978a). As will be discussed in later chapters, all three species of thornbill at Wollomombi, foraged differently in MSF than when on their own. Furthermore the dis-similarities themselves depended on which other species were accompanied, so it is reasonable to assume that quite apart from improved safety, membership of MSF also confers benefits in foraging.

Thompson *et al.* (1974), in a simulated model, concluded that although there was no difference in the capture rate of insects between birds in and not in flocks, those not in flocks ran a higher risk of doing badly (i.e. captures not commensurate with effort). Thompson *et al.* also concluded that among flocks, larger flocks would have a lower capture rate of prey than smaller flocks, but at the same time ran less risk of doing badly. They finally concluded that the major value in the flocking habit was in minimizing risk of failure rather than enhancing the capture rate. This view seems to be supported by field studies by Moynihan (1962) and Cody (1971) which concluded that it must be more cost-effective to forage over ground with an MSF than to waste time independently in an area that has already been depleted by other birds.

134. To sum up, membership of MSF probably confers advantages of reduced risk of predation, perhaps an opportunity to take prey flushed by other birds, opportunities to learn about food resources from other species, and the avoidance of areas that may have already been depleted of food. Possible disadvantages are: having to move to a feeding site to which a species may not be well-adapted to exploit, and having to share in any abundant food source found. Of course there is probably a 'trade-off' between the advantages and disadvantages e.g. accepting less than optimal foraging in order to reduce risk of predation. The advantages to a nuclear species which already forms large flocks of its own (e.g. Buff-rumped Thornbills) are less clear. Followers that forage at heights different from the nuclear species (especially above them) may extend the range of surveillance of the flock; followers that have alarm calls arouse the whole MSF but may attract attention to themselves only; followers, too, can pass on information about food sources to the nuclear species; and possibly large followers such as the Grey Shrike-thrush may make food available to a smaller nuclear species by its habit of tearing bark and turning over large objects. Disadvantages are: an MSF may 'invite' other species to the feeding-site of the nuclear species, which the follower may not have otherwise exploited; the uncoordinated foraging of other, usually monogamous, species on their own may be

unlikely to seriously deplete areas that the nuclear species would eventually exploit on its own. On balance it seems that, of the three thornbills, the Brown is the most advantaged by MSFs and that the two gregarious species are to a large extent passive members of them.

135. There was little evidence to support the convincing data of Morse (1970) in North America, which showed that frequency and participation in MSF increased when food was scarcest. Both at Canberra (Bell 1980a) and in this study, MSF were most numerous and largest, during autumn, when insects had not reached their lowest abundance. This was probably because there were most individuals and species in the area at that time. The effects of mixed-species flocking upon the foraging of the three species of thornbills will be dealt with in the chapters on that subject.

PART III

FORAGING BEHAVIOUR

INTRODUCTION

136. In order to define the differences in resource partitioning between species, past workers have used a variety of different measurements to identify separating mechanisms between species. Merely identifying diets is an inadequate basis on which to measure resource partitioning between species of insectivorous birds. Quite apart from the misleading biases inherent in dietary evidence (see Chapter 11), two species of similar diet may not compete for the same resources because each may be adapted to take their prey in different places.

137. Most workers use height from ground as one measure of difference between species in foraging location (e.g. Hartley 1953, MacArthur 1958), except for ground and grassland species (Cody 1968). The foraging site (or substrate) from which a species takes its prey is also used in most studies (e.g. Colquhoun and Morley 1943, Gibb 1954) except when comparing aerial-feeding species (e.g. Hespenheide 1975). Sometimes, with highly specialised groups such as bark-foragers, a particular substrate may be further divided (e.g. different textures of bark, Noske 1980). Some workers use another measurement of foraging site, in addition to substrate, that of the 'inner' or 'outer' parts of the crown of a tree (e.g. MacArthur 1958, Verbeek 1975) but this seems possible only where trees have regular crowns or where forests are homogenous. The method of foraging (e.g. sallying, hovering, probing etc) is often used (e.g. Root 1967, Croxall 1977).

138. The foraging by species on different types or taxa of plants seems to be much less used than the preceding measurements of resource partitioning. One reason may be that early studies were mostly in the fairly depauperate forests of the Northern Hemisphere, although some workers (e.g. Hartley 1953) did recognise that birds did not forage randomly on conifers and broad-leaved vegetation. Also, MacArthur and MacArthur (1961) had gained support for their emphasis on forest structure, rather

than plant species diversity, as a determinant of bird species diversity. However, more recent studies, including some in the Northern Hemisphere, have shown that the plant species foraged upon may be an important separating mechanism (e.g. Balda 1969, Franzreb 1978, Holmes and Robinson 1981).

139. Other measurements sometimes used include differences in the speed of foraging (e.g. Williamson 1971, Morse 1978), differences in morphology (e.g. MacArthur 1958, Hespenheide 1971) and foraging success (e.g. Cameron 1975). Speed of foraging and morphology seem very strongly dependent on other factors measured, e.g. the foraging site used and abundance and size of prey may determine the speed of movement, and morphological differences may be related to the substrate foraged upon. Foraging success can only be measured if both the prey and the beak of the bird can be clearly seen at all times, an impossibility with thornbills.

140. For this study I decided to record substrate, plant species, height above ground and foraging method of the three species of thornbills. The irregular shape of eucalypts at Wollomombi made impracticable the delineation of 'inner' and 'outer' parts of tree canopies. Speed of foraging was measured, but not included in the analysis of resource-partitioning; only for assessing seasonal differences related to food supply within each species. Morphology was studied but for comparison with foraging data, because it initially appeared that the three species were rather unspecialised gleaners of similar size and appearance.

METHODS

141. My aims were to make quantified comparisons between the three species, between time of day and season for each species and between different social groupings of each species, for the following aspects of foraging: substrate foraged upon, plant species foraged upon, height of foraging, and foraging method used. To achieve these aims I set a target of foraging observations on 150 birds of each species each month during 1978/79 and 1979/80. Because 1979/80 was very dry I extended coverage to 1980/81 but at a reduced rate (90 birds per month). No data

were collected during rain or high wind. When possible monthly data were evenly distributed between morning (first light to four hours after first light), afternoon (four hours before last light to last light) and mid-day (the period in between morning and afternoon, varying according to day-length).

