

## PART A

### INTRODUCTION AND METHODS

## Chapter 1

## INTRODUCTION

## 1.1 General Background

In most avian forest communities throughout the world, there are at least four insectivorous guilds (groups of species which use similar resources): (1) leaf or foliage gleaners, (2) salliers or flycatchers, (3) ground foragers, and (4) bark foragers. The importance of the bark foraging guild has been demonstrated by several studies in the United States of America. Nearly a quarter of the variance in foraging behaviour among 22 species in a hardwood forest of the north-east was related to bark foraging, though only four species were involved (Holmes *et al.* 1979). In oak woodland of the south-west, Landres and MacMahon (1980) identified five guilds, of which two were associated with bark.

The bark foraging woodpeckers (Picidae), nuthatches (Sittidae) and creepers (Certhiidae) figure prominently among the permanent residents of north-temperate forests (e.g. Willson 1970; Morse 1971). Members of other insectivorous guilds typically migrate during winter, or switch to other foods, such as seeds and fruits, and wander over large undefended areas in mixed flocks (Morse 1970; Austin and Smith 1972). Many bark foragers maintain territories throughout the year, suggesting that their food is both evenly distributed and economically defensible (Brown 1964, 1969). Active insects are abundant in bark during summer and inactive, dormant stages occur in or under bark during winter (Morse 1971; Karr 1976). In addition, most species of bark foragers become at least partly vegetarian in winter (Kilham 1958; Stallcup 1968; Bock 1970; Anderson 1976; Conner 1979; Williams and Batzli 1979a).

The Australo-Papuan treecreepers (Climacteridae) and sittellas (Neosittidae) are the only families in Australia specialized for climbing on tree-trunks and branches (Orenstein 1977). In their movements and general appearance, these birds superficially resemble the creepers and nuthatches respectively, families which are absent from the Australasian region. This region also entirely lacks the order Piciformes (including the

woodpeckers), many species of which excavate their own nest cavities, even in hard, living trees (Short 1974). Additionally, some woodpeckers chisel deep into wood to extract wood-boring larvae, a habit that is known for only two Australia birds, the Yellow-tailed Black Cockatoo, *Calyptorhynchus funereus* (Cacatuidae) (e.g. McInnes and Carne 1978) and the Shrike-tit, *Falcunculus frontatus* (Pachycephalidae). The parrot-like bill of the latter is used effectively for tearing and stripping sheets of peeling bark and nests of leaf-tying caterpillars, as well as for excavating in live twigs and dead branches. Yet this species forages as much in the foliage as it does on bark (Noske in prep.).

In contrast to North American bird communities, where up to five species of woodpeckers, three species of nuthatches and a creeper may co-exist, Australian mainland communities rarely contain more than three species of specialized bark foragers. Most species of treecreepers are allopatric or segregated by habitat to some extent (Keast 1957) and only one species of sittella occurs. Tasmania lacks both treecreepers and sittellas (Ridpath and Moreau 1966), but their niche is filled by several species of birds, each of which is slightly more specialized for bark foraging than its mainland relatives (Keast 1968). On the mainland, many non-climbing species exploit bark in search of insects or other food such as honeydew, including several species of honeyeaters (Meliphagidae) (Keast 1968; Ford and Paton 1976), thornbills (Acanthizidae) (H.L. Bell, pers. comm.) and Australo-Papuan flycatchers (Pachycephalidae) (Huddy 1979), but few of these show special morphological adaptations for this niche.

Three species of treecreepers occur in south-eastern Australia: the White-throated, *Climacteris leucophaea*, Red-browed, *C. erythroptera*, and Brown, *C. picumnus*. In a short preliminary study (Noske 1979), I compared the foraging behaviour and basic social organization of these three species during the non-breeding season at Wollomombi Falls in north-eastern New South Wales. The Brown spent much time on the ground whereas the smaller White-throated and Red-browed were almost totally arboreal. The last two species were very similar in their foraging behaviour, but the White-throated was normally solitary, while the Red-browed occurred in pairs or groups of three or four.

The differing social organizations of the White-throated and Red-browed Treecreepers posed several interesting questions, since such differences are usually linked with differing ecologies. Crook (1964) related differences between ploceine weaverbirds in their social organization (in particular, group size, nest dispersion and mating systems) to ecological factors such as the distribution and availability of food and the impact of predators. The relatively scattered and predictable food of forest-dwelling insectivorous species favoured monogamy and territorial defence, whereas the ephemeral but locally superabundant food of savannah-dwelling granivores favoured flocking and polygamy. To counter predation, the nests of the former were well-spaced and cryptic, while the conspicuous nesting colonies of the latter were built in inaccessible locations.

The White-throated and Red-browed Treecreepers are unlikely to experience different predation pressures where they coexist, but their differential selection of tree species for foraging (Orenstein 1977; Noske 1979) suggested that the social Red-browed exploited less evenly dispersed resources than the solitary White-throated. The discovery of communal breeding in several species of treecreepers, including the Red-browed and Brown (Orenstein 1976; Noske 1980) provided further impetus for a detailed investigation of the social organization of these birds, particularly since several workers have related communal breeding (where three or more birds attend a nest) to localized food resources and specialized habitat requirements (Gaston 1978; Stacey 1979; Koenig 1981; Emlen 1982).

While studies of comparative ecology (resource partitioning) and comparative ethology of congeners have enjoyed great popularity over the past two decades, studies paralleling that of Crook, in which these aspects are combined along with other life history information, are scarce (McKinney 1978). Few studies have compared the ecology of related communal and non-communal species (Brown 1974: 71). The present work aimed to investigate the possible relationship between behaviour and ecology in the three treecreepers of south-eastern Australia, and the Varied Sittella, *Daphoenositta chrysoptera*. The latter was included to provide more insight into the methods of resource use by Australian bark foragers. Most aspects of the life histories of these species were examined (including vocalizations,

roosting and nesting biology), as such information is not yet available for the great majority of Australian birds.

## 1.2 Taxonomy of the Study Species

### *Treecreepers*

While there is now general agreement that the Australo-Papuan treecreepers represent a distinct family (Climacteridae), unrelated to the northern treecreepers (Certhiidae), their affinities with other Australian passerine families remain unclear. Mayr (1963) suggested that Climacterids are closely allied to Acanthizids, but Harrison (1969a) favoured a Meliphagid derivation. In leg musculature, however, *Climacteris* is similar to the Paradisaeidae and Ptilinorynchidae (Orenstein 1977). Sibley and Ahlquist (in press), on the basis of DNA hybridization, also place *Climacteris* in an assemblage containing bowerbirds, which is distant from Acanthizids or Meliphagids.

*Climacteris* is confined to the Australian mainland, except for one species in montane New Guinea. Keast (1957) recognized six species belonging to three groups, based primarily on patterns of sexual dimorphism. In the first group, females have a deep orange patch on the cheek, which is lacking in males. This group contained only one species - the White-throated Treecreeper (*leucophaea*), in which Keast included the Little Treecreeper (*minor*) of North Queensland and the Papuan Treecreeper (*placens*). Although Schodde (1975) separated the Little Treecreeper, I questioned his criteria (Noske 1978) and Boles and Longmore (in press) have recently collected an intermediate form between the ranges of, but isolated from, the other two. Like Orenstein (1977, *in litt.*) the latter consider *minor* and *leucophaea* as conspecific, but treat *placens* as a distinct species.

Keast's second group contained the Red-browed Treecreeper (*erythroops*) of the humid south-east and the semi-arid White-browed Treecreeper (*affinis*) (Figure 1.1). In both species, the female has rufous edges to the feathers of the chest, as well as a rufous line above the brow, while in the male these markings are absent. Sexual dimorphism of plumage

FIGURE 1.1: *Distribution of the three groups of treecreepers and five races of Varied Sittella on mainland Australia*



 **White-throated**



 **Red-browed**

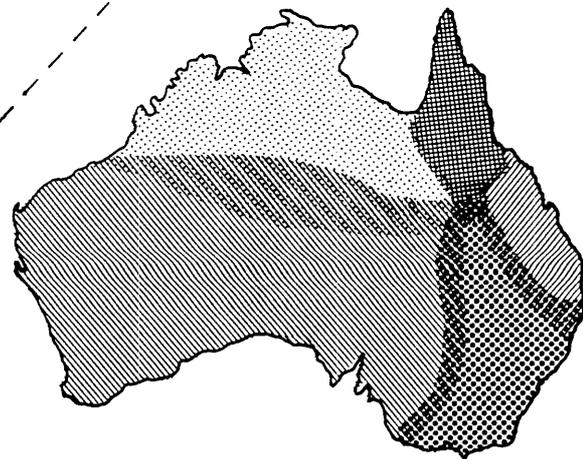
 **White-browed**



 **Brown**

 **Rufous**

 **Black-tailed**



**Varied Sittella**  
(5 races)

is much stronger in the Red-browed, where the face (including the lores, superciliary, and behind and below the eye) is uniform dark reddish-chestnut in females, and orange-brown in males.

The third group comprised three allopatric species (Figure 1.1): the Brown Treecreeper (*picumnus*), Rufous Treecreeper (*rufa*) and Black-tailed Treecreeper (*melanota*). The first two are virtually parapatric "sibling" species, very similar in plumage and voice. Females have the feathers of the chest marked with rufous (as in the previous group) but in males, this area is marked with black. The third species, however, has quite different vocalizations (unpubl. data) and while the female has chest markings typical of this group, the male has a black throat with white streaks. Yet this species shares with the other two species the characteristic habit of "tail-bobbing" (pers. obs.), hitherto overlooked by reviewers of the genus.

Orenstein (1977) compared the climbing adaptations of *Climacteris* with other bark-climbing birds and found that the White-throated was the most specialized of its genus, having shorter legs (proportions of hind-limb elements relative to sternum length), longer toes, and reduced pads on the plantar surface of the foot. In these features it resembled other genera such as the Spotted Creeper, *Salpornis*, of Africa and India, and the Coral-billed Nuthatch, *Hypositta*, of Madagascar, more than its congeners. The broad, well-developed foot pads on members of the Brown and Red-browed Treecreeper groups were viewed as an adaptation to their semi-terrestrial habits, increasing the surface area of the foot in contact with the ground. Orenstein considered the White-throated to be the most arboreal of the genus, but he observed foraging behaviour of Red-browed for only 90 minutes. Yet despite its longer hind-limbs and shorter toes (unpubl. data), the latter is just as arboreal as the White-throated (Noske 1979).

### *Sittellas*

Traditionally associated with the nuthatches (Sittidae) (Rand 1936; Mayr 1963) because of similarities in foraging locomotion and general morphology, the sittellas are now generally placed in a family of

their own (Neosittidae). From an analysis of leg muscles, Orenstein (1977) concluded that the resemblances between the nuthatches and the sittellas were due to convergence. Sibley and Ahlquist (1982) have recently shown from DNA hybridization that the sittellas are more closely related to the Australo-Papuan flycatchers (Pachycephalidae). Like the Australo-Papuan treecreepers, the sittellas are restricted to New Guinea and the Australian mainland but absent from Tasmania.

In Australia, the family is represented by five morphologically distinct taxa (Figure 1.1), formerly regarded as separate species but now treated as members of a single species, the Varried Sittella, *Daphoenositta chrysoptera* (Schodde 1975). This decision follows the demonstration of hybridization between all forms wherever they come into contact (Mayr 1950; Parker 1970; Ford 1980; Short *et al.* in press a,b). Of the two species found in New Guinea, one (*papuensis*) has been given conspecific status with *chrysoptera* (Diamond 1972; Schodde 1975), while the other, the Pink-faced Sittella (*D. miranda*) has been retained.

### 1.3 Thesis Structure

This thesis is presented in four parts. The remainder of this part (A) concerns the general methods used in the study, and compares the morphology and habitats of the four study species. The social organization and breeding biology of each species is described and contrasted in Part B. Factors underlying the evolution of communal breeding are examined in Chapter 7, and the general behavioural and ecological attributes of the communal treecreepers compared with those of other communal breeders studied to date. Part C deals with the foraging ecology of the species, attempting to answer questions, such as the following: which features of the foraging niche are most important in separating the species? Is there any significant intraspecific (specifically, temporal or sexual) variation in foraging behaviour which might affect interspecific niche relations? To what extent does the availability of food on bark reflect their foraging behaviour and diet? Finally, in Part D, I combine information from all chapters and attempt to relate the social behaviour and life history characteristics of each species (particularly in the treecreepers) with its ecology.

## Chapter 2

## STUDY SITES AND GENERAL METHODS

## 2.1 Study Sites

Of the three treecreepers in south-eastern Australia, the Brown has the widest distribution but is more typical of the inland slopes and plains than of the wetter tablelands and coast (Figure 2.1). The Red-browed has the most restricted range, occurring mainly on the tablelands (of the Great Dividing Range), but extending to the coast in some areas. These two species are rarely syntopic but each commonly coexists with the third species, the White-throated. The White-throated occurs throughout the range of the Red-browed and, indeed, it is doubtful if the latter occurs anywhere without the former (Orenstein 1976; Noske 1979). The Varied *Sittella* is found over the entire region, though is more plentiful on the tablelands and slopes than on the coast or inland plains.

