

## CHAPTER 5

GEOGRAPHICAL VARIATION5.1. INTRODUCTION

White (1920) claimed that the Rufous Scrub-bird consisted of two subspecies:

1. *Atrichornis rufescens jacksoni*, confined to the Macpherson Range.
2. *Atrichornis rufescens rufescens*, occurring south of the Macpherson Range and occupying the remainder of the species' range.

The main characteristics said to distinguish *jacksoni* from *rufescens* were generally darker plumage (both upperparts and underparts), heavier barring on the throat, and a longer bill. This subspecific division was supported by Jackson's (1920) observation that the song of Macpherson Range birds differed from that of birds in the Dorrigo district. Jackson described the "ordinary call" of males on the Macpherson Range as "rather like 'chit', short and shrill, varied from 5 to 12 'chits' uttered rapidly". The ordinary call of males in the Dorrigo district was described as "a prolonged and shrill note, resembling 'chirp-chirp-chirp-chirp', usually with about half a second duration between each call, but sometimes the interval is a little longer, and the sound lowers in pitch towards the last 'chirps'".

In recent years White's subspecific division of *A.rufescens* has met with both acceptance (e.g. Chisholm 1951; Macdonald 1973) and rejection (e.g. Keast 1961; King 1981; R.Schodde pers. comm.). The aim of the research described below has been to resolve this confusion through a fresh and detailed analysis of geographical variation in the Rufous Scrub-bird.

In reviewing the implications of modern subspecies concepts to Australian ornithology Ford (1974) concluded:

"In future studies on geographical variation the emphasis should be not on naming every morphologically differentiated population but on accurately describing the trends in variation ..... When these trends are analysed and zones of secondary intergradation have been determined, subspecific names can then

be applied so as to reveal the major discontinuities and uniformities in variation."

This approach contrasts sharply with that adopted at the time of White's (1920) study when the primary aim of geographical variation analysis was to name new subspecies. The primary aim of the present study is to describe objectively trends in geographical variation in the Rufous Scrub-bird. This information will be used as a basis for the secondary aim of revising the bird's infraspecific taxonomy. A revision of this kind should be viewed simply as an interpretation of data on geographical variation. This interpretation must be based on a sound concept of the subspecies.

Since the 1950's, the subspecies concept has been the topic of considerable controversy (e.g. Wilson and Brown 1953; Brown and Wilson 1954; Edwards 1954, 1956; van Son 1955; Hagmeier 1958; Pimental 1958, 1959; Inger 1961; Hale 1970; Selander 1971; Sneath and Sokal 1973; Ford 1974; Amadon and Short 1976; Key 1981). Ideas concerning the subspecies concept understandably reflect those relating to the concept of species. The three most popular species concepts have been the typological (or Linnean) species concept, the biological species concept, and the evolutionary species concept (see review by Lovtrup 1979). The three subspecies concepts discussed by Ford (1974) closely parallel these species concepts. The "taxonomic subspecies" is defined as a geographical aggregate of phenotypically similar local populations that differ from all other subdivisions of a species. These principles parallel those of the typological species. Ford (1974) has reviewed the numerous objections that have been made to the taxonomic subspecies concept. The three most important criticisms are:

1. The concept allows splitting of clinal populations into named subspecies.
2. The concept allows every distinguishable population to be described as a subspecies, thereby making "subspecies" synonymous with "local population" or "deme".
3. The concept allows lumping of phenotypically indistinguishable populations that have evolved independently through convergent or parallel evolution.

Numerous authors have argued that the subspecies category should be given some evolutionary connotation (e.g. Edwards 1954, 1956; van Son

1955; Pimental 1958, 1959). They have suggested that the term should be applied only to distinguishable allopatric populations, possessing the potential to evolve into separate species yet still potentially capable of interbreeding. Selander (1971) and Ford (1974) have pointed out the practical taxonomic difficulties of applying a purely evolutionary concept of subspecies. A similar conflict between theoretical and practical considerations has arisen at the species level (see reviews by Sokal and Crovello 1970; Sokal 1973; Wiley 1978; Lovtrup 1979). For example, while the evolutionary species concept offers several theoretical advantages for evolutionary research it is impractical as a basis for taxonomic classification. The now popular biological species concept serves as a compromise between the theoretical disadvantages of the evolutionary species concept. Ford (1974) has proposed a similar compromise at the subspecies level, namely the "taxo-evolutionary subspecies" or "biological subspecies" concept. This is the concept adopted in this thesis.

The main features defining a taxo-evolutionary subspecies are:

1. The characteristics distinguishing the subspecies must be acquired during allopatry (i.e. during isolation from other subspecies).
2. The similarities between populations grouped into a subspecies must not be due to convergent or parallel evolution.

Ford (1974) intended that this definition should cover situations in which a previously isolated population has expanded its range and is now in secondary contact with other subspecies. He suggested that zones of secondary contact are distinguishable from zones of primary intergradation because "nearly all steep zones of intergradation probably result from secondary contact". However in recent years several workers have shown that sharp contact zones can be either primary or secondary. Sharp primary intergradation has been predicted by various models of parapatric speciation (e.g. Bush 1975; Endler 1977; White 1978; Barton and Hewitt 1981). Despite sound theoretical arguments supporting the idea of parapatric speciation, evidence to date suggests that this phenomenon is very rare (e.g. Key 1981; Mayr 1982). Key (1981) believes that most cases of parapatric speciation represent the second stage of a speciation process that began in allopatry. The view adopted in this chapter is that the mode of speciation responsible for a sharp contact zone between two subspecies is of little relevance to the validity of those taxa.

While such a zone is most likely to represent a secondary contact following allopatric differentiation, the possibility of parapatric speciation should not be ignored. The important point is that the populations on either side of the zone can be viewed as subspecies regardless of the mode of speciation by which they have arisen.

In the present analysis of geographical variation in the Rufous Scrub-bird considerable emphasis is placed on song variation. Data on vocalizations were much easier to obtain for this species than were data on morphology. Collection of specimens for morphological study was considered unwise due to the species' apparent rarity. Attempts to live-trap the bird met with little success (see Chapter 3).

The use of vocal characteristics in avian systematics has often been discouraged (see reviews by Lohrl 1963; Lanyon 1969; Selander 1971; Mundinger 1979, 1982; Kroodsma and Miller 1982). I believe that many of the problems traditionally associated with the use of vocalizations in infraspecific systematics can be largely overcome by applying strict precautions to the analysis and interpretation of vocal variation. The problems most likely to be encountered in studies such as this are:

1. Geographical differences in vocalizations may be learnt rather than genetically based. Recent research on the ontogeny of vocal behaviour in birds has suggested that vocalizations are usually partly inherited and partly learnt; the basic underlying structure of vocal patterns is genetically based whereas the fine structure is learnt (e.g. Catchpole 1979; Mundinger 1979; Kroodsma 1982; Marler and Peters 1982). Mundinger (1979, 1982) has suggested that systematic studies should concentrate on the underlying genetically based component of vocalizations. One way in which this can be achieved is by studying songs of birds reared individually in social isolation. This was clearly impractical in the case of the Rufous Scrub-bird. An alternative in field studies is to analyse variation in basic structure only, ignoring the fine details of vocalizations (Mundinger 1979). While this latter approach was employed in the present study I nevertheless did not know to what extent learning was responsible for observed song variation. However, I feel that this problem is of less relevance to infraspecific systematics than has often been claimed. In terms of the biological species concept, species are defined as "groups of actually or potentially interbreeding natural

populations which are reproductively isolated from other such groups" (Mayr 1966). This definition implies that the importance of a taxonomic character should be based on the degree to which that character affords reproductive isolation between populations and not the degree to which the character is genetically based. The same principle should apply at the subspecies level.