142. Thornbills are so small and active, and their prey generally so minute, that it is usually impossible to see if a bird has taken, or even attempted to take prey. Thus any move not known to be otherwise was assumed to be a foraging move. Each bird had to perch before observation began and the first observation was made at the next perch or feeding site to which the bird moved. For each bird observed the unit of data was a foraging move. A foraging move was one move, in the course of foraging, from one perch to another. Each bird was observed for five moves, of which the foraging method and site was recorded, followed by ten moves for which time and distance moved were recorded. Data were not collected for any move definitely known not to be involved in foraging e.g. collecting nest-material, chasing, preening, sunbathing etc.

143. For the ten moves involving distance and time I recorded distance moved and time taken, for ten moves, from the perch at which a bird was first seen then along its route travelled to its arrival at the tenth perch. Distance was estimated only but was initially checked by pacing (one pace : 0.75 m); I soon found that an accuracy of ± 10% was easily attainable. Time was taken by stop-watch. I soon found that it was possible to record the first five of the ten moves simultaneously with the five on foraging data, and did so in most cases.

144. Data were written into notebooks. This was a deliberate choice by me and facilitated rough collations of data as I progressed, and obviated the time lost in having to re-run tape. However a major drawback was that I often lost sight of the party of birds under observation while writing down data and so had to search again for another party.

145. Overall I aimed to collect, each month, for each species, 750 observations (450 in 1980/81) of 150 individuals (90 in 1980/81), each observation giving the substrate, plant species, height and foraging

method, and for each bird observed ten observations giving distance moved and time. For each bird I also recorded date/time, time of day, identity if known, location on map if identity was known, numbers of own and other species also present. In practice, I found it easy to handle these data while observing, particularly as many of them were the same for all five moves of an individual bird. For some 12,000 sets of observations I doubt if I had to abandon observation for more than fifty because of failure to keep track of the data.

146. Overlap of similarity for each pair of species was calculated using Schoener's (1968) equation:

$$\alpha : 1\tfrac{1}{2} \sum_{i=1}^{s} \left| Px_i - Py_i \right|$$

where α: overlap and Px_i and Py_i are the frequencies of observation of species x and y in category i.

147. Seasons of the year are: spring (September, October and November) summer (December, January and February), autumn (March, April and May) and winter (June, July and August).

CHAPTER 7

SUBSTRATE FORAGED UPON BY THORNBILLS

INTRODUCTION

148. A major factor in ecological separation of syntopic species is their use of different substrates on which to forage. Taking prey from different substrates would enable two species to co-exist (even in the same tree) by exploiting food resources not available to each other. My aim in measuring use of substrate by the three species was to establish the degree to which substrate contributed to ecological separation between species.

149. The substrate foraged upon is that from which food is taken, but because of the difficulty in observing thornbills actually taking insects, the substrate on which the bird appeared to point its beak, at the completion of a foraging move, was also assumed to be that from which food was taken. The substrate foraged upon was very often, but not always, that on which the bird perched. An example where they could differ would be a hovering bird taking insects from a leaf.

150. As Jackson (1979) and others have pointed out there are many different types within each general class of substrate. Leaf substrates may vary from the tightly packed needles of a conifer to the broad, entire, leaf of a *Ficus*. In this chapter no differentiation is made between different types within a class of substrate, such differentiation being left to later chapters e.g. on plant species foraged upon, where although a species may feed on, say, bark it will be shown to prefer foraging on the bark of particular different species of plant.

151. The literature is generally vague about the substrate foraged upon by thornbills. The more recent works (e.g. McGill 1970, Abbott 1973, Frith 1976) describe Brown Thornbills as moving through foliage, implying that they forage off leaves. Both McGill (1970) and MacDonald (1973) recognized that Buff-rumped Thornbills foraged upon the ground

bark and foliage but Frith (1976) stated 'usually on the ground'. All references describe Striated Thornbills as feeding in the tops of trees, implying foraging upon foliage. McGill (1970) also stressed 'as well as in cracks or under layers of bark'.

METHODS

152. The method of collection of foraging data is given in paragraphs 142 and 143. The substrate recorded was that on which the bird was seen to take, or attempt to take food, or if it was not seen to do so, the one towards which it pointed its beak, or the one on which it was perched following a move. Substrates recorded were:

a. Ground; including grass tussocks, logs, stumps, stones and cow-dung;

b. Bark; including trunks, limbs, branches, hollows, lichen, strips of hanging bark. Branches were distinguished from limbs by either (1) lacking woody bark, or (2) if both branch and limb on a tree had woody bark, branches were of a diameter less than the length of a thornbill.

c. Leaves; including mistletoe clumps, insect nests and flowers.

d. Air, which included only those cases where flying birds took, or attempted to take, flying prey.

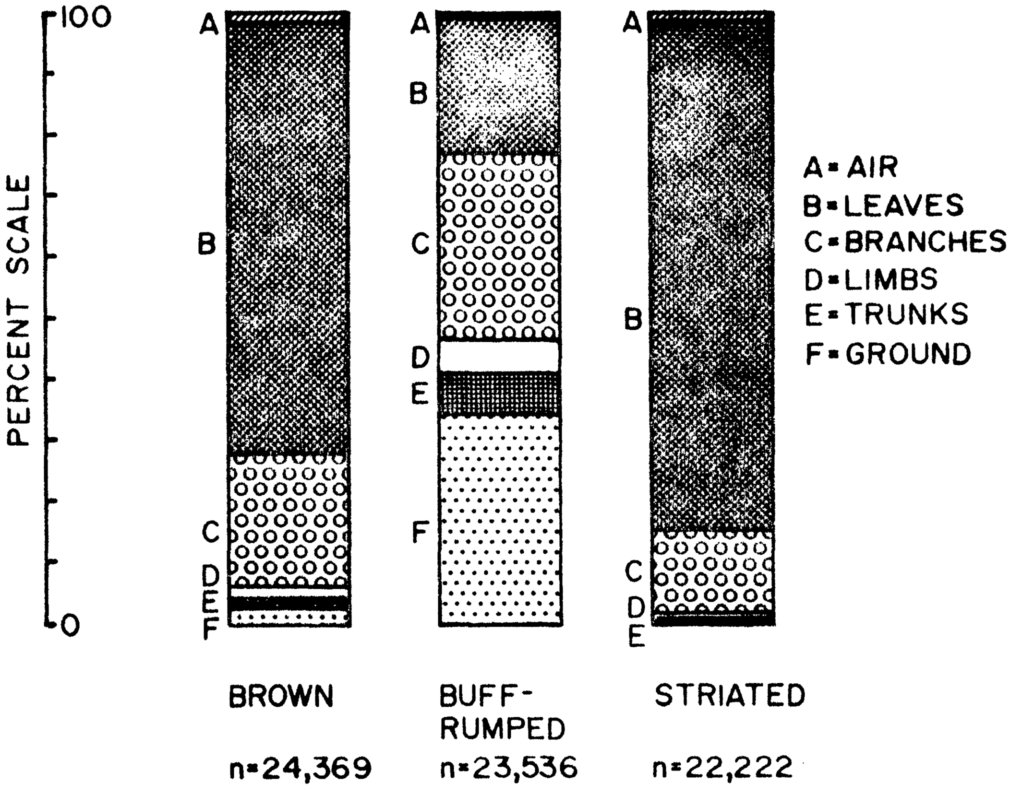
In some cases, where data for subcategories were few, they have been included, for presentation, as part of the major category.