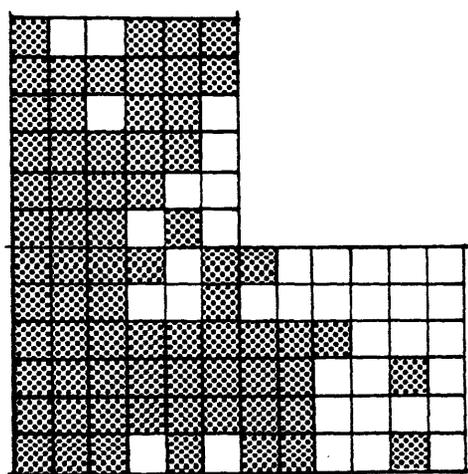
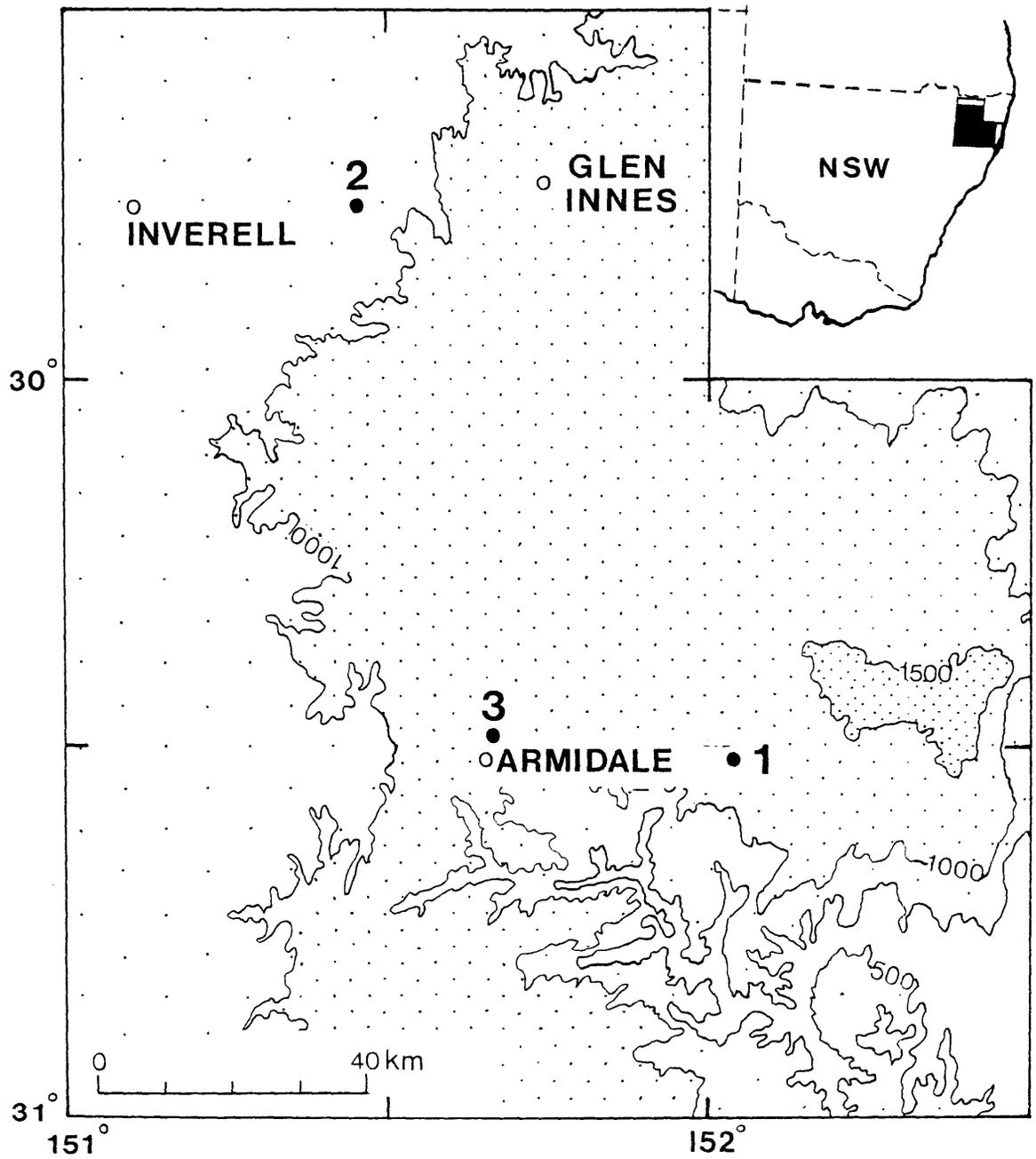
As I had already established the general demography of the White-throated and Red-browed at Wollomombi Falls Reserve, I continued to study these species there, adding the sittella. Swan Vale was chosen as the site to study the Brown as this species was uncommon at Wollomombi (Table 2.1) and on the eastern side of the Northern Tablelands generally (Figure 2.1). Additional observations of all species except the Red-browed were made at my home, Stringybark Hill. Details of the location, climate, vegetation and topography of all three sites are summarized in Table 2.1.

All sites supported open, dry sclerophyll forest or woodland, dominated by eucalypts (Figure 2.2). Each site had representatives from at least three groups of eucalypt (hereafter termed 'tree-types'), which differed markedly in bark texture and structure. Ironbarks, present only at Swan Vale, were covered by very hard, heavily-corrugated bark. Stringybarks, the commonest trees at all sites, were characterized by softer fibrous bark except for the outermost branches and twigs, which had a smooth surface (Figure 2.3). Boxes usually possessed thin, flaky or scaly bark on the trunk and a variable amount of smooth bark on the branches, depending

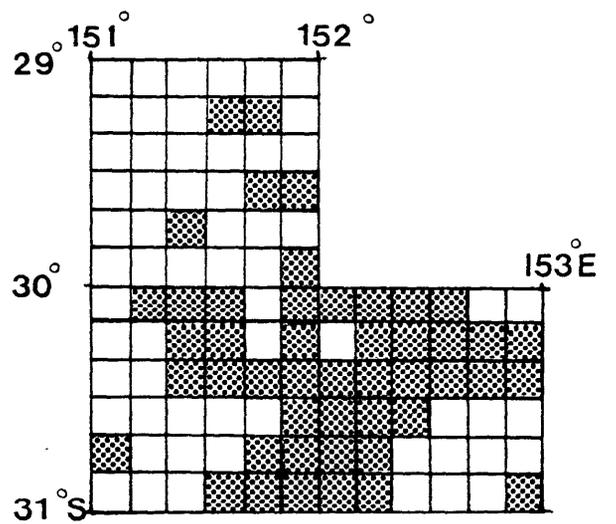
FIGURE 2.1: *Location of the three study sites and distribution of the Red-browed and Brown Treecreepers in north-eastern New South Wales*

1, Wollomombi Falls; 2, Swan Vale;  
3, Stringybark Hill

White-throated Treecreeper found in each  
10' grid square depicted; distributional  
data (pers. obs.; G. Holmes, S. Debus  
and H.A. Ford, pers. comm.)



**BROWN**



**RED-BROWED**

TABLE 2.1 : Characteristics of the three study sites

	WOLLOMOMBI FALLS	SWAN VALE	STRINGYBARK HILL
General Location (see Fig.2.1)	40 km E of Armidale, on eastern edge of Tablelands (30°32'S, 152°02'E)	100 km NW of Armidale, on western edge of Tablelands. (29°47'S, 151°28'E)	2 km N of Armidale. (30°29'S, 151°41'E)
Altitude (m)	900 - 950	770 - 810	1030 - 1040
Mean Annual Rainfall* (mm)	815	1085	753
Approx. area of Study Site (ha)	40	90	20
Topography and general description of habitat	Relatively undisturbed open forest situated on edge of deep gorges and surrounded by cleared grazing land; bisected (N-S) by a deep valley, and further dissected by several creeks and dry gullies.	Included open grazing paddocks with scattered patches of timber, and part of adjoining forest (on eastern side). Bounded by rocky hill-sides to north, cropland to south and permanent creek to west.	Semi-cleared hill, in grazing country. Narrow remnant strips of forest beside roads and isolated trees in open paddocks.
Dominant** Trees	Stringybarks ( <i>E. caliginosa</i> , <i>E. laevopinea</i> ) Boxes ( <i>E. melliodora</i> , <i>E. conica</i> , <i>E. sp. aff. cypellocarpa</i> ) Gums ( <i>E. blakelyi</i> , <i>E. amplifolia</i> and some <i>E. viminalis</i> along creeks).	Stringybark ( <i>E. macrorhyncha</i> ) Gums ( <i>E. dealbata</i> ; some <i>E. viminalis</i> along creeks) Ironbark ( <i>E. crebra</i> , mainly confined to eastern half) Box ( <i>E. melliodora</i> in pure and mixed stands)	Stringybark ( <i>E. caliginosa</i> ) Box ( <i>E. melliodora</i> ) Gums ( <i>E. blakelyi</i> , <i>E. viminalis</i> )
Understorey trees/tall shrubs	<i>Acacia filicifolia</i> <i>A. diphylla</i> <i>Jacksonia scoparia</i> <i>Exocarpus cupressiformis</i> <i>Angophora floribunda</i>	<i>Acacia leucoclada</i> <i>Angophora floribunda</i> <i>Casuarina cunninghamii</i> (margins of river)	<i>Acacia filicifolia</i> <i>Jacksonia scoparia</i> <i>Angophora floribunda</i>
Study Species#	White-throated Treecreeper Red-browed Treecreeper (Brown Treecreeper) Varied Sittella	White-throated Treecreeper Brown Treecreeper (Varied Sittella)	(White-throated Treecreeper) (Brown Treecreeper) Varied Sittella

\* sources: Wollomombi Falls, R. Edgar (1940-1980);  
Swan Vale, M.C.M. Woods (1958-1979);  
Stringybark Hill, Laureldale Res. Stn. (1960-1980)

\*\* all *Eucalyptus* species; given in approximate order of abundance

+ sparse or locally dense

# brackets, less than six individuals present and/or not studied

FIGURE 2.2: *Habitats at the two major study sites*

Open woodland at Swan Vale (upper) and  
forest at Swan Vale (middle) and  
Wollomombi Falls (lower)



FIGURE 2.3: *Texture of bark on three major types of eucalypts*

Upper, stringybark (left, trunk; right, thin branch with strips of peeling bark); lower left, box trunk; lower right, gum trunk



on the species. In contrast, gums were predominantly smooth-barked, often with some rough bark at the base of the trunk (rarely extending more than a metre above the ground). These trees shed their outer bark in sheets or long curled strips ('ribbons'), which often collected in the forks of branches. Similarly, the smooth branches of boxes (with the exception of *Eucalyptus conica*) were often festooned with hanging ribbons.

Understorey trees were sparsely distributed throughout each site, and small shrubs (e.g. *Olearia*, *Casinia*) were in localized patches (at Wollomombi) or absent. Both Swan Vale and Stringybark Hill included areas which were completely cleared. Dead trees (which had been ring-barked) and stumps had been left standing in many clearings at Swan Vale.

Total rainfall at Wollomombi was very close to average in the first two years of the study but below average in 1979 and 1980. This was mainly due to little rain during the 1979-80 summer (Figure 2.4). Rainfall at Swan Vale was below average in 1977 and 1979 but above average in 1978.

## 2.2 General Methods

Monthly field trips of five to seven days were made to Wollomombi and Swan Vale from March 1977 to May 1980 and May 1977 to January 1980, respectively. Swan Vale was usually visited in the second week of each month and Wollomombi in the last week. However, brief additional trips were undertaken to both sites frequently during the breeding season (mainly spring and summer for all species) and occasionally in 1980 and 1981. Observations at Stringybark Hill commenced in February 1977 and continued until late 1982, but were mainly confined to the breeding season.

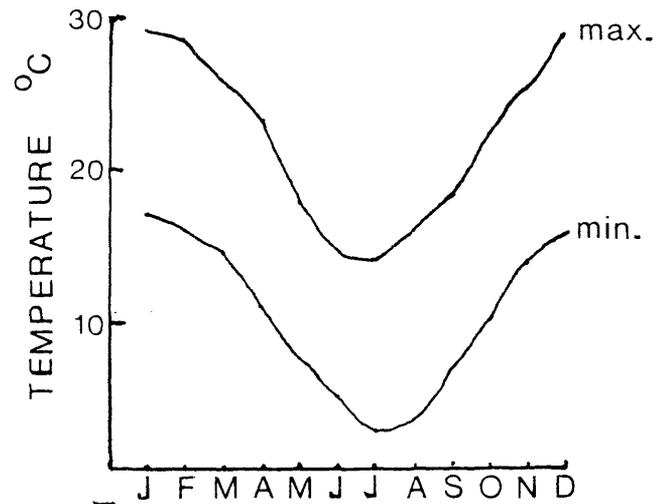
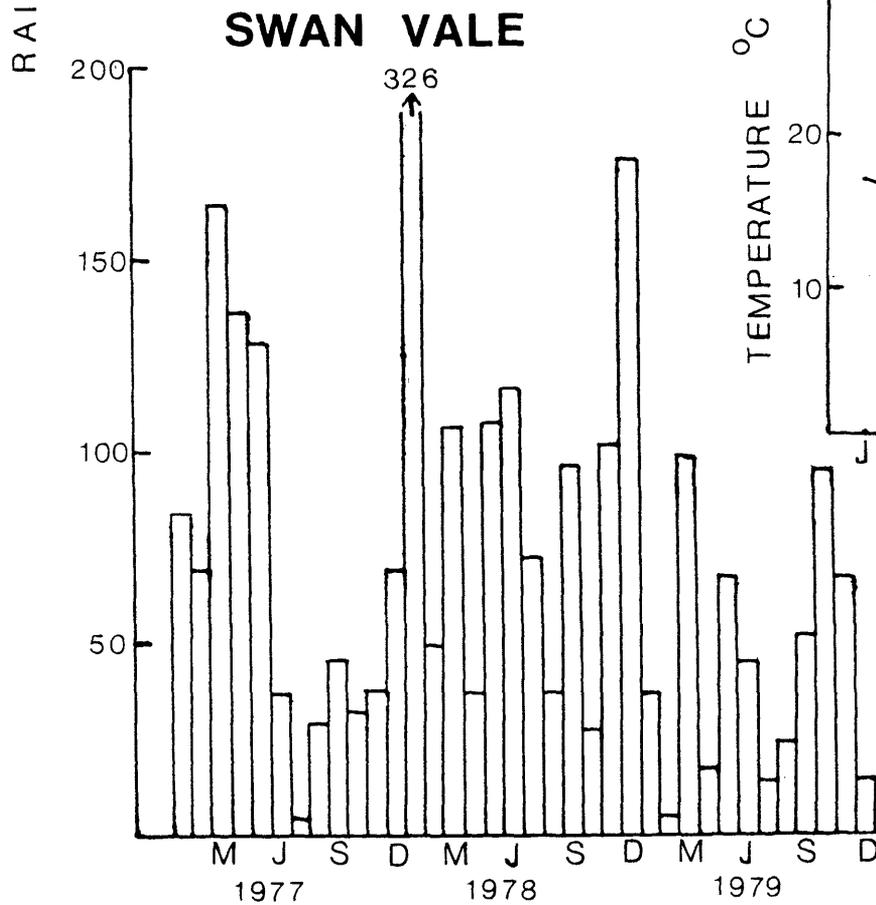
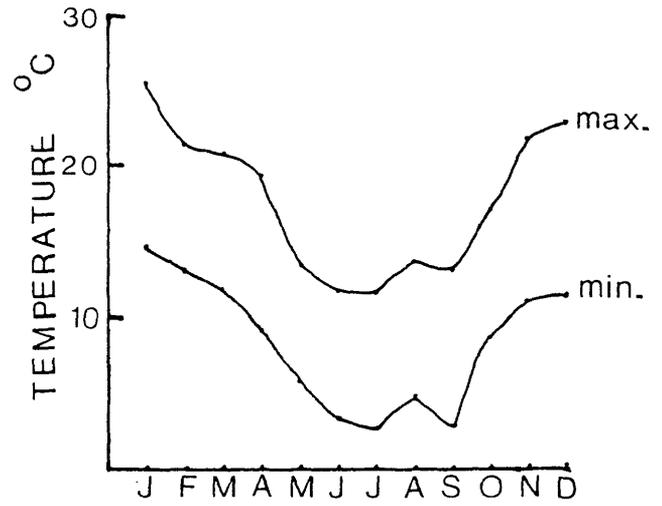
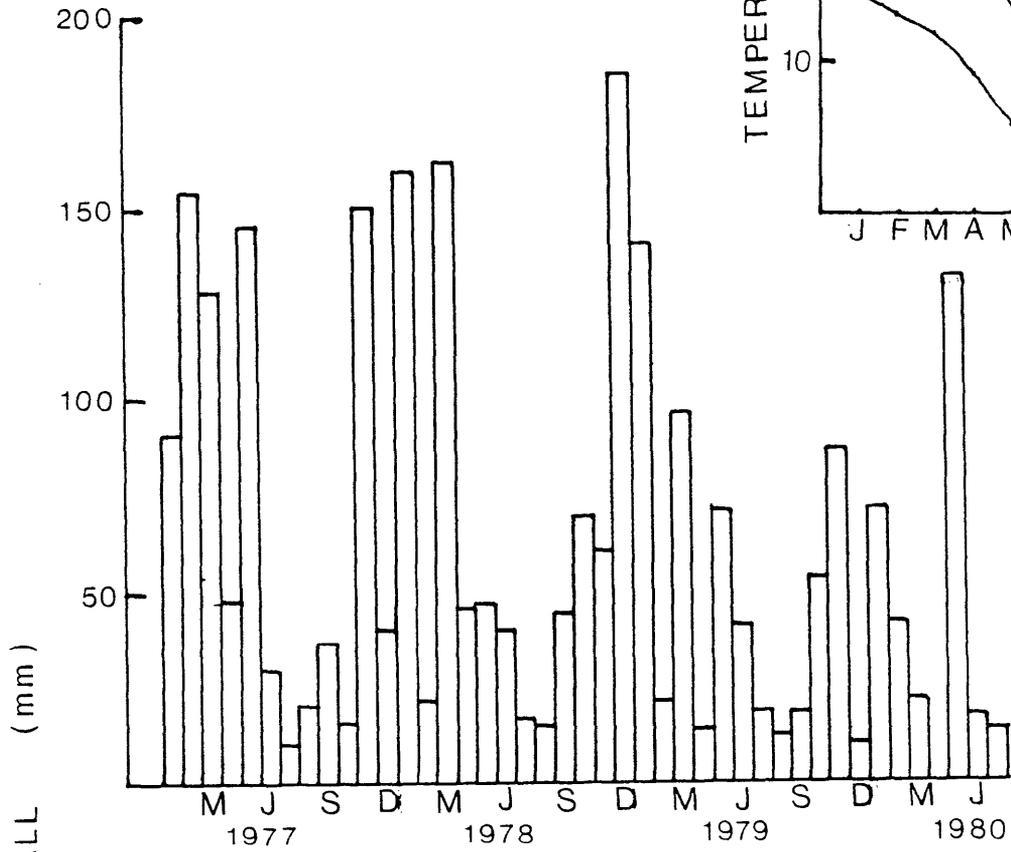
### 2.2.1 Capture and marking of birds

