

Chapter 5

RED-BROWED TREECREEPER

Red-browed Treecreepers occur usually in pairs or groups of three, rarely four, adults which occupy and defend territories year-round. Previously I (Noske 1979) used the term "home range" in reference to these territories, because few aggressive encounters between groups had been witnessed and there was considerable peripheral overlap. In the absence of evidence to the contrary, this species and other communally-breeding species of treecreepers (see Noske 1980) are assumed to be monogamous.

5.1 Sex Ratios and Population Structure

Males predominated in the breeding population at Wollomombi over the three years of intense study; the sex ratio for all seasons combined was 1♂:0.6♀. The decreasing disparity in sex ratios between the first (1:0.4) and the second (1:0.9) year of the study coincided with a rise in the number of pairs and a corresponding drop in the number of larger groups (Table 5.1). Few data were collected on sex ratios of juveniles as young in their first month were impossible to sex reliably in the field (see Section 3.1.2). Females predominated marginally in the fully sexed broods (5♂♂:7♀♀), as well as the combined total, including broods in which only one member was sexed (8♂♂:10♀♀). Information in ABBS (supplied by D. Purchase) are equivocal: sex ratios favoured females in juveniles (5♂♂:10♀♀) as well as in adults (54♂♂:60♀♀), but a substantial proportion of birds was not sexed (8 juveniles; 33 adults).

Of the 20 group-years, 13 (65%) consisted of more than a simple pair and of these, twelve contained two or more males, and the remaining one, two females (Table 5.1). Thus, with one exception, all auxiliaries were males. Of the nine auxiliaries, three were banded as adults and the remainder as immatures (Figure 5.1). All of the latter served as auxiliaries in their natal territory and at least two of these assisted both their parents, while another bird assisted his father and step-mother. Three of

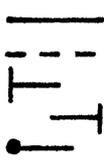
TABLE 5.1: Group composition of Red-browed Treecreepers* at Wollomombi Falls over three years

	$\sigma\sigma$	$\varphi\varphi$	Number of groups				Total
			1977	1978	1979		
Pair	1	1	-	3	4	7	
Trio	2	1	4	3	2	9	
	1	2	-	-	1	1	
Quartet	3	1	2	1	-	3	
<hr/>							
Total individuals	20		19		17	56	
$\sigma\sigma/\varphi\varphi$	14/6		12/7		9/8	35/21	
Number of groups	6		7		7	20	
Fledglings produced	11		5		6	22	

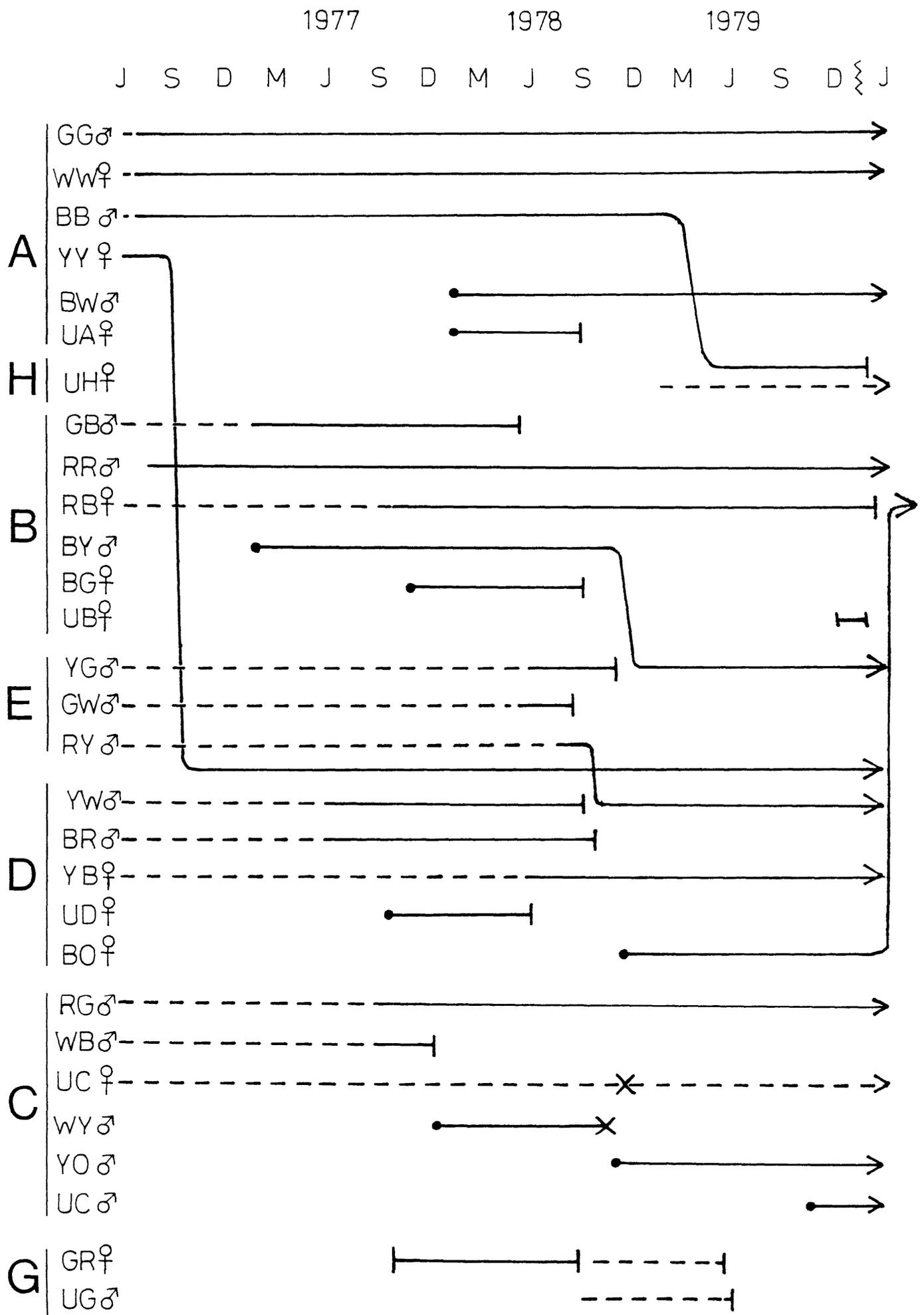
* includes group F, whose territory was situated outside the study site; group consisted of a trio in 1977 and 1978, and a pair in 1979

FIGURE 5.1: *History of individual Red-browed Treecreepers at Wollomombi Falls over the study period*

Large letters refer to group/territory as shown on Figure 5.2


 banded
 - - - unbanded
 |— date of appearance
 —| date of disappearance
 •— date of fledging

Young which disappeared within 6 months of fledging, excluded



the birds banded as immatures acted as auxiliaries for two years, and the other three (including the female), for one year. Two of the latter subsequently emigrated (BY σ , BO ♀) and the other almost certainly died (BR σ). Of the birds banded as adults, one acted as an auxiliary for at least two years (RR σ) and another, for at least three years (BB σ), including the 1976-77 season.

5.2 Mortality and Dispersal

In contrast to the almost complete disappearance of young White-throated Treecreepers within two months of fledging, only nine (41%) of the 22 known Red-browed fledglings (in Table 5.1) disappeared within that period. However, only six of the remaining 13 "survived" the following winter. Of the 20 birds (14 $\sigma\sigma$:6 ♀♀) banded or re-trapped as adults between June 1976 and June 1980 (excluding GB σ - see Figure 5.1), four (20%) died within twelve months of banding, but eight (40%) survived until the end of 1982; three of which were at least six years old. There was no evidence of differential mortality between the sexes, and deaths occurred in all seasons. Four birds (2 $\sigma\sigma$:2 ♀♀) changed territories within the study site, to become breeders in the new territory.

Apart from the preponderance of males in the breeding population, several lines of evidence suggest that dispersal is greater among females than among males. Of the six young that survived their first winter, four (3 $\sigma\sigma$:1 ♀) became auxiliaries, while the other two (both female) disappeared just prior to the breeding season (Figure 5.1). Another female (YY ♀) which disappeared from her natal territory at the beginning of the 1976 breeding season apparently emigrated. Indeed, the appearance of four immigrant females (GR ♀ and unbanded ♀♀ in territories *B*, *C* and *G*), coincided with the breeding season. As all were in adult plumage, they must have been born during the previous season or earlier. At another site (one kilometre from Wollomombi Falls), where both young in a nest were colour-banded, the male nestling became an auxiliary during the next breeding season, while his sister disappeared less than three months before the breeding season. Moreover, the only Red-browed ever recorded at Stringybark Hill, eight kilometres from the nearest breeding population of this species, was female. However, as this lone, diseased individual was found at the end of the breeding

season, and still possessed juvenile plumage, some post-breeding dispersal must occur.

5.3 Territoriality

The breeding population of Red-browed averaged about one half that of the White-throated over the study period (Table 5.1, excluding territory *F*), yet there was complete spatial overlap. This resulted from the much larger territories of Red-browed, which averaged 9.6 hectares. The boundaries of these territories did not alter appreciably over the study period, despite changes in the number of occupants (Figure 5.2). However, after at least three years as an auxiliary in territory *A*, $BB\sigma$ took a mate (possibly a sibling) and defended a small compartment of his natal territory, where he attempted to breed. In addition, one section of the north-west sector was temporarily occupied by an unbanded pair between September 1978 and May 1979.

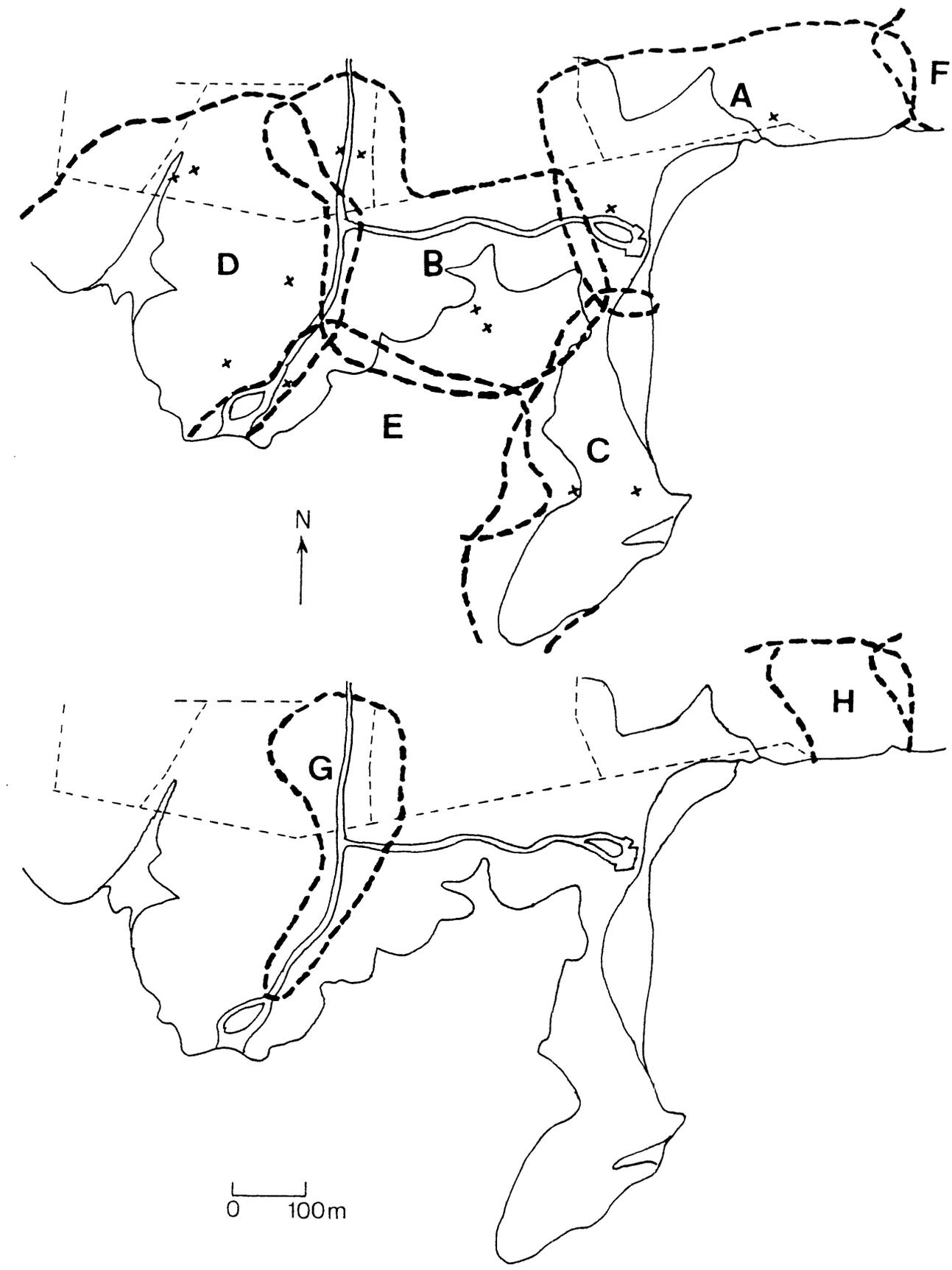
The history of the north-west sector is noteworthy. During 1976, it was usually occupied by a lone bird ($RR\sigma$) who rejoined his presumed natal group (*B*) in October, and shared the combined area with its members. From December 1977 to May 1978 this bird often accompanied an immigrant female ($GR\eta$) who resided in the northern area, though the male was frequently hostile towards her. In May, immediately after the death of the primary male ($GB\sigma$) in group *B*, $RR\sigma$ rejoined that group where he succeeded as the breeder. Meanwhile, $BR\sigma$ from group *D* began to associate with $GR\eta$ in her area, precipitating in a vigorous fight between the former and $RR\sigma$. However, the female soon died and was replaced by an unbanded pair who defended the area against the surrounding groups. Although this pair probably mated, they failed to breed and from January 1979 made frequent excursions south, in the area of overlap between territories *B* and *D*. Finally, $RR\sigma$ reclaimed the area for his group after the unbanded pair disappeared in May-June 1979.

5.4 Social Interactions

Aposematic displays, such as the "clicking" of the White-throated Treecreeper, were absent in the Red-browed. Only eight out of 26 interactions

FIGURE 5.2: *Distribution of group territories of Red-browed Treecreepers at Wollomombi Falls. Upper, 1977 breeding season; lower, territory of group G (in 1978 breeding season) and subterritory H (in 1979 breeding season); other territory boundaries unchanged*

Dark, broken lines, territory boundaries ;
thin, unbroken lines, contours and creeks ;
small crosses, roost-sites
Letters correspond to those on Figure 5.1
(far left)



between two groups involved any physical violence, while in the remainder, supplantings and chasings occurred. Pursued birds commonly displayed submissively, with fully-spread wings and tail while climbing, or with lowered head and partly-raised, fluttering wings when stationary. Some interactions involved only one member from each group, whereas others included all members. During a fierce combat between two adult males (RR σ and BR σ) in the area of overlap between their respective territories, their female companions simply watched. This was the most intense battle witnessed, the males wrestling on the ground with their legs locked for at least nine minutes before one (BR σ) retreated. The latter was never seen again.

Of the 26 interactions between two birds from different groups in which both participants were identified, 13 involved males only, and six, females only. Males won each of the remaining (seven) intersexual conflicts. Within the "family" group, a strict dominance hierarchy occurred (Figure 5.3), where females were always subordinate to males, regardless of age, and younger birds were subordinate to older birds of the same sex. Almost a half of the 70 recorded aggressive interactions within groups occurred between the primary male and female, but such quarrels were short-lived, most consisting of a single displacement.

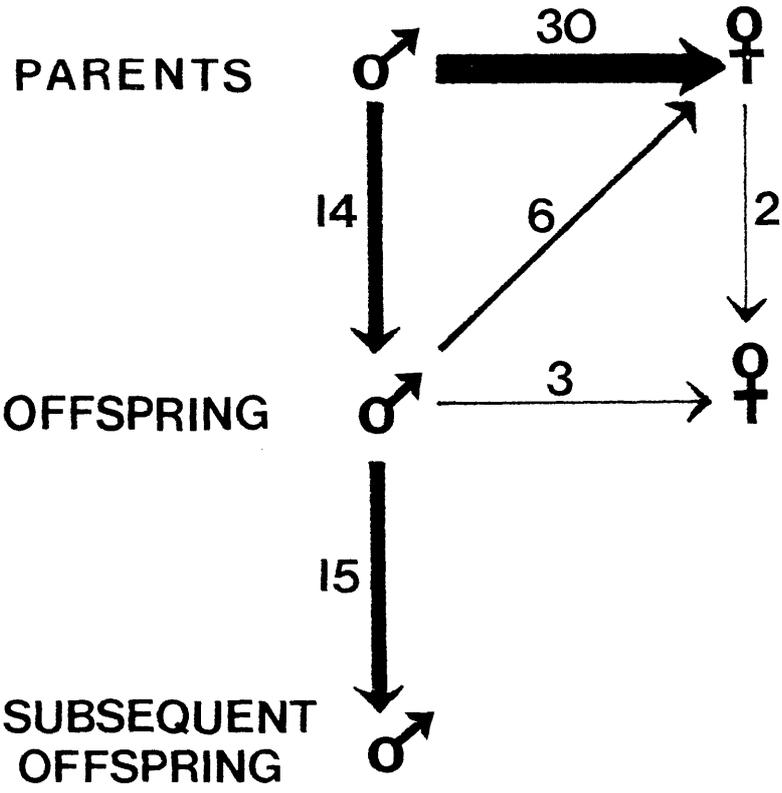
In all but two of the 120 separate interactions (involving 171 displacements) between Red-browed and White-throated, the former was the aggressor. This is consistent with previous findings (Noske 1979). I saw White-throated forage on nest-trees of the Red-browed or inspect their nests on five occasions, but this precipitated in interspecific aggression only once. Thus, neither species vigorously defended their nests against each other.

5.5 Courtship Feeding

As in the White-throated and other treecreepers, the breeding female is fed both prior to and during the incubation period. In the Red-browed, both the primary male and auxiliaries fed the female before laying, though auxiliaries were never observed to copulate. Thus, feeding of the female may not be related to courtship. In contrast to White-throated, feeding of the female was confined to the breeding season (September-January)

FIGURE 5.3: *Dominance hierarchy within Red-browed
Trecreeper groups*

Values represent total number of aggressive
displacements observed



and the month preceding it, with only a few records in July. The provisioning of the female by auxiliaries probably varied with age or experience of the auxiliary, as well as stage of the nesting cycle. Overall, primary males contributed 69% of the 70 feedings where auxiliaries were present. In 60 minutes of observations away from the nest (6 x 10 minute intervals), females were fed 31 times, i.e., the overall feeding rate was 31 per hour.

5.6 Copulation

Copulation was witnessed three times, involving three different pairs. In each case, prior to copulation, the female was perched on a near vertical branch or trunk with the head lowered, tail slightly raised and wings quivering. On two occasions, the male hopped about her with an insect in his bill, while on the other occasion he merely "chattered" softly beside her. Brief coition quickly followed.

5.7 Vocalizations

Four adult calls and one juvenile call were recognized.

1. *Chatter*. The commonest call, consisting of a rapid, slightly descending succession of sibilant notes.
2. *Retort*. A short, disyllabic (occasionally trisyllabic) call, the last syllable lower in pitch; usually delivered immediately after a *chatter*, and frequently followed loud calls of other species.
3. *Grate*. Harsh, low-pitched sound uttered during group interactions and intraspecific or interspecific altercations.
4. *Shrill Call*. A loud, high-pitched upward-inflected note quickly repeated up to four times; infrequently heard, usually during intraspecific conflicts.

5. *Juvenile/Food-begging Call.* A monotonal series of high-pitched, insect-like notes when being fed by adults.