RESULTS

153. Appendices A, B, and C show the distribution, by months, seasons and years of substrates foraged upon by Brown, Buff-rumped and Striated Thornbills respectively. These data are summarised in Figure 33. As shown, there is a high similarity between Brown and Striated Thornbills (87.5%), moderate similarity between Brown and Buff-rumped (50.7%) and a fairly low similarity between Buff-rumped and Striated (38.2%). While

Figure 33

Distribution of observations of foraging moves, by substrate foraged upon, by thornbills at Wollomombi

PERCENT SCALE
100
0
A
B
C
D
E
F
A
B
C
D
E
F
A
B
C
D
E
A= AIR
B= LEAVES
C= BRANCHES
D= LIMBS
E= TRUNKS
F= GROUND
BROWN
BUFF-RUMPED
STRIATED
n=24,369
n=23,536
n=22,222

Brown and Striated Thornbills primarily foraged upon leaves, Buff-rumped Thornbills foraged mainly on the ground and on trunks, limbs and branches.

154. Figure 34 shows the distribution, by months, of foraging substrates used by Brown Thornbills, comparing, by X^2 Test, foraging on particular substrates by seasons, with foraging on that substrate over the whole study; Brown Thornbills foraged significantly more on leaves during spring 1979, summer 1979/80, summer 1980/81 and autumn of 1981 (see Table 11 for X^2 values).

155. Foraging on leaves was lowest during autumn and winter of 1980 when drought had seriously defoliated the vegetation (see Chapter 2). Foraging on the ground, rarely important with Brown Thornbills, rose significantly in that same winter (see Table 11) when the birds were seen, for the only time in the study, to forage on the ground travelling up to fifty metres at a time. Foraging on flowers, although relatively unimportant, noticeably occurred twice yearly in each of the three years, in spring and in late summer, corresponding to the flowering periods of *Acacia irrorata*.

156. There were no significant differences in the data on substrates foraged upon by Brown Thornbills, by time of day for each major substrate for each year . From my data attributed to colour-banded birds, no significant differences, in choice of substrate, occurred between pairs in different territories or between sexes in each pair.

157. Figure 35 shows the distribution of substrates for the Buff-rumped Thornbill. While the overall data showed, in Figure 33, that the species favoured bark substrates (42.7%) and the ground (34.2%), with leaves at only 22.2%, they mask pronounced seasonal changes that are depicted by Figure 35. Foraging on ground substrates was significantly more frequent in all three winters and in the autumn of 1980 (see Table 11). Foraging on bark substrates was significantly higher in all three summers and the spring of 1980 (Table 11). Leaf-foraging was significantly higher in spring, summer and autumn of both 1978/79 and 1980/81, but was not so in 1979/80 at the height of the drought. Ignoring the drought in 1979/80, when many trees and shrubs were wholly or partly defoliated (see Chapter 3) the pattern appears to be one of predominate ground and bark foraging in late autumn and winter, switching to mainly leaves and bark in early spring, changing to a greater emphasis on bark during late spring, summer and early autumn.

Figure 34

Distribution of observations of foraging moves, by substrate, of Brown Thornbills at Wollomombi. (Total n: 24369, monthly mean 676, monthly range 390-955)