Adult birds were captured for marking by two methods. Up to six mist-nets were erected on each trip to Wollomombi and Swan Vale during the first nine months, and sporadically afterwards. To cover the whole area at each site, nets were concentrated in one portion of the site one month, and another, the next. Despite checking at intervals of 20 to 30 minutes,

FIGURE 2.4: *Monthly rainfall and average minimum and maximum temperatures over the study years at Wollomombi Falls and Swan Vale*

Sources: for Wollomombi Falls, Styx River Meteorological Station (temperatures) and R. Edgar, owner of adjacent property (rainfall); for Swan Vale, Inverell Research Station (temperatures) and M.G.M. Woods, owner of adjacent property, (rainfall)

# WOLLOMOMBI FALLS



two treecreepers at Wollomombi were killed by predatory birds while trapped in mist-nets. The second method involved catching treecreepers at roost during the night with a butterfly-net, mounted on a 2.5 metre long wooden rod. A torch was used to illuminate the roost-site while the net was placed over the bird (if roosting on the tree-trunk), or roost-hole, and quickly scooped when the bird flew into it.

The latter method required locating roost-sites, but was nevertheless less time-consuming than mist-netting, and no casualties were recorded. About 17% and 14% of adult White-throated and Brown respectively, were caught in this manner, the roost-sites of the other species usually being inaccessible. Towards the end of the study, one Brown was caught while incubating during the day, and another while brooding during the night, by placing the butterfly-net over the nest-entrance. Neither abandoned their nests.

All species were marked using the same scheme: two coloured celluloid bands (see Section 2.3) were placed on the left leg and a numbered aluminium band (issued by CSIRO) on the right. This scheme prevented confusion between the aluminium band (which often appeared white in the field) and white celluloid bands, but reduced the number of permutations possible. Black bands were generally not used on treecreepers as these birds have blackish legs. Similarly, the bright yellow legs of sittellas precluded the use of yellow bands on this species.

Acetone was used to seal the join on celluloid bands but despite this several Brown lost one or both such bands after three years. As this species foraged extensively on the ground band losses were probably caused by abrasion with soil and litter. Each of the five individuals concerned were re-trapped and given new bands. One Red-browed and one Brown developed swollen abscesses around the celluloid bands; these bands were removed from both birds when re-trapped, but only the Brown recovered. The injured leg of the Red-browed caused it to stumble frequently when foraging and presumably led to its death.

### 2.2.2 Observations

On each field trip, I checked every known individual to monitor population and territory changes, as well as reproductive success (measured

as number of fledged young) during the breeding season. Locations of birds were marked on gridded maps and activities other than foraging (e.g. social interactions, roosting and nesting behaviour) recorded in note-books or on tape-recorder. Details of methods employed in the collection of foraging data and assessments of food availability are described in Chapters 9 and 11 respectively.

I attempted to find as many nest- and roost-sites as possible. In the case of treecreepers, this often involved following birds for over an hour, only to lose the subject when it flew to the distant site. Nests were watched for periods of 30 minutes or more to record incubation spells, feeding rates and the identity of visitors. Hides were not used as the birds were generally not wary of humans; 10 x 40 binoculars were usually sufficient to identify birds, but a telescope was employed when it was necessary to view nests from a long distance.

An aluminium extension ladder permitted access to most nests less than 12 metres from the ground, but nests above this height or at the end of horizontal hollow limbs were not inspected. For several unstable, hollow trees at Swan Vale, the ladder was secured to a tractor (when available), parked at the base of the tree. A thin "pencil" torch was used when examining nest-holes of treecreepers and extracting young. The open, cup-shaped nests of sittellas were rarely accessible, but where possible, contents were checked from the nearest vantage point by holding a mirror, attached to the end of a pole, directly above the nest. Heights of trees, nests and roost-sites (greater than 3 metres) were determined using a Suunto inclinometer.

Nestling treecreepers were extracted from nest-holes by hand where possible. However, as most nests were too deep or narrow to permit this, a noose of fishing-line (housed in a rigid but malleable metal pipe) was used to draw the bird out as well as to return it, by the neck. This procedure never resulted in injury to the bird. Some nests were inspected at frequent intervals (after watches) to determine incubation and nestling periods, and growth rates of young. Nests with well-developed young were usually not examined owing to the danger of causing them to leave prematurely. In a few instances when the age of young was unknown, nestlings

flew while I was climbing their tree, but in all cases remained in the nest when I returned them.

### 2.2.3 Collection of birds

For a detailed examination of the morphology and diets of the study species, specimens of each were collected from areas two to twelve kilometres outside the study sites. Additional specimens of sittellas were taken from the Northern Rivers region in the north-eastern corner of New South Wales, extending north and east from Glen Innes (see Figure 2.1). These specimens represented a hybrid population between the nominate "Orange-winged Sittella", *D.c. chrysoptera*, of south-eastern Australia (the region including the study sites depicted in Figure 2.1: inset) and the "White-headed Sittella", *D.c. leucocephala*, of central-coastal Queensland (Noske unpubl. ms.; Short *et al.* in press b). These hybrids differed from local birds mainly in head coloration.

Birds were shot using a .410 shotgun, and dissected within two hours of collection. Each specimen was sexed internally and its gonads stored in a 10% formalin solution. The stomach and intestines were removed and preserved in 70% alcohol. Tongues and claws were viewed in the laboratory under a microscope to make accurate measurements. Weight and moult were recorded for collected specimens as well as for live birds during banding operations. Details of the analysis of stomach contents are presented in Chapter 11.

## 2.3 Terminology and Abbreviations

Communal breeding refers to the system in which more than two birds attend a nest or dependent young. Though the term 'cooperative' has been used interchangeably with 'communal' in this context, I have chosen the latter because of its wider use in the literature (see also Brown 1978: 127). 'Group' is used rather than 'flock' to describe permanent or semi-permanent associations of individuals (Rowley *et al.* 1979). Like Rowley (1981: 232), I regard pairs as the smallest 'group'. Birds other than the presumed breeding (primary) pair in each group are termed 'auxiliaries' in accordance with Dow (1980a). However, as no terms have been advanced to

replace 'helping', the provisioning behaviour of the auxiliaries, this term is (reluctantly) used here.

'Huddling' refers to the situation where members of a group sit together along a branch, side by side (see Figure 3, Rowley 1968; King 1980). This term is used in preference to 'clustering', which is perhaps best restricted to the peculiar roosting configuration of species of wood-swallows (Artamidae), where individuals crowd together on vertical surfaces (e.g. Stokes and Hermes 1979; see Figure 2, Rowley 1968). 'Clumping' has been coined mainly in connection with allopreening behaviour (Kunkel 1974) and implies as great a degree of contact as clustering.

Throughout the thesis, the seasons are defined as summer, December to February; autumn, March to May; winter, June to August; and spring, September to November. ABBS refers to the Australian Bird-Banding Scheme administered by the Division of Wildlife Research, CSIRO. The Nest Record Scheme (NRS) is operated by the Royal Australasian Ornithologists Union; the number following references to the scheme specify the cards (nest number and year) from which the information was extracted.

Individual birds are designated by their colour-bands, which are abbreviated as follows (in brackets): white (W), red (R), orange (O), yellow (Y), light green (G), dark green (D), blue (B), magenta (M) and black (N). The letter U signifies unbanded birds, followed by the letter of the group to which they belonged, or their status (M = mated; U = unmated).

Chapter 2  
MORPHOLOGY, PLUMAGE AND HABITATS  
OF THE STUDY SPECIES

3.1 Treecreepers

3.1.1 Mensural characters

*Interspecific Comparisons*

Noske (1979) found no significant difference between the White-throated and Red-browed Treecreepers in body length or bill dimensions, based on twelve and nine specimens respectively, from several localities in the Armidale region. Examination of a larger sample collected during the present study revealed that White-throated had significantly longer wings than Red-browed (Table 3.1 and 3.3), a difference supported by data in Keast (1957) and Orenstein (1977), though they made no interspecific comparisons. Despite this, Red-browed were slightly, but significantly heavier than White-throated at or near Wollomombi (Tables 3.1 and 3.2).

There were no significant differences between these two species in the length of the bill, tongue, tarsus or tail but the furcation at the tip of the tongue was significantly deeper in the Red-browed than in the White-throated (Tables 3.1 and 3.3). In addition, the White-throated had a significantly more curved hind-claw than the Red-browed. Data in Orenstein (1977) suggested that the Red-browed has a longer hind-claw than the White-throated, based on measurements of the external chord. However, as Norberg (1979) stated, it is the curvature of the claw (rather than its length) that is important in increasing its ability to cling to bark.

The Brown Treecreeper is about one and a half times as heavy as the other two species (Table 3.2), though not much longer in the body (Noske 1979: Table 2) or wing (Orenstein 1977: Table 9). Overall, there was no significant difference between the Brown and White-throated at Swan

TABLE 3.1: *Results of comparisons (t-tests) between White-throated and Red-browed Treecreepers in mensural characters* †

MORPHOLOGICAL CHARACTER	t	df	significance#
BILL-LENGTH	1.22	37	NS
BODY WEIGHT	2.67	93	**
TAIL	1.12	48	NS
TARSUS	0.79	43	NS
WING	8.52	38	***
HIND-CLAW CURVATURE	2.38	53	*
TONGUE	1.47	46	NS
TONGUE-TIP FURCATION	12.20	53	***

† means and methods of measurements shown in Tables 3.2, 3.3; only birds from Wollomombi region used in this table

# \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ ; NS - not significant,  $p > 0.05$

TABLE 3.2: Mensural characters\* of the three treecreepers

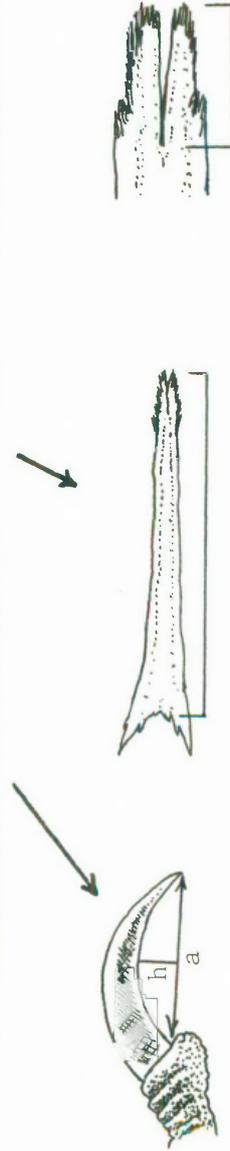
SPECIES	SEX	BILL LENGTH (mm)	BODY WEIGHT <sup>†</sup> (g)	TAIL (mm)	TARSUS (mm)
WHITE-THROATED TRECREEPER					
Wollomombi	♂	14.5 ± 0.12 (11)	22.5 ± 0.24 (29)	64.0 ± 0.71 (10)	24.3 ± 0.20 (8)
"	♀	14.0 ± 0.09 (7)	21.5 ± 0.27 (25)	61.9 ± 1.24 (7)	24.1 ± 0.37 (6)
Swan Vale	♂	14.5 ± 0.26 (7)	23.5 ± 0.33 (14)	63.9 ± 0.97 (6)	24.2 ± 0.25 (6)
"	♀	14.2 ± 0.13 (7)	22.1 ± 0.27 (17)	63.3 ± 0.98 (8)	24.4 ± 0.21 (7)
RED-BROWED TRECREEPER	♂	14.1 ± 0.13 (13)	22.8 ± 0.23 (26)	64.1 ± 0.55 (10)	24.3 ± 0.15 (10)
	♀	14.1 ± 0.19 (8)	22.8 ± 0.47 (15)	64.1 ± 0.59 (8)	24.5 ± 0.33 (8)
BROWN TRECREEPER	♂	14.6 ± 0.14 (15)	37.2 ± 0.34 (38)	72.2 ± 0.56 (13)	28.0 ± 0.16 (16)
	♀	13.8 ± 0.15 (13)	33.8 ± 0.47 (20)	69.6 ± 0.63 (13)	26.9 ± 0.19 (14)