All calls were given by both sexes. The first two calls were typically uttered antiphonally by the primary pair, one member *chattering* and the other, responding with the *retort*. The *grate* was often delivered after this duet, or in unison, by a third member of the group. Such vocal exchanges between group members probably aided group cohesion, or, alternatively, helped to maintain individual space, when birds foraged in the same tree. There did not appear to be any discrete "incubating call" (as in the White-throated), but when receiving food from males, the female sometimes gave a soft, drawn-out version of the *chatter*. A soft hissing sound was also heard twice when the primary male met the female at the nest, and once, prior to and during coition.

5.8 Roosting

The last calls of the day of Red-browed were consistently earlier than those of White-throated; the mean difference (\pm SE) on nine evenings was 17.4 (\pm 1.36) minutes. One Red-browed was seen entering its roost 15 minutes before the last White-throated call was heard. In addition to roosting earlier than the White-throated, the Red-browed probably awoke, or at least became active, later than the White-throated. The first calls of the Red-browed were never heard before those of the White-throated. A Red-browed left its roost-site in the morning 14 minutes after the first White-throated call.

The roost-sites of Red-browed, in contrast to those of the White-throated, were enclosed. All but two of the 15 sites were in the hollow tops of broken tree-trunks (mostly live boxes), or in hollow spouts of dead trees. These sites were significantly higher than those of White-throated at Wollomombi, ranging from 2.5 to 12.0 metres ($\bar{x} \pm$ SE = 6.6 \pm 0.76 m). Few roost-trees of Red-browed were situated on the margins of territories, but despite the social nature of this species, the sites used by members of the same group were apparently widely-spaced (Figure 5.2).

5.9 Breeding Season and Brood Frequency

Nest-building commenced in late August and laying peaked in early September and early October (Figure 5.4). Information compiled by M.T. Goddard suggests a similar laying schedule in the Dorrigo region (70 km east of Wollomombi) with young from early nests occurring in late September and early October. At Wollomombi, two late clutches were begun in December, the first (early December) belonging to a group with young that had fledged about 20 days earlier. The owners of the second nest (in late December) had been feeding apparently well-grown nestlings which never fledged, in the previous month.

Two groups raised two broods successfully in one season, both in 1977-78, but second broods were not attempted in other years, despite some early first broods. Both successful second broods were raised in nests different from the first.

5.10 Nest-sites

The nest-sites of Red-browed resembled their roost-sites. In contrast to those of the White-throated, most nests of the Red-browed were situated in hollow dead branches of live trees or entirely dead trees (Table 5.2). Stringybarks were used least frequently. The majority of the nests in trunks concerned dead trees which had lost their branches. Of the 20 nests at Wollomombi, four were used twice and another, three times. The height of the 26 nests (including repeats) ranged from 5.3 to 20.0 metres, though a nest, two kilometres from Wollomombi, was as low as 1.8 metres. Including the latter, Red-browed nests averaged 10.2 ± 0.85 metres (SE), which was significantly higher than White-throated nests at Wollomombi ($t = 2.04$, 50 df, $0.02 < p < 0.05$).

5.11 Building

In this species, both sexes, including auxiliaries, brought building material to the nest though most of the initial construction was probably done by the female. Females carried stringybark in five of the 20 building visits witnessed, but males took only fur or other lining in

FIGURE 5.4: *Estimated laying dates of final eggs (upper) and dates of broods of undetermined age (lower) in Red-browed Treecreepers*

Open bars, Wollomombi Falls; cross-hatched bars, Dorrigo region, M.T. Goddard *in litt.*

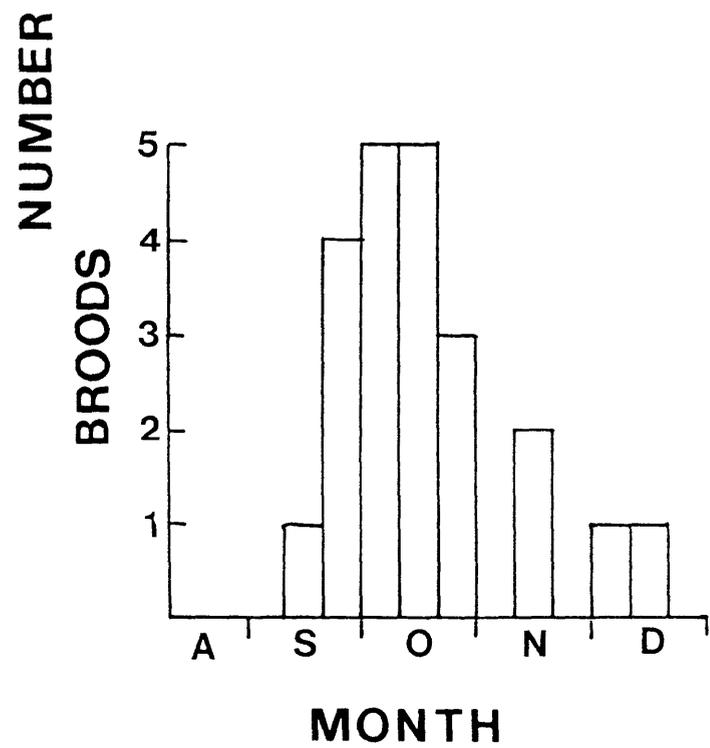
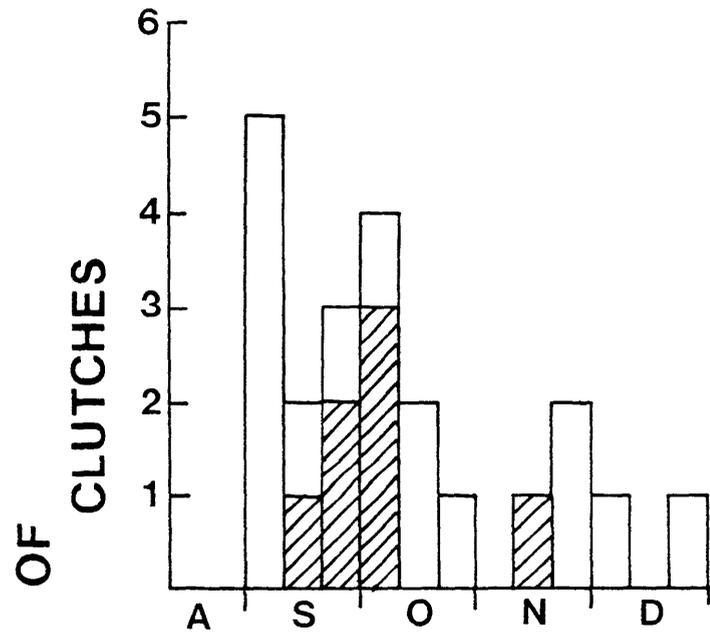


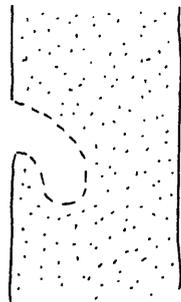
TABLE 5.2: Nest-sites* of Red-browed Treecreepers

Tree	Stringy-bark		Box [†]		Gum		Dead	Total
	H	S	H	S	H	S		
Trunk	-	-	-	1	-	1	5	7
Branch	-	1	3	5	-	5	7	21
TOTAL	-----		-----		-----		-----	28
	1		9		6		12	

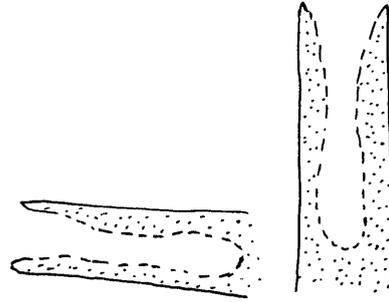
* all from Wollomombi Falls study site; except one (2 km from Wollomombi); includes repeats

† comprises *E. melliodora* (6) and *E. sp. aff. cytellocarpa* (3)

H = hole (live)



S = hollow spout (dead)



six visits. Once a male gave material to the female, who then flew to the nest. Bill-sweeping (see Section 4.11) was performed by both sexes (four times each), mostly before and during the incubation period. One female, however, swept vigorously for over ten minutes, when its nest contained young.

5.12 Clutch Size and Laying Routine

According to most popular texts, the Red-browed Treecreeper lays two or three, occasionally even four, eggs (e.g. Frith 1969; Orenstein 1976; Pizzey 1980; Beruldsen 1980). Despite this claim, I have been unable to locate authentic documentation of any clutch size other than two. M.T. Goddard (*in litt.*) provided details of 29 nests in the Dorrigo area over 24 years, all of which contained either two eggs or two young. All five clutches I examined at Wollomombi were of two eggs, and I never recorded more than two fledglings per brood. Howe (1921) gave the clutch size of Red-browed as two, and described five nests in southern Victoria, each with two eggs. The six complete clutches of this species held by the Australian Museum (Sydney) and National Museum of Victoria are C/2, but the only pertinent information in NRS is of one brood of two nestlings (NRS 1/78).

At the only nest where laying was observed, the second egg was probably laid in the afternoon (13:00 \pm 2.00 hours), at least 44 hours after the first. Incubation probably began before the second egg was laid, as the incubating bird was flushed on three of the six inspections of the nest when only one egg was present, after sitting for at least 15 minutes on one occasion.

5.13 Incubation and Nestlings

The minimum incubation period at two nests was 17 days 6 hours and 17 days 22 hours, but another nest gave a maximum period of 18 days 23 hours. The latter is about four days shorter than the incubation period of the White-throated. The nestling period of the two species however, was probably much the same, two Red-browed nests giving minimum periods of 25 days and 25 days 8 hours. Consistent with other species, only female

Red-browed incubated and brooded on the 72 occasions when the "sitter" was sexed. Brooding continued for at least twelve days after the eggs hatched. Only a few incubating sessions were timed: the maximum was 35 minutes. The duration of 21 brooding sessions ranged from 1.5 to 16 minutes ($\bar{x} \pm SE = 7.6 \pm 1.00$), probably decreasing as the young grew. Attendance apparently dropped gradually during the nestling period (Table 5.3).

All group members fed the nestlings and removed their faecal sacs, even in the group containing two females. On several occasions, auxiliary males presented food to the primary male or female, who transferred it to the young. In 124 observations at nests with auxiliaries, the overall feeding contributions of both primary males (42%) and females (32%) exceeded that of auxiliaries (26%). Feeding rates over three stages of the nestling period varied from 8.1 to 10.7 per hour (Table 5.4) averaging 9.6 per hour for almost 15 hours of observations.

5.14 Fledglings and Reproductive Success

Of five broods observed on their first day or two as fledglings, three were found in hollow dead spouts of trees up to 50 metres from the nest, and the other two, in the open. Juveniles from three different broods were still being fed at 57, 61 and 80 days post-fledging respectively, suggesting that young are still dependent two months or more after leaving the nest. During the 1977-78 breeding season, the three simple pairs raised more fledglings on average than the three larger groups (1.0 versus 0.7) but the reverse occurred in the following season (0 versus 2.0). Nevertheless, overall productivity of trios and quartets was three times greater than that of pairs (1.6 versus 0.5 fledglings per year, over six and 12 seasonal breedings, respectively).

5.15 Conclusions

In sharp contrast to the White-throated, over half of the young produced by Red-browed remained in their natal territory for over two months. This was probably due in part to a longer period of dependency, but a substantial proportion (27%) were tolerated within their families for over six

TABLE 5.3: Attendance of brooding female Red-browed Treecreepers

Age of young (days)*	Obs. time (mins)	% brooding attendance	Complete brooding session (mins) [†]	
			\bar{x}	SE
1	78	50.0	11.3	2.91
5	68	33.8	7.5	3.33
7	98	30.6	9.8	4.32
11	75	25.3	4.7	2.14

* post-hatching; nestling(s) at one and five days pertain to same nest; other two pertain to different nests; all nests with one auxiliary attending

† excludes sessions of less than one minute (as feeding sometimes took this long) and incomplete sessions (i.e., observations begun or terminated during session)

TABLE 5.4: *Feeding rates* during nestling period of Red-browed Treecreepers*

Age of nestlings [†] (days)	Obs. time (mins)	Feeding rate (per hour)
1 - 8	244	8.1
9 - 16	163	10.7
17 - 25	476	10.1
TOTAL	883	9.6

* combined observations from six nests, all observation periods \geq 30 minutes; rates include some visits in which brooding ♀ was fed, but excludes visits in which no food was seen; no adjustments made for number of auxiliaries, or time of day

† nestling period divided into three stages (about 8 days each); age of young at several nests extrapolated from fledging dates

months. As evident from the Stringybark Hill observation, some post-breeding dispersal probably occurs but this may be largely confined to females, as was dispersal of "yearling" birds prior to the next breeding season. The latter point suggests that females are physiologically capable of breeding in their first year, as there would be little advantage in dispersing if they could not. Alternatively, if sexual rivalry occurs among females for breeding status, mothers may not tolerate their daughters when breeding commences, forcing them to disperse. The relative importance of these factors and presumably others awaits resolution.

The recruitment of breeders from territories within the study site and the longevity of many individuals suggests a fairly old and isolated population, consistent with the localized distribution of this species generally (see Figure 2.1). Howe (1982) concluded that Red-browed required large, uninterrupted tracts of forest, since they were almost totally absent from small "islands" of forest in cleared areas nearby. That the territories of Red-browed are much larger than those of the White-throated implies that the former requires more space to obtain sufficient resources. Large territories, inability to colonize new habitats, and prolonged parental care would appear typical attributes of a specialized species. The slow development of adult plumage (see Section 3.1.2) might also be correlated with the protracted period of dependency.

Chapter 6

BROWN TREECREEPER

The communal habits of the Brown Treecreeper were only recently recognized (Orenstein 1976; Noske 1980) and until now, never detailed. Males predominate as in the previous species, but unlike the latter, individuals of this species may attend more than one nest (Noske 1980). This appears to be the result of temporary relaxation of territoriality, a phenomenon hitherto undescribed among Australian birds.

6.1 Sex Ratios and Population Structure

Males outnumbered females in the breeding population at Swan Vale, comprising about two-thirds of the total number of birds in all three years (Table 6.1). Boehm (1982) recorded a similar sex distribution ($1\sigma:0.62\text{♀}$ or 62% males) among 147 Brown Treecreepers banded in South Australia. Although less than half (48%) of the 1,008 adults banded through ABBS were sexed, a preponderance of males ($1\sigma:0.81\text{♀}$) occurred (data compiled by D. Purchase). This was also the case with juvenile and immature birds of which only 41% were sexed ($38\sigma\sigma:20\text{♀♀}$), though no nestlings were sexed. The sex ratio of nestlings and fledglings at my study sites, however, was close to parity (Table 6.2).

As all breeding groups in the three main years at Swan Vale contained only one female, auxiliaries were always males, although one probable exception occurred in 1981. Similarly, trios at both Stringybark Hill and Wollomombi incorporated two males. The composition of breeding groups at Swan Vale was confused by partial disintegration of territorial boundaries between related groups during the breeding season. While simple pairs were prevalent in 1978 (Table 6.1), the breeding males of at least three pairs spent considerable time in territories other than their own, where they attended nests as auxiliaries (see Section 6.3). Thus, members of several groups combined to form temporary quintets and sextets at several nests during the study period.

TABLE 6.1: Group structure* of Brown Treecreepers at Swan Vale over three breeding seasons

	1977	1978	1979	Total
Pair	2	5	2	9
Trio	2	1	4	7
Quartet	2	2	2	6
Total individuals	18	21	24	63
♂♂/♀♀	12/6	13/8	16/8	41/22
Number of groups	6	8	8	22
Fledglings produced	12	10	8	30

* this table is necessarily over-simplified, owing to the habit of some individuals of sharing two territories; thus although the full complement of birds in territory (A: 1978) during the nestling stage was six, three of these "belonged" to other groups; all auxiliaries were males

TABLE 6.2: Sex ratios of juvenile* Brown Treecreepers at study sites

		1977	1978	1979	1980/81	Total
Swan Vale	♂	4 (5)	4	1 (2)	2	11 (13)
	♀	2 (4)	4	2 (3)	2	10 (13)
Wollomombi Falls/ Stringybark Hill	♂	1	2	1	2	6
	♀	1	2 (3)	4	1	8 (9)

* sexed either as nestlings or fledglings

() includes broods in which one or more young were unsexed

6.2 Mortality and Dispersal

Seven (22%) of the 32 birds banded or re-captured as adults disappeared within twelve months of banding (or 24 months in the case of birds banded as nestlings). Of these seven, five were female, suggesting higher mortality or dispersal among adults of this sex than among males. As at least two of these females and four other breeding females (who lived longer) died during the breeding season it is possible that the incubating and brooding activities of this sex exposes them to greater predation than males. Indeed one (GB♀) died while incubating, as her remains were found on the three eggs she had laid 23 days previously.

One half of the 26 known fledglings disappeared within their first three months: seven within two months post-fledging and six, afterwards. Another six (at least five females) disappeared between six and twelve months post-fledging, and the remaining seven (all males) lived for over two years. One juvenile female (NN♀) was seen 300 metres from her natal territory, two months after she fledged and was never seen again; her brother (DD♂) appeared in the same area two weeks later and also disappeared soon afterward.

Two first-year females emigrated during winter after at least six months in their natal territory (Figure 6.1). One (BG♀) became a breeder in another territory on the southern edge of the study site; the other (YW♀) accompanied an unmated male (BY♂) over 700 metres from her natal territory for at least one month before she disappeared. Her sister (DD♀) however, remained "at home" where she mated and attempted to breed in her first year, but apparently died soon afterwards. This case was perhaps exceptional because both parents of this female disappeared from the territory less than two months after she fledged (Figure 6.1). When banded in June/July 1977, group *E* contained two adult females but during August, one of them (BR♀) began to forage apart from the other group members, and by mid-September had disappeared.

6.3 Territoriality and Communalit

As with the previous species, the boundaries of the original territories altered little over the study period despite fluctuations in the

FIGURE 6.1: *History of individual Brown Treecreepers at Swan Vale over the study period*

Large letters refer to group/territory as shown on Figure 6.2

———— banded

- - - - - unbanded

┌─── date of appearance

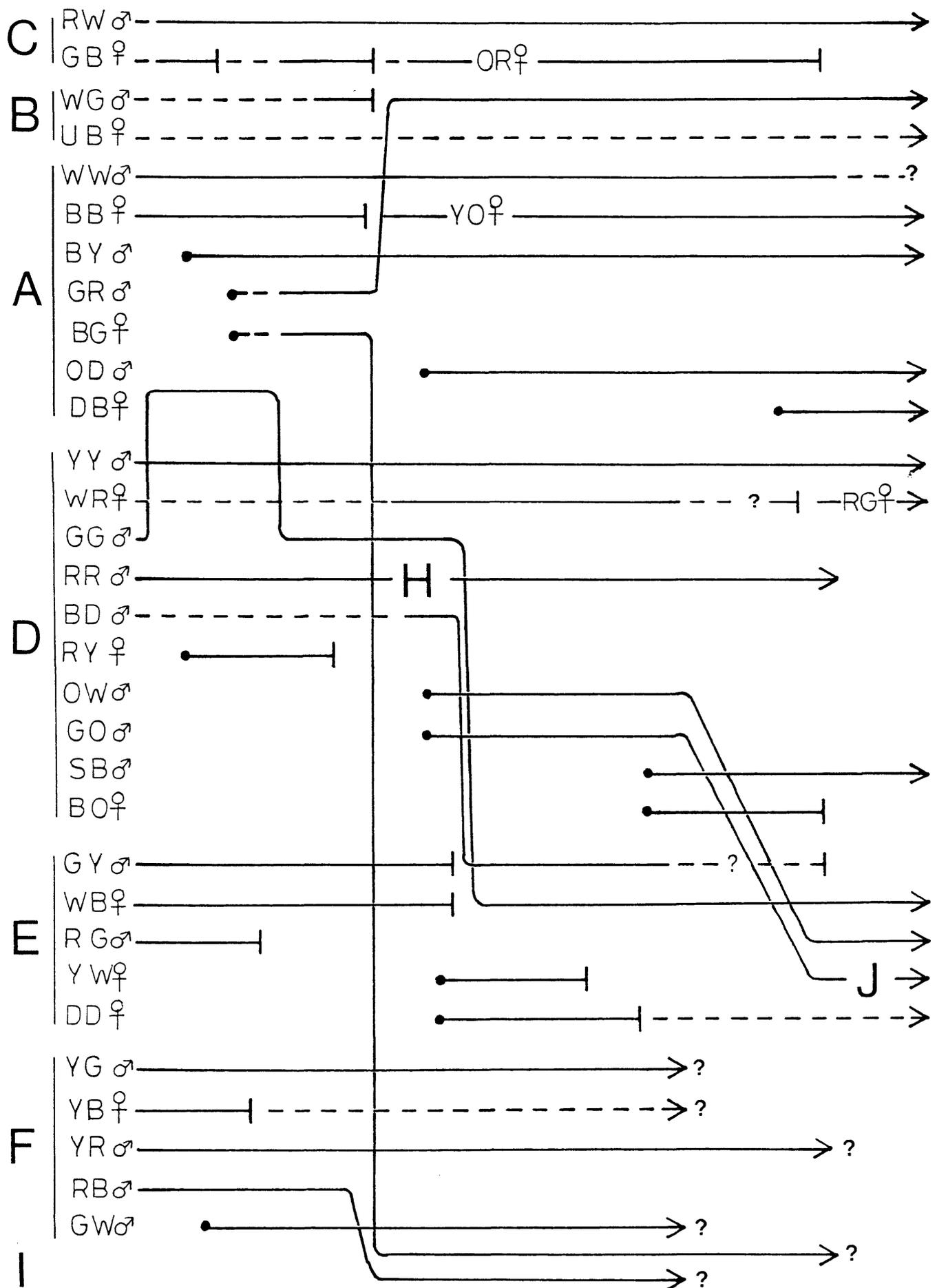
└─── date of disappearance

●─── date of fledging

Young which disappeared within 6 months of fledging, excluded

1977 1978 1979 1980

J S D M J S D M J S D M J S D M



number of occupants. The size of the six original territories was positively correlated with the number of occupants ($r_s = 0.96$, $N = 6$, $p < 0.01$), the two pairs holding the smallest territories (6.8 and 7.3 ha) and quartets possessing the largest areas (19.6 and 20.5 ha). The comparatively large size of territories and the "sharing" of territories by individuals in later years precluded accurate assessment of small scale expansions or contractions in the foraging range of groups concomitant with increases or reductions in membership. Some territories overlapped marginally (Figure 6.2), but less so than in the Red-browed, possibly because of the more dissected nature of the habitat at Swan Vale compared to Wollomombi.