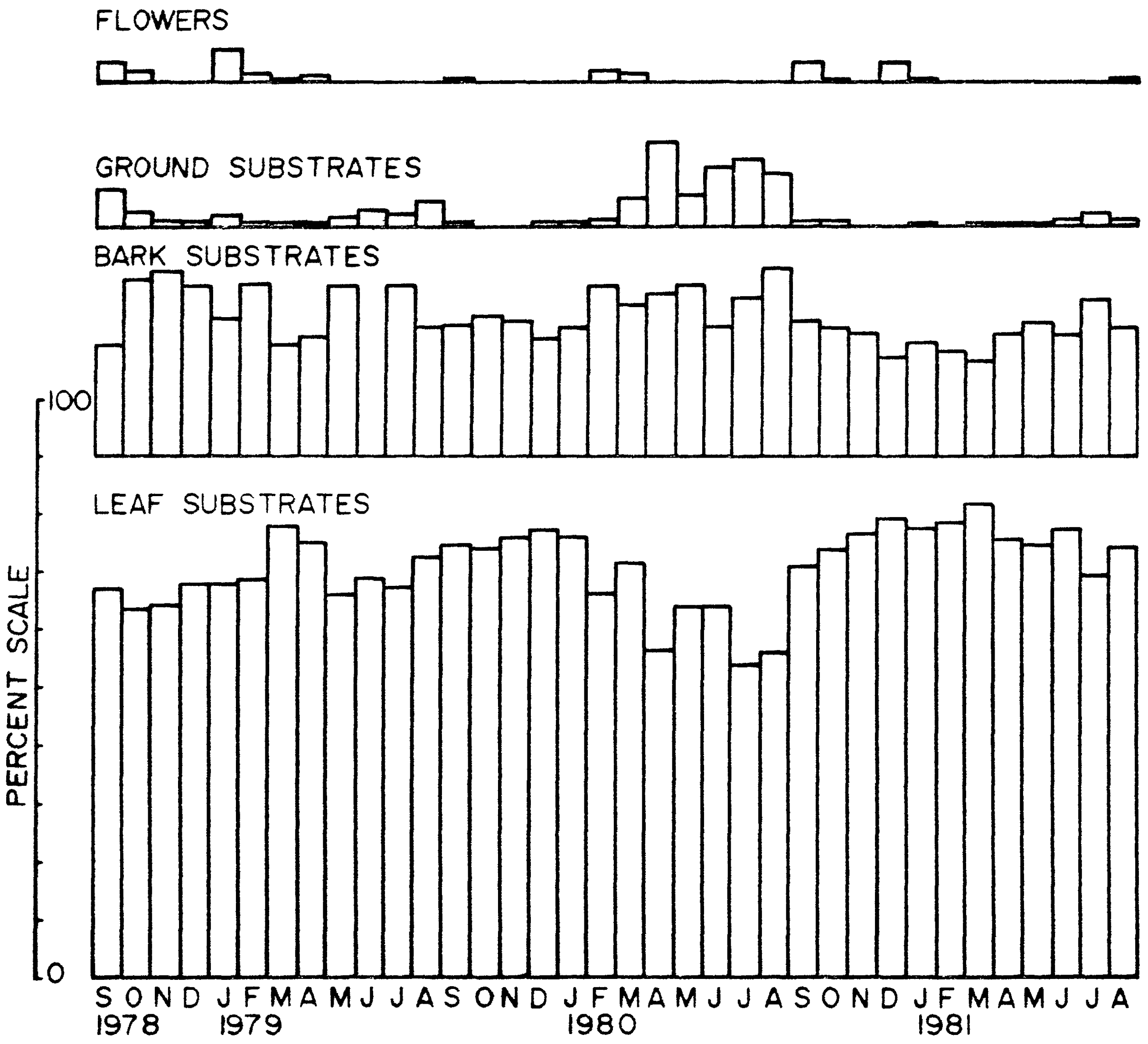

FLOWERS
GROUND SUBSTRATES
BARK SUBSTRATES
LEAF SUBSTRATES
PERCENT SCALE
100
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

Figure 35

Distribution of observations of foraging moves, by substrate, of Buff-rumped Thornbills at Wollomombi. (Total n: 23, 536; monthly mean 654; monthly range 300-825) (lower box of bark substrates are trunks and limbs)

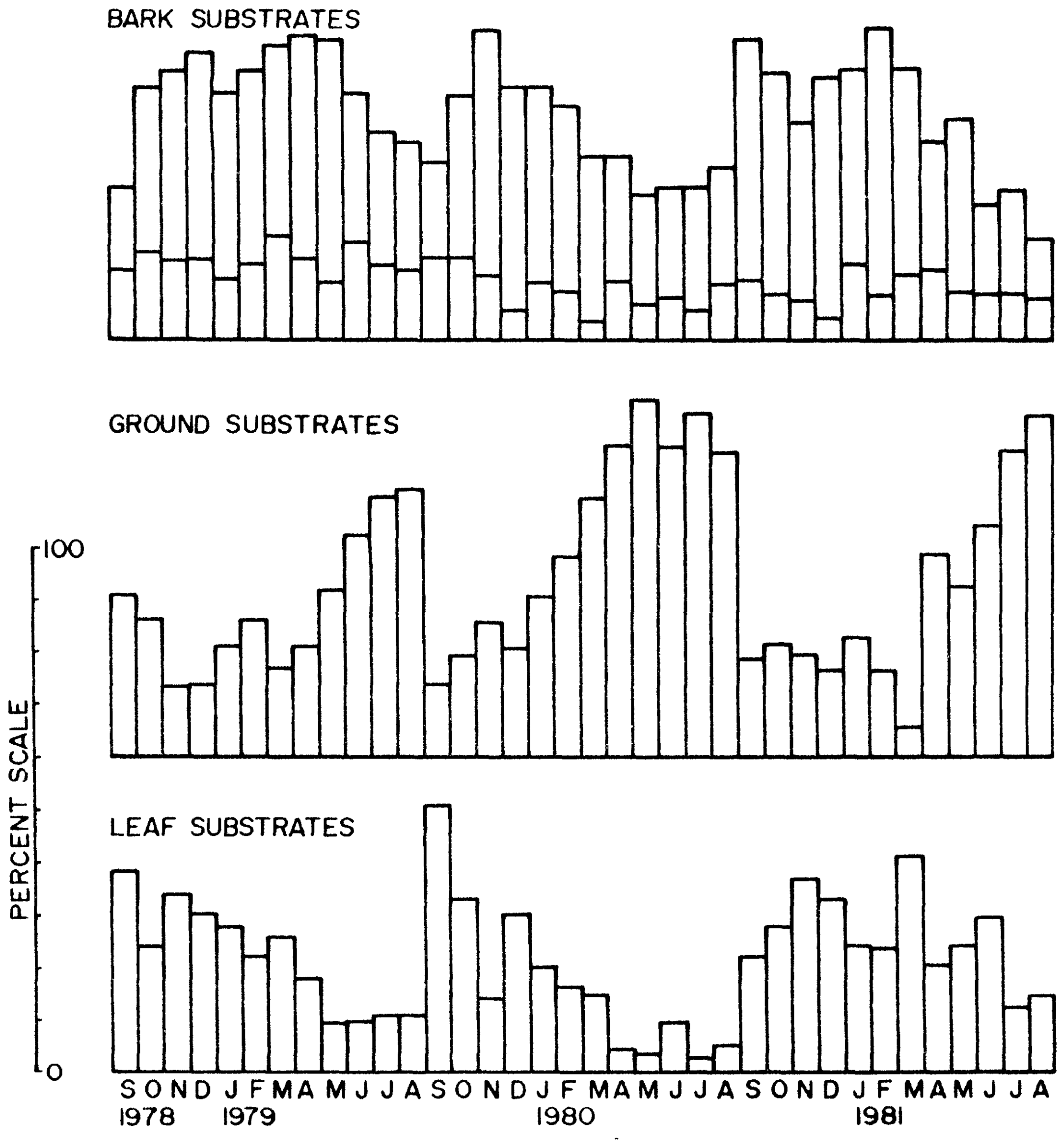

BARK SUBSTRATES
GROUND SUBSTRATES
LEAF SUBSTRATES
PERCENT SCALE
100
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