\* values represent mean ± standard error (sample size in brackets);  
; vertical bar by means indicates that values are not significantly different ( $p > 0.05$ );  
; only adults measured

† includes data from live birds trapped at both study sites

TABLE 3.3: Mensural characters\* of White-throated and Red-browed Treecreepers from the Wollomombi region

SPECIES	SEX	WING-LENGTH (mm)	HIND-CLAW <sup>+</sup> CURVATURE	TONGUE LENGTH (mm)	TONGUE FURCATION DEPTH (mm)
WHITE-THROATED TREECREEPER	♂	91.6 ± 0.43 (11)	3.89 ± 0.05 (15)	11.8 ± 0.19 (13)	1.34 ± 0.05 (29)
	♀	88.8 ± 0.51 (9)	3.89 ± 0.09 (15)	11.5 ± 0.12 (8)	
RED-BROWED TREECREEPER	♂	86.3 ± 0.43 (11)	4.03 ± 0.09 (13)	12.1 ± 0.07 (0)	2.39 ± 0.07 (26)
	♀	85.4 ± 0.16 (8)	4.12 ± 0.08 (12)	11.7 ± 0.09 (8)	



\* as in Table 3.2

+ ratio  $\frac{a}{h}$ , following Norberg (1979); the smaller the value the greater the curvature; juveniles included

Vale in bill length ( $t = 0.52$ , 40 df,  $p > 0.05$ ). Orenstein's (1977) data show that the Brown has the shortest bill of the three species relative to its wing-length.

#### *Intraspecific Comparisons*

White-throated at Swan Vale were heavier than those at Wollomombi (Table 3.2), though the difference was significant only in males ( $t = 2.26$ , 41 df,  $p < 0.05$ ). Males were significantly heavier than females at both sites ( $t = 2.88$ , 52 df and  $t = 3.27$ , 29 df, at Wollomombi and Swan Vale respectively, both  $p < 0.01$ ). Males also had significantly longer bills than females at Wollomombi ( $t = 3.27$ , 16 df,  $p < 0.01$ ) but not at Swan Vale ( $t = 0.82$ , 12 df,  $p > 0.05$ ). In contrast, Red-browed exhibited no sexual differences other than in tongue length ( $t = 3.52$ , 15 df,  $p < 0.001$ ). Orenstein (1977: 60) also noted no sexual difference in wing-length in this species. However, there was strong sexual dimorphism in the Brown in all characters measured ( $p < 0.001$  for weight, bill and tarsus and  $p < 0.01$  for tail) (Table 3.2).

#### 3.1.2 Juvenile plumage

##### *White-throated Treecreeper*

Mellor (1915) and White (1915: 142) were among the first to suggest that the conspicuous patch of orange-chestnut on the rump and upper-tail coverts of young White-throated Treecreepers was peculiar to females. Howe (1921) reported a nest containing two young, one of which had an "orange cheek-patch and bright red rump" and the other having "no cheek-patch and a grey rump...slightly washed with rufous". Another nest contained four young, all with the bright rufous rump, but Howe neglected to mention whether they had orange cheek-spots.

My repeated examinations of young at two nests, and casual inspections at many other nests indicated that nestlings could be sexed nine days after hatching. At this time the tiny quills emerging from the cheeks were deep reddish-orange in females and pale buff in males. However, one or two days earlier, the feathers of the rump and upper-tail coverts burst from their quills. At one nest, all of these feathers were entirely rufous on two eight-day old female sibs (sexed later by cheeks), but grey

on their brother. One of the females at another nest had rufous on only four of its ten upper-tail coverts, and pale grey tips to some of the rufous rump feathers, while her sister and brother resembled the female and male young of the first nest, respectively.

Data for 70 sexed nestlings or fledglings (31♂:39♀) show that the rufous on the rump (and upper-tail coverts) was uniform on the great majority of young females, but patchy on the remainder (13%); none had entirely grey rumps (Table 3.4). Males had all-grey rumps in 68% of cases; two birds showed extensive rufous and the remainder had chestnut edges to some of the rump feathers. The sex of two handled birds was indeterminate; one had a grey rump and the other a rufous rump, but both possessed cheek patches of an intermediate colour (deep buff). Determination of rump colour of fledglings in the field was probably less accurate than that of nestlings in the hand. One fifteen-day old male nestling possessed chestnut flecks near the tips of twelve rump feathers, but these were not apparent eleven days later when it fledged.

The age at which most White-throated lose the rufous colouring on the rump has not yet been established. This is partly because few birds of known age have been recaptured and because banders generally failed to record rump coloration or the methods used to assess age. Of 221 "juveniles" (including nestlings and immatures) banded through ABBS up to 30 June 1979, 51 (23%) were subsequently recovered (D. Purchase, pers. comm.) but only one of these was banded as a nestling. Thirty birds banded as "juveniles" were re-trapped as "adults" within four months of banding (data provided by D. Purchase). Only one "immature" was banded as late as August, while another banded as "immature" in May was recaptured one month later as an "adult". Assuming "juveniles" were distinguished by rufous on the rump, and "adult" by their lack of it, these data indicate that the rufous usually disappears within the first few months of life, as suggested by Wilson in Frith (1969: 375).

My observations suggest that the rufous on the rump of young White-throated persists for long periods on some birds. On one female at Wollomombi, traces of rufous were visible in the field for at least four years. Another female retained the rufous for at least 14 months, though it

TABLE 3.4: *Sexual dimorphism in rump coloration of juvenile\* White-throated Treecreepers*

AMOUNT OF RUFOUS ON RUMP				
SEX <sup>†</sup>	Uniform	Patchy	None	TOTAL
♂	2	8	21	31
♀	34	5	0	39
TOTAL	36	13	21	70

\* includes both nestlings and fledglings

† sexed on basis of colour of lower cheek, which is deep orange in females, and whitish to pale buff in males

was not discernible in the field after the first six months. A third female (banded as a juvenile in February at Stringybark Hill) showed gradual diminution of rufous when re-trapped in April and July but this colour was still visible in the field in September just before the bird disappeared.

Juvenile White-throated also typically possessed creamy or buffish-white streaks with black edges along the shafts of the lower scapulars and occasionally the back. Although all of the juveniles handled or collected during this study possessed this character, it was not always noticeable in the field. The distinctness and number of streaks varied considerably between individuals, even siblings of the same sex. Moreover, several adult females at Wollomombi retained whitish streaks on their scapulars for at least two years.

Strangely, I can find no reference to this character in the literature. North (1906) described similar markings on the greater wing-coverts of immature birds and on only "a few of the feathers of the back"; yet I have never noted these streaks on the wing-coverts. North (1906) also erroneously stated that young birds just before leaving the nest have the forehead and crown "dull dark brown without any paler margins to the feathers". Most nestlings I handled had the "scalloped" forehead typical of older birds, though even in adults this area is variable in colour.

Other plumage features I noted on well-feathered nestlings were (1) thin grey margins to the white feathers of the lower throat and chest, giving a scaly effect; (2) reduced area or absence of white on lores; and (3) a strong cinnamon wash to the under-tail coverts and occasionally the breast and abdomen on some birds. A few females had a cinnamon tinge on the crown and on the tips of the outer tail feathers. In addition, late nestlings had blackish-brown legs with bright yellow behind the "knee", on the tips of the toe-nails and on the underside of the toes. The bill was blackish-grey with a yellow cutting-edge and base to the lower mandible, while the gape was pale cream. Some of these features remained on birds after they fledged.

Apart from whitish streaks on the scapulars, and occasionally rufous patches on the rump, juvenile males are difficult to distinguish from adult males. This fact possibly explains, in part, why there are approximately four times more juvenile females banded than juvenile males (based on records of ABBS, supplied by D. Purchase). Other possible reasons for this disparity are discussed in the next chapter. As adults are usually moulting at the time juveniles are present, the "fresh" plumage (particularly remiges and rectrices) of the latter contrasts with the worn plumage of the former when in the hand.

#### *Red-browed Treecreeper*

In contrast to the bold black and white-striped undersurface of adult Red-browed Treecreepers, juveniles of this species have a plain brownish-grey breast, though often with some white streaks only visible in the hand. Additionally, the reddish- or orange-brown region on the face of adults is mid-grey on juveniles. Thus, juvenile Red-browed superficially resemble Brown Treecreepers. Young nestlings have flesh-grey legs, with paler claws, but older birds have blackish-grey legs.

Of two nestling sibs examined and colour-banded about 22 days after hatching, only one had faint reddish markings, partly hidden, on the chest. This bird was subsequently verified as a female and the other as a male. Yet young Red-browed cannot be reliably sexed in the field until at least 30 days after fledging. A few reddish-chestnut stripes were noted on two females at 35 and 36 days post-fledging, while on another bird of the same age (later sexed as female) these markings were not apparent. One female showed reddish-chestnut specks on the forehead at 52 days, though two others (one in the hand) did not exhibit this feature at 85 and 87 days. Females with incomplete facial markings were recorded from 114 to 153 days, but another was almost indistinguishable from adults at 145 days.

Development of the orange-brown face of males was also slow. Two birds at 50 and 60 days post-fledging showed little evidence of colour on the face in the field, while "incomplete" markings were noted on three birds from 90 to 108 days. One male was apparently indistinguishable from adults at 120 days post-fledging. Thus, it appears that adult plumage in this species is attained between four and five months after fledging.

### *Brown Treecreeper*

North (1906) and later texts (e.g. Frith 1969, Orenstein 1976) described the immature Brown Treecreeper as having ill-defined streaking on the underparts and rufous-washed flanks and undertail-coverts, but failed to note the dark dorsum of young birds compared to adults. The dark-grey crown contrasts with the chocolate-brown back and wings, resembling the plumage of Red-browed Treecreepers (both juvenile and adult). On adult Brown, these parts are greyish-brown and dull earth-brown, respectively. Moreover, the eyebrow, cheeks, and breast of juveniles are grey rather than buff, and the upper throat whitish in young males. Adult plumage is acquired by about two months after fledging except for a cinnamon suffusion on the flanks, which remains for over a year on some birds.

Despite the weak sexual dimorphism in the plumage of adult Brown, nestlings of this species can be sexed at an earlier age than Red-browed owing to the distinctive markings of the male. Between 14 and 16 days after hatching, the feathers emerging from the lower throat quills of males show black freckles, which eventually develop into the black-spotted white "bib" of fledglings of this sex. The rufous markings on the lower throat of females are discernible on 20-day old nestlings in the hand, but generally invisible on fledglings in the field. As in the Red-browed, nestling Brown have flesh-grey legs, darkening with age, and a pale cream-coloured bill and gape with dark grey along the top of the culmen and tip of the mandible. The pale gape is visible on birds up to at least three months after fledging.

#### 3.1.3 Habitats

The White-throated Treecreeper is the most catholic of the genus in its habitat requirements, occurring in all types of rainforest to fairly open sclerophyll woodland, though not extending as far west as the plains. Holmes (1973) noted that this species was particularly abundant in the cool-temperate rainforests dominated by Antarctic Beech, *Nothofagus moorei* - a habitat similar to that frequented by the Papuan Treecreeper (H.L. Bell, pers. comm.). I have been impressed by its abundance in cypress pine forests (*Callitris*) on the north-west slopes, perhaps the "dry" equivalent of the closed forest communities of more humid environments. In the Moree

district on the western edge of its range, Morse (1922) recorded this species only in *belah* (*Casuarina cristata*) forests, another apparently favoured habitat in drier areas (pers. obs.). Within its range the species is also commonly encountered in river oaks (*C. cunninghamii*), which often form dense closed forests along streams. It also occurs in exotic pine forests (Gepp 1976; Driscoll 1977; pers. obs.).

Despite statements by several authors to the contrary (e.g. Kikkawa *et al.* 1965; Slater 1974; Orenstein 1976), the Red-browed rarely penetrates climax rainforest (pers. obs.; Morris *et al.* 1981) but typically occurs in eucalypts such as Flooded Gum (*E. grandis*), Blue Gum (*E. saligna*) and Tallow-wood (*E. microcorys*) on the edges of rainforests or emerging above regenerating rainforest. Among its habitats is sub-alpine woodland, dominated by Snow Gum (*E. pauciflora*) but sometimes mixed with other gums (*E. dalrympleana*, *E. nitens* and *E. stellulata*) all of which are mostly smooth-barked trees. The fondness shown by Red-browed towards such trees has been noted previously (Orenstein 1977; Noske 1979) but the species is also a common inhabitant of forests composed almost exclusively of predominantly rough-barked eucalypts (e.g. New England Blackbutt, *E. andrewsii campanulata*; Messmate Stringybark, *E. obliqua*; Brown Barrel, *E. fastigata* and many peppermints). However, it completely avoids the drier areas dominated by *Callitris* or ironbarks, both entirely rough-barked trees.

Though possibly originally confined to the woodland and savannah of the inland slopes and plains, the Brown Treecreeper has undoubtedly benefitted from the clearing activities of humans, and now occurs, albeit patchily, throughout the tablelands and coastal plains on the edges of forests and around clearings. It particularly favours disturbed areas, where there is an abundance of dead timber (e.g. Hindwood 1966; Orenstein 1976). In arid inland regions it is most common along eucalypt-lined watercourses, rarely penetrating far into the *Acacia*-dominated communities. Like the Red-browed, this species avoids the interior of *Callitris* forests.

#### 3.1.4 Summary of interspecific differences

Orenstein (1977) drew attention to the distinctiveness of the White-throated compared to its congeners, in terms of modifications of the hind-limb (see Section 1.2). He also noted that the bill of the White-

throated was thinner and straighter than those of its congeners. The view that the White-throated is divergent from the other species is strengthened by a comparison of several plumage and soft-part characteristics summarized in Table 3.5. As already indicated (Section 3.1.2), the juvenile plumages of the Red-browed and Brown are closer to each other than either is to the White-throated.