Three of the original territories were subdivided to accommodate extra breeding units in subsequent years (Figure 6.2). Two such compartments or "sub-territories" were formed in 1978 when one of the auxiliary males in each of the two 1977 quartets ($D:RR\sigma$ and $F:RB\sigma$) mated with an immigrant female. After the demise of the group formerly occupying territory E , the auxiliaries from the neighbouring territory D ($BD\sigma$ and $GG\sigma$) appropriated the vacant area, and its three "orphans" (less than two months post-fledging). The two young produced by group D ($GO\sigma$ and $OW\sigma$) shared the two territories, until the disappearance of $BD\sigma$, whereupon one of them ($GO\sigma$) established his own "sub-territory" within territory E while the other joined $GG\sigma$ in the remaining area.

Territory-sharing was also evident in the eastern territories ($A-C$). Soon after fledging, the young from the first 1977 brood of group A were often seen in the adjacent territory C , where they were fed by the occupants, a simple pair whose first nest had failed. The male of this pair ($RW\sigma$) sometimes crossed the border into territory A to feed these young, though previously (and subsequently) this bird and the primary male of group A defended their territories against each other. The two young (including $BY\sigma$) continued to use territory C as well as their natal territory until the following breeding season, when $RW\sigma$ took a new mate (Figure 6.3). After at least one unsuccessful breeding attempt, this bird made repeated incursions into territory A to attend the nest of group A . The surviving young from this nest shared territories A and C during the following non-breeding season, as did $BY\sigma$ for the second year.

FIGURE 6.2: *Distribution of group territories of Brown Treecreepers at Swan Vale in the first breeding season*

Solid lines, territory boundaries in 1977 breeding season ; broken lines, subsequent subdivisions.

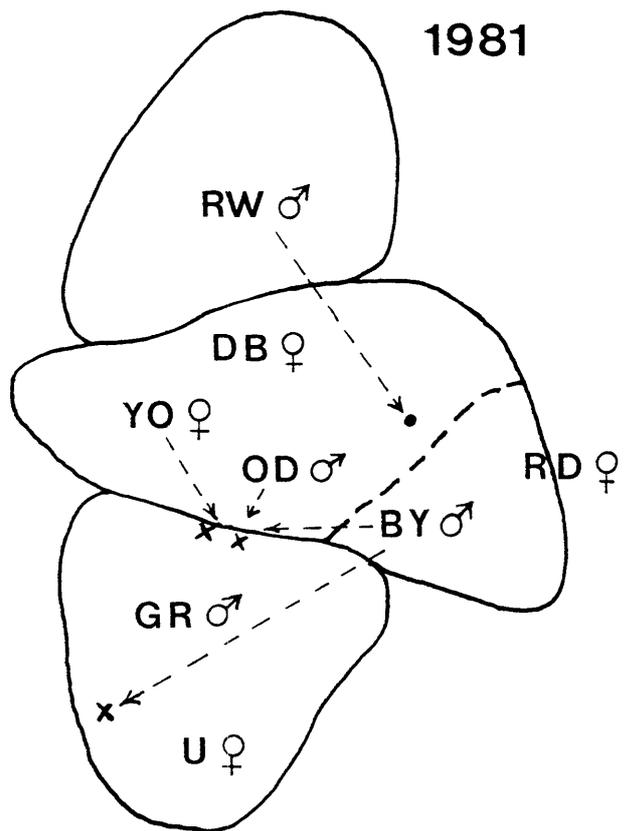
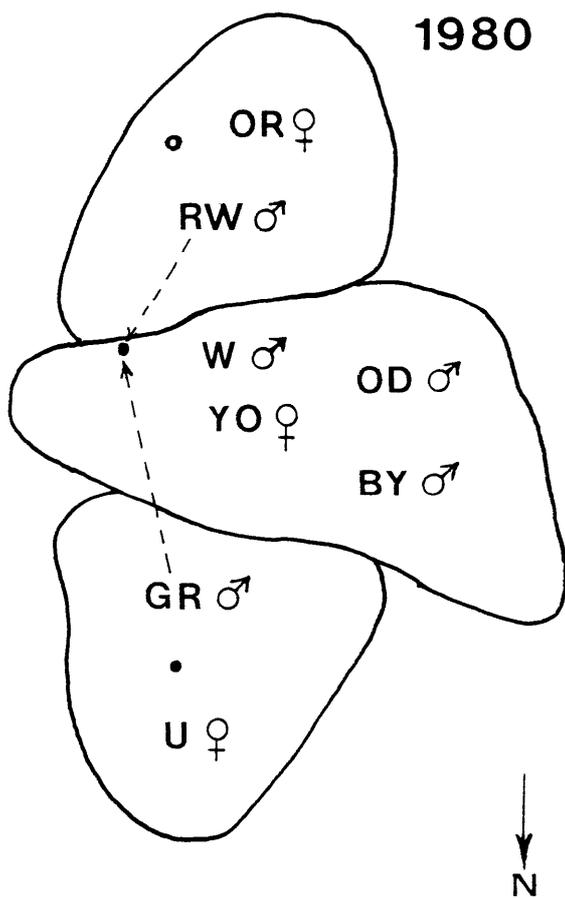
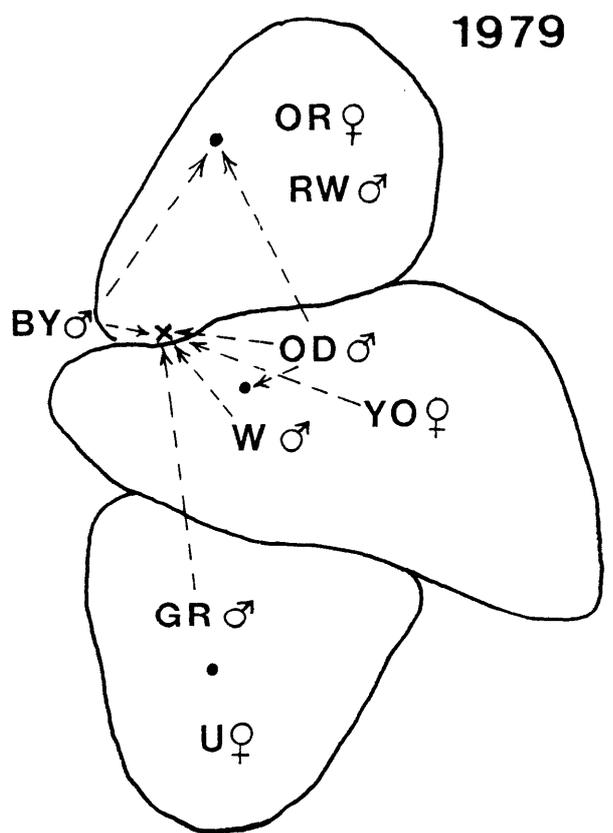
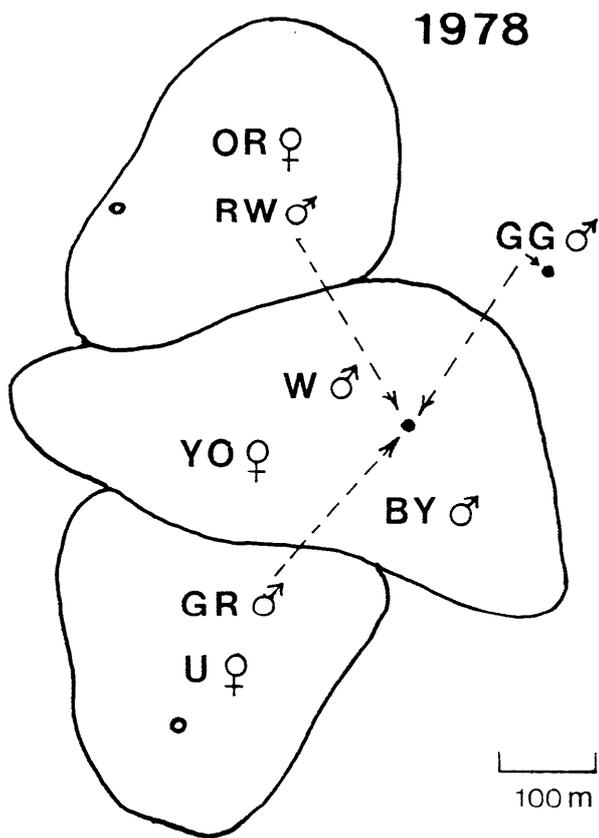
Letters correspond to those on Figure 6.1 (far left)

 trees
 creeks



FIGURE 6.3: *Group composition and helping behaviour of Brown Treecreepers in the three eastern territories at Swan Vale over four successive breeding seasons*

- successful nests
- unsuccessful nests
- ✕ location of fledglings
- ← provisioning
- W♂ = WW♂



Of the auxiliaries whose pedigree was known, most attended nests of their parents or father and step-mother (Table 6.3). Three individuals fed the young of their brother or step-brother (1981) and one fed the young of his mother and step-brother (1982). The relationship between auxiliaries and breeders in most other cases was obscured by the unknown pedigree of the former. There were only four definite instances of females attending young other than their own. Three of these involved breeders feeding fledglings which were presumably unrelated or distantly-related to them (GB♀ - 1977; YO♀ - 1979, 1981). In each case, the fledglings were on or near the boundary between their natal territory and that of the breeding female concerned (Figure 6.3). The auxiliary role of the yearling DB♀ in her natal territory (Figure 6.3, 1981) was unique and may have been connected with the disappearance of the breeding male (her father), as well as the frequent absence of the breeding female (her mother) from the nest she attended.

It is conceivable that territory *C* originated from subdivision of the larger territory *A*, and that RW♂ (*C*) split off from group *A* in the same way RR♂ and RB♂ did from their presumed natal groups (*D* and *F*, respectively). If so, he was probably related to the breeder of territory *A* (WW♂), and his continued interest in the young of that group over three seasons was possibly equivalent to that of GR♂, who repeatedly infiltrated territory *A* to feed its young, even after he had acquired breeding status. Similarly, the attendance of YY♂'s (*D*) nestlings by RR♂ after the latter had become a breeder, may also suggest close kinship between these birds. Though some cases of "outside help" involved breeders whose own nesting attempts had failed (Table 6.3), this was not always so. For example, GR♂ (*A*) attended his father's and his own young contemporaneously in two seasons (Table 6.3: 1979, 1980). Several non-breeders attended nestlings or nestlings and fledglings in two territories on the same day, sometimes visiting two nests within one hour (e.g. GG♂ - 1978; OD♂ - 1979, 1980; BY♂ - 1981).

6.4 Intraspecific Aggression

Aggression among group members was recorded less frequently in this species than in the Red-browed, but the few data suggest a dominance hierarchy within "families" similar to the one shown by that species.

TABLE 6.3: Instances of helping from within and outside groups/territories in Brown Treecreepers at Swan Vale

Year	WITHIN				OUTSIDE ^a			
	Aux- iliary	Breeder ♂ (territory)	Relationship ⁺ to breeding pair	Stage [#]	Aux- iliary	Breeder ♂ (territory)	Relationship ⁺ to breeding pair	Stage [#]
1977	RR♂	YY (D)	?	N	GG♂	WW (A)	?	N
	BD♂	YY (D)	?	N	*RW♂	WW (A)	?	F
	RC♂	GY (E)	?	N	*CB♀	WW (A)	?	F
	RB♂	YG (F)	?	N				
	YR♂	YG (F)	?	N				
1978	BY♂	WW (A)	son/step	N	GG♂	WW (A)	?	N
	GG♂	YY (D)	?	N	*GR♂	WW (A)	son/step	N
	BD♂	YY (D)	?	N	*RW♂	WW (A)	?	N
	YR♂	YG (F)	?	B	GW♂	RB (I)	b?	F
	GW♂	YG (F)	son/step	B	YR♂	RB (I)	b?	F
1979	OD♂	WW (A)	son	N	BY♂	RW (C)	?	N
	GO♂	YY (D)	son	N	OD♂	RW (C)	?	N
	OW♂	YY (D)	son	N	**GR♂	RW (C)	?	F
	GG♂	YY (D)	?	B	**WW♂	RW (C)	?	F
	YR♂	YG (F)	?	N	**YO♂	RW (C)	NR	F
	GW♂	YG (F)	son/step	N	GG♂	BD (E)	b?	N
	UP♂	YG (F)	?	N	*RR♂	YY (D)	?	N
					*RB♂	YG (F)	?	N
1980	OD♂	WW (A)	son	N	**GR♂	WW (A)	son/step	N
	BY♂	WW (A)	son/step	N	*RW♂	WW (A)	?	N
	SB♂	YY (D)	son/step	B	OW♂	GG (E)	?	N
1981	OD♂	? ?	?/son	N	BY♂	GR (B)	brother/NR	N
	BY♂	? ?	?/step	N	OD♂	GR (B)	step-brother/NR	F
	DB♀	? ?	?/daughter	N	**YO♀	GR (B)	step-mother/NR	F
	SB♂	YY (D)	son/step	N	SB♂	OW (E)	brother/?	N
					*OW♂	YY (D)	son/step	F
				*GG♂	YY (D)	?	F	
1982 ^b	OD♂	BY (A)	step-brother/ son	N				

a includes birds which established a "sub-territory" on original territory

+ son = son of both breeders; son/step = son of breeding ♂, step-son of breeding ♀;
b? = brother?, i.e. breeding ♂ originally auxiliary in same territory, thus probably
also son of breeder in original territory; NR = probably not related (as immigrant)

N = fed nestlings (usually also building and feeding ♀ and fledglings); B = building
only (nest failed sometimes); F = fed fledglings

* breeder

** successful breeder (i.e. produced fledglings)

b J. Courtney (pers. comm.)

Breeding males displaced auxiliaries and among siblings, older birds dominated younger birds. Both breeding and auxiliary males were observed to attack the breeding female twice each, and a first-year male displaced his mother once, although the reverse also occurred once. Aggressive interactions between groups were recorded 42 times, involving over 50 chases, usually across territorial borders or zones of overlap. Seven chases occurred between WW^σ (*A*) and RW^σ (*C*), in which the former was dominant four times and the latter, the remainder.

Intense aggression was apparently avoided through the frequent employment of an appeasement display similar to that in the Red-browed. When approached by the dominant bird, the subordinate bird usually crouched (head lowered and back arched), raised the wings slightly and fluttered them vigorously for several seconds. On several occasions, birds spread their wings for up to 30 seconds, presumably also denoting submission. As with the Red-browed, one intense battle was witnessed in the Brown. The protagonists wrestled on the ground with legs locked and wings spread, jabbing at each other with their bills for at least two minutes. This battle took place on the border of territories *A* and *B* just after the breeding male in the latter territory disappeared, and was a small part of a long confrontation involving all members of group *A* (including GG^σ) and two unbanded birds (presumably including the widow of territory *B*).

6.5 Vocalizations

I recognized six calls, which are described in Table 6.4. As with the Red-browed, antiphonal and simultaneous calling by two or more birds occurred, and all of the calls were given by both sexes, though the *pre-mating call* is probably mainly confined to males. The juvenile food-begging call of this species was barely distinct from the common call of adults, but there was a distinct *pre-mating call*, reminiscent of the White-throated. During courtship and nesting female Brown solicited food with the same call that accompanied submissive behaviour by either sex in intra-specific encounters. The evolution of a distinct alarm call (*rattle*) in this species is presumably related to their semi-terrestrial habits.

TABLE 6.4: Vocalizations of Brown Treecreepers

Name	Sex	Description	Context and other comments
1. Staccato	♂ ♀	High-pitched, often repeated, single notes with slight upward inflexion; a succession some-times develops which descends scale	Familiar call; juvenile food-begging call identical except thinner and higher-pitched
2. Rattle (alarm)	♂ ♀	Sustained, harsh, rasping noise	Frequently emitted when disturbed or when mobbing other species; also a component of <i>cackle</i> during intraspecific aggressive encounters
3. Cackle	♂ ♀	Variable call (possibly combination of several different calls), often consisting of rapid succession of strident notes or <i>rattle</i> rising the scale, punctuated by slower notes, falling in pitch	Mainly given in response to descending <i>staccato</i> calls and occasionally develops into short canary-like whistle
4. Pre-mating call	♂ occas. ♀	Chatter of six to ten monotonal notes, thinner than <i>staccato</i> notes, repeated up to 100 times or more with an interval of a few seconds between each chatter	Uttered by males on three occasions and female once, prior to pre-mating behaviour
5. Begging call	♂ ♀	Soft, high-pitched sound ("dring")	Given by females when accepting food on or off the nest; by both sexes during appeasement displays
6. Chirp	?	Soft, downward-inflected note	Heard infrequently; probably also a component of <i>cackles</i>

6.6 Courtship Feeding and Copulation

As in the Red-browed, both primary and auxiliary males fed the female prior to and during the breeding season. Such feedings took place both on the ground and in trees, and before being fed females sometimes crouched submissively, fluttered the wings, fanned the tail and gaped the bill, while uttering *begging calls*.

Copulation was witnessed twice, though pre-copulation behaviour and calls were noted on two other occasions. As with the Red-browed, the female crouched low with quivering wings (see also Orenstein 1976: 456) and raised her tail, before the male mounted, but this took place on horizontal branches in each case. The distinctive *pre-mating call* (see Section 6.5) was repeated continuously for up to ten minutes, mostly while stationary, once by a female and thrice by males. The males uttered this call while holding an insect in the bill, whereas the female's bill was empty during her call. When the partner arrived, both birds hopped excitedly between branches, often facing each other and occasionally bowing. The pre-mating display described by Orenstein (1976: 456) was similar: the male bowed back and forth in front of the female before sidling behind her and mounting.