2. Vocalizations may be adapted to suit particular acoustic environments (e.g. different habitats) and therefore prone to convergent or parallel evolution in different populations. Similar problems are encountered in analyses of morphological variation (Selander 1971). In the present study the likelihood of convergent or parallel evolution between populations is assessed on the basis of environmental data collected in conjunction with the song data. Observed relationships between song characteristics and environmental factors are compared with predicted relationships derived from previous research on this problem (e.g. Morton 1975; Nottebohm 1975; Bowman 1979; Hunter and Krebs 1979; Gish and Morton 1981; Wiley and Richards 1982).
3. Geographical variation in vocalizations may be complicated by the existence of dialects. Many authors have made a distinction between "dialects" which are song differences occurring over short distances within contiguous populations, and "geographical variation" which refers to differences occurring over long distances between populations that do not normally interbreed (Nottebohm 1969; Thielcke 1969; Orejuela and Morton 1975; Catchpole 1979). The function of dialects is still unclear despite the large amount of research that has been devoted to the phenomenon (e.g. Nottebohm and Selander 1972; Baker 1975; Lemon 1975; Nottebohm 1975; Handford and Nottebohm 1976; Avery and Oring 1977; Baptista 1977; Jenkins 1977; Baker and Mewaldt 1978; Martin 1979; Adkisson 1981; Baker 1982; Mundinger 1982; Trainer 1983). Under the terms of the taxo-evolutionary concept we are concerned only with geographical variation in vocalizations; i.e. variation probably acquired during allopatry. Nevertheless, dialects complicate geographical variation and there may even be difficulty in distinguishing between these two phenomena. In the present study I attempted to overcome these problems by detailed analysis of song variation at a variety of spatial scales.

Despite precautions such as those discussed above, no study of geographical variation in vocalizations can hope to remove totally problems associated with learning, convergent or parallel evolution, and dialects. Probably the best way of testing the systematic importance of observed variation in vocalizations is by searching for correlations with other characteristics. The existence of sibling species of birds is often initially recognized on the basis of vocal variation, and then confirmed by the elucidation of subtle, previously overlooked, morphological differences (Selander 1971; Ford and Parker 1973). This method of confirming the systematic importance of vocal variation is adopted in the present study. The analysis of song variation is followed by a detailed analysis of the morphology of all available museum specimens.

5.2. VOCALIZATIONS OF THE RUFIOUS SCRUB-BIRD : GENERAL CHARACTERISTICS  
AND SOME DEFINITIONS

General descriptions of vocal behaviour in the Rufous Scrub-bird have been given by Jackson (1911, 1920, 1921), Chisholm (1921, 1948, 1951), Favalaro (1931), Marshall (1935), Robinson (1974, 1975), Smith (1976a, 1976b), and Smith and Robinson (1976).

Territorial males possess a very large vocal repertoire. The most frequently used and apparently most species-specific component of this repertoire is the loud and penetrating "chipping song" (see Fig.5.1). The remainder of the male's repertoire consists largely of mimicry of other species. A wide range of species are mimicked. Frequently the copied calls or songs are modified rather than being faithfully reproduced. This modification makes it hard to distinguish between mimicked vocalizations and species-specific vocalizations.

Females vocalize much less than males. In the past it has generally been accepted that females are only capable of producing simple call notes. The most common of these is a soft "tick-tick". Casual observations during the present study have suggested that the female can also engage in complex song duetting with the male. This duetting is softer than the male's full song, but much more complex. Duetting was heard on only 12 separate occasions during the present study.

The following analysis of geographical variation in Rufous Scrub-bird vocalizations deals only with male chipping songs. The terminology to be used in describing these songs is as follows (see Fig.5.1):

1. Syllable. A sound continuous in time.
2. Phrase. A sequence of syllables comprising a distinct subunit of song clearly separated in time from preceding and following subunits.
3. Bout. A sequence of song in which a particular phrase of chipping is repeated with little variation at more or less regular intervals. Although an individual male is capable of producing a variety of chipping phrases, these are always delivered in discrete bouts rather than in a mixed sequence. These bouts usually last for approximately 10 minutes. Successive bouts of chipping may be separated by either

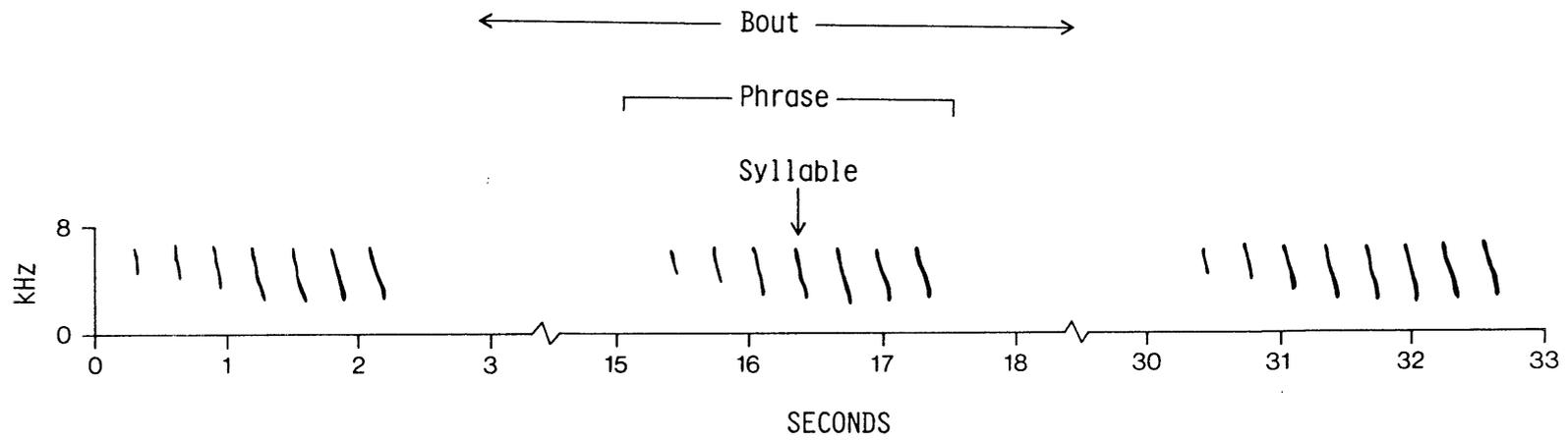


FIGURE 5.1. Sonogram of a typical section of chipping song illustrating definitions of "syllable", "phrase", and "bout".

a period of mimicry, a period of silence, or an abrupt change from one type of chipping phrase to another.