Table 11

Differences Between Mean Annual and Seasonal Frequencies of Use of Substrates by Thornbills. X^2 Values (all d.f. 1). Significance Values and Direction of Departure of the Seasonal Value from the mean (+: higher than mean, -: lower than mean) are shown

Brown Thornbill		Spring	Summer	Autumn	Winter
1978/79					
1979/80	Ground			+ 277.049 P <0.005	+ 504.600 P <0.005
	Leaves	+ 6.726 P <0.01	+ 5.785 P <0.025		
1980/81	Leaves		+ 11.878 P <0.005	+ 9.070 P <0.001	

Buff-rumped Thornbill		Spring	Summer	Autumn	Winter
1978/79	Ground				+ 88.497 P <0.001
	Bark		+ 26.870 P <0.001		
	Leaves	+ 116.562 P <0.001	+ 38.407 P <0.001	+ 66.862 P <0.001	
1979/80	Ground			+ 386.387 P <0.001	+ 268.260 P <0.001
	Bark	+ 23.867 P <0.001	+ 11.293 P <0.001		
1980/81	Ground				+ 157.808 P <0.001
	Bark		+ 34.316 P <0.001		
	Leaves	+ 21.327 P <0.001	+ 19.646 P <0.001	+ 20.857 P <0.001	

Striated Thornbill		Spring	Summer	Autumn	Winter
1978/79	Leaves	- 5.189 P <0.025			
1979/80	Leaves			- 8.092 P <0.005	- 14.570 P <0.005
1980/81					

*: all increases, except for Striated Thornbill which are decreases.

158. As for the Brown Thornbill, Buff-rumped Thornbills showed no significant difference in use of substrates between times of the day, between the different breeding groups or between individuals within each group.

159. Figure 36 shows that there were differences in the substrates used by Buff-rumped Thornbills according to the number of individuals present. There was a direct correlation between the frequency of ground foraging and the size of group and a negative correlation between frequency of bark foraging and the size of group. (Spearman Rank Correlation $r = 1.000$ $P < 0.01$ in both cases).

160. The distribution of foraging substrates used by the Striated Thornbill is shown in Figure 37. There was little seasonal variation in the species' preference for foraging on leaves. Significant decreases in foraging upon leaves occurred in spring 1978, autumn of 1980 and winter of 1980 (see Table 11). The decreases in 1980 coincided with the defoliation caused by the drought. There were no significant differences by size of groups as for the Buff-rumped Thornbill. I had insufficient data on colour-banded individuals to assess any differences between groups or individuals.

161. All three species showed some changes in use of substrates when in MSF. These changes are shown in Figure 38. X^2 Tests for significance were made by comparing numbers of observations in each category, for each species combination, against the number of observations of that category for the thornbill species when on its own. Brown Thornbills foraged significantly more on the ground when accompanying Buff-rumped Thornbills and White-browed scrub-wrens, more on bark when with Striated Thornbills (surprisingly, considering the latter's preference for leaves), and more on leaves when with the Superb Fairy-wren. Buff-rumped Thornbills when in flocks with flocks of Striated Thornbills foraged more on bark and when in small parties (1-3 birds) among Striated flocks foraged more on both bark and leaves, almost abandoning the ground. Surprisingly, flocks of Buff-rumped Thornbills foraged more than expected on the ground when with flocks of Varied Sittellas and Superb Fairy-wrens. Striated Thornbills showed little change except for foraging more on bark when in flocks

Figure 36

Substrates foraged upon by Buff-rumped Thornbills, by size of party. (X^2 Test observations of substrate in party-size category against overall mean)