Of the three groups, only the White-throated inhabits rainforests. Indeed, the Little and Papuan Treecreepers (considered conspecific with the White-throated by Keast 1957) are confined to montane rainforests in North Queensland and New Guinea, respectively. The striking difference between the eggs of the White-throated and those of its congeners, commented on by others (North 1906; Harrison 1969a), suggests that this species evolved under different nesting conditions or predator regimes. Unmarked (white) eggs are typical in hole-nesting birds, presumably because there is little need to camouflage them (Van Tyne and Berger 1971) and/or because white eggs are more easily seen by parents in dark holes. The relatively unmarked eggs of the White-throated may be an adaptation for visibility by parents in the extreme dark conditions of rainforests, where it presumably originated (e.g. Frith 1976: 605).

## 3.2 Varied *Sittella*

### 3.2.1 Mensural characters

*Sittellas* are substantially smaller than treecreepers, weighing approximately half that of the White-throated and Red-browed (Tables 3.1 and 3.6). In general appearance, the *sittella* is stockier and shorter-tailed than treecreepers, and the bill, in contrast to the tapering, slightly decurved one of the treecreepers is uniformly slender and slightly upturned (Figure 3.1).

Male *sittellas* were significantly longer-billed than females ( $t = 12.11$ , 64 df,  $p < 0.001$ ), a fact independently found by Short *et al.* (in press a). Males also had a significantly longer wing than females ( $t = 3.88$ , 63 df,  $p < 0.001$ ), but there was no significant sexual difference in weight ( $t = 1.45$ , 59 df,  $p > 0.05$ ). The hind-claw of males was signifi-

TABLE 3.5: *General characteristics distinguishing the White-throated Treecreeper from its congeners*

	SPECIES - GROUPS	
	WHITE-THROATED *	RED-BROWED † BROWN
SEX MARKINGS # (FEMALES)	Dark orange cheek spot	Reddish-chestnut stripes on chest (small in <i>picumnus</i> )
BILL SHAPE #	Thinner, straighter	Stouter, gradually curved
BILL COLOUR	Black with greyish-white base to lower mandible	All black
CROWN	Pale edging to fore-crown ("scalloping")	Uniform (dark)
EYEBROW	None	Distinct, contrasting with crown (except in <i>melanura</i> )
LORES	Narrow white stripe parallel with gape	Same colour as crown
JUVENILE PLUMAGE (DORSAL)	Rump-patch (orange-chestnut) on females; narrow white streaks with black edges on scapulars (variable)	Similar to adult; no rump patch or streaks on scapulars
LEGS AND TOES (NESTLINGS)	Brownish-black with bright yellow behind "knee"; tips of toenails and soles yellowish	Flesh-grey with whitish tips to toenails
EGG COLOUR	White, sparingly dotted with dark-brown	Pink to pinkish-white densely marked with red-brown and lilac-grey
HABITAT	Rainforests, sclerophyll and pine forests (native and exotic)	Sclerophyll forests and woodlands only

\* includes Little and Papuan Treecreepers, though evidence based entirely on White-throated (considered nonspecific by some)

† Keast's (1957) groups lumped

# also noted by Keast (1957) and/or Orenstein (1977)

TABLE 3.6: *Mensural characters\* of the Varied Sittella*

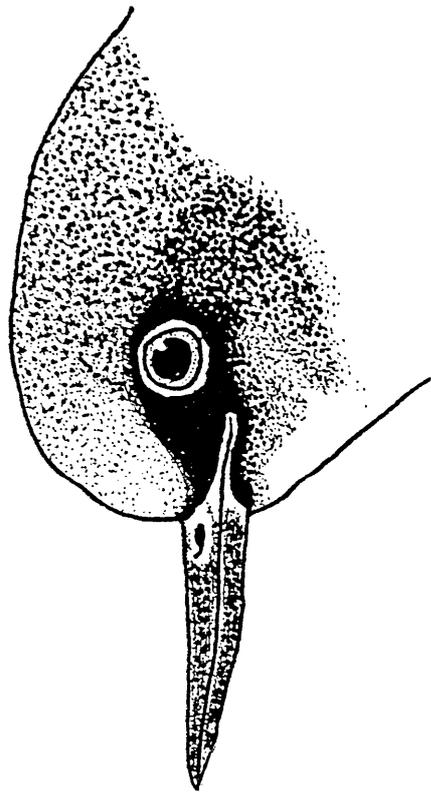
SEX	BILL LENGTH (mm)	BODY WEIGHT (g)	WING (mm)	TAIL (mm)	TARSUS (mm)	HIND-CLAW <sup>†</sup> CURVATURE (mm)
Northern Rivers	♂ 11.9±0.06 (31)	11.3±0.12 (28)	79.2±0.33 (29)	37.9±0.35 (27)	17.4±0.12 (29)	4.09±0.06 (26)
"	♀ 10.5±0.16 (14)	11.2±0.16 (14)	76.9±0.61 (13)	37.2±0.86 (11)	17.2±0.20 (13)	4.50±0.12 (10)
Armidale-	♂ 12.0±0.12 (15)	11.5±0.27 (13)	80.0±0.67 (17)	-	-	-
Wollomombi	♀ 10.8±0.05 ( 8)	10.9±0.33 ( 6)	78.6±0.48 ( 7)	-	-	-

\* values represent mean ± standard error (sample size in brackets); vertical bar by means indicates that values are not significantly different ( $p > 0.05$ ); only adults measured

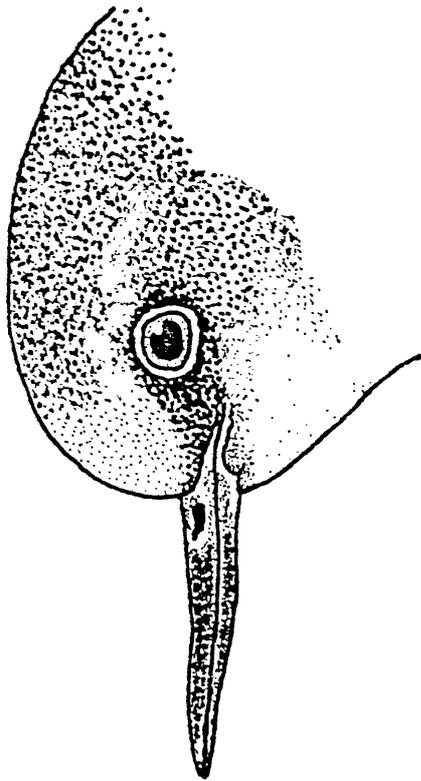
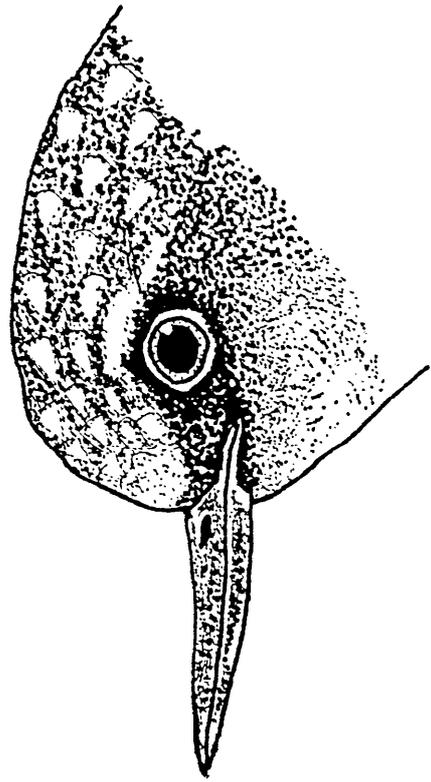
† measured as shown in Table 3.3

FIGURE 3.1: *Head coloration of Varied Sittellas in the Armidale region*

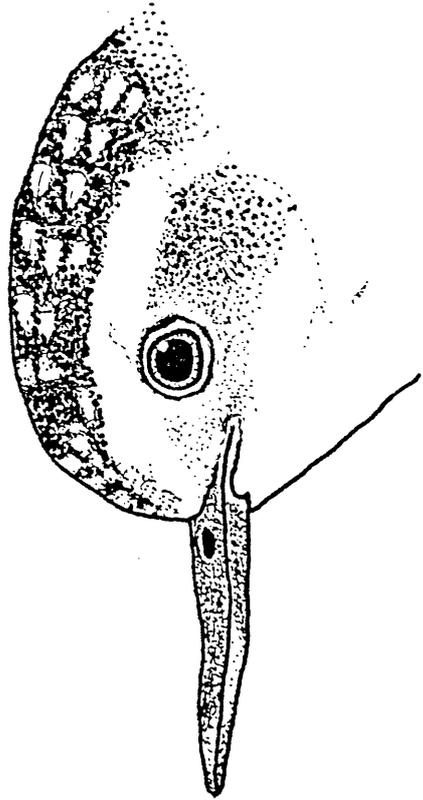
Upper, adults; lower, juveniles



♀



♂



cantly more curved than that of females ( $t = 3.18$ , 34 df,  $p < 0.01$ ). Despite differences in head coloration, birds from the Armidale–Wollomombi region did not differ significantly from the Northern Rivers birds in the length of the bill or wing, or in weight, even when compared intrasexually.

### 3.2.2 Sexual dimorphism and juvenile plumage

Boles (1980) and Noske (1980) questioned the widely-accepted sexual dimorphism in plumage of the Varied Sittella, in which males have pale faces and throats, and females, black faces (and streaked or black throats in eastern forms). Boles (1980) argued that the south-western *D.c. pileata* was monomorphic based on an examination of museum skins, but using the criterion of bill-length, it is apparent that many of these were mis-sexed (Noske unpubl. data). Noske (1980) pointed out the weak sexual dimorphism in adults of the nominate race, *chrysoptera*, suggesting that plumage variation in this subspecies was also related to age.

Juveniles of the species are characterized by white streaks on the dorsum (Figure 3.1), which disappear during their first (juvenile) moult between two and three months after fledging, at least in *chrysoptera* (Noske 1980, unpubl. data). The greater wing-coverts however, are retained until the next (annual) moult, so that sittellas bearing buff or whitish tips to these feathers are usually identifiable as "sub-adult" (see also Short *et al.* in press a). Birds in their first-year plumage also have duller (brownish) legs than the adults.

The throat of some adult male *chrysoptera* in the Armidale region was well-streaked whereas those of young males were always white. Females attained a streaked throat soon after their first (juvenile) moult, but had the characteristic black face before they fledged. Nestlings were therefore probably sexually dimorphic, though the sexes were most readily separable as sub-adults (Figure 3.1), particularly since males retained a faint whitish superciliary stripe for at least two years (pers. obs.).

In this study, males were identified (when unbanded) by the combination of a white or lightly streaked, pale throat and pale (white to pale grey) cheeks or superciliaries. Though females occasionally had white in the centre of the throat, the sides of the throat and cheeks were

usually dark grey and the lores and orbital ring, black, often contrasting sharply with a whitish-grey forehead (Figure 3.1). Nevertheless, some birds could not be reliably sexed in the field, and were thus classed as "unsexed" in foraging observations.

### 3.2.3 Habitats

While both New Guinea species of sittellas are confined to montane rainforests (Rand 1936; Diamond 1972), the Australian species avoids rainforests, including cool-temperate forests, but occurs in most other wooded habitats. This includes the inland *Acacia*-dominated communities (e.g. mulga, gidgee), tropical paperbark (*Melaleuca*) woodlands, and tall wet sclerophyll forests of sub-coastal regions. Like the White-throated Treecreeper, this species inhabits *Callitris* forests and *Casuarina* thickets (pers. obs.).

PART B

SOCIAL ORGANIZATION AND  
BREEDING BIOLOGY

## Chapter 4

## WHITE-THROATED TREECREEPER

Individuals or pairs of White-throated Treecreepers maintain and defend territories strongly throughout the year. During the non-breeding season (February to August), the male and female of each pair tend to forage in separate parts of their combined range. As these areas are largely mutually exclusive and intra-pair aggression is not uncommon, I concluded elsewhere that the species holds individual territories (Noske 1979). However, individual spacing appears to vary considerably between pairs during the non-breeding season, and as the ranges of both pair members overlap extensively in the breeding season, the term "territories" is used here to refer to the combined range of a pair.

## 4.1 Sex Ratios

As pairs constituted the breeding units of White-throated Treecreepers, the adult sex ratio was approximately even. Information from ABBS (provided by D. Purchase) is corroborative: of 963 birds banded as adults up to 30 June 1979, 488 were males and 475 females (1.00♂:1.03♀). However, among sexed juveniles there were about four times as many females banded as males (29♂♂:124♀♀). If it is assumed that all juveniles of unknown sex (68) were male, the ratio improves to 1♂:1.3♀, but judging from those recovered, at least some were female. Recovery data verify this disparity in sex ratios (assuming equal mortality/dispersal in both sexes); of 34 juveniles recaptured, 22 were female (1♂:1.8♀). Yet it is possible that some juvenile males were incorrectly identified as adults or free-flying, as explained in the previous chapter. My data (Table 4.1), however, also show an overall bias towards females in nestlings and fledglings, though ratios were not significantly different from parity, even when data from all sites were combined ( $\chi^2 = 2.32$ , 1 df,  $p > 0.1$ ).

TABLE 4.1: Sex ratios of juvenile\* White-throated Treecreepers at three sites

Site	N <sup>†</sup>	Sex	Season				Total	$\chi^2$ #
			1977	1978	1979	1980		
Wollomombi Falls	21	♂	2	9	5	-	16	0.95
		♀	4	9	9	-		
Swan Vale	13	♂	3	2	2	-	7	2.33
		♀	6	5	3	-		
Stringybark Hill	5	♂	3	1	2	1	7	0
		♀	0	2	3	2		

\* nestlings and fledglings; inclusion of the latter assumes equal mortality of sexes as nestlings; all young banded as nestlings were observed again as fledglings

† number of broods sampled

# all values non-significant

## 4.2 Mortality and Dispersal

Of the 27 adults banded at Wollomombi (14♂♂:13♀♀) up to February 1980, five (3♂♂:2♀♀) disappeared within one year of banding (Figure 4.1). At Swan Vale, however, half of the 14 adults (6♂♂:8♀♀) banded in 1977-78 disappeared within one year of banding (3♂♂:4♀♀). Therefore, assuming these birds died, annual mortality was as high as 50% at Swan Vale but only 19% at Wollomombi. Yet only four (15%) of the 27 birds at Wollomombi survived to November 1982 following a two-year drought. There was no evidence of differential mortality between the sexes. The time of disappearance was recorded for 18 birds from all sites. Of the ten males, half "died" during the breeding season (August to January), while six of the eight females "died" during this period.