### 5.3. METHODS

#### 5.3.1 Song

Songs were sampled from all of the study areas described in Chapter 2, between January 1980 and January 1983. Two methods of collecting song data were employed:

##### Taped Songs

Recordings were made on a Uher 400 Report-L tape recorder at 19.05 cm/s, with input from a Uher dynamic microphone mounted on a 60cm parabolic reflector.

The basic sample unit was a bout of chipping song (described above). At least 10 consecutive phrases were recorded for each bout. The following information was also noted for each recording:

1. The precise location of the territory (recorded on 1:25,000 Topographic Maps).
2. Habitat type classified on a three-point scale: 1 = territory totally surrounded by rainforest, 2 = territory situated on ecotone between rainforest and open forest, 3 = territory totally surrounded by open forest.
3. Altitude to nearest 100 metres a.s.l. (estimated from topographic maps).
4. Date.
5. Time of day.
6. Weather. Dry bulb temperature, relative humidity, wind, mist, rain, and cloud cover were recorded in the manner described in Chapter 3.
7. Distance between the microphone and the bird.
8. Recording level setting used during the taping.

Sound spectrograms were produced with a Kay Electric Model R 662 B Sona-Graph. In this thesis, spectrograms are used only to illustrate different types of song. The song variables used in the following analyses were measured by other means.

Three variables were measured by playing tapes at  $\frac{1}{4}$  speed (see Fig.5.2):

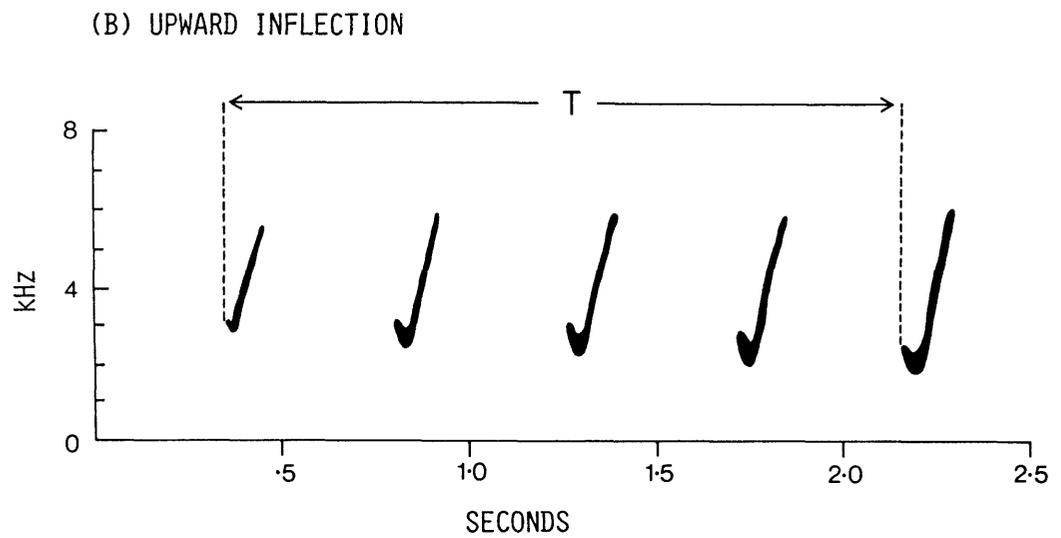
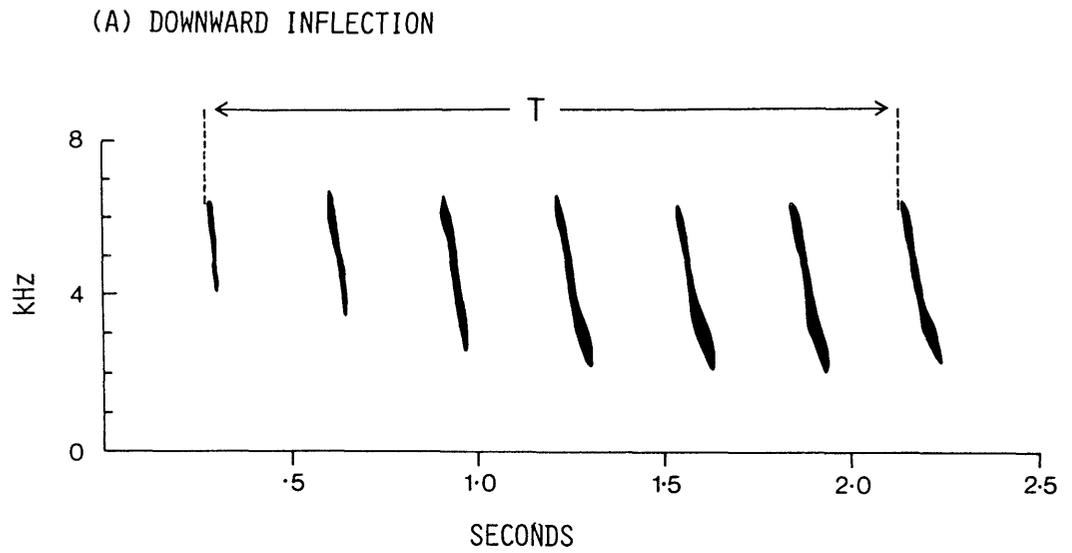


FIGURE 5.2. Sonograms of two chipping phrases illustrating song variables defined in the text.

1. Inflection of syllables. Bouts of chipping were classified according to whether they involved upward or downward inflected syllables. Bouts of chipping always contained syllables of one type only - i.e. either all upward inflected or all downward inflected.
2. Number of syllables per phrase. The value for each bout was the average obtained from 10 consecutive phrases.
3. Syllable interval. This was the average time separating the onset of syllables within a phrase. The average syllable interval for a phrase was calculated as:

$$\text{Syllable interval} = \frac{T}{(n-1)}$$

where T = the time between the onset of the first syllable and the onset of the last syllable (see Fig.5.2). This was timed with a stopwatch while playing the tape at  $\frac{1}{4}$  speed, then divided by 4 to give an estimate at normal speed.

n = the number of syllables in the phrase.

Syllable interval was estimated to the nearest millisecond. The value for each bout was the average obtained from 10 consecutive phrases.

The frequency structure of song bouts was analyzed using a Hewlett Packard Model 3582A Spectrum Analyzer. This produced a power spectrum in which amplitude (dB) was plotted against frequency (0-10kHz). The instrument settings used were : flat top passband shape, RMS averaging mode (64 samples), input signal trigger mode. The frequency spectrum for a song bout was the average of 64 sample scans. This average frequency spectrum was plotted on a Y.E.W. Type 3086 X - Y Recorder. The spectrum was used to measure the following variables (see Fig.5.3):

1. Mean frequency (to nearest 0.1 kHz). This was calculated as:

$$\text{Mean frequency} = \frac{\sum(A \times F)}{\sum A}$$

where F = frequency at the midpoint of one of ten 1 kHz divisions between 0 and 10 kHz (i.e. the values of F were 0.5, 1.5, 2.5.....9.5 kHz)

A = the amplitude associated with a particular F value. This was measured in terms of dB below the modal amplitude of the spectrum.