6.7 Interspecific Agonism, Mobbing and Nest Defence

Aggressive interactions between the White-throated and Brown Treecreepers at Swan Vale were witnessed 19 times, involving 37 displacements. In all cases, the larger Brown was dominant. Despite these occasional squabbles, there was no evidence to suggest the operation of interspecific territoriality, as proposed by Orenstein (1976: 456) since large areas of overlap occurred between the territories of the two species, and in some cases, complete overlap. Indeed, it is difficult to see why these birds, so different in morphology (see Section 3.1.1) behaviour and foraging ecology would defend territories against each other.

Mobbing behaviour was seen nine times. Five of these involved potential predators, one a Red-bellied Black Snake, *Pseudechis porphyriacus*, and another a feral cat. In the remaining three instances, solitary Yellow-footed Marsupial Mice, *Antechinus flavipes*, were harassed as they scurried

between holes in hollow logs or stumps on or near the ground. The birds hopped agitatedly around the hole containing the mammal, spreading their wings repeatedly and emitting *rattles* (Table 6.4) almost incessantly; these activities continued for almost an hour on one occasion which took place below an occupied nest tree.

Identical behaviour was recorded when trios of birds tormented an Owlet-Nightjar, *Aegotheles cristatus* and a Brush-tailed Possum on separate occasions, both at the entrance to hollow spouts high in trees. These two species and *Antechinus* might compete with treecreepers for nest and roost-sites. A roost-site of Brown Treecreepers near Cunnamulla, Queensland, was subsequently occupied by an Owlet-Nightjar (unpubl. data). Another victim of mobbing by this species was a Ring-tailed Possum, *Pseudocheirus peregrinus*, resting in foliage during the day, though this mammal roosts and nests in arboreal stick nests.

Yet another display is used by this species when defending young members of the group. Frequently when I approached fledglings, climbed nests containing young or examined nestlings in the hand, adults nearby made short low flights, fluttering vigorously for a few seconds then gliding on up-stretched wings sometimes accompanied by *rattles*. These peculiar "butterfly" flights presumably serve to distract or deter potential predators.

6.8 Roosting

The Brown roosted solitarily in similar situations to the Red-browed, usually hidden within dead hollows. All but two of the 41 roost-sites found at Swan Vale were in old (ring-barked) dead trees or stumps. Approximately one half of the hollows were below the top of vertical trunks, and the other half, in oblique broken branches. Two such sites were also used for nesting. The two exceptional roost-sites were also below the top of hollow, severed trunks but retained the external "live" bark (one a stringybark, and the other an ironbark); both were located in the forest. Thirty sites ranged in height from 1.1 to 10.4 metres ($\bar{x} \pm \text{SE} = 4.3 \pm 0.35$ m). At Stringybark Hill, two sites were under slabs of peeling bark on the trunks of dead gums, and the remaining four in hollows of dead trees. An immature

bird at Wollomombi roosted in a large hole in the trunk of a box twice, and another occupied a regular White-throated roost-site one night (Noske 1977), exceptional as it was exposed. The remaining seven sites of Brown at Wollomombi were in hollow dead tree trunks, three of which were at some time used by Red-browed instead.

6.9 Breeding Season and Brood Frequency

At Swan Vale, laying commenced in late July-early August, while the first clutch recorded at Stringybark Hill was in mid-August (Figure 6.4). This was about three weeks earlier than the first clutches of White-throated at both sites. At Tenterfield (160 km north of Armidale), eggs were found as early as mid-July twice (M.T. Goddard *in litt.*), but most occurred in mid-August (Figure 6.4). Latest clutches found in that district were in early October, whereas at Swan Vale, eggs were once recorded in November. Thus although the breeding season of Brown at Swan Vale began earlier than that of the White-throated, it finished at about the same time, or even later.

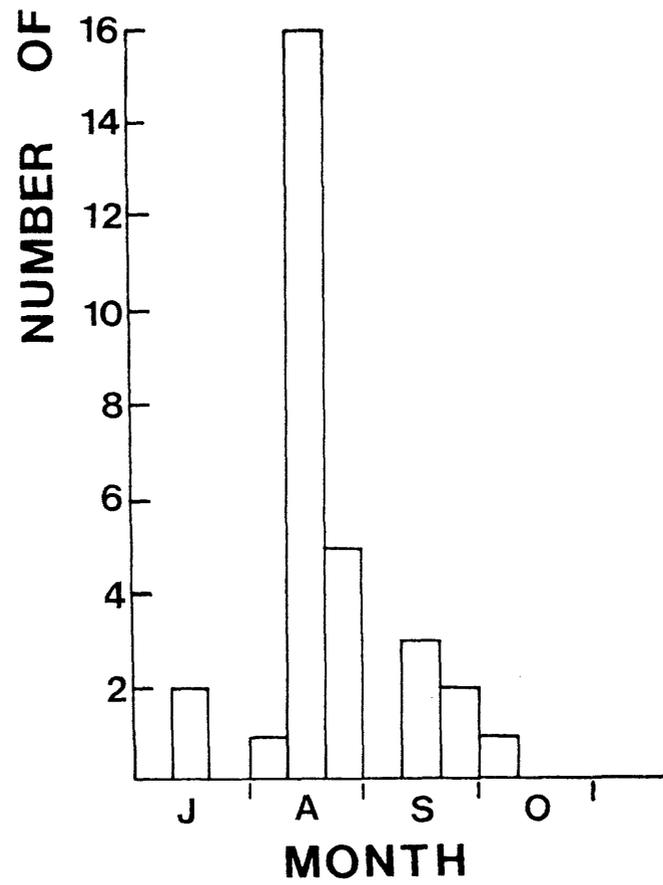
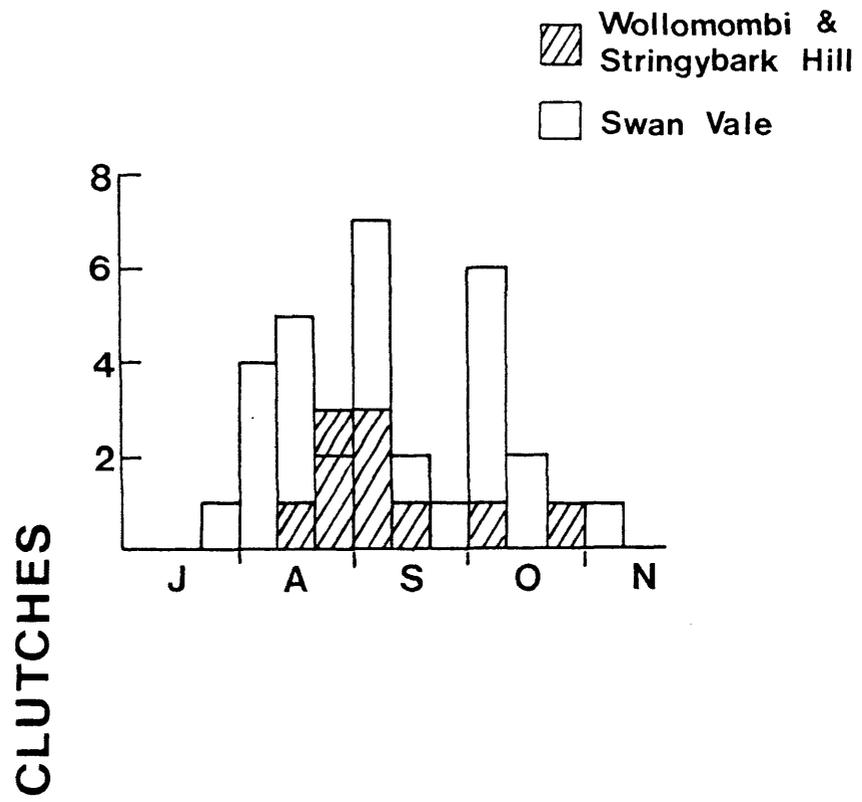
Despite statements by some (e.g. Hyem 1936; Beruldsen 1980), this species is clearly multi-brooded at times. At Swan Vale, one trio (A) raised two broods (five fledglings) successfully in the 1977 season, and two groups (A, C) attempted second broods (unsuccessfully in 1979). In three seasons at Stringybark Hill, second broods succeeded once (1979) and failed twice. The successful second clutch at Stringybark Hill was laid only 14 days after the first brood fledged from the same nest. A nest at Swan Vale was being refurbished about ten to 15 days after the first brood fledged. J. Hobbs (NRS: 7/67 and 8/67) recorded hatching of a clutch 33 to 44 days subsequent to the fledging of an earlier brood from the same nest.

6.10 Nest-sites

All but six of the 41 nests at Swan Vale were built in old, hollow dead trees or stumps. Of the exceptions, four were in dead spouts of live gums (one repeat) and the remaining two nests in a hole in a live stringybark. The same hole was used successfully by White-throated in 1977, but

FIGURE 6.4: *Estimated laying dates of final eggs of Brown Treecreepers at the study sites (upper) and other localities in north-eastern New South Wales (lower, M.T. Goddard in litt.)*

Dates extrapolated as explained in Figure 4.3



both Brown clutches laid in the following two years failed. Of the 41 sites, 63% were in vertical hollows, and the remainder in horizontal or oblique spouts. Ignoring two rotten fenceposts, about one half of the nests in dead trees were situated in the main axis or trunk, and the other half in broken branches.

Eight sites at Swan Vale were used twice: once in the same season, four in consecutive seasons, and the remaining three, between two and four years apart. At Stringybark Hill, a hollow dead spout of a live stringybark was used four times in three seasons, and at Wollomombi, a hollow branch of a mostly-dead stringybark, three times in three seasons. Nest-sites at Swan Vale were significantly higher in the 1977 season than in either the 1979 or 1980/81 (combined) seasons ($t = 2.85$, 21 df, $p < 0.01$ and $t = 3.13$, 19 df, $p < 0.01$ respectively). Similarly, sites in 1978 were lower than those in 1977 (means = 4.9 and 7.1 metres, respectively), but the difference was not significant ($t = 1.63$, 15 df, $p > 0.1$).

Overall, heights of sites at Swan Vale varied from 1.2 to 12.2 metres ($\bar{X} \pm SE = 4.9 \pm 0.41$), a similar vertical range to roost-sites. At Wollomombi, the height of seven nests built by the same pair over five seasons varied from 1.3 to 11.6 metres ($\bar{X} \pm SE = 8.3 \pm 1.48$ m). The depth of seven nest-holes varied from 25 to 60 centimetres, though another nest-hole at Swan Vale in 1951 was 86 centimetres deep (J. Courtney *in litt.*); records in NRS gave a similar range of depths. The diameter of entrances to nest-holes ranged from 6 to 13 centimetres.

6.11 Building

As in the previous species nest-building was shared among all members of the group, but much of the initial heavier material was brought by the female (Table 6.5). One female at Stringybark Hill carried dried grass 13 times to her nest in 17 minutes, while another at Wollomombi took bark five times in seven minutes. However, males took most of the lining (including fur, feathers, snakeskin and thistle-down), a habit which continued through the incubation and nestling stages, almost until fledging. Four males carrying material visited one nest within 17 minutes; two of the auxiliaries arrived simultaneously and waited until the incubating female

TABLE 6.5: Contributions (%) of attendants at all nests (combined) of Brown Treecreepers with auxiliaries

Activity	Primary ♂	Auxiliary ♂♂	♀	N
Building* I	14.3	7.1	78.6	14
II	56.3	28.1	15.6	32
Feeding incubating ♀ ⁺	51.2	48.8	-	41
Feeding young ⁺	30.9	48.3	20.8	298
Removing faecal sacs [#]	41.7	30.5	27.8	36

* building stages: I - bark or grass; II - lining (fur, feathers or snakeskin)

+ visits to the nest without food excluded; feeding of ♀ while sitting only; no account taken of size/quality of food

includes several data from other sites owing to small sample sizes for Swan Vale

departed before entering the nest. "Bill-sweeping" was performed on seven occasions, twice by females and the remainder, by males. Snakeskin was used twice and fur once but the material was unidentified in the remaining cases. One female swept around the entrance to its nest for over 15 minutes on the day before it laid, while a male swept inside its nest for two minutes during the mid-nestling stage.

6.12 Clutch Size and Laying Routine

Owing to the addition of nest lining during and following egg laying, the clutch size of this species (like other treecreepers) may occasionally be underestimated. Complete or partial concealment of clutches was recorded at four nests when inspected between the laying and hatching dates. Nevertheless, C/3 were about three to four times more common than C/2 at my study sites (combined) and at Tenterfield (Table 6.6). Clutches of two eggs were more frequent in NRS records from more southerly locations.

Eggs are probably laid at intervals of about 24 hours. One C/3 was laid within three days and a C/2 within two days. However, the third (and final) egg of another clutch was laid at least 42 hours after the second; hatching was never observed at this nest, but two of the nestlings were substantially larger and heavier than the other suggesting that incubation had started before the completion of the clutch. Moreover, the weights of three nestlings at another nest ranged from 9.5 to 21.3 grams, indicating a difference in age of two to three days (unpubl. data).

6.13 Incubation

Hyem (1936) asserted that the "eggs take 15 days to hatch and the young leave the nest 15 days later", but gave no supporting details. This claim was iterated by Hindwood (1966) and Orenstein (1976). Courtney and Marchant (1971) calculated the incubation period at one nest to be 12 days 8 hours (\pm about $1\frac{1}{2}$ days) but one of the three eggs never hatched and the third egg was apparently laid after incubation had commenced (J. Courtney, pers. comm.). If the first two eggs laid were the ones that hatched the

TABLE 6.6: Clutch size of Brown Treecreepers

	C/2	C/3	Total	Average
Swan Vale*	5	21	26	
Wollomombi Falls/ Stringybark Hill	1	6	7	
TOTAL	6	27	33	2.82
Local ⁺	9	26	35	
NRS	12	17	29	
TOTAL	21	43	64	2.67
GRAND TOTAL	27	70	97	2.72

* includes 5 nests (at same locality) recorded in Courtney and Marchant (1971)

+ data provided by M.T. Goddard

above determination may be an underestimate. Information recorded at another nest (NRS: 1/78) gives a minimum period of 14 days 6 hours.

My data suggest the incubation period is closer to 16 days (Table 6.7), only one day more than Hyem (1936) contended. However, Hyem apparently underestimated the nestling period of the species, which according to Table 6.7, varies from 20 to 25 days. This variation, not evident in the other species, probably relates to the comparatively accessible nests of the Brown and the consequent vulnerability of their nestlings to potential predators, resulting in frequent premature fledging.

Attendance by incubating females during observations at five nests at Swan Vale totalling 9.1 hours was approximately 57%. However, during 140 minutes of continuous observation at one Wollomombi nest, the female incubated for 72% of the time. The average duration (\pm SE) of 35 incubating sessions was 11.8 (\pm 1.39) minutes, slightly higher than that for periods of absence ($\bar{X} \pm$ SE = 9.4 \pm 1.46 mins; N = 25). The longest incubating sessions were recorded at Stringybark Hill (over 60 minutes once) and Wollomombi (45 minutes).

As with the other species of treecreepers, the female alone incubates and broods the young. Males continue to feed the female for at least a few days after the young hatch. The average rate of feeding of sitting females for combined watches totalling 5.9 hours (minimum 37 minutes) was 6.3 per hour. Auxiliaries were seen feeding the incubating female on the nest almost as often as primary males (Table 6.5), but considering the greater number of auxiliaries involved, their efforts were less than the latter. Begging young probably provided a greater stimulus for auxiliaries to feed than the sitting female.

6.14 Feeding of Nestlings

All group members fed the nestlings and removed their faecal sacs. At nests with three or more attendants, the overall feeding contribution of auxiliaries was almost as great as that of the primary pair (Table 6.5) but this may vary according to the number of auxiliaries in the group (Figure 6.5). Four auxiliaries at one nest provided 60% of the food (Figure 6.5)

TABLE 6.7: *Incubation and nestling periods* of Brown Treecreepers*

	Minimum			Maximum	
	Days	Hours		Days	Hours
INCUBATION PERIOD	16	0	————→	17	20
	14	5	————→	16	5
	16	1		18	0
NESTLING PERIOD	25	1	————→	26	1
	23	20	————→	25	20
	+ 17	0	————→	22	0
	26	2		25	0
	17	5		24	1
	+ 21	0		24	0
	+ 21	0		20	2
	+ 21	0		+ 21	0
+ 19	0				
+ 19	0				

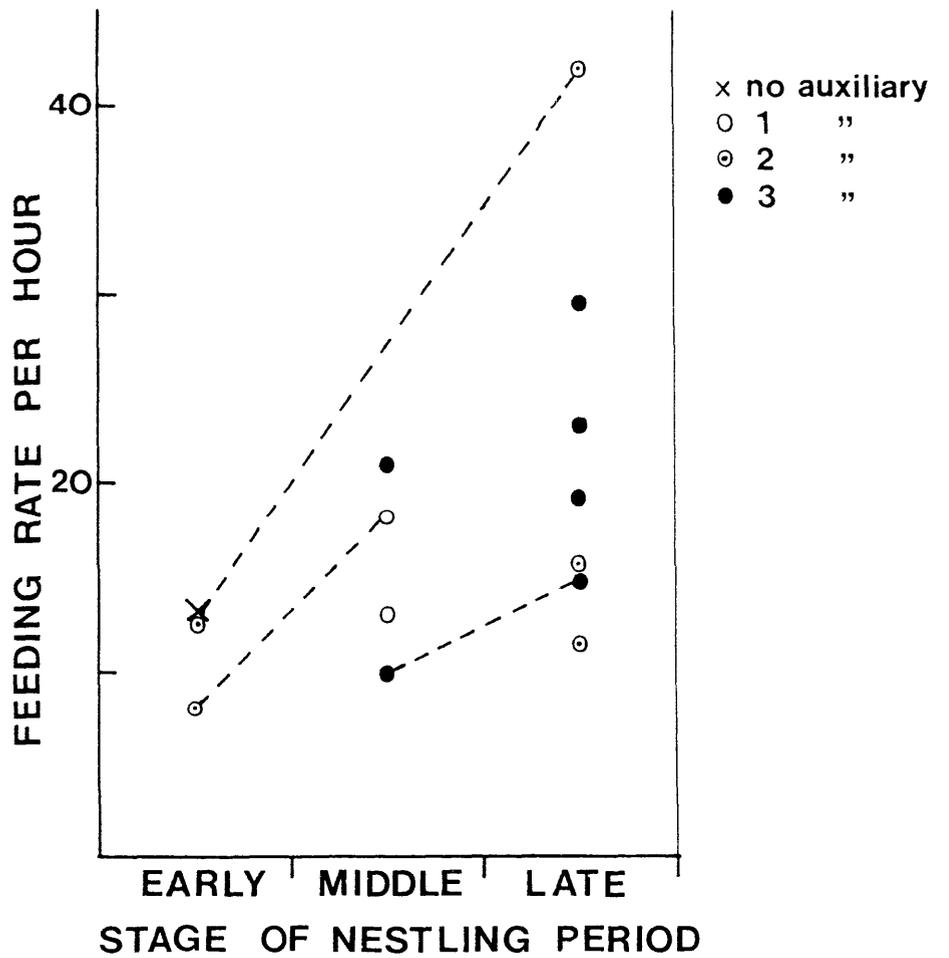
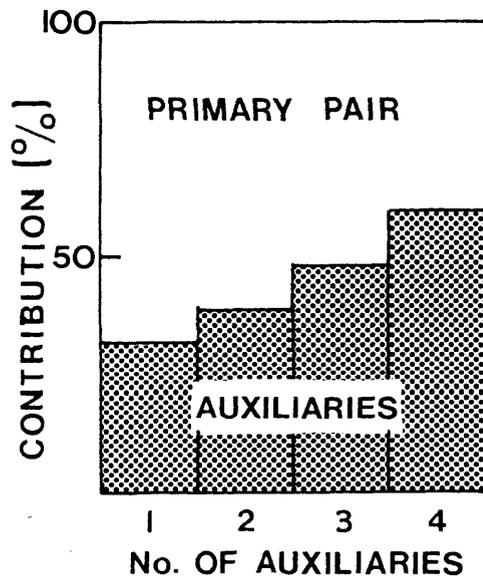
* arrows connect data pertaining to the same nest;
where no arrow data pertain to different nests

+ calculated from data in NRS; all other periods
personal observation

FIGURE 6.5: *Contributions of auxiliary Brown Treecreepers at nests with different numbers of attendants during the late nestling stage (upper) and feeding rates at each nestling stage (lower), at Swan Vale*

In upper graph, each bar represents one nest; nests with one, two, three and four auxiliaries observed for 180, 223, 135 and 164 minutes, respectively.