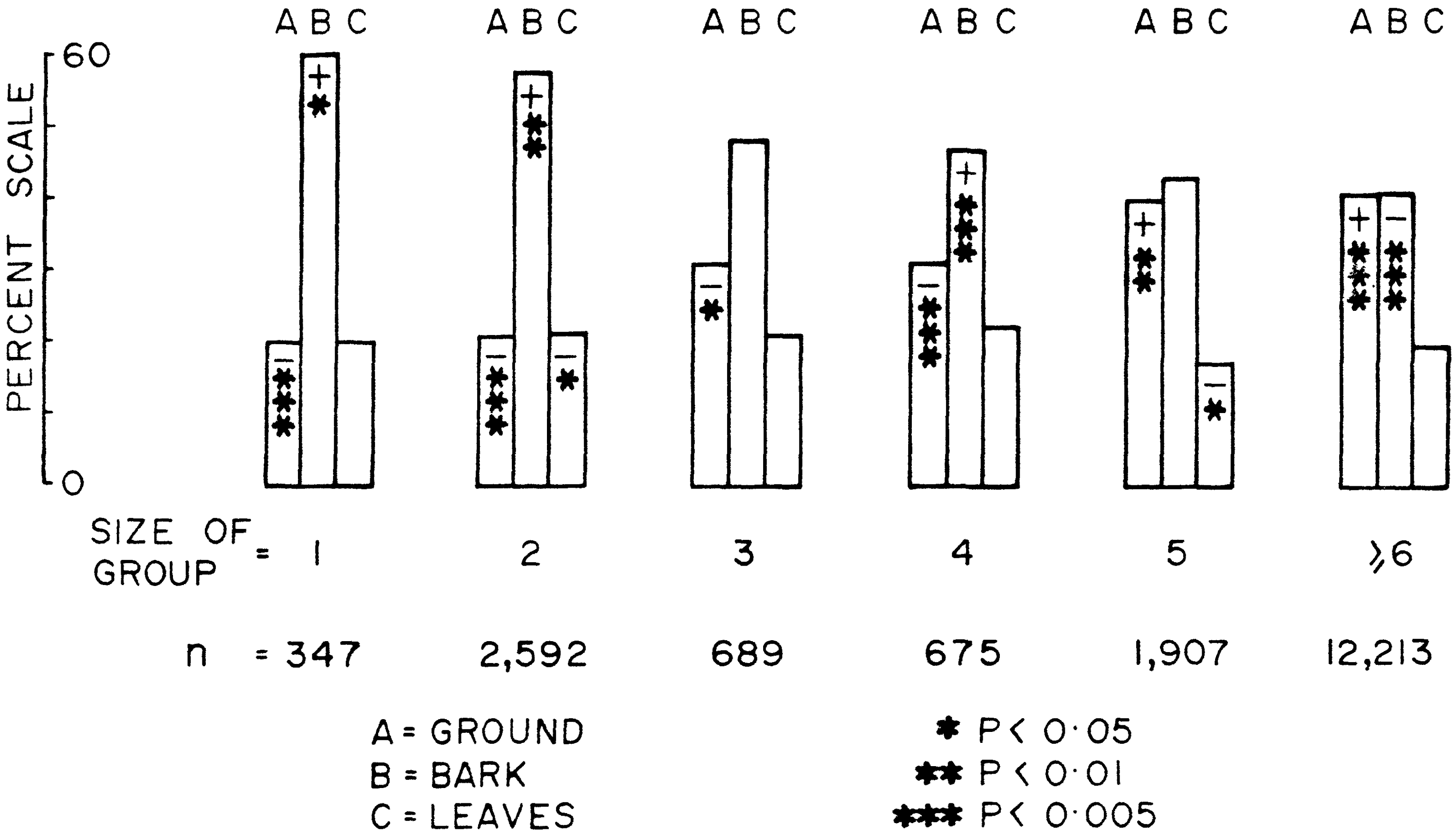

A B C
PERCENT SCALE
60
0
SIZE OF GROUP = 1
2
3
4
5
⩾6
n = 347
2,592
689
675
1,907
12,213
A = GROUND
B = BARK
C = LEAVES
* P < 0·05
** P < 0·01
*** P < 0·005
+
−

Figure 37

Distribution of observations of foraging moves, by substrates, of Striated Thornbills at Wollomombi (Total n: 22 232; monthly mean 617; monthly range 280-835)

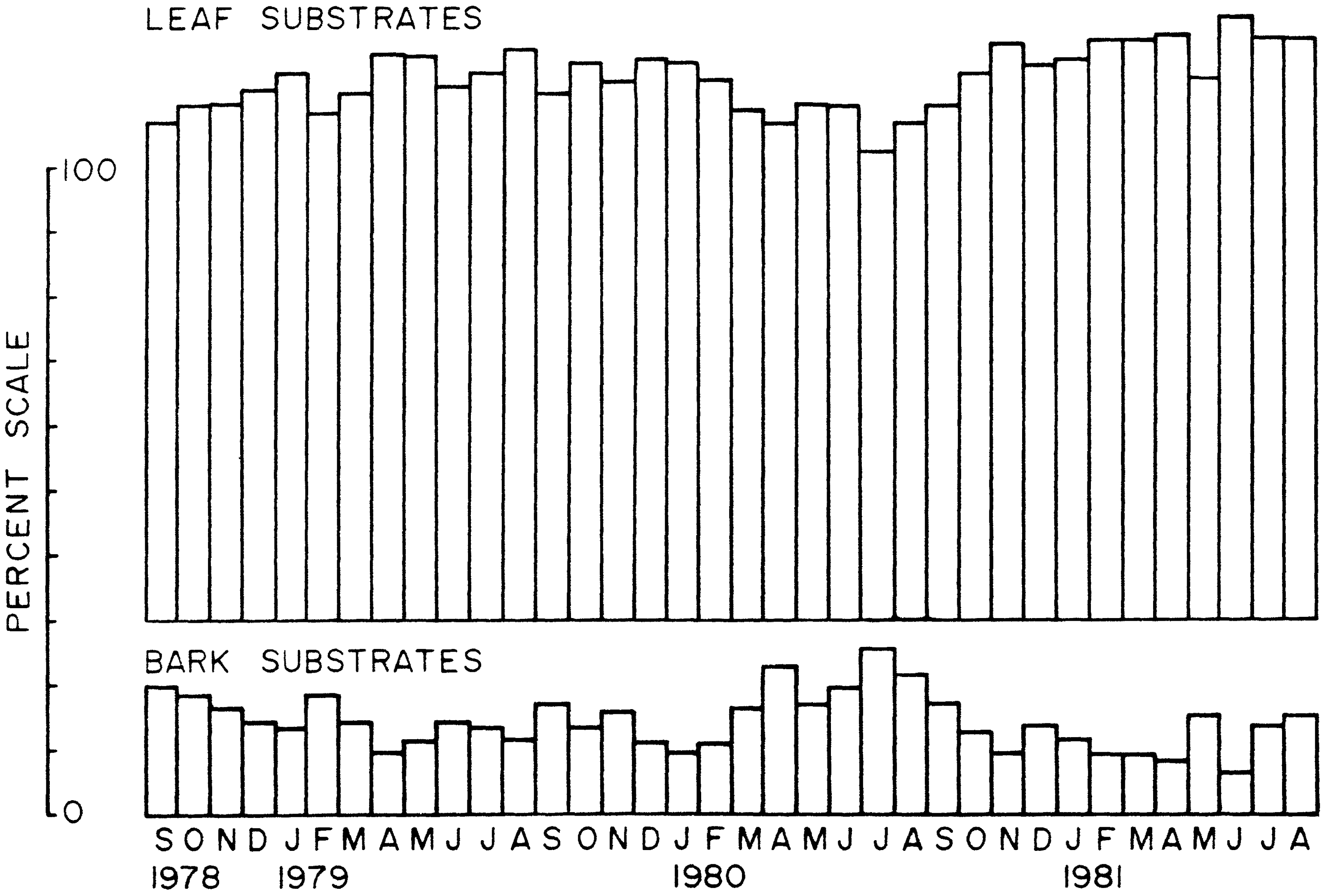
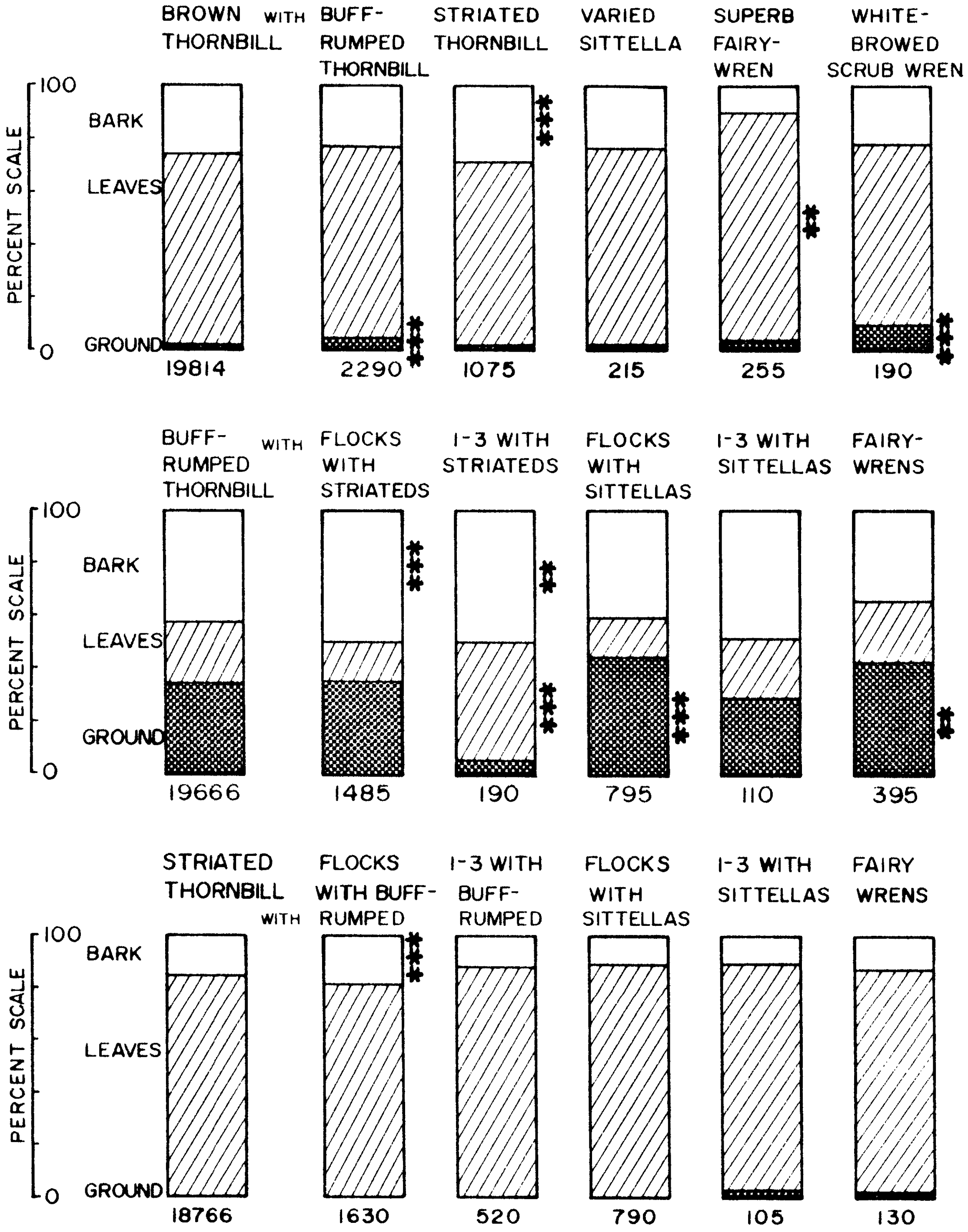