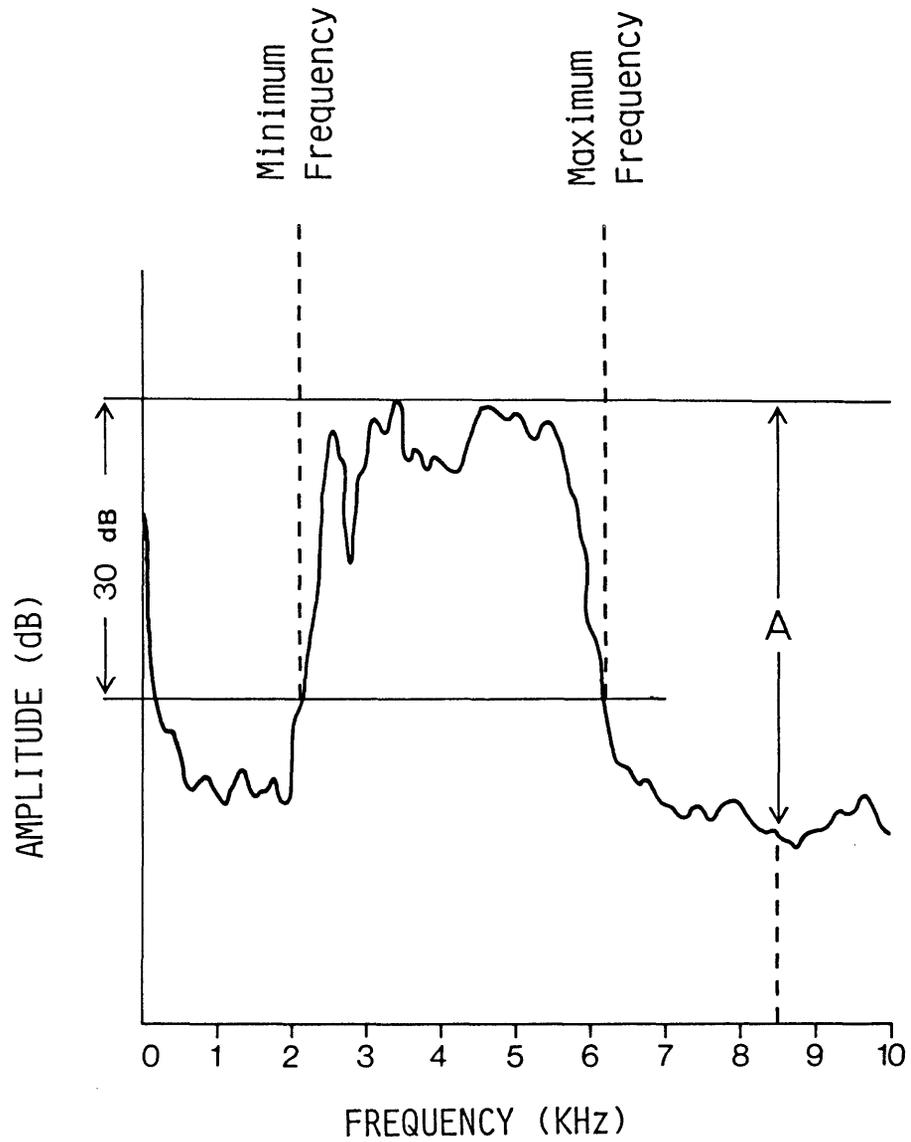
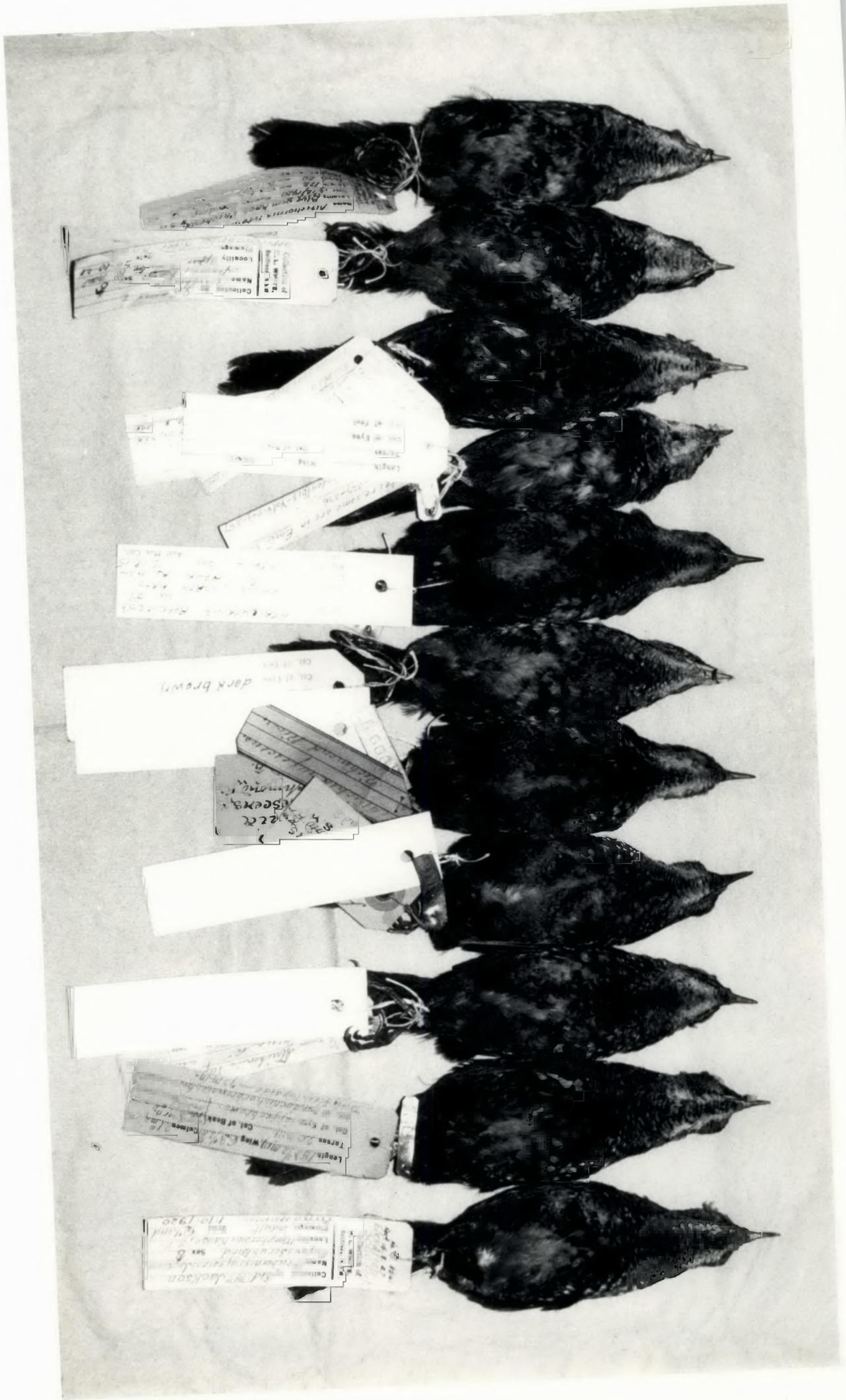


FIGURE 5.3. A typical frequency spectrum obtained from a bout of chipping, illustrating song variables defined in the text.