In lower graph, total observation periods for the three stages in sequence : 283, 421 and 626 minutes; dashed line connects observations at the same nest



while at another nest with nestlings of the same age, the four auxiliaries provided 72% of the food during 90 minutes of continuous observation. At the latter nest, however, the female spent most of the time attempting to distract the observer, with incessant mobbing behaviour. Primary males provided more food than their mates overall (Table 6.5) but this may have been partly due to the wariness of females, such as the one above. There were insufficient data to analyze the effects of other factors likely to influence the relative feeding contributions of attendants (e.g. age or experience of auxiliaries and size or quantity of food; see Stallcup and Woolfenden 1978). Yet evidence suggests that the provisioning efforts of auxiliaries are significant, and probably reduce the efforts of the primary pair in most cases.

Food delivery rates, recorded during watches of not less than 30 minutes varied from 8.0 to 42.0 per hour, the average for 22.2 hours being 17.9 per hour. However, during a watch of two hours at Wollomombi, recently-hatched young were fed only eight times (4.0 per hour). These feeding rates exclude non-feeding visits, which were mostly by auxiliaries, though occasionally primary males brought nest material instead of food. Feeding rates probably increased as the young grew (Figure 6.5), but other factors such as number of attendants, brood size and time of day were not considered. Brown *et al.* (1978) however, showed that the rate of feeding of nestling Grey-crowned Babblers, *Pomatostomus temporalis*, was independent of the number of helpers.

6.15 Fledglings and Reproductive Success

On their first day or two out of the nest, young Brown invariably sheltered in hollow spouts of dead trees, where they called and received food as they did in the nest. Such trees were refuges for young birds which fledged prematurely, as well as those that remained nestlings for the full term. One brood which had spent 23 or 24 days in the nest were still sheltering in hollow spouts five days after fledging. However, from 20 days post-hatching, some nestlings made short climbing excursions outside the nest-hole. Fledging of brood members apparently took place over several hours when all fledged on the same day. Sometimes they flew to the same

tree and remained together, but more often they separated, forcing the adults to feed at two or three sites.

Juveniles become independent between 30 and 40 days after fledging. Birds from two different broods were still being fed 32 days after fledging. Yet at Stringybark Hill one 45 day old (post-fledging) male from an early brood fed the nestlings in a later brood, and even removed their faecal sacs. Seven days later, his sister was also seen feeding the second brood. This was the only nest at which I observed "helping" behaviour by juvenile treecreepers.

Pairs with auxiliaries produced more offspring than those without in all seasons, though on a *per capita* basis, "groups" were no more successful than simple pairs in 1978 (Table 6.8). Breeding success was highest in 1977 when nests were higher than in other years (see Section 6.10). The pair at Wollomombi produced six fledglings over four seasons (1.5 per year), with assistance from a son in one season only. The group at Stringybark Hill produced nine fledglings (2, 4, 3) over three seasons (as a trio, quartet and pair, respectively), averaging 0.8 per individual. Thus, these two somewhat isolated populations were more productive than the population at Swan Vale overall (Table 6.8).

6.16 Conclusions

Many aspects of the social organization and breeding biology of the Brown Treecreeper resemble those of the Red-browed. Differences between these two species in their ecology perhaps explain the greater complexity of communal behaviour in the former. The habitat of the Red-browed was relatively homogeneous and well-timbered, while that of the Brown was dissected and largely open. Ground feeding in such open situations expose the Brown to predation from terrestrial reptiles and mammals (particularly the introduced fox, *Vulpes vulpes*). Animals living in groups can detect and deter predators more efficiently than solitary ones (see review by Bertram 1978).

The need for improved surveillance and protection from predators in this species is reflected in the evolution of a distinct "alarm" call (absent in the White-throated and Red-browed), which is an important element

TABLE 6.8: Reproductive success* of Brown Treecreepers at Swan Vale over three breeding seasons for pairs with and without auxiliaries

	Year	Year		Total average	N	
		Without	With		Without	With
Per breeding unit	1977	0	3.0	2.0	2	4
	1978	1.0	1.7	1.3	5	3
	1979	0.5	1.2	1.0	2	9
TOTAL AVERAGE		0.7	1.8	1.4	9	13
Per individual	1977	0	0.9	0.7	4	14
	1978	0.5	0.5	0.5	10	11
	1979	0.3	0.4	0.3	4	20
TOTAL AVERAGE		0.3	0.5	0.5	18	45

* expressed as number of fledglings produced per pair/group (upper) and per adult individual (lower); N = number of breeding units (upper) and number of adults (lower)

of mobbing behaviour and defence of young birds. The characteristic tail-bobbing of this species and other ground-frequenting treecreepers (pers. obs.) may also have an anti-predator function, as it occurs mainly when birds are agitated or excited. Such conspicuous, rapid movements of the tail may serve to warn conspecifics of danger, or to discourage potential predators by advertising alertness (Woodland *et al.* 1980), or both. Though there does not appear to be any rigid or organized sentinel system as exists in some other ground feeding communal species (e.g. *Turdoides*, Gaston 1977, 1978), wary individuals often fulfil the role of a sentry for short periods while other members of the group continue or resume foraging.

Another advantage of group-living in many gregarious species is the improved ability to locate and exploit patchily distributed food. However, this appears to be of little importance to the Brown and Red-browed Treecreepers, in which group members forage separately (rarely closer than three metres) and roost solitarily. The possibility of "social facilitation" in foraging is investigated more thoroughly in a later chapter.

Chapter 7

COMPARISON OF TREECREEPERS IN RELATION
TO COMMUNAL BREEDING

The essential difference between the life history strategies represented by the White-throated on the one hand, and the Red-browed and Brown on the other, is in their treatment of offspring. In the White-throated, ostracism of progeny leads to widespread dispersal, while the tolerance and retention of young in the other two species results in reduced dispersal, and ultimately in communal breeding. Brown (1974) compared the behaviour and general ecological characteristics of communal and non-communal species of New World Jays (Corvidae). Demographic features of the communal species were low dispersal, high survival (longevity), deferred maturity and low fecundity. As such features are typical of population densities at or near the theoretical carrying capacity of their environment, he viewed communal behaviour as a 'K-selected' strategy, while non-communal species were regarded as relatively 'r-selected'; several other workers have used this analogy (Emlen 1978; Gaston 1978, 1980). The non-communal White-throated certainly exhibits greater dispersal than its communal relatives, and there is some evidence of lower survival and higher fecundity in this species relative to the other treecreepers.

The mortality rate of White-throated at Swan Vale was much higher than that of the Brown, and while mortality rates (in the first year after banding) of White-throated and Red-browed at Wollomombi were similar, about a third of the Red-browed banded between 1976 and 1979 survived into 1982, compared with only 14% of the White-throated. The population structure of the Red-browed (and the Brown) was thus "older" than that of the White-throated. All three species of treecreepers are apparently capable of breeding in their first year (pers. obs.), but as Koenig and Pitelka (1981:262) point out, several communal species, previously thought to exhibit delayed sexual maturity, have been shown to be capable of breeding as yearlings. Woolfenden (1981:260) further suggests that the lack of breeding opportunities is a more likely explanation of delayed breeding in the Florida Scrub Jay *Aphelecoma coerulescens*, than inability to attain sexual maturity.

There is some evidence in both the Red-browed and Brown that groups with auxiliaries breed more successfully than those without auxiliaries (pairs). This is consistent with evidence for many, but not all, communal breeding species studied to date (see Brown 1978 and Emlen 1978 for reviews). Yet on a *per capita* basis, reproductive success among communal breeders is usually inversely related to group size (Koenig 1981; Koenig and Pitelka 1981). Brown (1974: 77) suggested, without documentation, that communal species of jays had lower reproductive rates (*per capita*) than non-communal species of jays. Indeed among the treecreepers, the White-throated raised more young per individual overall than either the Red-browed at Wollomombi, or Brown at Swan Vale (Table 7.1). Dow (1980b) cited evidence from several Australian studies that indicate reproductive success of communal breeders is generally low. He suggested that the long life-spans of communal breeders (e.g. Fry 1980) permitted a more "leisurely approach to reproduction", auxiliaries providing the breeder with the means to reduce reproductive effort. Such energy savings may also increase the opportunities for a second, or even a third brood (references in Brown 1978: 133). Indeed, the communal Red-browed and Brown Treecreepers occasionally raised second broods, while the White-throated did not, but this may be largely due to other factors (e.g. protracted courtship and larger incubation period of the latter) and has not, in any case increased fecundity in the former as Table 7.1 shows.

Communal breeding has been reported in over 60 species from 20 families of Australian birds (Dow 1980a), though the regularity with which these species breed communally probably varies greatly. In some species, group living appears almost obligatory (e.g. *Corcorax*, *Manorina*), while others (e.g. *Malurus cyaneus*) are socially opportunistic from year to year (Dow 1980a,b). The ecological and behavioural diversity of species exhibiting communal breeding has impressed many (e.g. Brown 1974, 1978; Rowley 1976; Emlen 1978), suggesting that the strategy has evolved independently many times. This diversity has not, however, discouraged workers from attempting to identify a common ecological link between such species.

Rowley (1965, 1976) and Harrison (1969b) proposed that communal breeding was an adaptation to an erratic and unpredictable, or harsh

TABLE 7.1 : Comparison of reproductive success of treecreepers

Year	No. of Fledglings	No. of Adults	Fledglings /Adult	No. of Fledglings	No. of Adults	Fledglings /Adult
	WHITE-THROATED					
1977	6	14	0.43	11	20	0.55
1978	16	18	0.89	5	19	0.26
1979	14	22	0.64	6	17	0.35
TOTAL	36	54	0.67	22	56	0.39
	RED-BROWED					
	WHITE-THROATED					
1977	-	-	-	12	18	0.67
1978	5	8	0.63	10	21	0.48
1979	5	8	0.63	8	24	0.33
TOTAL	10	16	0.63	30	63	0.48
	BROWN					

climate, enabling species to maximize reproductive output during favourable conditions, and this hypothesis has recently been supported by Emlen (1982). Dow (1980a,b), on the other hand, stressed the stable and equable nature of the Australian environment, and, as mentioned above, viewed communal breeding as a strategy which lowered rather than increased reproductive effort. In fact, Brown (1974) originally hypothesized that communal breeding should be associated with stable and climax environments but he later (Brown 1978) retracted this idea.

After a systematic, quantitative analysis of environmental (mostly climatic) variables likely to affect the distribution of communal breeders, Dow (1980a) concluded that no single factor could account for the incidence of communal breeding in Australia. He showed that communal breeding species in Australia were least numerous in deserts, and most numerous in tall mesic forests. By contrast, Gaston (1980) suggested that semi-arid scrub and dry deciduous woodland provided the optimal conditions for the evolution of group territorial behaviour (and communal breeding), and implied that moist forests were not conducive to this strategy. The Brown and White-throated Treecreepers appear to conform to this pattern. The communal Red-browed however, is an inhabitant of mesic environments, though it may have evolved in drier habitats. Indeed, the closest relative of the Red-browed, the White-browed, is the driest-adapted of all treecreepers, and is almost certainly non-communal (Noske 1980, unpubl. data). Interestingly, of the four species of *Cissolopha* (New World Jays) studied by Raitt and Hardy (1979), the least social (*C. beecheii*) lives in a more arid, seasonal environment than its congeners.

Koenig and Pitelka (1981) and Emlen (1982) emphasized the role of resource localization in the evolution of group-living and communal breeding. Central to their thesis is the assumption that most communal breeders are specialized in their habitat or resource requirements. In such cases, all optimal habitats are filled ('saturated') and young are forced to remain on their natal territory, moving only when another 'good' area becomes vacant (see also Stacey 1979). Non-communal species, by contrast, are able to take advantage of 'marginal' habitats and dispersing young stand a good chance of establishing territories and breeding on their own. The White-throated Treecreeper is more generalized in its habitat

requirements than its congeners, and thus able to colonize "new" habitats such as small patches of timber in cleared areas, and exotic pine forests (see Section 4.16). That the Red-browed and Brown Treecreepers have narrower habitat requirements is suggested by the observation that they have not colonized such habitats, and in the case of the Red-browed, its localized distribution. Large territories in the latter also possibly indicates more specialized resource requirements than in the White-throated.

As auxiliaries often enhance the reproductive success of breeders or at least ease their burden (Brown *et al.* 1978), the benefits of the communal breeding strategy to breeders (the recipients) are obvious. But what advantage could accrue to auxiliaries (the donors)? Since auxiliaries forfeit the opportunity to breed in order to "aid" other individuals, it has commonly been assumed that "helping" is altruistic. The fact that auxiliaries are often the offspring of the breeding pair and therefore helping to raise their own siblings led to the conclusion that kin selection was important in the evolution of helping behaviour (e.g. Brown 1974, 1978, 1979; Bertram 1978). Koenig and Pitelka (1981), however, warned against this interpretation. They contended that cooperation among siblings is due largely to the intimate social bond between individuals that have grown up together rather than to any genetic advantage gained.

Several authors have argued that helping is actually an indirect strategy for personal gain - a selfish rather than altruistic act (Zahavi 1974; Rowley 1978; Woolfenden and Fitzpatrick 1978; Woolfenden 1980, 1981; Ligon and Ligon 1978a; Ligon 1980, 1981). Woolfenden and Fitzpatrick (1978) demonstrated that male Florida Scrub Jay auxiliaries increase their own chances of becoming breeders by helping through a process called "budding". By their provisioning efforts, auxiliaries help to increase the size of the group, which in turn leads to expansion of the territory. The dominant male auxiliary then takes possession of a segment of the group territory, where he pairs with a female (always from outside the group) and commences breeding. A similar process seems to operate in the communal treecreepers. Although not the result of territorial expansion, three auxiliary Brown and one auxiliary Red-browed gained breeding status by subdivision of their former group territories.

Helping is not always directed at closely-related individuals. The principle of "reciprocal altruism" or "reciprocity" was originally proposed by Trivers (1971) to account for presumed acts of altruism directed at distant relatives or unrelated individuals. Simply stated, selection will favour such behaviour when there is a good chance that the donor (auxiliary) will be "repaid" in the future by the recipient. The studies of Ligon (1980, 1981) and Emlen (1981) provide some support for this hypothesis. Ligon and Ligon (1978a) suggest that in the Green Woodhoopoe, *Phoeniculus purpureus* nestlings (whether related or not) are a valuable resource to auxiliaries, which utilize them in establishing a new territory and in helping to raise their young when they become breeders. That several groups of this species contained hard-working auxiliaries, which were unrelated to either members of the breeding pair, they believed, weakened the kin selection explanation for communal breeding. Brown (1979), however, criticized their interpretation, arguing that kin selection requires neither discrimination by relatedness nor individual sacrifice, and was thus, not inconsistent with their findings. Clearly the precise roles of individual and kin selection have yet to be determined.

Several features of the nesting behaviour of the Brown Treecreeper are unusual among communal breeders. In this species, breeders often accepted help from brothers or even unrelated birds, at least during the nestling and fledgling stages. By contrast, of 56 auxiliary Florida Scrub Jays, all but five helped their parents or one of their parents (plus step-parent) (Woolfenden 1975). Four of the remaining five helped their brothers. Normally, however, breeders in this species did not tolerate the intrusion of any individuals other than their own young. In the Brown Treecreeper, it was not uncommon for non-breeders and even breeders to attend two nests in different territories contemporaneously. I can find no references to such activities in other communal breeding species. In the Mexican Jay, *Aphelocoma ultramarina* (Brown 1970, 1972) and several species of jays belonging to the genus *Cissilopha* (Hardy 1976; Raitt and Hardy 1976), communal flocks often contain two or more breeding pairs which nest concurrently within a common territory but there is no evidence of sub-territories or areas within the flock-territory being defended (Brown 1972). Most flock members fed at two nests simultaneously, but parents showed a

significant preference for feeding their own nestlings during the early stages. A breeding White-fronted Beeeater, *Merops bullockoides*, may become a helper at another nest, and subsequently a breeder again, but groups in this species are mobile and their membership fluid (Emlen and Demong 1980; Emlen 1981).

Why should Brown Treecreepers that have attained breeding space and status, continue to attend nests in the other territories? This situation is exemplified by GR σ who repeatedly visited and fed his father's young, even when busy with young of his own. One simple explanation has been suggested above: perhaps there is a chance that his father's young will eventually help him in his own breeding efforts. Indeed, his fledglings were once attended by an individual he had helped to raise, though this occasion may have been mediated by the location of the young on the border of the two territories. When RW σ eventually produced nestlings of his own (in the third season), they were attended by two birds that he had fed as nestlings and/or fledglings (OD σ , BY σ). The latter auxiliary contributed as much food to the young as the breeding female. With so many active attendants, a nestling might experience difficulty in identifying its true parents. Brown and Brown (1980) doubted that young Mexican Jays were capable of recognizing their parents or siblings. Perhaps auxiliaries are manipulating the young they feed into believing that they are closely-related, in order to be helped by them subsequently.

Another possible incentive for breeding males to visit the natal territory during the period of relaxed territoriality is the opportunity to become acquainted with the breeding female there, particularly if he stands a chance of taking over the territory in the event of her mate's death. The helping of breeders by their brothers may serve a similar function, though the possibility of succeeding may be limited by the presence of other (especially older) non-breeders. Some workers have suggested that by helping, auxiliaries gain valuable experience in nesting. A period of "apprenticeship" (Rowley 1976) might indeed be useful to yearlings, but is of doubtful significance to birds that have already attained breeding status yet still help, as in the case of the Brown Treecreepers discussed above. Although some studies have shown that novice breeders produce fewer young than experienced breeders (e.g. Woolfenden 1975; Koenig 1981), this is not universal (e.g. Rowley 1965, 1981).

A direct relationship between group size and territory size has been found for some communal species (e.g. Ridpath 1972; Parry 1973; MacRoberts and MacRoberts 1976; Woolfenden and Fitzpatrick 1978), but not for others (e.g. King 1980; Rowley 1981; Sherrill and Case (1980)). That territories of the Red-browed and Brown Treecreepers did not change appreciably in shape or size over the study period, and yet were large enough in some cases to be subdivided, argues that the territories of these species sometimes contain more than adequate resources for a simple pair. Indeed, even the relatively small territory *C* accommodated one or two "extra" birds from territory *A* intermittently during both the breeding and non-breeding seasons. Rowley (1981) found that territories in the Splendid Wren *Malurus splendens* were remarkably stable over seasons, and concluded that they had more than "just enough" resources. The conservativeness of territorial dimensions in the two treecreepers, however, was possibly partly due to the survival of most of the breeding males for the duration of the study. If auxiliaries inherit their natal territory in these species, as happens in many communal breeders (see Woolfenden and Fitzpatrick 1978), one might expect them to continue to defend the area with which they are familiar if possible.

Communal breeders commonly have skewed sex ratios (Fry 1972; Ridpath 1972; Dow 1973, 1978; Brown 1974; Woolfenden 1976; Zahavi 1976; Emlen 1978; Lennartz and Harlow 1979; Dyer and Fry 1980; Rowley 1965, 1981). However, even sex ratios also occur (Counsilman 1977; Rowley 1978; Ligon and Ligon 1978b). Assuming inbreeding is deleterious it would be advantageous for a population to expel some young from their natal grounds. In many communal breeders, breeding males rarely, if ever, mate with their daughters, so females disperse earlier and farther than males (Rowley 1965, 1981; Zahavi 1974; Woolfenden and Fitzpatrick 1978). Males tend to be sedentary because they stand a better chance of inheriting the natal territory or succeeding as a breeder in a neighbouring territory. Thus females are likely to breed sooner than males, but may also suffer higher mortality by wandering from the relative safety of their natal territories (Woolfenden and Fitzpatrick 1978).