LEAF SUBSTRATES
BARK SUBSTRATES
PERCENT SCALE
100
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1978
1979
1980
1981

Figure 38

Distribution of observations of foraging, by substrate, by thornbills when with, or not with, MSF. (X^2 probabilities, ***: $P < 0.005$; **: $P < 0.01$). (n shown: number of moves)


BROWN THORNBILL
WITH
BUFF-RUMPED THORNBILL
STRIATED THORNBILL
VARIED SITTELLA
SUPERB FAIRY-WREN
WHITE-BROWED SCRUB WREN
PERCENT SCALE
100
0
BARK
LEAVES
GROUND
19814
2290
1075
215
255
190
BUFF-RUMPED THORNBILL
WITH
FLOCKS WITH STRIATEDS
1-3 WITH STRIATEDS
FLOCKS WITH SITTELLAS
1-3 WITH SITTELLAS
FAIRY-WRENS
PERCENT SCALE
100
0
BARK
LEAVES
GROUND
19666
1485
190
795
110
395
STRIATED THORNBILL
WITH
FLOCKS WITH BUFF-RUMPED
1-3 WITH BUFF-RUMPED
FLOCKS WITH SITTELLAS
1-3 WITH SITTELLAS
FAIRY WRENS
PERCENT SCALE
100
0
BARK
LEAVES
GROUND
18766
1630
520
790
105
130

in company with Buff-rumped flocks. These changes, particularly for the Buff-rumped Thornbill, may represent hanges in foraging height more than a choice of substrate.

DISCUSSION

162. The literature (see paragraph 151) correctly describes the Brown Thornbill as mainly foraging on foliage. The Buff-rumped Thornbill is also correctly described as foraging on ground, bark and foliage, except by Frith (1976) who considered ground to be the main substrate used. No-one seems to have recognized seasonal change, from ground to arboreal feeding, by the Buff-rumped Thornbill. Striated Thornbills are correctly described as foliage-gleaners of the tree canopy, but McGill's (1970) emphasis on bark foraging by the species was not confirmed in this study. At Wollomombi only 64 out of *ca.* 22,000 observations were of foraging on trunks or limbs.

163. Only the Buff-rumped Thornbill used trunks and limbs as a major substrate (i.e. > 5% of all foraging). Other predominantly bark-feeding groups such as woodpeckers Picidae (e.g. Ligon 1968), creepers, Certhiidae (e.g. Norberg 1979), and treecreepers, Climacteridae (e.g. Noske 1978) show that they are morphologically adapted to the bark-feeding role, particularly with long and deeply curved claws. Although, as will be shown later (Chapter 12) Buff-rumped Thornbills have claws more adapted to bark-foraging than do the other two species, the difference is minor.