Collected by M. W. Jackson  
Name: *Spizella monticola*  
Sex: ♂  
Locality: *St. Louis, Mo.*  
Date: *1/10/1920*

Length: *110*  
Wing: *65*  
Tail: *45*  
Col. of Head: *Dark*  
Col. of Eyes: *Dark*

Length: *110*  
Wing: *65*  
Tail: *45*

Length: *110*  
Wing: *65*  
Tail: *45*

SC 222  
M. W. Jackson  
1/10/1920

Col. of Eye: *Dark*  
Col. of Head: *Dark*  
dark brown

Length: *110*  
Wing: *65*  
Tail: *45*

Length: *110*  
Wing: *65*  
Tail: *45*  
Col. of Eye: *Dark*  
Col. of Head: *Dark*

Collected by *M. W. Jackson*  
Name: *Spizella monticola*  
Sex: *♂*  
Locality: *St. Louis, Mo.*  
Date: *1/10/1920*

Collected by *M. W. Jackson*  
Name: *Spizella monticola*  
Sex: *♂*  
Locality: *St. Louis, Mo.*  
Date: *1/10/1920*

## PLATE 6

Series of male Rufous Scrub-bird specimens demonstrating absence of latitudinal variation in plumage. Localities top to bottom: Chichester R., Chichester R., Dorrigo, Dorrigo, Dorrigo, Lionsville, Richmond R., Richmond R., Tweed R., Macpherson Ra., Macpherson Ra.



2. Maximum frequency (to nearest 0.1 kHz). The frequency above the mean at which amplitude dropped to more than 30dB below the modal amplitude.
3. Minimum frequency (to nearest 0.1 kHz). The frequency below the mean at which amplitude dropped to more than 30dB below the modal amplitude.
4. Frequency range. The difference between maximum frequency and minimum frequency.

### Untaped Songs

The collection and analysis of taped songs proved to be very time-consuming. A method of directly measuring song variables in the field was therefore developed. Three variables were measured:

1. Inflection of syllables.
2. Number of syllables per phrase.
3. Syllable interval.

The only differences between these variables and those measured from taped songs lay in the method and precision of estimation. The time between first and last syllables used in calculating syllable interval was timed at normal speed and therefore lacked the precision achieved using slowed down tapes. Number of syllables and syllable interval were not averaged over several phrases. Instead, I listened to at least 5 phrases in a song bout before measuring one that seemed typical of that bout. Number of syllables was estimated to the nearest syllable and syllable interval was estimated to the nearest 10 milliseconds. The following variables were also recorded for each untaped song sample (in the manner described for taped songs): territory location, habitat type, altitude, date, time of day, weather.

### 5.3.2 Morphology

Attempts to develop suitable live-trapping techniques for this species met with little success (see Chapter 3). Only one live-trapped individual was ever examined. The analysis of morphological variation therefore relied heavily on study of museum specimens. The following 34 specimens were examined:

Queensland Museum (QM)

0695, 0696, 3862

Australian Museum (AM)

A9997, 0778, 05017, 05018, 05015, 017638, 021406, 022835, 029406,  
029407, 029408

National Museum of Victoria (NMV)

55794

H.L. White Collection, Melbourne (HLW)

2716, 2717, 2718, 2719, 2720, 2722, 2724, 2725, 2726, 2727, 2728,  
2729, 2730, 7465, 8539, 8540, 8541, 8542, 8543

All specimens from AM, NMV, and HLW were examined together in one session at the National Museum of Victoria. Measurements were taken as follows:

1. Culmen from tip of bill to insertion at skull, to nearest 0.1mm.
2. Wing as flattened chord, to nearest 1.0mm.
3. Tail from tip of longest rectrix to insertion at base, to nearest 1.0mm.
4. Tarsus from the notch on the back of the inter-tarsal joint to the distal edge of the last complete scale before the toes separate, to nearest 0.1mm.

## 5.4. RESULTS

### 5.4.1 SONG

#### 5.4.1.1 Preliminary Analysis of Song Variables

Before embarking on an analysis of geographical variation a preliminary analysis was made of the song variables in order to assess their distributions and inter-correlations.

The data obtained from 160 taped song bouts (combined from all localities) are summarized in Fig.5.4. In this figure each point represents the mean of 10 phrases of a song bout. For the sake of clarity no indication is given of the variation between phrases within each bout. However, in relation to the depicted variation between bouts, variation within bouts was very small. The average standard deviation of number of syllables within a bout was 0.69. The average standard deviation of syllable interval within a bout was 0.0096 (seconds). The distribution of bouts displayed in Fig.5.4 is of particular interest. If the means of these bouts formed clusters this would suggest the existence of distinct song types. If the bouts did not form clusters but were instead continuously distributed, this would suggest a gradation between song bouts with no distinct types. The inflection of syllables is a discrete variable by definition because only two values are possible - i.e. a bout has either all upward syllables or all downward syllables. On the other hand, number of syllables and syllable interval appear to vary continuously rather than forming discrete clusters (see Fig.5.4).

The taped song bouts provided a valuable means of checking the accuracy and precision of measurements obtained from untaped songs. This was achieved by initially replaying the taped bouts at normal speed (19cm/sec) and estimating the song variables in the manner used for untaped songs. These estimates could then be compared to those obtained by subsequent slowing down of the tape and averaging over 10 phrases. The inflection of syllables was correctly assessed for all 160 bouts. The relationship between estimates of number of syllables obtained using the "untaped song" and "taped song" techniques is depicted in Fig.5.5. The two estimates were strongly correlated ( $r = 0.993$ ;  $df = 158$ ;  $p \ll 0.001$ ). Note that the points closely fit the line  $Y = X$ , suggesting that the