All 27 nestlings and dependent juveniles banded at the three sites (14 at Stringybark Hill), disappeared within two months after fledging. At Wollomombi, six banded birds were last seen in their natal territories 30 days (three birds), 37 days (two) and 45 days (one) after fledging. The maximum period between fledging and the disappearance of five birds from two broods at Stringybark Hill was 40 days. Dependent juveniles at all sites were prevalent in November and December, after which few birds other than breeding residents were observed. Over three years, five juveniles from elsewhere were seen in the territory at Stringybark Hill (for one or two days each) during January and February, and another bird in late November.

While the above observations indicate that mass dispersal of juveniles occurs at the end of the breeding season, there have been no recoveries of juveniles away from their banding sites. Recovery of juveniles at their banding sites, ignoring those recaptured (and thus possibly still dependent) was as high as 14.5% (data supplied by D. Purchase), though some may have been immigrants when banded. During winter 1980 at Wollomombi however, two adult males were replaced by birds which had been banded as juveniles in January/February 1979 on the study site but had not been seen in the intervening period. Neither of the young males inherited his natal territory.

FIGURE 4.1: *History of individual White-throated  
Treecreepers at Wollomombi Falls over  
the study period*

Large letters on far left signify (pair)  
territory as shown on Figure 4.2

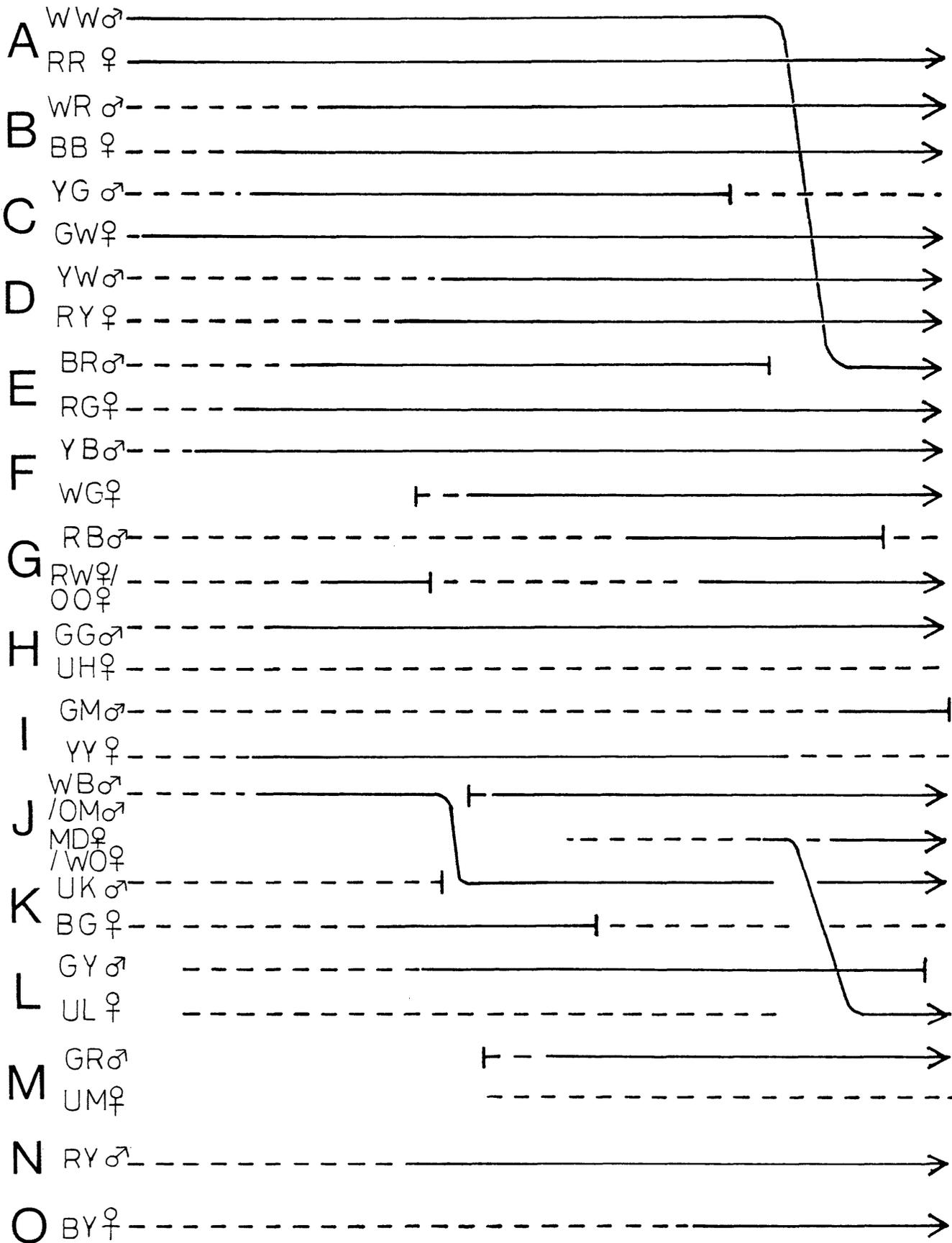
—	banded
- - -	unbanded
┌	date of appearance
└	date of disappearance

1977

1978

1979

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



### 4.3 Territoriality and Population Structure

Average territory size for nine pairs at Wollomombi (during 1978) was  $5.9 \pm 0.47$  (SE) hectares and for four pairs at Swan Vale,  $5.8 \pm 0.34$  hectares. Both these sites supported woodland or forest of relatively even density while at Stringybark Hill where grassland and woodland occurred, the single pair ranged over 14.5 hectares.

The boundaries of several territories at Wollomombi changed during the study period (Figure 4.2). During the first year, two males (WB and YB) holding adjacent territories failed to secure mates and consequently did not breed. In early December 1977, one of these males (WB) vied with another (YR) for acquisition of a territory, in which the recently-widowed female was tending fledglings. After a battle lasting at least 75 minutes, the latter male retreated. Subsequently, YB $\sigma$  expanded his range to include part of the area vacated by WB. In the second year the appearance of GR $\sigma$  (at the tip of the western spur) caused the constriction of the territory immediately to the north (Figure 4.2). Finally, an unbanded pair moved into the north-west corner of the study site during the latter half of 1979 coinciding with contractions of territories to the south and west (Figure 4.2). Though not measured continuously, some territories at Swan Vale definitely changed shape during the study period.

At least one bird at each of the main sites changed territories during the study. At Wollomombi, one male (WW) left his mate of at least two year's standing (RR $\phi$ ) for a recently-widowed female in an adjacent territory (RG $\phi$ ). This male continued to visit his former mate for several months and courtship fed both females, though only the new mate nested. At Swan Vale, a female who had bred successfully one year left her mate the next to join a widower in a larger, adjacent territory.

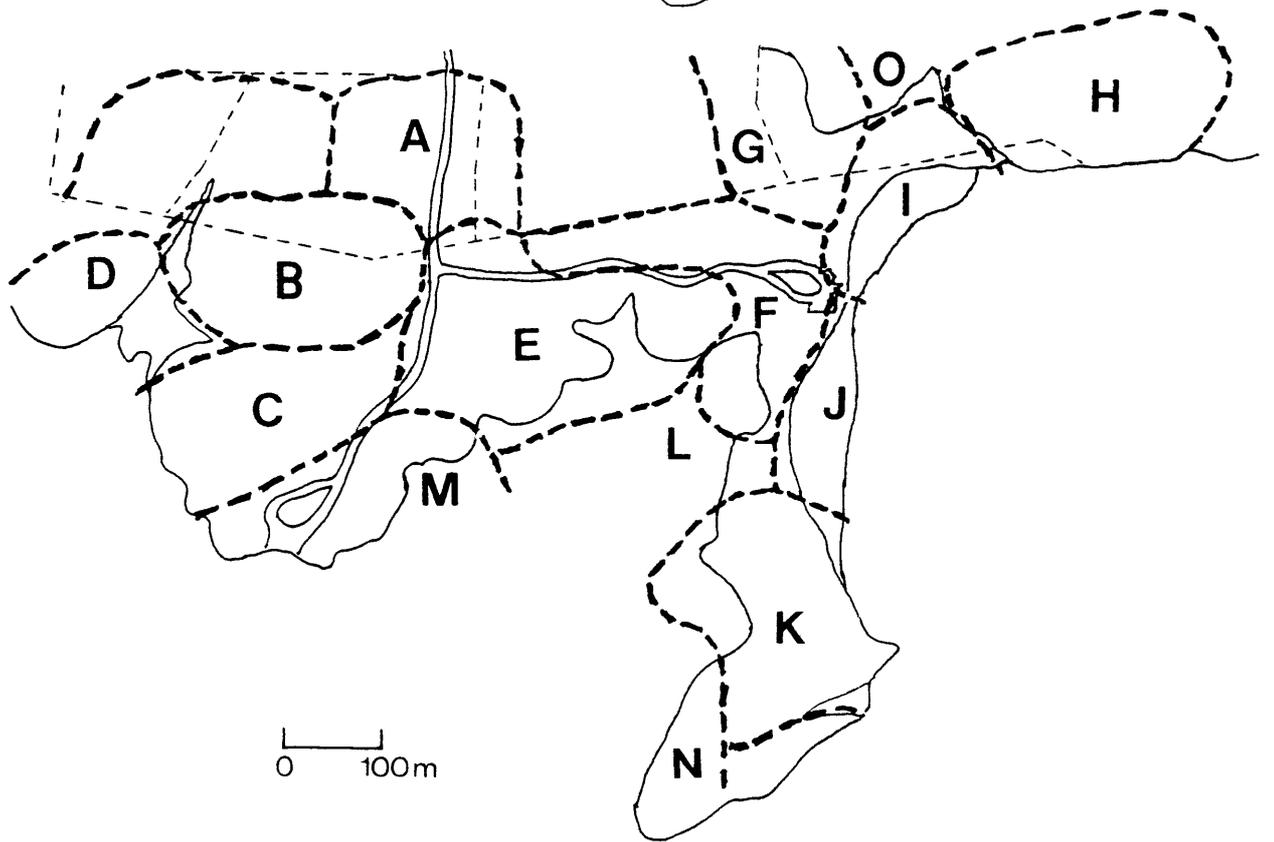
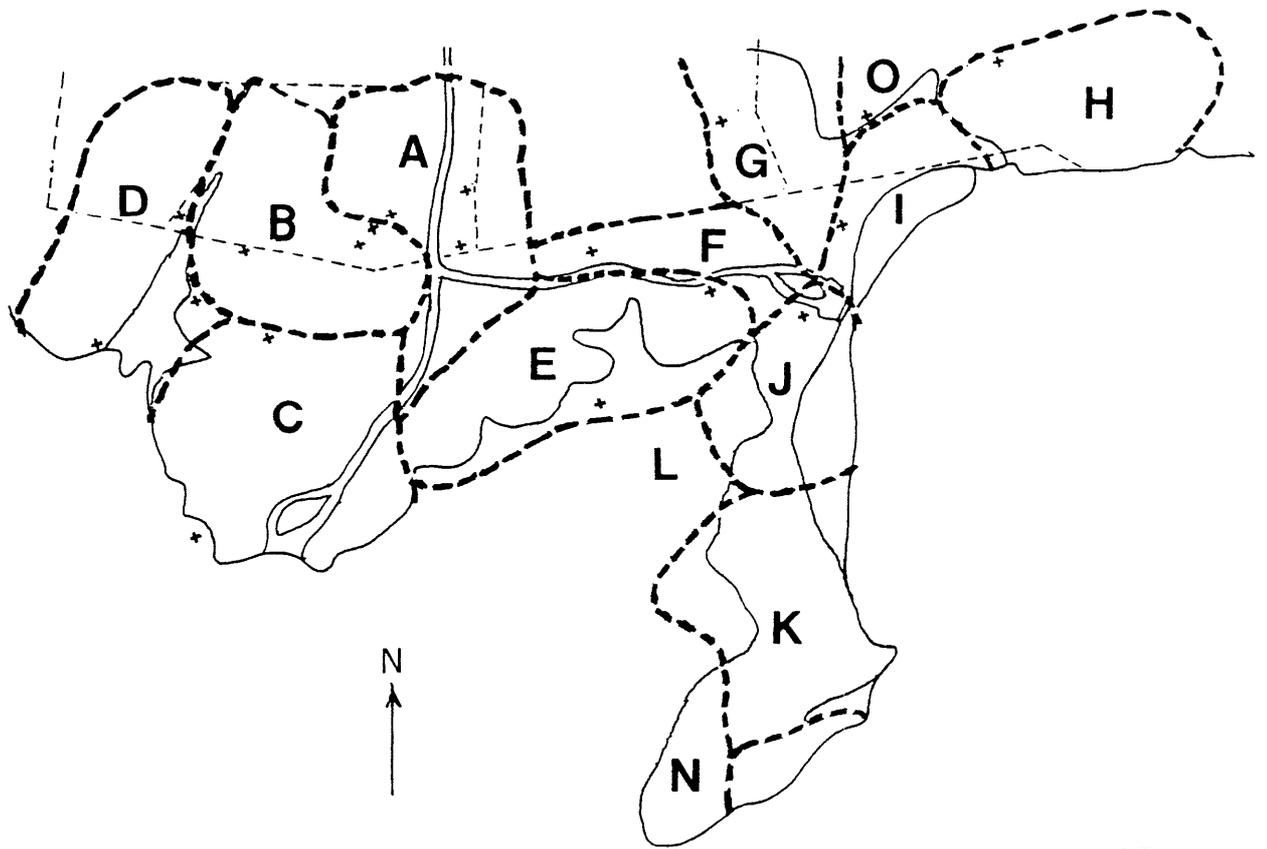
### 4.4 Social Interactions

When two or more White-throated Treecreepers from different territories met near a common boundary, one or more typically commenced an aposematic display in which the tail was quickly flicked open and shut

FIGURE 4.2: *Distribution of territories of White-throated Treecreepers at Wollomombi Falls during 1977 (upper) and 1979 (lower) breeding seasons*

Dark, broken lines, territory boundaries ;  
thin, unbroken lines, contours and creeks ;  
small crosses, roost-sites.