Dispersal-related mortality is evident in the Red-browed and Brown Treecreepers, in which auxiliaries are almost exclusively males. One

female Red-browed and two female Brown (at Swan Vale) emigrated within the study sites to become breeders in territories, which were not adjacent to their natal territories. Only one female Red-browed (*D*: BO♀) was an auxiliary, and it subsequently succeeded as the breeder in a neighbouring territory. Both male Red-browed that filled breeding vacancies were known to originate from adjoining territories. When one group (*E*) of Brown at Swan Vale disintegrated, its territory was immediately seized by the non-breeding males from the adjacent territory, and the oldest of these became the breeder. Age and position in the family dominance hierarchy may be important in determining whether a non-breeder becomes a breeder in the new territory or not. Woolfenden and Fitzpatrick (1977) suggested that intra-familial dominance hierarchies in Florida Scrub Jays were important in establishing and maintaining the actual or potential reproductive positions of birds in the population.

Chapter 8

VARIED SITTELLA

While the literature is replete with references to the gregarious nature of the Varied Sittella, there has been no detailed study of its social organization. The infrequency with which parties of these birds are encountered in inland regions has probably contributed to the widespread belief that they are nomadic (e.g. Hindwood 1966; Pizzey 1980). Yet nomadism is a doubtfully adaptive strategy for a specialized insectivore such as the sittella, and large home ranges may be a more tenable explanation. Orenstein (1976: 451) asserted that sittellas do not maintain territories, "but wander widely within an area...in small flocks...but up to 30 outside the breeding season". My observations at both Wollomombi and Stringybark Hill, however, indicate that individuals occupy large yet discrete areas, which they defend against individuals from adjoining areas. Thus, I refer to these areas as territories, though at times the borders between some groups may dissolve (see below).

Sittellas breed communally (e.g. Rowley 1976; Dow 1980a) and although normally only one female lays in a nest there are reports of two females incubating and brooding simultaneously at one nest (Hindwood 1966; L. Short *in litt.*). The species is multi-brooded, young from early broods attending subsequent broods in the same season (Hando 1970; Noske 1980). When roosting, all members of the group huddle together, side by side, along a horizontal branch (McGill 1967; Beruldsen 1978). Their tendency to huddle is sometimes seen during the day, when it leads to allopreening (Noske 1980), though this activity generally involves only two or three birds at a time. Group members usually foraged in the same tree simultaneously and flew in a tight formation to the next tree.

8.1 Demography

The canopy-dwelling and high-flying habits of sittellas rendered them difficult to trap. Over 26 years (up to 1979), only 171 free-flying

sittellas were banded through ABBS, and of these, four were re-trapped, each within 13 months of banding (information supplied by D. Purchase). Despite intensive mist-netting at both Wollomombi and Stringybark Hill, only seven and eight birds were caught over three years at these sites, respectively. Another five were colour-banded as nestlings or fledglings at the latter site. Quarterly censuses over two years within the 40 hectares at Wollomombi suggested a population varying between 17 and 28 adults (Figure 8.1). The main group at Stringybark Hill comprised five to eight birds, which ranged over about 20 hectares.

Wilson in Frith (1969) claimed that in the south-eastern highlands, sittellas occurred "always in groups of six to eight", while in central and western Australia, T. Keartland (in North 1906) observed them "in flocks of six to twelve". McGill (1967) watched a group of eleven settle to roost in Western Australia and P. Slater (in Dow 1980a) counted ten birds attending a nest in northern Queensland. Group size during censuses at Wollomombi varied from two to nine ($\bar{X} \pm SE = 5.4 \pm 1.91$; $N = 33$). Figure 8.2 shows the size of 44 groups (excluding juveniles) recorded either in north-eastern New South Wales (pers. obs.) or central Queensland (Short *et al.* in press a). Mean group sizes ($\pm SE$) for these two regions were 4.9 (± 0.49) and 4.5 (± 0.50), respectively. Simple pairs were recorded in about 20% of cases in both areas (Figure 8.2). However, at Wollomombi, only two of the 23 nests observed were attended by simple pairs, which later fused to form a quartet.

Sub-adults (or first-year birds) comprised almost one-third of the birds in groups of three or more collected in north-eastern New South Wales during both July and December. The primary moult of sub-adults was more advanced than that of adults in each of three groups collected in December (Figure 8.3). Primary moult was least developed on the males with the most enlarged testes, presumably the breeding males. Yet among groups collected in central Queensland immediately prior to breeding, Short *et al.* (in press a) found little difference between sub-adults and adults in gonadal condition. They believed that all group members were capable of breeding, regardless of age. Interestingly, in one flock of the closely-related Pink-faced Sittella (see Section 1.2), Rand (1936: 307) found "birds with enlarged gonads, adult birds showing no enlargement of their gonads and birds in immature plumage".

FIGURE 8.1: *Approximate distribution of group territories of Varied Sittellas at Wollomombi Falls*

Values represent range of number of inhabitants

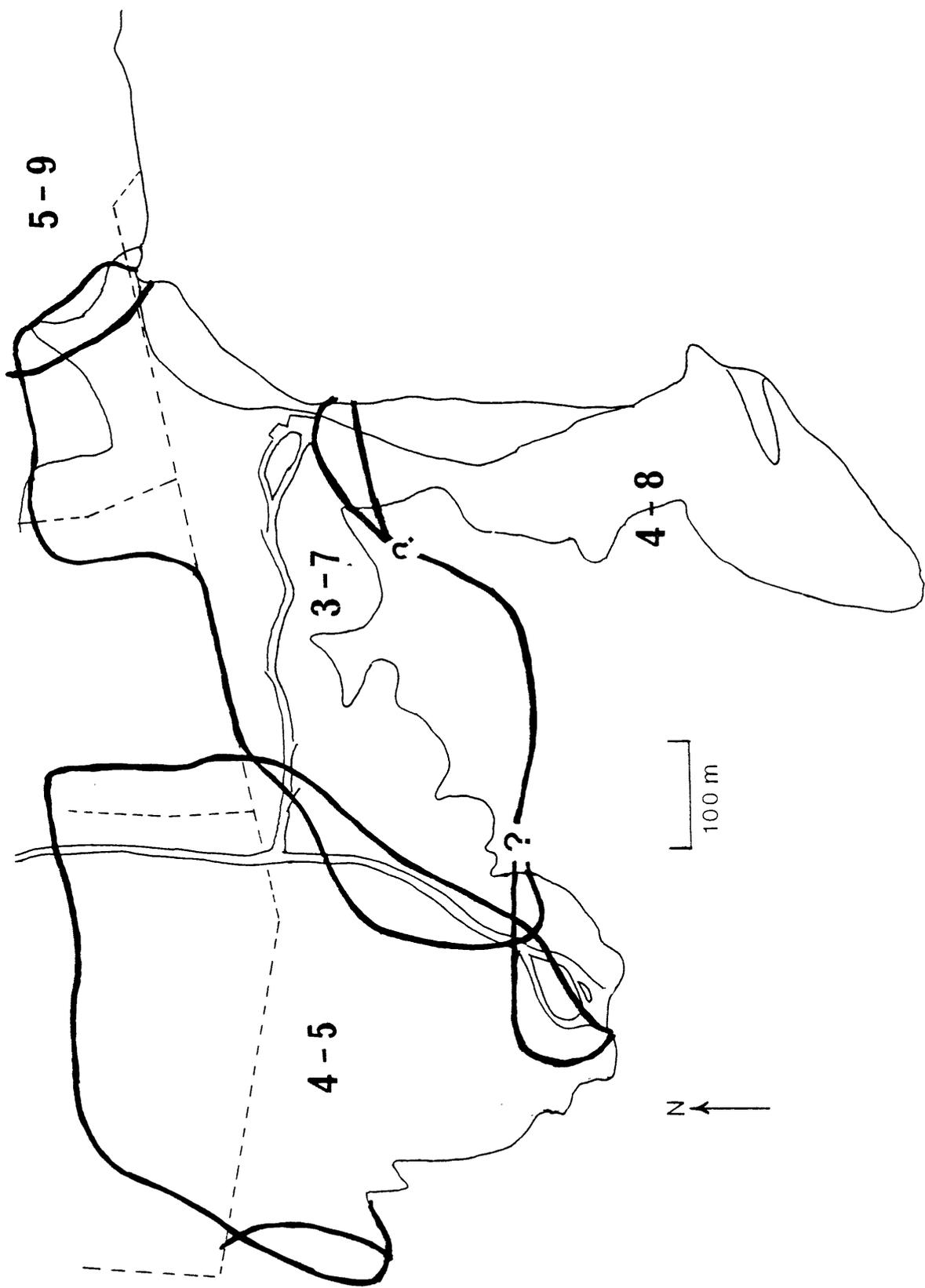


FIGURE 8.2: *Frequency of different group sizes in Varied Sittellas observed in north-eastern New South Wales (pers. obs.; excluding Wollomombi Falls), and central Queensland (Short et al in press a)*

Juveniles excluded

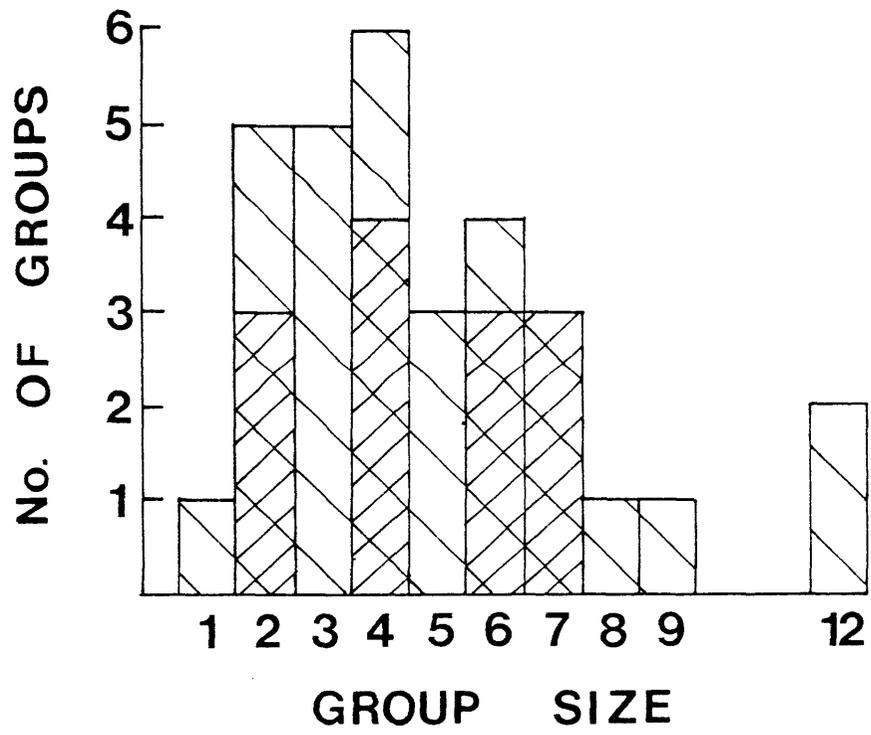
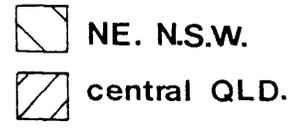
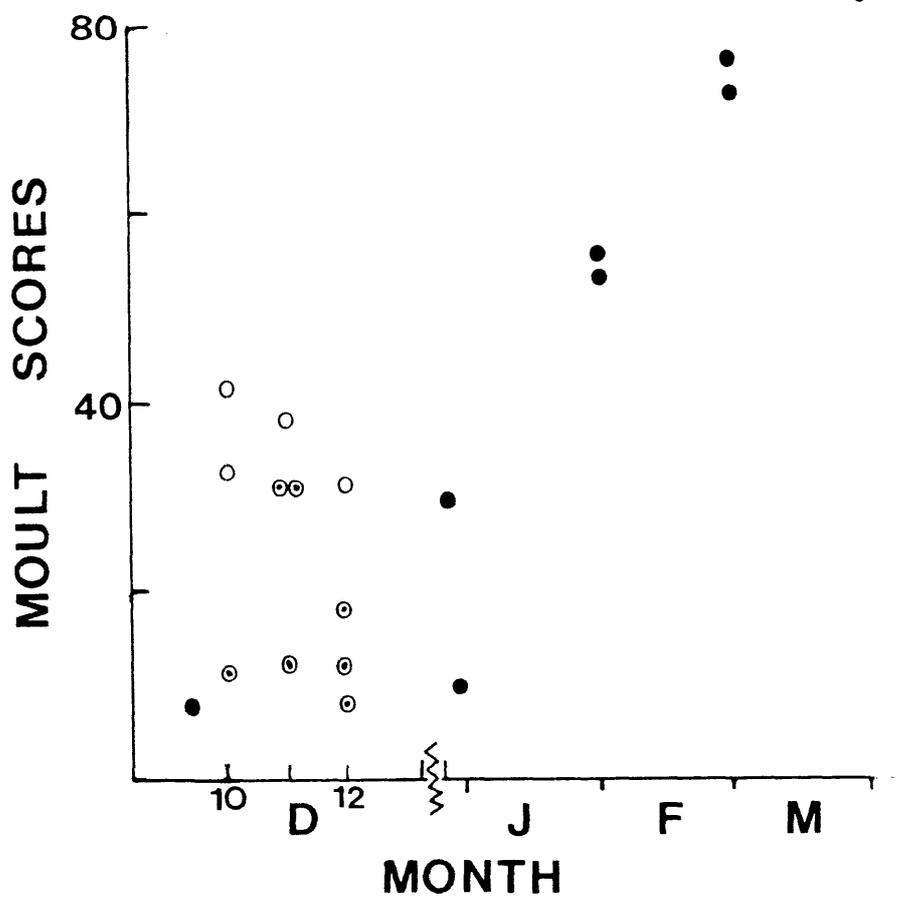


FIGURE 8.3: *Moult of primaries of Varied Sittellas collected in north-eastern New South Wales*

Primaries for both wings scored as follows:

old feather	= 0
missing feather	= 1
quill/bursting	= 2
half-grown feather	= 3
3/4 grown feather	= 4
full-grown feather	= 5
(maximum for each wing = 50)	



- Northern Rivers sub-adults
- ⊙ " " adults
- Wollomombi "

The composition of groups at Wollomombi was apparently dynamic. In February 1977, eight or more birds occupied territories *A* and *B*, but in the following month this "flock" split into two groups. At the beginning of the next breeding season, group *A* had split into two pairs, but coalesced for subsequent breeding attempts. Group *B* also divided into at least two groups, one (a trio) of which occupied the north-eastern section of the territory exclusively in two successive breeding seasons, but shared it with others during one non-breeding season. In February 1980, members of two groups (*A* and *B*) amalgamated after breeding and remained together for at least three months, separating before the following breeding season. Finally, at Stringybark Hill in 1982 a group of twelve birds separated into at least three breeding units. Though the breeders in two of these units occupied exclusive areas, two non-breeders shared both areas and "helped" both units in breeding attempts.

8.2 Sex Ratios

In one adult quartet at Wollomombi and another at Stringybark Hill (Noske 1980), the sex ratio was even. Yet among 43 adults and sub-adults collected from 14 or 15 groups in north-eastern New South Wales, males outnumbered females in the ratio 2.3:1. Excluding single specimens taken from larger groups, this ratio becomes 2.5:1. Three quartets and one sextet contained only one female, while another sextet contained two females. The sixteen sexed birds collected near Wollomombi showed a similar skew (2.2:1) and two trios (one at Wollomombi and another at Stringybark Hill) comprised an adult pair with a sub-adult male.

By contrast, Short *et al.* (in press a), found no evidence of sexual imbalance in groups collected in central Queensland. Although they concentrated on sampling the breeding pair of each group, two quartets contained at least two females and another, definitely three females (L.Short *in litt.*). L.Short (*in litt.*) also found two females brooding young simultaneously at one nest. Hindwood (1966:84) reported a similar instance, in which "two females used the same nest, laying a total of seven eggs in it ...both sat together, side by side". If it is assumed that groups contain only one breeding male, these observations indicate polygyny. During the

Harold Hall Expeditions, 78 sexed adult sittellas were collected across Australia, of which 45 were male (1.36♂:1♀) (data extracted from Hall 1974).

8.3 Vocalizations

Though I did not record calls of this species systematically, its vocal repertoire is apparently very limited. Only four calls were identified, each designated by their broad context:

1. *Contact*. Single note ("chip") repeated monotonously, while foraging, sometimes developing into a rapid chatter.
2. *Rallying*. A drawn-out double note, the first often slightly higher in pitch than the second, both with a rising inflexion.
3. *Food-begging*. Shrill chatter, higher-pitched than *contact* call; uttered by both incubating female and young birds.
4. *Submission*. A soft, sustained wheezing note emitted occasionally when an individual approached another closely or prior to copulation.

The almost incessant *contact* call probably served to maintain spacing between individuals while they forage in the same tree. In contrast, the purpose of *rallying* calls was apparently to unite the members of a group before leaving the tree, so that the group could fly in a tight cohesive bunch to the next tree. Thus, *rallying* calls expressed either an individual's diminishing interest in a tree or intention of flight, though other group members usually responded gradually.

8.4 Social Interactions and Roosting Behaviour

Sittellas are essentially passive. Although several encounters between groups were witnessed, none resulted in overt hostility. When birds from two or more groups met on the borders of territories supplantings or chases took place between only a few birds, while the majority spectated.

Wing-quivering as seen in young begging for food and in females before copulation, was a frequent component of such interactions, presumably signifying submission. Agonistic interactions within groups were rarely seen and allopreening was infrequent, never involving more than three birds at a time. Thus, in order to learn more about social relations within a group, I focused on roosting, a regular and predictable behaviour, in which all group members participated.