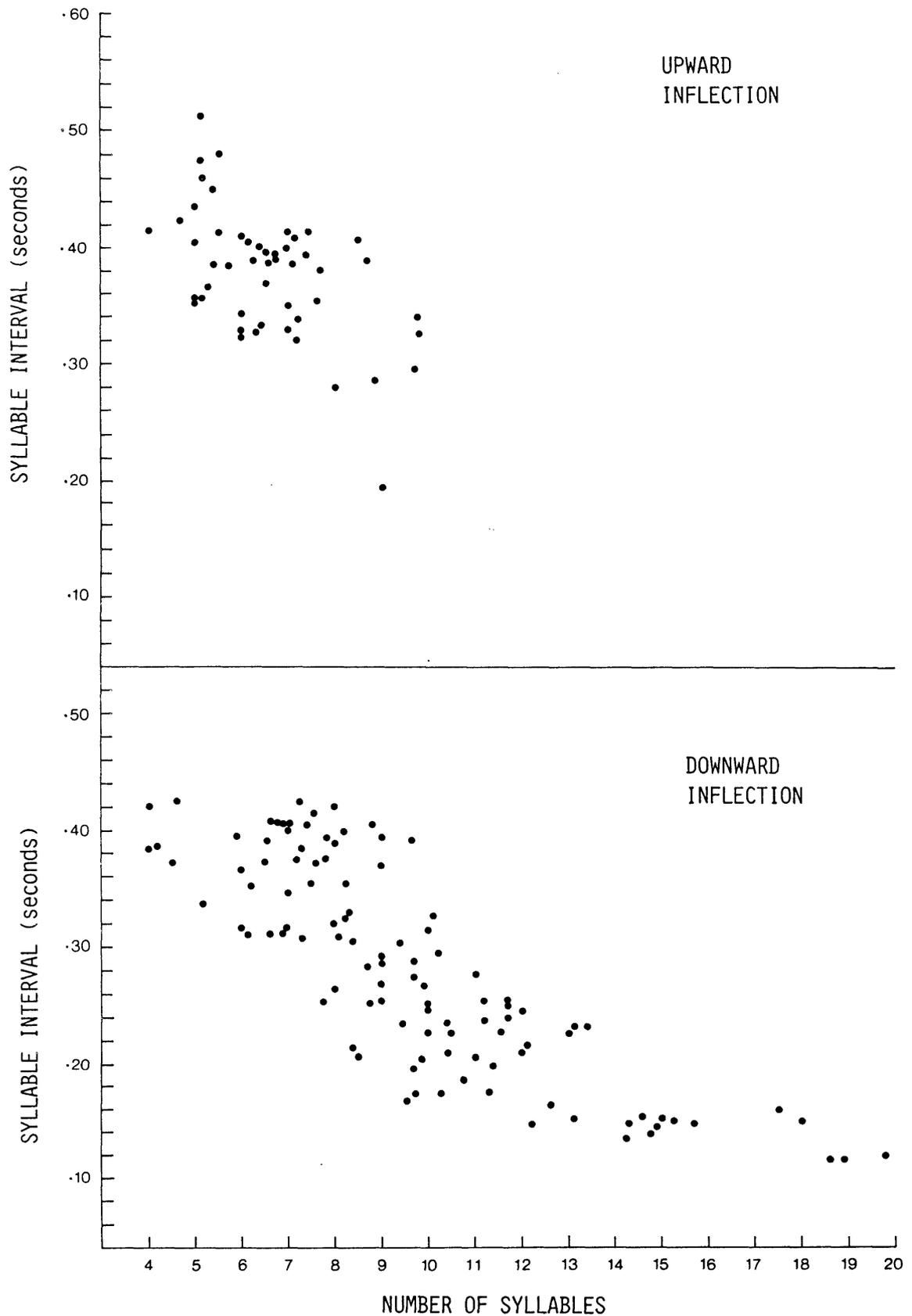


FIGURE 5.4. Distribution of taped song bouts in relation to three song variables: syllable inflection, syllable interval, and number of syllables. Each point represents the mean of 10 phrases sampled from a single bout.

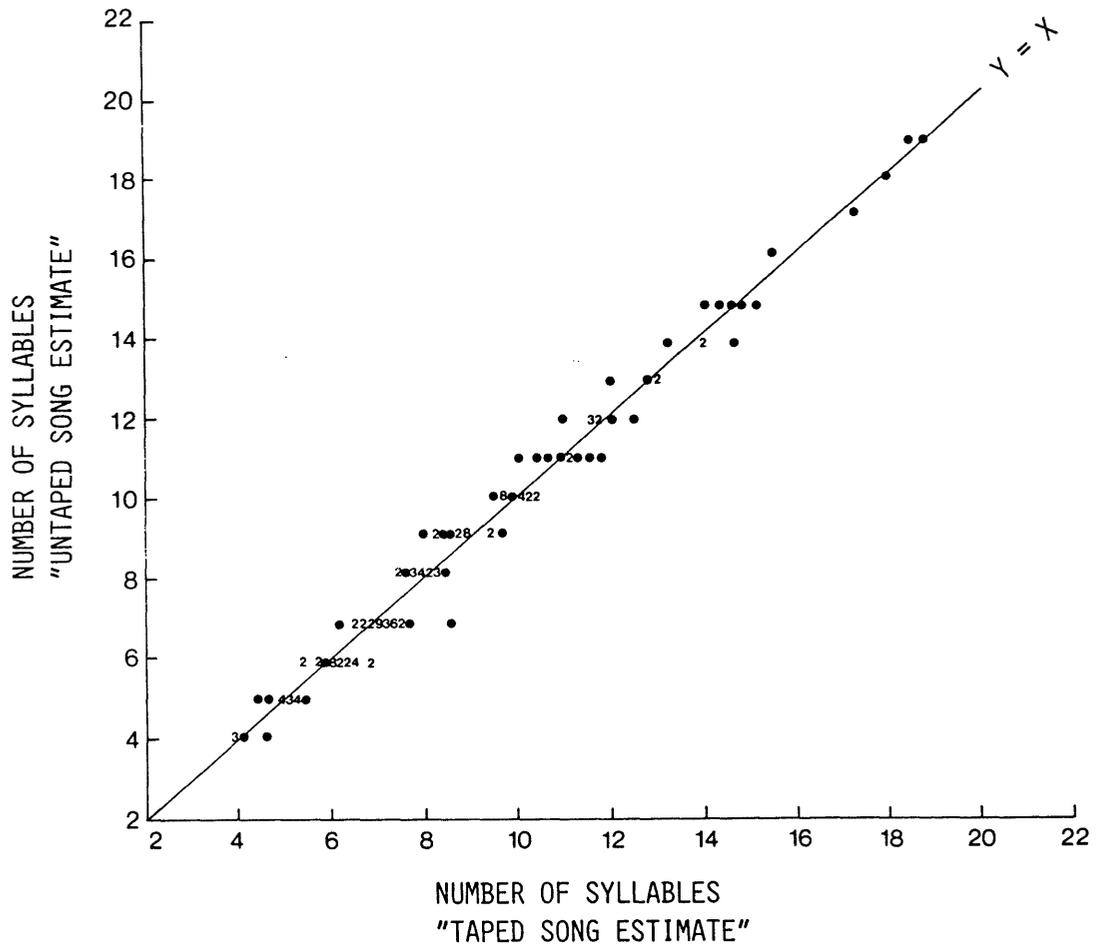


FIGURE 5.5. Relationship between estimates of number of syllables obtained using the "taped song" and "untaped song" methods. (Numbers indicate number of bouts falling on a single point.)