Letters correspond to those on Figure 4.1  
(far left)



repeatedly, producing a clicking sound. This display (hereafter referred to as "clicking") probably functioned as a warning signal to potential trespassers, the volume and frequency apparently varying with the proximity of participants. Birds clicked while flying or climbing, maintaining a distance of no less than five metres, often in adjacent trees. Such essentially passive encounters comprised 32% of all social interactions at Wollomombi (Table 4.2) and were less common between females than between males, or between males and females of different territories (inter-pair).

In 54% of recorded interactions between members of two (occasionally three) neighbouring pairs, violence erupted. These high intensity border disputes usually involved physical scuffles (Table 4.2), in which the participants sparred while scampering up tree trunks and tumbling towards the ground with feathers flying. The wings and tail were often fanned, bills gaped and forehead feathers raised. Such fights were again less frequent between females than between males or opposite sexes and rarely occurred between members of the same pair. High intensity interactions varied in duration, one battle between two males lasting over 75 minutes.

Moderate intensity interactions consisted of supplantings and chases, with little or no physical contact. The majority of these interactions occurred within pairs (Table 4.2) during the non-breeding season and were apparently related to invasions by one bird into the "favoured" areas of its mate, but other factors may have been involved (e.g. age of birds, history of pair and proximity to roost-sites). Clicking was infrequent in intra-pair conflicts (Table 4.2).

Neither sex won consistently in intersexual aggressive encounters, but males dominated females more than the reverse, both within and between pairs (Table 4.3). Dominance relations within several pairs appeared to be volatile. For example, during observations totalling 278 minutes at a tree oozing sap, the female "owner" (RG♀) displaced and/or chased both her mate (BR♂) and the owner of the adjacent territory (YB♂) at least twice, but was also chased by these males at least once each. At Stringybark Hill the adult female attacked her mate ten times (involving over 40 supplantings) while the reverse occurred only once. In altercations between parents and offspring of families containing young of both sexes, juvenile males were

TABLE 4.2: Frequency and context of three types of social interactions in White-throated Treecreepers

General intensity of interaction	Intensity			Total
	Low	Moderate	High	
Major characteristic	Clicking only	Supplantings	Scuffles	
Inter-pair				
$\sigma\sigma$	17	3	17	37
$\text{♀♀}$	10	-	8	18
$\sigma\text{♀}$	14	8	13	35
Intra-pair	3	42	3	48
TOTAL	44	53	41	138

TABLE 4.3: *Outcomes of intersexual (adults) and juvenile-adult aggressive interactions in White-throated Treecreepers*

		Aggressor (dominant)		
		♂	♀	Total
ADULT	Intra-pair	28	12	40
	Inter-pair	18	8	26
TOTAL		46	20	66

		Adult (dominant)		
		♂	♀	Total
JUVENILE (subordinate)	♂	5	17	22
	♀	19	3	22
TOTAL		24	20	44

harassed mostly by their mothers, and juvenile females by their fathers (Table 4.3). Though juveniles usually tolerated each other, twelve intersexual altercations among siblings were recorded, in which males were dominant nine times.

Clearly, systematic and detailed observations of pairs of known age and history are required in order to gain a better understanding of social relations in this species. During the breeding season, intra-pair barriers dissolve and pair members commonly forage in the same tree concurrently without any overt sign of hostility.

#### 4.5 Courtship Feeding and Pre-copulation Display

Although one unmated male at Stringybark Hill fed or attempted to feed a female each month from February to September, courtship feeding in mated pairs at Wollomombi and Swan Vale was mainly confined to the breeding season, commencing in earnest during late August (with only a few records in July) and rarely extending beyond early October. Feeding continued during the early nesting stages, particularly the incubating period. When off the nest, females were fed quite frequently: the average rate for pooled observations totalling 365 minutes was 16.9 per hour. Females did not always accept offerings by the male and on several occasions the latter eventually ate the food. "Courtship feeding" by females was seen only twice, involving one pair in May.

At the onset of the breeding season, male White-throated displayed frequently, presumably to attract their mates. Crescendo calls, consisting of around six notes, were given repeatedly at intervals of several seconds for up to five minutes. Sometimes, the bird called while perched near the base of a thick, horizontal or sloping branch. This vocal display accompanied by wing-shivering and tail-cocking was witnessed six times at Wollomombi, once at Swan Vale and nine times at Stringybark Hill. Observations of one male at the latter revealed that it displayed at the same sites (one branch in each of two trees) on six consecutive days. Of the 15 displays observed, eleven attracted mates and although only one

actually culminated in copulation, it is assumed that this display is a normal precursor to copulation.

The following sequence of events were typical of this presumed pre-copulation display. While calling, the male tilted his tail gradually upwards until almost vertical; the wings were at first drooped, then held horizontally, shivering rapidly with each call. After the female arrived, perching behind the male, the latter lifted one or both wings to display the pale cinnamon bar on the underside, and raised his head intermittently. He sidled slowly towards the female waving his shivering wings and rocking from side to side. The inactive, spectating female then flew off the branch, and the male eventually ceased displaying. On several occasions however, he pursued the female while calling and shivering wings excitedly. Once the female rested on a vertical trunk, wherecoition was finally achieved.

#### 4.6 Female Displays

On four occasions, I saw females display when close to males in a fashion reminiscent of the male's pre-copulation display. Three of these involved immature females between December and mid-February and followed harassment by the male. The birds drooped the wings and raised the tail slightly, displaying the conspicuous bright rump patch typical of young females. Another instance concerned an adult female which raised its tail and spread its wings when pursued by two males during an intense interaction involving five birds in late May. The displaying of the rump, at least by young birds, may serve to appease the male owners of the territories they traverse.

#### 4.7 Vocalizations

Table 4.4 summarizes the characteristics and contexts of ten calls identified during the present study. Three or four calls were given solely by males and one, possibly two, other calls were generally distinctive of females. An additional call, heard only at Swan Vale, was a high-

TABLE 4.4: Vocalizations of White-throated Treecreepers

Name	Sex	Description	Context and other comments
1. Pipe	♂ ♀	Sharp notes with slight downward inflexion given singly or in succession, lasting up to five minutes	Commonest call; single notes often give prior to leaving trees (when foraging), by incubating bird when leaving the nest and at dusk when approaching roost-site
2. Crescendo	♂	Series of loud crescendo notes (rarely more than ten), variable in tempo	Territory-advertisement and Courtship; heard most frequently at beginning of breeding season (particularly in early morning); also commonly uttered during intraspecific agonistic encounters
3. Trill	♂	Rapid tremor accompanied by lowering of the head	Given during intraspecific agonistic encounters; also during courtship feeding prior to and during transfer of food
4. Soft whistle	♂	Thin, high-pitched notes with upward inflexion ("whit"), quickly repeated up to eight times	Uttered during intersexual encounters, often interspersed with the preceding and following call
5. Buzz	♂ ♀	Harsh, low-pitched nasal notes	In intersexual encounters and intrasexual physical scuffles
6. Descending call	♀*	Melodious series of descending notes, initially fast then gradually slowing down	Infrequently uttered by females during intraspecific conflicts (both intra- and intersexual); also occasionally produced by males during vocal displays
7. Squeal	♀?	High-pitched, sustained notes with upward inflexion; single or repeated	In intraspecific encounters; details unknown; uncommon
8. Chuckle	♂ ♀	Low-pitched, guttural call, somewhat reminiscent of Kookaburra	Sometimes given when holding food in the bill; included in vocal displays by males
9. Incubating	♀	Monotonal series of morse-code like notes, resembling insects	Given only during incubation period when female is off the nest, especially when male in close proximity
10. Food-begging	♂ ♀	Explosive chatter (nestlings) or soft trill (fledglings)	The only call of nestlings and fledglings, intensifying when adults approach with food

\* primarily given by this sex.

pitched downward-inflected note sometimes uttered by males when accompanying their mates during the breeding season. During both the breeding and non-breeding season, unmated males gave prolonged medleys of mostly male-diagnostic calls continuing for up to 20 minutes. These "vocal displays" were uttered while foraging and presumably served to attract potential mates, as well as advertize territory ownership. Two similar, yet distinctive food-soliciting calls occurred - one given by the incubating female, and the other by dependent young.

#### 4.8 Roosting

White-throated Treecreepers were among the last birds to go to roost at all study sites. The last calls of the day were usually given well after sunset. Most of the known roost trees of this species were situated close to the boundaries of territories (Figure 4.2), or the interface of the non-breeding ranges of paired birds. As birds often called just before arriving at the roost-site, and possibly when departing in the morning, the position of roosts may be important for territorial defence or advertisement.

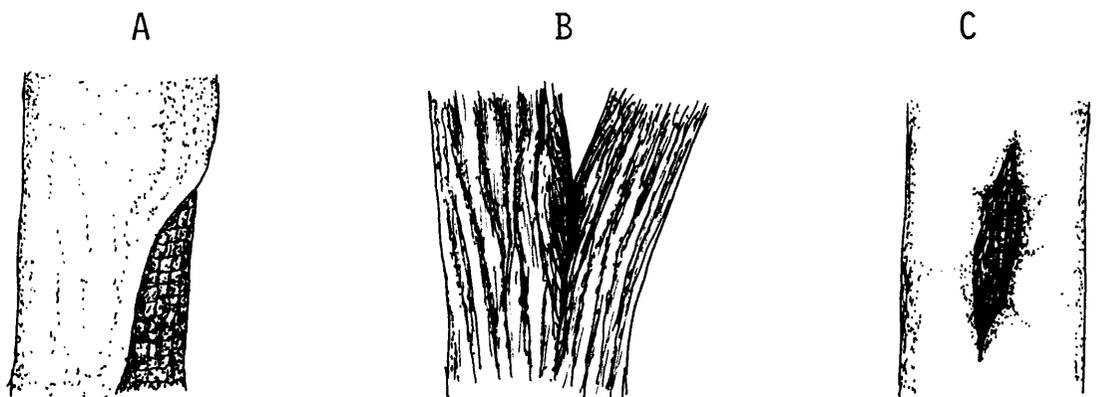
With few exceptions, this species slept in external situations with part or whole of the body exposed. When asleep, the head is hidden among the feathers of the back (Noske 1977). At Wollomombi, 75% of the 24 known sites were either burnt surfaces at the base of live trees or stumps, or depressions at the junction of two tree-trunks (Table 4.5). Other sites included fissures on trunks, shallow cavities formed by broken-off limbs, and directly beneath swellings or loose bark. At Wollomombi and Stringybark Hill, live stringybarks were most commonly used and at Swan Vale, live ironbarks. The species is apparently not averse to using man-made constructions: one slept on a wall under the eaves of the house at Stringybark Hill (Noske 1977), and another just below the ceiling in a public toilet at Wollomombi. Other records include a cavity of a chimney (Dickison 1933) and an old garage (Bryant 1934). Heights of roost-sites at Wollomombi ranged from 0.7 to 6.2 metres. Mean heights ( $\pm$  SE) for the three study sites were 3.03 ( $\pm$  0.39), 2.98 ( $\pm$  0.49) and 3.38 ( $\pm$  0.64) metres.

TABLE 4.5: *Roost-sites\* of White-throated Treecreepers*

	Type of tree				Total
	Stringy-bark	Box/Iron- <sup>†</sup> bark	Gum	Dead	
A. Burnt surface	5	3	2	-	10
B. Live surface	13	4	-	-	17
C. Overhang/fissure	3	4	4	6	17
TOTAL	21	11	6	6	44

\* study sites combined; each roost-site counts as one observation

† ironbarks at Swan Vale only



Sites were used repeatedly but not constantly, and once flushed, the occupants rarely returned to the same site that night. At least three sites were used by one bird at Wollomombi. At Swan Vale, one site was used by both pair members, the male apparently occupying it while the female incubated, and the latter before and after her "confinement". Some sites may have special significance: one female at Wollomombi used the same site (a conspicuous tree) as that used by her predecessor.

#### 4.9 Breeding Season

Though building was recorded in the last two weeks of August in most years at Wollomombi and Stringybark Hill, eggs were not recorded until early September. At Stringybark Hill, the first eggs for three consecutive seasons were laid on September 1, 7 and 10. Peak laying at Swan Vale, however, occurred about three weeks before that at the other sites (Figure 4.3). The last nests in the two latter areas showed a similar lag. Laying was not recorded beyond mid-November.

#### 4.10 Nest-sites

The majority of nests at all three sites were built in holes entering the trunks of stringybarks or gums, or at the bend of large limbs (Table 4.6). Most of the remaining nests were situated in hollow, dead branches (spouts) of live trees, but few dead trees were used. Of the 20 different sites at Wollomombi, at least six were used for two consecutive seasons; at Stringybark Hill, one site was used for three seasons, though unsuccessfully in the last. The height of 25 nests at Wollomombi ranged from 4.0 to 13.4 metres ( $\bar{X} \pm \text{SE} = 8.1 \pm 0.56$  m); while at Swan Vale and Stringybark Hill they ranged from 0.6 to 8.2 metres ( $5.2 \pm 0.68$  m and  $5.2 \pm 0.64$  m, respectively). Nest dimensions were not recorded systematically, but the diameter of the entrance to six nests varied from three to eleven centimetres. The depth of eight holes measured from the nest platform to the lower edge of the entrance varied considerably from 18 to 60 centimetres ( $\bar{X} = 33$  cm).