8.4.1 Roost-sites

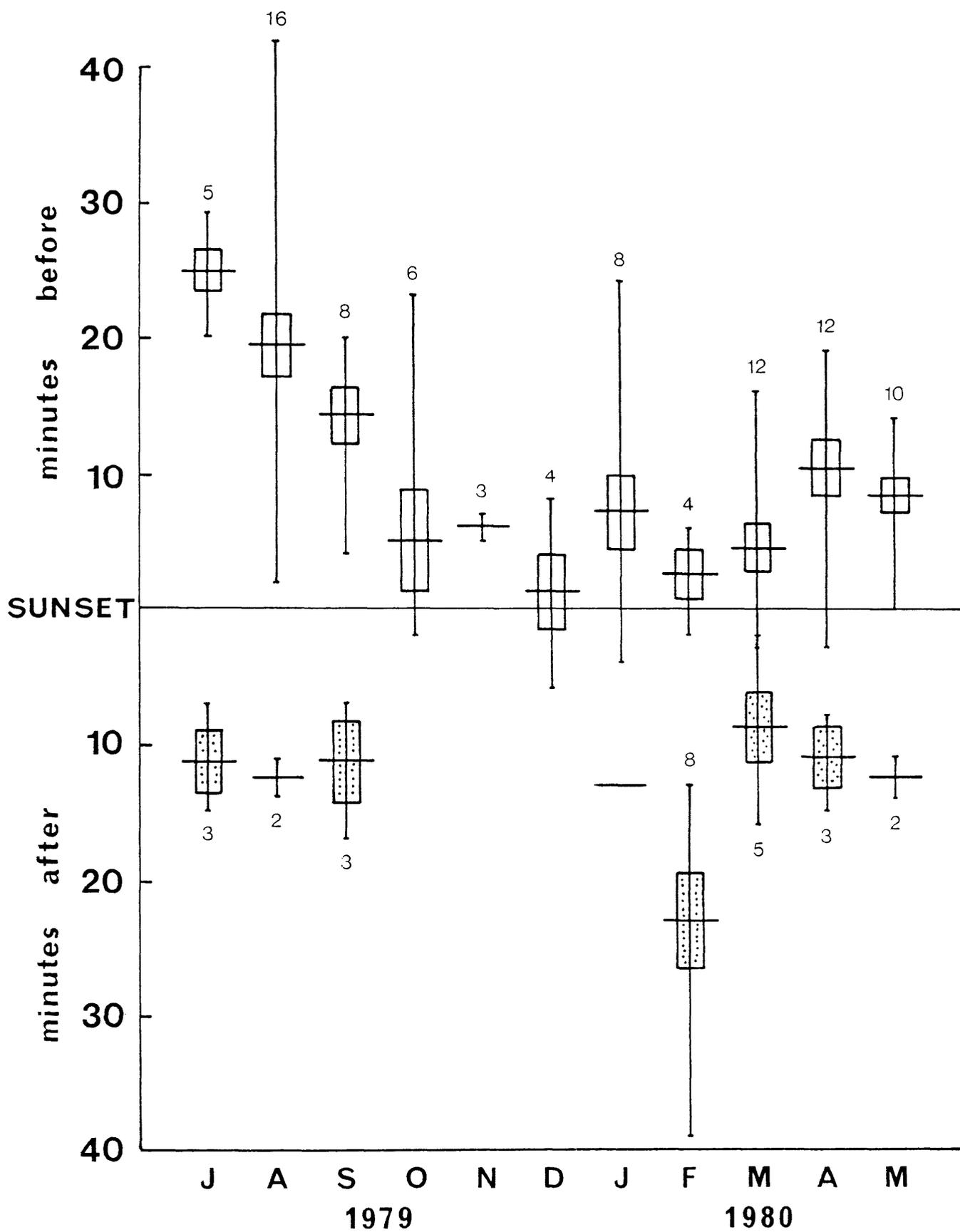
On 120 nights between January 1979 and September 1980, I noted the roosting behaviour of a marked group of sittellas at Stringybark Hill. These birds settled to roost earlier than other local species, invariably before sunset (Figure 8.4). Most other species, including the Striated Thornbill, *Acanthiza lineata*, which huddled in groups of three to nine (pers. obs.), roosted after sunset. The thornbills roosted 26 minutes later on average than the sittellas. On each of four mornings, I noted up to ten other species (including Striated Thornbills) actively foraging three minutes or more before the sittellas even awoke. Yet the sittellas did not depart from the roost-site until another ten minutes later on three mornings and seven minutes on the other.

The sittellas always roosted at the base of a thin (about 3 cm in diameter), horizontal or slightly upward-inclined dead branch, the innermost bird touching the adjoining branch, which in most cases formed a "roof" over the roost-branch (Figure 8.5). Despite the apparent abundance of such situations in most large trees at Stringybark Hill, the group was known to use only 15 different sites in 13 trees dispersed over their entire territory (Figure 8.6). All trees were eucalypts, mostly stringybarks, and two of the six most frequently used trees were dead (Table 8.1). Roost-sites ranged in height from 7.6 to 16.8 metres, the average (\pm SE) over 120 nights being 14.0 (\pm 0.29) metres. With one exception, the sites were located in the upper half of the tree, less than 11.3 metres from the top; the mean interval between the top of tree and the site (\pm SE) was 5.63 (\pm 0.32) metres.

The group switched sites frequently and unpredictably. At one extreme, three different sites were chosen on three consecutive nights,

FIGURE 8.4: *Times of roosting of Varied Sittellas (upper) and Striated Thornbills (lower, stippled), in relation to sunset (mid-line) at Stringybark Hill*

Times represent the arrival of the last member of the group at the roost site; only final sites are considered if two sites or more were visited; boxes signify one standard error either side of the mean; number of observations shown at top or bottom of range



← BREEDING →

FIGURE 8.5: *The colour-banded group of Varied Sittellas at Stringybark Hill huddling at a roost-site*

From left to right : WW♂ , UM ♀, BB ♂, UU♀ ,
OO ♀ and NN ♂ ; all birds except WW ♂ and
OO ♀ in the inclined (pre-sleeping) posture

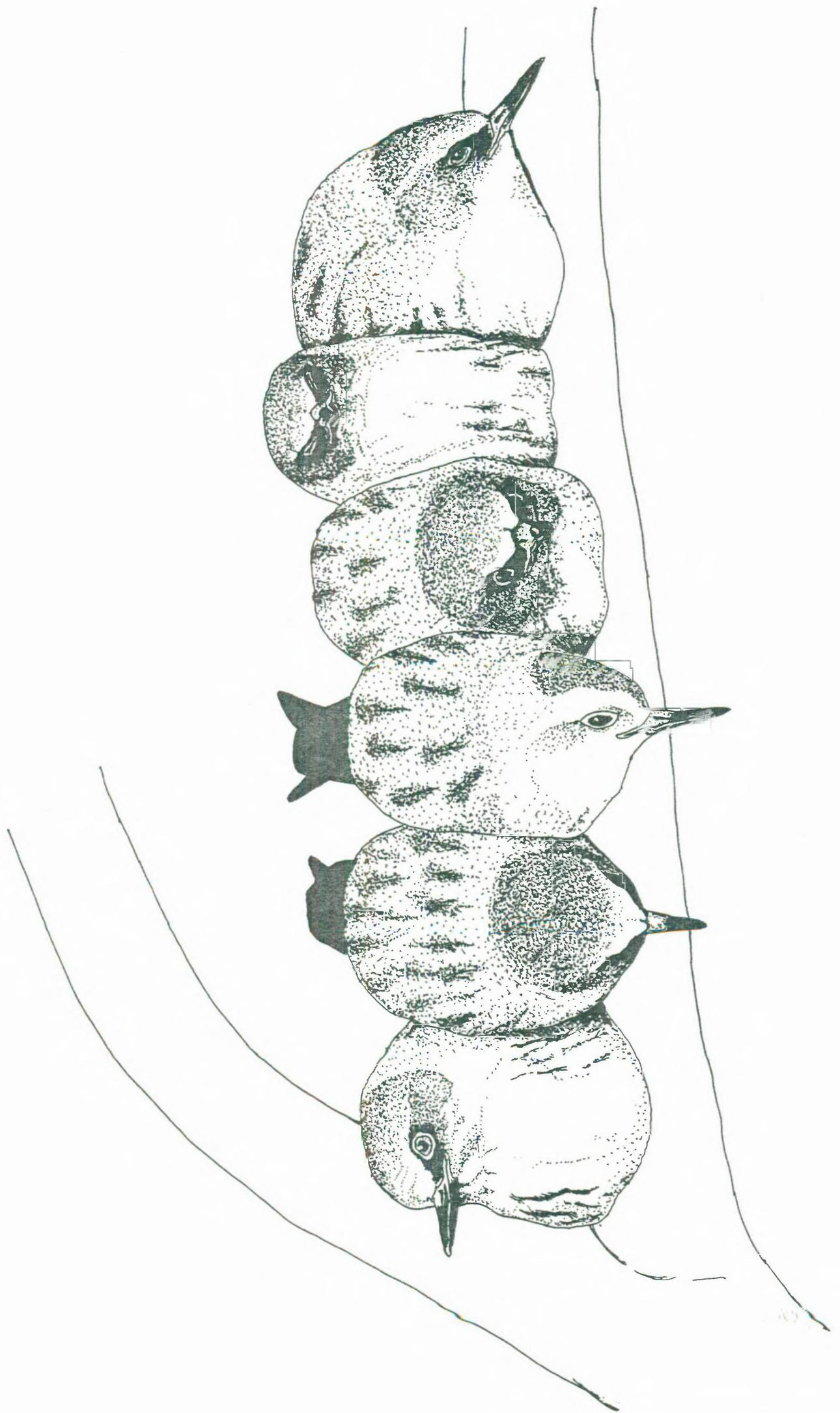


FIGURE 8.6: *Dispersion of major roost-sites of the colour-banded group of Varied Sittellas at Stringybark Hill*

Boundary of group territory indicated by broken line

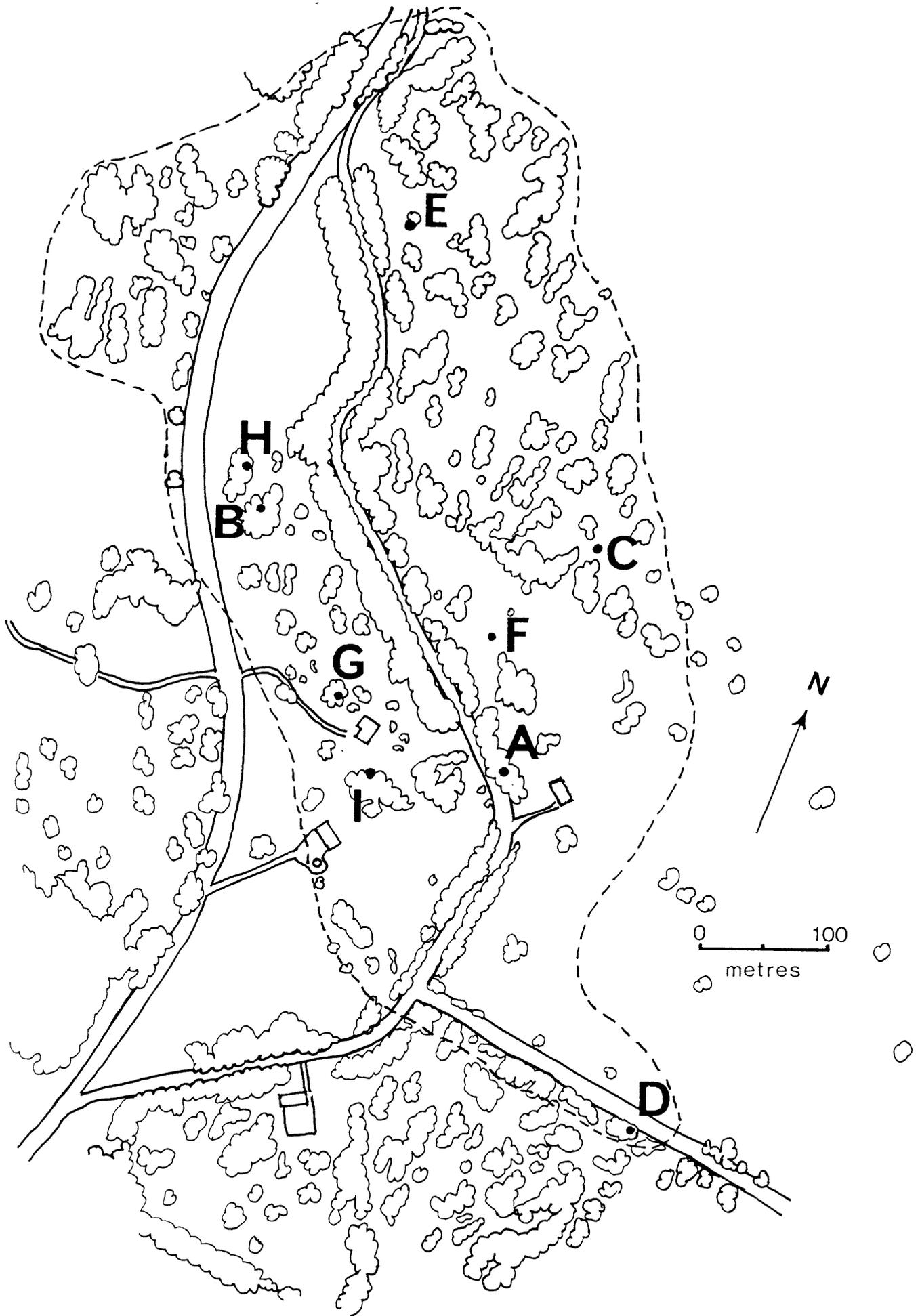


TABLE 8.1: Characteristics of the six roost-sites most frequently used by the colour-banded group of Varied Sittellas at Stringybark Hill

Tree site	Tree type	Height of roost (metres)	Total times used	Longest period of continuous use (days)	Orientation* of branch (degrees)
A	Stringybark	15.9	40	19	ESE
B	Stringybark	9.1	22	6	NNE
C	Dead	16.2	19	12	N
D	Gum	16.8	10	3	ENE
E	Gum	14.6	9	3	S
F	Dead	12.2	7	5	ESE

* measured from base towards tip, using compass

whereas the longest recorded period of continuous use was 19 days (Table 8.1). As the birds often flew long distances directly to the site, they did not appear to be selecting those closest to where they last foraged. One site (Figure 8.6:D) was also used by a neighbouring group of eight birds, which succeeded in supplanting the study group at least once.

8.4.2 General behaviour at roost

Prior to roosting, the members flew in a tight bunch to the roost-site or an adjacent tree, splitting up immediately before landing. Sometimes autopreening followed but usually one or two individuals started towards the roost-site. The first two or three birds often arrived in quick succession, but rarely simultaneously; the remainder usually staggered their arrival, the total "settling" period lasting three to five minutes on most nights. Each new arrival climbed along the underside of the branch, and squeezed up between any two birds already present, gradually forcing the outermost bird to shift farther outwards. When settled, all birds faced the same direction leaning head downwards and tail upwards at an angle of up to 45 degrees from horizontal, as Beruldsen (1978) noted. This posture was maintained only while the birds were awake; eventually each tucked its head over the shoulder, assuming a more erect stance (Figure 8.5).

After the last bird settled the group were usually quiet and inactive. Sometimes, however, there was a short period of re-shuffling of internal positions usually caused by one seemingly indecisive individual. On several evenings, the group became restless before all members had settled, and flew suddenly to a second site. If the group was still "undecided", it returned to the original site, or chose a third one. One night, it attempted to settle five times (involving three trees), eventually returning to its first choice.

Once settled, the birds never turned round, even when disturbed from behind. Each time I approached a roost-site from the rear, or walked under it, the birds merely increased their inclined posture so as to observe me from the underside of the branch. However, "escape" reactions were induced by three diurnal species of birds (Horsfield Bronze-Cuckoo, *Chrysococcyx basalis*; Eastern Rosella, *Platycercus eximius*; Noisy Miner, *Manorina melanocephala*), none of which is known to prey on small

birds. In each case, one or more of the sittellas called, apparently triggering a sudden "explosion" of birds in all directions.

8.4.3 Individual behaviour at roost

The two adult males were the first two to arrive at the roost-site with few exceptions (Table 8.2); the breeding male (NN σ) was first in 81% of cases. Whenever the auxiliary male (WW σ) preceded the breeder, the former hopped off the site at the approach of the latter. The breeding females (RR f and her replacement UM f) were third to arrive on most nights, but UM f was sometimes preceded by her son (BB σ). Both times that UM f preceded the second male, she left quickly upon his arrival, and returned soon afterwards. All instances when RR f was last (Table 8.2) occurred just prior to incubation, when she arrived four to ten minutes after the others had settled. She was absent from the roost after incubation began.

The two adult males occupied the ends of the huddle on all but one of the 120 nights (Tables 8.3 and 8.4). The breeder (NN σ) occupied the outermost position in 72% of observations, and WW σ , the remainder. The sharing of the two end positions by these birds did not appear to be related to changes in social status or choice of sites. The positions of other group members were less predictable, but some significant association between individuals and positions were found. At six to nine months of age, GB σ and WD f were associated with the middle and second (from the inside) positions, respectively, but after the disappearance of the latter and the arrival of the next generation of young, GB σ moved to the penultimate position (Table 8.3). During their first two months after fledging, BB σ and OO f mostly occupied the positions next to either end (Table 8.3), but subsequently moved to the inner half (Table 8.4). The association of UM f with the penultimate position after the loss of GB σ (Table 8.4) did not seem to be related to the identity of the adult male beside her (nine versus eleven times beside NN σ and WW σ , respectively).

Observations of roosting in two other groups of sittellas indicated that the arrangement of individuals described above was not unique. On three nights, the two colour-banded males in a quartet at Wollomombi arrived first at the roost, and the two unbanded females wedged themselves between them; the males thus occupied the end positions. In a quintet,

TABLE 8.2: Arrival order* of the colour-banded Varied Sittellas at roost-sites at Stringybark Hill when the group contained five (upper) and six (lower) birds†

Bird	Age# (months) or status	Sequence					
		1st	2nd	3rd	4th	5th	6th
NN♂	α	14	-	-	-	-	-
WW♂	β	-	14	-	-	-	-
RR♀	α	-	-	4	1	5	5
GB♂	6 - 9	-	-	1	2	4	4
WD♀	6 - 9	-	-	2	4	1	1

NN♂	α	24	5	2	-	-	-
WW♂	β	7	24	-	-	-	-
UM♀	α	-	2	21	6	2	-
BB♂	2 - 6	-	-	7	9	10	5
OO♀	2 - 6	-	-	1	6	13	11
UU♀	β	-	-	-	10	6	15

* first column indicates first bird to arrive, column 2, the second, etc.; total number of observations for each column unequal in upper table because some evenings I only noted the first two or three arrivals; nights on which the breeding female was absent due to nest attendance were excluded

† corresponding to the following periods: late July to late October 1979 (upper) and mid-February to early September 1980 (lower)

α, β = breeders and non-breeders respectively, of unknown age

TABLE 8.3: Roosting positions* of the colour-banded Varied Sittellas at Stringybark Hill when the group contained five (upper) and seven (lower) birds

Bird	Age (months) or status	Positions						
		1	2	3	4	5	6	7
WW♂	β	31 ⁺⁺	-	-	-	-	-	4
WD♀	6 - 9	-	18 ⁺⁺	8	9	-	-	-
RR♀	α	-	9	10	16 ⁺	-	-	-
GB♂	6 - 9	-	8	17 ⁺⁺	10	-	-	-
NN♂	α	4	-	-	-	-	31 ⁺⁺	-

WW♂	β	12 ⁺⁺	-	-	-	-	-	-
OO♀	1 - 2	-	6 ⁺⁺	4	1	1	-	-
UM♀	α	-	3	1	4	2	2	-
GB♂	12 - 13	-	3	3	1	-	5 ⁺⁺	-
UU♀	β	-	-	1	3	8 ⁺⁺	-	-
BB♂	1 - 2	-	-	3	3	1	5 ⁺⁺	-
NN♂	α	-	-	-	-	-	-	12 ⁺⁺

* position 1 = innermost (at base of branch), position 5 = outermost (towards tip); association between birds and positions were tested (χ^2) by comparing observed frequencies of occupation with expected values, based on assumption that each bird had an equal chance of occupying each position; due to problems of partial dependence only levels of $p < 0.01$ (+) and $p < 0.001$ (++) were considered; no sign indicates association is absent or negative; other symbols as in Table 8.2

TABLE 8.4: Roosting positions* of the colour-banded Varied Sittellas at Stringybark Hill when the group contained six birds

Bird	Age (months) or status	Positions					
		1	2	3	4	5	6
WW♂	β	26 ⁺⁺	-	-	-	-	26 ⁺⁺
OO♀	2 - 6	-	26 ⁺⁺	18 ⁺⁺	6	2	-
BB♂	2 - 6	-	18 ⁺⁺	19 ⁺⁺	3	12	-
UM♀	α	-	8	8	16 ⁺⁺	20 ⁺⁺	-
UU♀	β	-	-	7	27 ⁺⁺	18 ⁺⁺	-
NN♂	α	26 ⁺⁺	-	-	-	-	26 ⁺⁺

* other symbols as in Tables 8.2 and 8.3

the colour-banded breeding male occupied the outermost position on the two nights I observed this group roosting.

Although sittellas were among the earliest species to roost, they were not necessarily the first asleep. In the intensively studied group, some birds went to sleep while it was light, but at least one stayed awake till dark. The minimum period from the time at which the last bird arrived at the site to when the last fell asleep on 21 evenings varied from 23 to 48 minutes ($\bar{X} \pm SE = 36.3 \pm 1.31$). The last bird fell asleep ten to 43 minutes ($\bar{X} \pm SE = 25.4 \pm 2.68$) after the first. These values are possibly under-estimated because the last bird was sometimes still awake when it was too dark to observe movements.