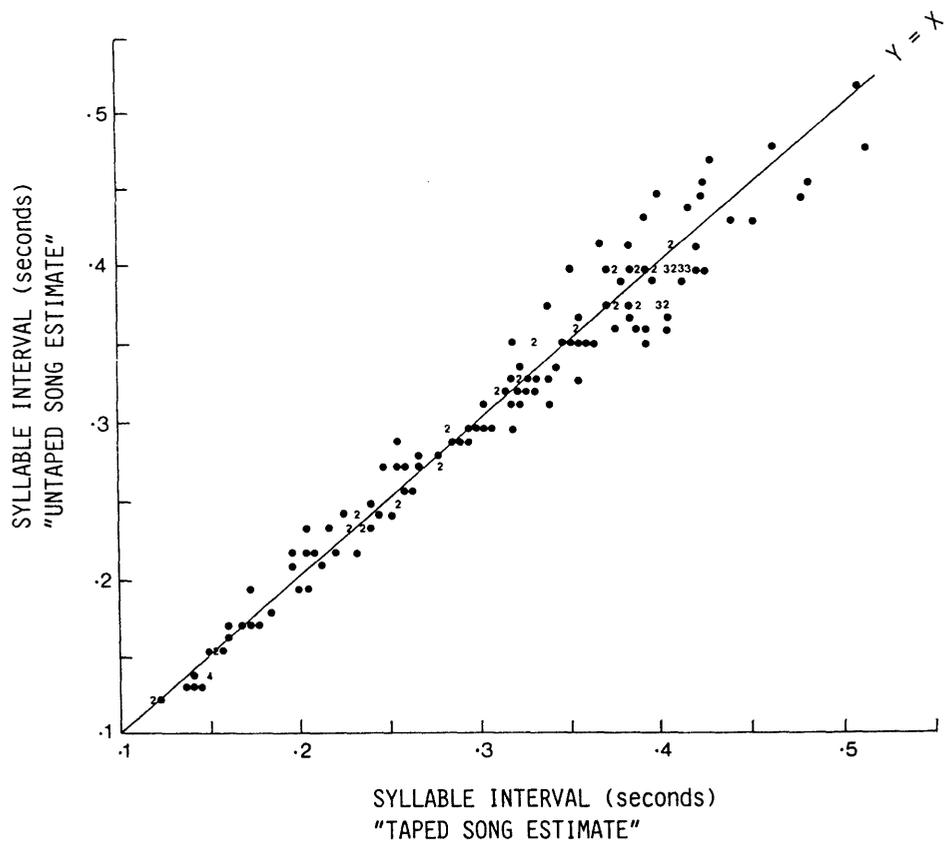


FIGURE 5.6. Relationship between estimates of syllable interval obtained using the "taped song" and "untaped song" methods. (Numbers indicate number of bouts falling on a single point.)

untaped song method yielded an accurate and precise estimate of syllable number. A similar relationship existed between the "untaped song" and "taped song" estimates of syllable interval depicted in Fig.5.6, which were also strongly correlated ( $r = 0.983$ ;  $df = 158$ ;  $p < 0.001$ ).

For the purposes of further analysis the taped song sample of 160 bouts was pooled with the untaped song sample of 660 bouts to give a total sample of 820 bouts. The data on song variables for these bouts are summarized in Fig.5.7. Note that the three song variables appear to be correlated. For the purposes of testing these relationships syllable inflection was assigned a score of 0 for upward inflected syllables and 1 for downward inflected syllables. The correlations between all three variables were highly significant ( $p < 0.001$ ; see Table 5.1a). Syllable number and syllable inflection were positively correlated with each other, while both were negatively correlated with syllable interval. In other words, phrases with few syllables tended to have a longer syllable interval and more often consisted of upward inflected syllables than phrases with many syllables.

The strong inter-correlations between song variables suggested that these variables could perhaps be combined into a single "index" describing song structure, thereby simplifying subsequent analysis of song variation within and between populations. This possibility was investigated by subjecting the three variables to principal component analysis using the FACTOR program of the SPSS Statistical Package (Nie *et al.* 1975). The results of this analysis are summarized in Table 5.1b. The first principal component accounted for 74.6% of the total variance of the three song variables and therefore represented an excellent index of song structure. A song bout's score on this component was calculated as:

$$\text{Song Score} = 0.332 \left( \frac{A - 0.685}{0.465} \right) + 0.413 \left( \frac{B - 0.873}{0.158} \right) - 0.408 \left( \frac{C - 0.320}{0.105} \right)$$

where A = syllable inflection; 0 for upward, 1 for downward

B =  $\log_{10}$  (number of syllables)

C = syllable interval in seconds

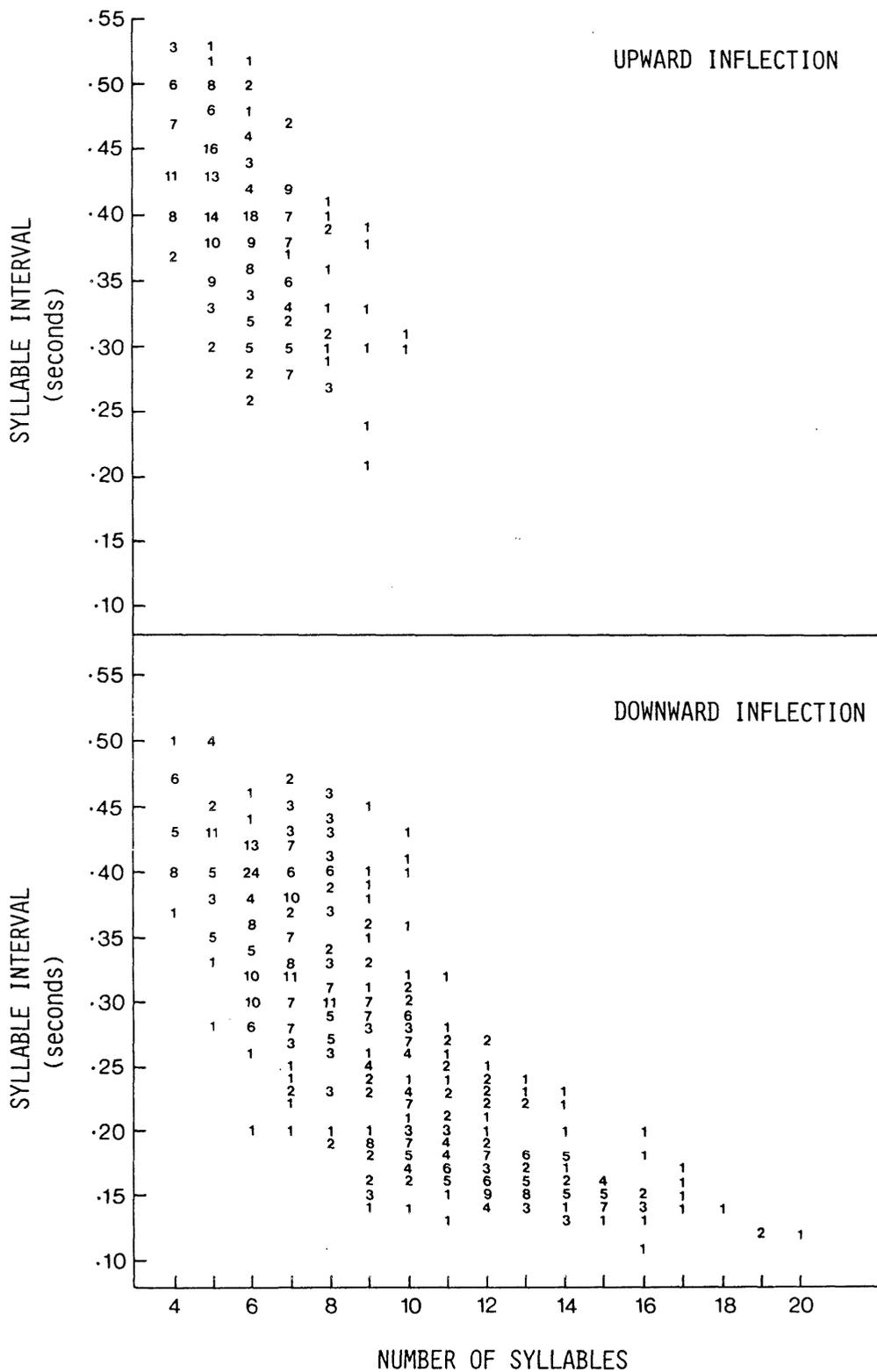


FIGURE 5.7. Distribution of combined taped and untaped song bouts (n=820) in relation to three song variables : syllable inflection, syllable interval, and number of syllables. Each number indicates the number of bouts falling on that point.