FIGURE 4.3: *Estimated laying dates of final eggs of White-throated Treecreepers at the study sites (upper) and other localities in north-eastern New South Wales (lower)*

Most data for study sites extrapolated from hatching or fledging dates or age of nestlings; lower graph, M.T. Goddard *in litt.*

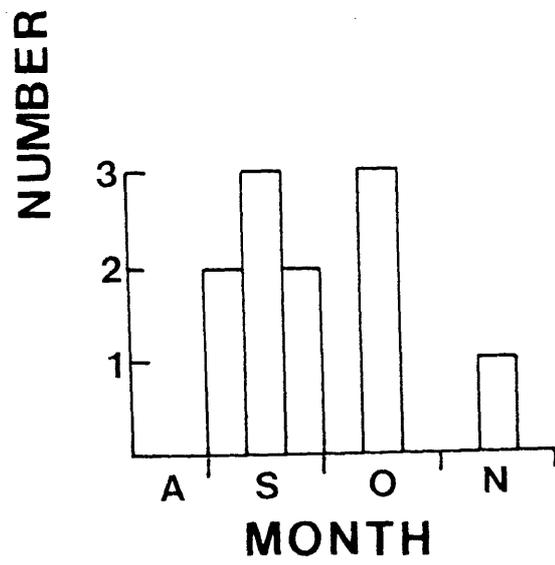
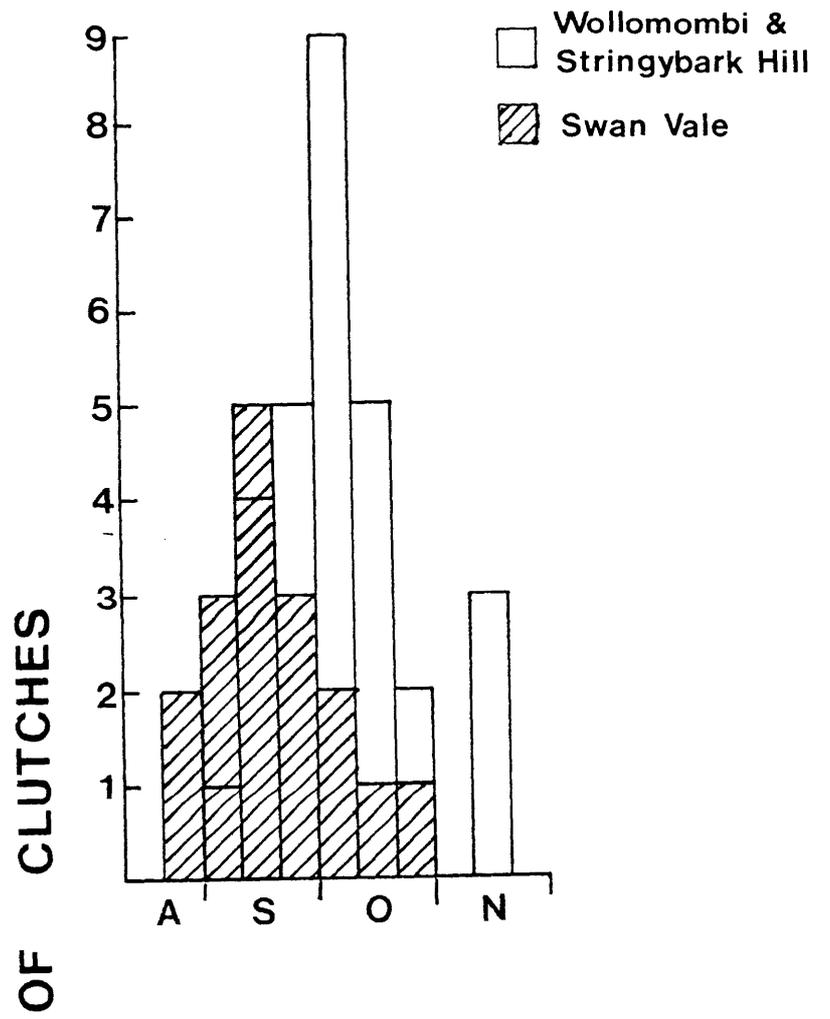


TABLE 4.6: Nest-sites\* of White-throated Treecreepers

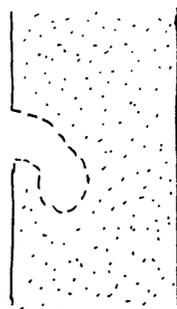
Tree	Stringy-bark		Box†		Gum		Other#		Dead	Total
	H	S	H	S	H	S	H	S		
Trunk	13	3	3	-	8	-	3	-	1	31
Branch	4	2	1	2	-	2	-	-	2	13
TOTAL	17	5	4	2	8	2	3	-	3	44
	22		6		10		3		3	

\* study sites combined; data include "repeats", viz. nests used more than once

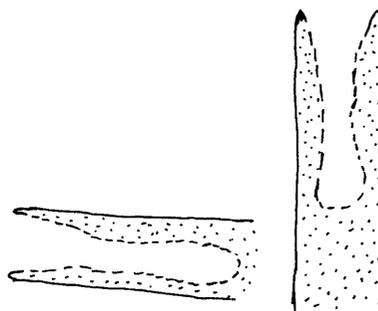
† mostly *Eucalyptus melliodora* (Yellow Box) and *E. conica* (Fuzzy Box)

# *Angophora floribunda* (apple) and *E. crebra* (ironbark) at Swan Vale

H = hole (live)



S = hollow spout (dead)



#### 4.11 Building

Building was performed exclusively by the female, though the male sometimes accompanied her to the nest, and frequently perched at the entrance with food for her. During the early stages of nest construction, females were observed tearing fibres of bark from the trunks of stringybarks and carrying them to the nest 36 times. Fur and hair were taken on another eleven occasions, twice from the carcass of a Brush-tailed Possum, *Trichosurus vulpecula*, and once from the remains of a cow.

Two previously undescribed habits of treecreepers associated with building deserve mention. In "bill-sweeping" (*sensu* Kilham 1968), the bird holds material in its bill and wipes it back and forth sideways over the bark surface inside and around the nest-hole, as well as on trees up to 20 metres from the nest. Such behaviour was observed in White-throated Treecreepers on 17 occasions, involving six different females. An unidentified thin, translucent substance (perhaps snake skin or insect wings) was used several times, and at Stringybark Hill, the female used pieces of a plastic bag procured from a spot over 200 metres from the nest. This bird usually bill-swept continuously for at least five minutes and once for almost 30 minutes. Sometimes, the material was deposited in the nest, though on at least one occasion, a Brush-tailed Possum was sleeping in the nest-hole at the time of sweeping. Less than 12 days after they were laid, the eggs were destroyed, probably because the possum reclaimed its roost-site.

Another habit of treecreepers is that of covering or partly covering their eggs with loose nest lining. On four out of five inspections of one White-throated nest at Wollomombi, one or more eggs were partly covered with fur, and in two nests at Stringybark Hill, the first egg was almost completely concealed. S. Marchant (NRS:2/76) described similar circumstances at a nest of this species. The incubating bird sometimes gathers lining before returning to sit on the nest (*pers. obs.*), so it is conceivable that this extra material is used to cover the eggs. Unfortunately the frequency of this habit cannot be gauged by examination of nest records in NRS since nest inspections invariably force the incubating bird to depart hurriedly. Whether the concealment of eggs is the accidental consequence

of excess lining, or an evolved anti-predator device remains to be resolved.

The minimum interval between the day on which building was first noted and the laying of the first egg for four nests was ten to 15 days. Yet little or no building activity was observed during the final three to six days at these nests. At Stringybark Hill, the female began to lay her third clutch in a new nest only seven days after the previous clutch was abandoned. Thus, building of this nest took less than a week.

#### 4.12 Clutch Size and Brood Frequency

Though some texts (e.g. Frith 1969; Orenstein 1976) suggest that the usual clutch of this species is three eggs (C/3), data compiled from both personal observations and other sources (Table 4.7) indicate that clutches of two eggs (C/2) are equally if not more common. Clutch size may depend to some extent on the individual. One female at Stringybark Hill laid six clutches of C/3, and another at Wollomombi four clutches of C/2. Unfortunately, data for broods (nestlings) are unreliable as one egg may be predated or if infertile, may be concealed beneath the young birds or buried in the lining of the nest. I recorded egg losses in seven nests, four of which were C/3. Howe (1921) found one nest containing four young, but this seems exceptional.

Howe (1921) claimed that this species rears two broods in a season, but of 44 nests I observed, only one (at Stringybark Hill) was started after a brood had already been raised earlier in the same season. Marchant (1981) has also found this species to be single-brooded normally. However, re-nesting may occur if early clutches fail. In one season at Stringybark Hill, the female laid three clutches (C/3), each in a different nest. The first nest was abandoned after a week of incubation, and the second after three weeks; none of the eggs hatched.

#### 4.13 Laying Routine

Eggs are apparently laid on alternate days, probably at intervals of between 30 and 48 hours. At two nests, the minimum interval between the

TABLE 4.7: Clutch size\* of White-throated Treecreepers

	$\frac{\text{Clutch size}}{\text{C/2}}$		C/3	Total	Average
Wollomombi Falls	9		3	12	
Swan Vale	1		2	3	
Stringybark Hill	-		7	7	
TOTAL	10		12	22	2.55
Local <sup>†</sup>	6		6	12	
NRS <sup>#</sup>	11		4	15	
TOTAL	17		10	27	2.37
GRAND TOTAL	27		22	49	2.45

\* assumes all clutches complete; data only for nests which were accessible

† other sites in the local region (N.E. N.S.W.); data provided by M.T. Goddard (10 nests), mainly from Tenterfield and Dorrigo, and personal observation (2 nests)

# from areas south of the local region; data extracted from R.A.O.U. Nest Record Scheme cards up to and including 1978/79 season

second and third eggs was 40 hours, while three other eggs were laid at least 25 hours after the preceding ones. Marchant (1980) claimed that the laying interval at one nest he observed was 48 hours, but he assumed that eggs were laid in the early morning. Re-examination of his data (NRS:5/77) shows that the minimum interval was 23 hours. Five eggs in four nests at Stringybark Hill (none of which were first eggs) were laid after 08:00, and at least three of these, in the afternoon or late morning (13:30  $\pm$  3:00, 14:30  $\pm$  3:00 and 15:15  $\pm$  2:45 hours).

#### 4.14 Incubation

Incubation began with the laying of the second (penultimate) egg at one nest, and the third egg at three others. However, disparities in the size and weight of nestling sibs at two other nests suggest that the commencement of incubation is variable. Detailed observations at four nests indicate that the incubation period of this species is 22 to 23 days (Table 4.8). At another nest I observed, the three eggs were incubated for almost exactly 24 days but none hatched. Successful hatching of three eggs took place over less than 29 hours at one nest, the last egg hatching between 09:30 and 12:30 (pers. obs.). Both eggs in another clutch (NRS: 3/76) hatched overnight between 17:00 and 05:45. Dickison (1933) reported hatching of three eggs on three successive days, but gave no supporting details. Asynchronous hatching presumably occurs when incubation begins before the final egg is laid.

Contrary to Orenstein (1976) only the female incubates in this species and probably all species of treecreepers (unpubl. data). In total, I observed female White-throated Treecreepers incubating 93 times, and brooding a further 23 times, but males never performed these duties. During the incubation period, females spent about three-quarters of their time on the nest. Combined observations of three nests at both Wollomombi (3.7 hours) and Stringybark Hill (7.5 hours) gave 75.2% and 73.8% attendance, respectively. The average duration of 18 complete incubating sessions (both sites pooled) was 24.1  $\pm$  3.58 (SE) minutes, though this was biased towards shorter periods; inclusion of nine additional incompletely-timed sessions yielded a slightly higher average of 26.1  $\pm$  3.14 minutes. Complete

TABLE 4.8: *Incubation and nestling periods\* of White-throated Treecreepers*

	Minimum			Maximum	
	Days	Hours		Days	Hours
INCUBATION PERIOD	22	17	→	23	5
	22	18	→	24	4
	† 21	22	→	22	6
	† 22	10	→	22	22
	20	2			
	19	4			
-----					
NESTLING PERIOD	26	4	→	26	20
	† 26	1	→	26	18
	25	22	→	28	9
	25	18			
	24	18			
	24	12			

\* arrows connect data pertaining to the same nest

† from Marchant (1980); all other data pers. obs.

sessions ranged from six to 53 minutes, though one session lasted over 64 minutes. Periods of absence were significantly shorter in duration, ranging from one to 20 minutes, and averaging  $10.0 \pm 1.47$  minutes (16 complete sessions).

At the same six nests, males fed their mates on the nest 1.9 times and 1.4 times per hour, on average, at Wollomombi and Stringybark Hill respectively. These feeding rates excluded seven visits, in which no food was brought by the male, or the female rejected his offering. Thus, while sitting, the female was fed rather infrequently in comparison to feeding rates off the nest (see Section 4.5) though these rates may vary according to the age of the eggs, as well as environmental factors such as time of day.

#### 4.15 Nestlings and Fledglings

Females continued to brood during the day for at least 14 days after the young hatched, though brooding sessions were not timed. Similarly, the rates of food delivery to nestlings were not recorded systematically, but during short watches between 20 and 70 minutes at five nests, they ranged from 4.7 to 16.0 per hour, the average for 5.0 hours being 8.7 per hour. I observed 32 feedings by males and 39 by females, indicating that both parents possibly shared this activity equally. Yet in two cases, single birds (one of each sex) successfully reared three young alone, following the death of their mates during the early stages of nestling development.

When approaching the nest, treecreepers invariably flew directly to the nest entrance, rarely climbing to it from below. When leaving the nest, however, they often climbed to a higher point in the tree before taking off. Faecal sacs voided by nestlings were carried well clear of the nest and dropped in flight. As nestlings were not visible, it is not known if the excrement of hatchlings was consumed by the adults (as it is in many passerines), though several nests were soiled when inspected after fledging.

The nestling period of the White-throated was about 26 days (Table 4.8). Newly-fledged young perched and climbed in the open, and were never seen sheltering in tree-hollows. On average, each pair at Wollomombi produced 1.33 fledglings over three years, but there was considerable annual variation. The number of fledglings produced (per pair) in 1978 was double that of the preceding year, though the latter may have been underestimated as I had assumed that re-nesting did not occur after the first nest failed. At Swan Vale, four pairs produced five fledglings in both the 1978 and 1979 seasons; average success (1.25 fledglings/pair) was thus remarkably similar to the combined average for Wollomombi. Young of three broods were still being fed 35 days after fledging but disappeared within 10 days afterwards. It seems, therefore, that juveniles disperse as soon as they reach independence.

#### 4.16 Conclusions

The strongly territorial, anti-social nature of the White-throated is reflected in many facets of its social organization, culminating in the eviction of offspring as soon as they reach independence. The resulting widespread dispersal of young is facilitated by the generalized habitat requirements of this species (see Section 3.1.3). Its ability to colonize "new" habitats is exemplified by its abundance in small isolated patches of sclerophyll forest (Howe 1982), as well as its presence in 20-year old plantations of exotic pine, *Pinus radiata* (Gepp 1976; Driscoll 1977). The pronounced sexual dimorphism of juveniles (see Section 3.1.2) may be adaptive in the context of dispersal. Dispersing youngsters presumably search for an unoccupied space or a vacancy in an established territory, where one of the owners has died. The conspicuous rump patch of females probably serves to subdue male territory-holders, or to attract potential mates by soliciting a feeding response. As no dominance hierarchy was evident in adults, there is presumably no social pressure to conceal one's sex. The female-biased sex ratio of juveniles is difficult to explain however, since there was no evidence of higher mortality among adult females, and there seems no reason to believe the costs of rearing the two sexes were different.