Without exception, the juvenile 00♀ or her brother (BB♂) were the first asleep - the female in 78% of cases (Table 8.5). BB♂ was the second asleep in almost 70% of observations. Either of the adult males was usually the last to go to sleep. In all but two of the 16 cases, the last bird asleep was in the outermost position. On all 14 nights that the two adult males were among the first three asleep, they occupied the innermost position.

Awakening was observed on four mornings only, but on at least three of these, the two adult males were the first awake. The young 00♀ was the last to wake on one morning, four minutes after all the others had woken. It took six minutes on one morning and seven minutes on another for all birds to awaken. When departing, all members "burst" from the site simultaneously, except on the first morning, when NN (in the outermost position) left a second or two before the other six. On this occasion, the birds autopreened for a further 13 minutes in the roost-tree.

8.4.4 Dominance

There was little evidence of a dominance hierarchy within the above group, apart from perhaps the sexual rivalry between females, and between males, immediately prior to and during the breeding season (see next section). However, WW♂ always acted submissively towards NN♂ when arriving at the roost-site, approaching him with head lowered and wings quivering. Yet NN♂ only displayed submissively towards WW♂ just before they disappeared in September 1982, suggesting the status of these two

TABLE 8.5: Order* in which the colour-banded Varied Sittellas at Stringybark Hill went to sleep

Bird	Age (months) or status	Sequence					
		1st	2nd	3rd	4th	5th	6th
00♀	2 - 6	28	6	2	-	-	-
BB♂	2 - 6	8	22	-	-	-	-
UM♀	α	-	2	9	5	2	1
UU♀	β	-	-	-	7	9	-
NN♂	α	-	-	12	1	1	7
WW♂	β	-	2	-	3	4	8
TOTAL ⁺		36	32	23	16	16	16

* first column indicates first asleep, column 2, the second, etc.; bird was considered asleep at the moment it tucked its head over its shoulder, even though its eyes may have closed some time beforehand; other symbols as in Table 8.2

+ totals are not the same for each category because I noted only the first bird asleep on 20 nights, only the first two on 16 nights, etc.

males had suddenly reversed. WW σ then became aggressive towards NN σ , attempting to prevent him from joining the roost on two nights. He also began to accompany the breeding female, indicating he had usurped NN σ as the breeder.

No aggression was observed between the sexes in adults, though a juvenile male was seen chasing a juvenile female several times. These chases probably represented "play" rather than aggression, but such interactions may serve to establish dominance relations between peers (Gaston 1977). Because dominant individuals tend to be the active participants in allopreening, Harrison (1965) proposed that this behaviour represented redirected aggression. In sittellas, young birds not uncommonly groom adults of the same or opposite sex so the direction of allopreening does not appear to reflect age or breeding status in this species.

In the group studied, the breeding male (NN σ) apparently led the others to the roost. The other group members rarely moved towards the roost-site while he was still foraging, and soon lost interest when they did. Moreover, this male initiated departure from the site on at least two nights (when another site was sought) and on one morning after the group awoke. Rowley (1978) found no evidence of a dominance hierarchy in White-winged Choughs, *Corcorax melanorhamphus*, which are obligate communal breeders, living in groups of up to 20 birds. Yet the oldest male in each group performed a "linchpin" role in group cohesion, and when he disappeared, the group usually disintegrated.

8.4.5 Sexual rivalry

Several observations at Stringybark Hill suggested that sexual rivalry occurred among adult females within a group. At nests in two consecutive seasons, the non-breeding adult female was prevented from feeding the nestlings by the breeding female. As the non-breeder approached the nest with food, the breeder quickly supplanted and chased her away (Noske 1980, unpubl. data). Moreover, just prior to nesting in both seasons, the breeder repeatedly attacked the non-breeder as the latter attempted to join the group at the roost. In the first season, the non-breeder was a first-year bird, unrelated to the breeder, and this individual disappeared soon after squabbles were observed at the roost. In the second season, the same

breeder harassed an adult female, which had joined the group following the expulsion of the above yearling. Significantly, neither this breeder nor her predecessor annoyed their own daughters. It is perhaps no coincidence that the only two solitary birds I have collected were female.

Possible rivalry between males was witnessed only once, just prior to the completion of a nest. The breeding male repeatedly supplanted and chased the two other male members of the group when they approached the nest with building material. As the breeding female had only recently replaced her predecessor and at the time of the above observations, spent most of her time in the nest vicinity, it is possible that the dominant male was guarding the female to avoid cuckoldry. Copulation was observed on four occasions, the female crouching over a branch, wings quivering, while the male spiralled the branch around her before mounting. As mating was a simple and short procedure, resembling behaviour at the roost in some aspects, "stolen matings" may sometimes occur as they do in the communal Splendid Wren (Rowley 1981: 250).

8.5 The Nest

The nest of sittellas is a deep open cup "built at the junction of an upright forked branch, sometimes against a slightly leaning single-stemmed branch, frequently a long dead one" (North 1906: 53). This accords with my observations of 57 nests, only three of which were built on live branches. The cup is decorated on the outside with pieces of bark, bound with spider web, so that the nest is usually well camouflaged against the branch on which it is built. The lining of bluish-green and grey lichen also approximates the colour of the eggs (Hindwood 1966; pers. obs.).

All but seven of 50 nests were built in stringybarks. Of the seven exceptions, three (at Wollomombi) were in Fuzzy Box, *Eucalyptus conica*, and two (at Swan Vale) in Tea-tree, *Leptospermum brevipes*. The height of nests varied from 6.0 to 19.0 metres, the means (\pm SE) for 14 at Wollomombi and ten at Stringybark Hill being 13.1 (\pm 1.08) and 11.3 (\pm 0.77) metres, respectively. All were situated in the upper half (mostly the upper third) of trees, averaging 5.8 metres below the top of the crown at both sites (SE = 0.80 and 0.90, respectively).

Nest-building was noted in late August at Wollomombi and Swan Vale, but as early as August 9 at Stringybark Hill (1979). My latest record of building was December 31 (at Wollomombi). Incubation was recorded from late August to late January, with a peak in late September (Figure 8.7).

8.6 Building

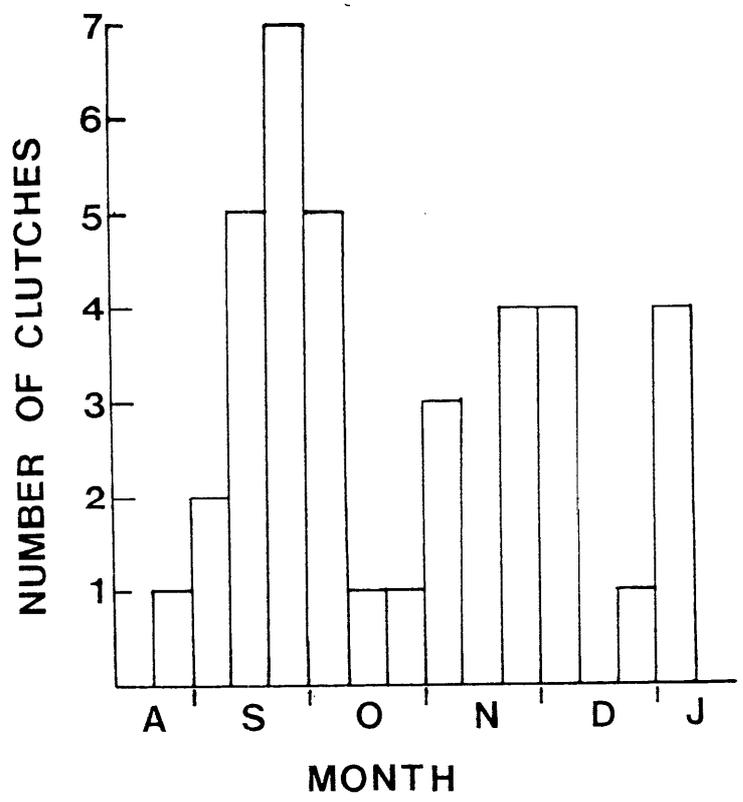
The bulk of the nest took between five and nine days to build, while the addition of material to the interior may occupy another ten days. Incubation at one nest began about 17 days after the first foundations were laid, but at three other nests, at least twelve days passed between the completion of the exterior and the commencement of incubation. During the last few days before laying, visits became infrequent. Up to a quarter of nests at Wollomombi and Stringybark Hill were abandoned just after their apparent completion (before laying), a characteristic of the species noted by H.G. Barnard (in North 1906: 58). However, one nest at Stringybark Hill was only half finished when deserted, and another (the fourth for the season) was started.

All five members of the Stringybark Hill group participated in the building of the nest at the start of the 1979-80 season, but at the last nest of that season many attempts by the auxiliary males to add material to the nest were thwarted by the breeding male (see Section 8.4.5). At one late nest elsewhere, I observed building by two juveniles probably less than two months old, corroborating other evidence of early brood young "helping" at subsequent nests of their group (Noske 1980). During the building stage individuals often visited the nest without bringing material, but sat on it, re-decorating the exterior with the bill and shaping the interior with trembling body movements. Queues sometimes formed as birds waited for their opportunity to visit the nest.

8.7 Clutch Size and Laying Routine

All nine clutches I was able to examine were of three eggs, and in NRS, eleven of the 17 nests with clutch size data were C/3, the remainder being C/2. The species appears to lay at intervals of 48 hours (*contra*

FIGURE 8.7: *Egg dates (when eggs or incubation first noted) of Varied Sittellas at the three study sites (combined)*



Courtney and Marchant 1971: 129) judging from personal observations at two nests, as well as information for two nests in NRS (4/65 and 3/69). Incubation in clutches of three eggs began with the laying of the second egg (pers. obs. at two nests; NRS: 2/67). At another nest I observed, one young fledged two days later than the other two young, possibly indicating that the first two eggs hatched two days before the last.

8.8 Incubation and Nestlings

Hindwood (1966) stated that incubation occupied between twelve and 13 days and the young reached the flying stage after about two weeks, giving a full nesting cycle of 26 to 27 days. Yet at two nests, I established that the full period was at least 38 days. Assuming the above laying routine the maximum cycle for one nest observed by S. Marchant (NRS: 3/67) was also 38 days. The maximum incubation period at this nest was about 17 days and the minimum at three others (pers. obs.; NRS: 3/65) was 16 days. Minimum nestling periods of 18 and 19 days were calculated from records at two (NRS: 1/70; pers. obs.) nests, and another gave a maximum of 20 days (pers. obs.). Thus, the incubation and nestling periods are possibly about four and five days longer, respectively, than Hindwood supposed.

As with the treecreepers, only female sittellas incubate. Over three seasons at Stringybark Hill I noted one breeder (RR♀) incubating or brooding 44 times; no other group members participated in these duties. Similarly, colour-banded males at Wollomombi never incubated. Incubating sessions lasted up to 45 minutes, averaging 22.1 ± 2.58 (SE) minutes for 27 observations, while the maximum period off the nest was 27 minutes, averaging 9.9 ± 1.93 (N = 14). Attendance for five watches of 60 minutes varied from 50 to 80%. Brooding was not timed, but continued for at least ten days after hatching at two nests. The incubating female was fed by most other group members including her daughters, both on and off the nest. While foraging with the rest of the group at this time she uttered food-begging calls almost continuously.

8.9 Feeding of Young

As Dow (1980a: 126) noted, sittellas do not fly directly to the nest when feeding the young, but jump from branch to branch in the nest-

tree before briefly pausing at the nest. In 63 minutes of watching a nest with three well-developed young attended by at least five birds, Dow recorded a feeding rate of 43.8 times per hour. Yet at Stringybark Hill I observed a nest with the same number of young and a similar complement of attendants, where the maximum feeding rate was 18.0 per hour during the four days prior to fledging. The average rate for combined observations totalling 12.5 hours was merely 13.1 per hour. Two of the attendants were juveniles, probably about two months old, which fed less frequently than the adults (Noske 1980: Figure 1). Even if they had fed as frequently as the adults the feeding rate at this nest would not have been as high as the one observed by Dow.

The contribution of the primary pair at the above nest was over half (58%) of the total effort by the group (Noske 1980). In the following season however, the combined contribution of the two auxiliary males in this group was equal to that of the primary pair, though fewer data were collected (N = 30). The non-breeding female at this nest (UU♀) did not feed the nestlings despite several attempts, but fed a fledgling at least once. All feeders at this nest removed faecal sacs. WW♂ was an auxiliary for at least two seasons, but at the beginning of the third (1980-81) season had apparently assumed a more dominant role than NN♂ and performed most of the building. Unfortunately, both males disappeared soon after the nest was begun.

Of 24 nests at Wollomombi, only three (12.5%) definitely produced fledglings, while at Stringybark Hill, seven (28%) of the 25 nests were successful. All 49 nests were apparently complete but up to twelve of these may have been abandoned before laying. However, one nest was definitely predated after an egg had been laid, and another at least a week after the young had hatched. Predation of nests is probably high judging by the number of nests destroyed.

Though well concealed, nests were often made conspicuous to the observer by the noise and excitement of birds when building, or when feeding the sitting female. Moreover, females often called while on the nest, one bird calling continuously for 25 minutes during an incubation session of 35 minutes. Such activities may be expected to attract predators or brood-parasites, but surprisingly, parasitism was recorded only once, involving the Brush Cuckoo, *Cuculus variolosus*. In common with many other communal

breeders, all group members united in their defence of the young. Whenever I examined nestlings or fledglings, all adults climbed around me at close range sometimes quivering their wings, presumably as a distraction tactic.

On their first day out of the nest, the two fledglings from each of two nests at Stringybark Hill became separated. In one case, they reunited in an established roost-tree (70 metres from the nest tree), where they roosted with the rest of the group. In the other case, they remained separated and roosted apart from the other group members. On the second night, one of these fledglings roosted with the others, while the other huddled with the third, newly-fledged, brood mate. All three fledglings joined the "adults" on the following night. They were last seen being fed 80 days after fledging, but were probably largely independent after two months, as were the young from the first nest.

8.10 Discussion and Conclusions

Unlike treecreepers, sittellas exhibit certain behavioural characteristics typical of "contact" species. Group members always roosted together, and occasionally allopreened, both activities involving huddling. The major calls seemed to be connected with the co-ordination of group activities, which were highly synchronized. Average group size was larger than in the social treecreepers, and though there was some evidence for a male-biased sex ratio, several breeding groups contained more than one female. Communal breeding occurs more regularly in the sittella, but nest losses were higher presumably owing to the exposure of their open nests. The passive nature of sittellas reflects the mutual tolerance among individuals necessary for their communal lifestyle. Intra-group aggression is minimal, though observations at the roost suggest the existence of a subtle form of dominance.

The roosting behaviour of the colour-banded group of sittellas was remarkably stereotyped despite several changes in group membership. Most significantly, the two oldest males were normally the first to arrive at the roost-site and invariably occupied the end positions when all members were settled. Some evidence suggests that other huddling species may exhibit a

similar configuration of group members at roosts. I watched roosting behaviour of a group of (1) six Striated Thornbills, including three fledglings, and (2) six Brown-headed Honeyeaters, *Melithreptus brevirostris*, with two or three fledglings, on three nights each. In all cases, the fledglings occupied central positions, flanked by the adults. Gaston (1977) found a similar structure in huddled roosting groups of Jungle Babblers (*Turdoides striatus*). He noted that the first bird to enter the roost was one of the breeding pair. The juveniles entered last by squeezing into the middle, but late-arriving adults sometimes joined onto the end of the roost.

Gaston (1977) concluded that age determined the positions of members of roosting babbler groups. Juveniles first perched in the centre of the roost, moving to the outer third when two to three months old, then to the edge or inner third as the next generation of juveniles arrived. This pattern differs somewhat from that of the sittellas. During their first two months, BB♂ and OO♀ mostly occupied the positions nearest to both ends, but subsequently moved to the inner half. Sex may be more important than age in determining roosting positions in sittellas. On the only night I observed roosting of the group after the two adult males disappeared, the sole remaining male (nine-month old BB♂) held the outermost position and his mother (UM♀), the innermost; yet UU♀ was older than the male. This was the only time I saw a female in an end position, and it was apparently due to lack of males.

The external position of adult males appears to confer both protection and thermal insulation on the young and female members of the group. However, it is doubtful that huddling evolved primarily for thermoregulation, as sittellas and Striated Thornbills huddled at their roosts throughout the warm months when minimum temperatures were as high as 20°C. Indeed, if heat conservation were important to young sittellas, one would not expect the fledglings (BB♂ and OO♀) to roost apart from the adults on their first few nights out of the nest. Among Estrildid finches, Kunkel (1974) noted a greater tendency for "clumping" in species which live in hot regions without great temperature fluctuations, than those inhabiting areas with large differences between day and night temperatures.

The outermost bird in the huddle could play a lookout or guard role, warning the others of impending danger. This bird had an unobstructed

view of the side and in most instances, stayed awake longer than the others. Moreover, the innermost bird, whose side-view was largely obscured by a branch, was sometimes among the first to go to sleep. It is significant that the two young birds were invariably the first asleep, often long before the others. Though this may have been related to fatigue resulting from inexperienced foraging, I believe that their lack of responsibility permitted the luxury of a long sleep.

In groups of Jungle Babblers, most of the sentinel activity during the day was performed by the breeding male or female who had a direct investment in its offspring, but among non-breeders, males acted as sentinels more than females (Gaston 1977). As new breeding males were recruited from within the group, Gaston reasoned that non-breeding males may benefit in the long-term by helping to maintain the strength of the group, in which they may succeed as breeders. Most females, on the other hand, dispersed after 18 months in their natal territory, and new breeding females were immigrants. A similar pattern may occur in the sittellas and could explain the occupation of the outermost roosting position by the non-breeding male (WW σ). Indeed, this bird apparently succeeded as breeder at the end of the study.

That predation is a significant factor in the roosting behaviour of sittellas is suggested by (1) the staggered sleeping times of group members, (2) the staggered arrival of birds at the roost-site, and possibly (3) the switching of sites. The first of these points is clearest: there seems little advantage in one or two birds staying awake for up to 48 minutes after settling to roost, unless there is more risk of attack from a diurnal or crepuscular predator. The second point assumes that if birds enter the roost gradually, they attract less attention from potential predators than if they arrived simultaneously. Finally, sittellas may discontinue use of a roost-site to avoid repeated exposure to predators in its vicinity. However, weather conditions, particularly wind direction, at the time of roosting may be a more important influence in the choice of sites. Exposure to wind probably forces all members of the group to face the one direction, even though this must restrict predator surveillance. The inclined "pre-sleeping" posture probably partly compensates for this reduced view of the surroundings, as well as facilitating a quick launch when escaping from a predator.

In this context, it is interesting that the sittellas roosted so early, since this might be expected to (1) increase the risk of predation from crepuscular predators, and (2) reduce foraging time. It could be argued that the bark-dwelling arthropods eaten by sittellas become too difficult to locate as light intensity falls. Yet the larger White-throated Treecreeper exploits the same substrates as sittellas and it is always among the last species to roost. The additional, albeit less substantiated, fact that sittellas awoke later in the morning than other species suggests that they were extremely efficient foragers. This may be related to their sociality, as individuals in groups benefit from an increased potential to detect predators and reduced time spent on vigilance (see Bertram 1978). Indeed, Nice (quoted by Norris 1958) observed that solitary Bronzed Grackles, *Quiscalus quiscula*, arose earlier than those roosting in a flock. Stokes (1979) presented evidence that communally-roosting species tended to roost earlier and awake later than solitary-roosting species. Yet several other huddling species tend to roost much later than sittellas; Striated Thornbills, Blue Wrens (pers. obs.) and White-winged Choughs (Rowley 1978) are such examples.

Kunkel (1974) suggested that clumping (or huddling) has a social function similar to allopreening in the maintenance of the pair bond. In sittellas, huddling at the roost probably promotes social harmony within the group and reinforces cohesion. The ritualized order of arrival of the adult males, and their monopoly of the end positions perhaps served to advertise their status to each other, as well as to other group members.