164. Jackson (1979) makes the point that bark crevices serve as sites for egg-laying and over-wintering by many kinds of arthropods that carry out the active part of their lives elsewhere. Thus trunks and limbs are likely to provide important reserves of winter food for Buff-rumped Thornbills, although Figure 35 shows no evidence of increased bark-foraging in winter by the species. Of those arthropods that do actively move across bark surfaces Jackson (1979) found in North America that ants were a major component, as did Noske (1982b) at Wollomombi (see Chapter 3). As will be shown later Buff-rumped Thornbills eat more ants than do the other two species. Jackson (1979) also made the point that the bark of

different species of plants vary considerably as sources of insects for birds, by virtue of the bark texture, which will be examined in the next chapter. Bark also serves as a diurnal resting-place for many nocturnal insects e.g. moths and chrysomelids.

165. All three species foraged off branches but Striated Thornbills much less so than the other two. I suggest that there would have been more difference between the species had the branch substrate been more finely divided, as was done in other studies (e.g. Cameron 1979 on fantails). However when planning the study I eliminated further subdivision of major substrates in order to keep the number of variables for each observation to manageable proportions. From observation I found that the Striated Thornbill strongly preferred the thinner branches and that Buff-rumped Thornbills favoured dead branches. Branches lack the deep fissures of bark found on trunks and limbs that shelter many inactive life-forms of arthropods, and also the soft matter of leaves on which phytophagous forms, particularly larvae, can feed. However they appeared to harbour the sedentary forms of scale insects (mostly Psylloidea with some Coccoidea) and were thus probably an important source of food to all three species, particularly before psyllids declined during the drought (see Chapter 3). However, as will be shown in the next chapter the three species differentiated between the various species of plants when foraging on branches.

166. All three species foraged off leaves to a major degree, the Buff-rumped Thornbill being seasonal in this respect. Leaves are the substrate on which grazing arthropods, especially larvae, mostly occur. However as will be demonstrated later what appears to be a substrate exploited by all three species is in fact finely divided by plant species and/or leaf structure.

167. No thornbill was seen to probe into the ground or turn over leaf litter and they appeared, when feeding on the ground, to take food off the surface of the ground, off fallen twigs, but most often, off the base of grass-stems. Only the Buff-rumped Thornbill was a major ground-forager. However, although the Brown Thornbill on average only foraged on the ground for 2.7% of its effort, the percentage during autumn and

winter of 1980 rose to 9.3%. This suggests that the ground offers a worthwhile foraging substrate when insects are scarce, as they were at that time (see Chapter 3), and particularly when so many plants had been defoliated.

168. Flowers were an insignificant substrate in the overall total of observations but for Brown Thornbills were important at particular times, chiefly spring and late summer, the two flowering periods of *Acacia irrorata*, on which most observations were made. The other two species fed much less on flowers, but at the same periods as did Brown Thornbills. It was not possible to identify food taken i.e. nectar, pollen or insects but test results, given in Chapter 11, suggest that all three could take nectar, especially the Brown Thornbill.

169. Although there were obvious differences in the use of substrate when thornbills were feeding in MSF as opposed to by themselves the differences may reflect changes in other habits (i.e. vertical distribution) from which the choice of substrate is not independent. Brown Thornbills, when with Striated Thornbills, which were mainly leaf-foragers, foraged more on bark and not on leaves. However as will be shown later, Brown Thornbills follow Striated Thornbills into the canopies of large trees, a place where there appears to be much greater surface areas of bark available than in the understorey normally favoured by Brown Thornbills. Brown Thornbills foraged more off leaves when with Superb Fairy-wrens. However the preferred habitat of the wrens, bushy undergrowth, would result in the thornbills, which follow the wrens (see Chapter 6), also staying in that habitat more than was usual. Increased foraging by Brown Thornbills on the ground, when with Buff-rumped Thornbills and White-browed Scrub-wrens, the nuclear species of many MSF, reflects those two species' predilection for ground-foraging (34% for Buff-rumped Thornbills; 38% from my data for the scrub-wren).

170. Buff-rumped Thornbills foraged even more on the ground when with Varied Sittelas and Fairy-wrens than they did when alone but there are apparent reasons for this. The Fairy-wren is itself a nuclear species of MSF that attracts other species and forages mainly close (< 2m) to the ground (53% of observations at Wollomombi). Thus it and the Buff-

rumped Thornbill are likely to be together only when the thornbill is itself foraging close to the ground. Similarly, the data when with the Sittella give a false picture. Of 225 observations of the Sittella less than half were below 2 m from the ground, but most observations below 2 m were when in company with the Buff-rumped Thornbill; no records above 2 m were with the thornbill. Thus it is really the Sittella that has changed, to foraging near the ground only when there are Buff-rumped Thornbills also doing so. When the Sittella is higher it has no apparent need to follow Buff-rumped Thornbills when the thornbills are foraging higher, because the Sittella is very much a nuclear species in its own right (see Table 9). The increase in bark-feeding of the Buff-rumped Thornbill when with Striateds in flocks is probably caused by the same reason as for Browns, i.e. access to higher levels of the vegetation where there are much greater surface areas of bark. However it is when small parties of Buff-rumped are with large parties of Striateds that the greatest differences occurred, with the Buff-rumped foraging greatly off leaves. This difference may result from the Striated attracting the Buff-rumped up into the canopy, where leaves are so much a proportion of the available substrate, but differs so much from when flocks of Buff-rumpeds join Striateds that it does seem that deliberate mimicry of feeding habits may possibly occur. The only change (to more bark-feeding) made by the Striated Thornbill, when in MSF, may also reflect a change in choice, because, as will be shown later, they were attracted downwards by Buff-rumped Thornbills,to levels where it appears there would be less, not more, bark available on which to forage. In general however the three species, when in MSF, did not appear to show, independently of other factors such as height and plant species, much imitation of other species in choice of substrate, as witnessed elsewhere (e.g. Morse 1970, in North America).

171. Overall, substrate by itself seems to play a minor part in the partitioning of resources between the three species of Thornbill. Browns and Striated overlap highly in choice of substrate. Even Buff-rumped Thornbills, although overlapping much less because of their preference for ground-foraging overlap 60-75% with the other two species during spring, when the Buff-rumpeds largely abandon ground-foraging. However, as will be shown, choice of substrate by plant species does involve a much more fine partitioning of resources.