TABLE 5.1

(a) Correlations between song variables. (b) Correlations of song variables with three unrotated factors derived from principal component analysis.

(a)

	Log <sub>10</sub> (Number of Syllables)	Syllable Interval
Syllable Inflection	0.517***	-0.484***
Log <sub>10</sub> (Number of Syllables)		-0.833***

\*\*\* p<0.001

(b)

	Factor 1	Factor 2	Factor 3
Syllable Inflection	0.74	0.67	-0.02
Log <sub>10</sub> (Number of Syllables)	0.92	-0.24	0.29
Syllable Interval	-0.91	0.30	0.28
Variance Explained (%)	74.6	19.9	5.5

This principal component score was used in all subsequent analyses of song variation. The combination of three variables into a single principal component allowed the use of powerful univariate methods of geographical analysis for which there are no suitable multivariate equivalents (see Gabriel and Sokal 1969; Selander 1971; Thorpe 1976).

The reader's interpretation of component scores in the following analysis will be aided by remembering the following rule: high scores represent bouts with more syllables per phrase, a shorter syllable interval, and less upward inflected syllables compared to low scores. Interpretation will also be aided by reference to Fig.5.8 in which a variety of song phrases illustrated by sonograms are plotted along the principal component.

#### 5.4.1.2 Variation Within Populations

For the purposes of analysis the study areas from which songs were sampled were considered as belonging to five geographical "populations" (see Fig.5.9). The grouping of localities followed the guidelines laid down by Gabriel and Sokal (1969). The populations were:

1. Border Ranges population incorporating Wiangarie, Lamington Plateau, and Mt. Barney.
2. Gibraltar Range population.
3. New England-Dorrigo population incorporating Point Lookout-Dorrigo Escarpment and Killiekrankie Mountain.
4. Hastings Range population.
5. Barrington Tops population.

All five populations were more or less isolated by barriers of unsuitable habitat. However it should be emphasized that the localities and population boundaries depicted in Fig.5.9 do not accurately represent the distribution of either the Rufous Scrub-bird or of habitat potentially suitable for the species. Detailed information concerning the distribution of the Rufous Scrub-bird and its habitat is presented in Chapter 6.

To analyze and interpret song differences between populations properly it is essential to know something about how song varies within a population. In testing differences between populations it is important

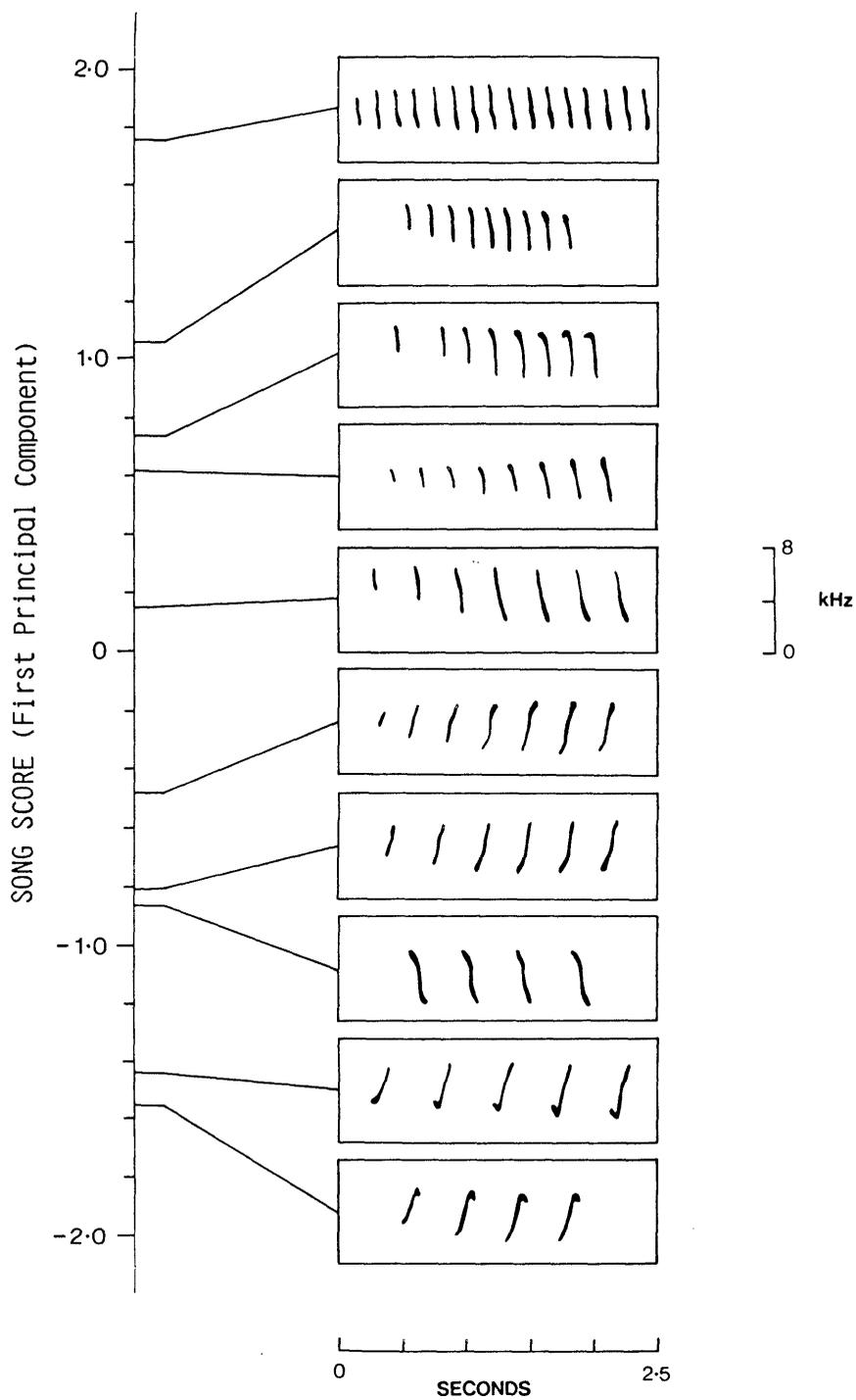


FIGURE 5.8. Principal component scores of a representative range of song phrases illustrated by sonograms.

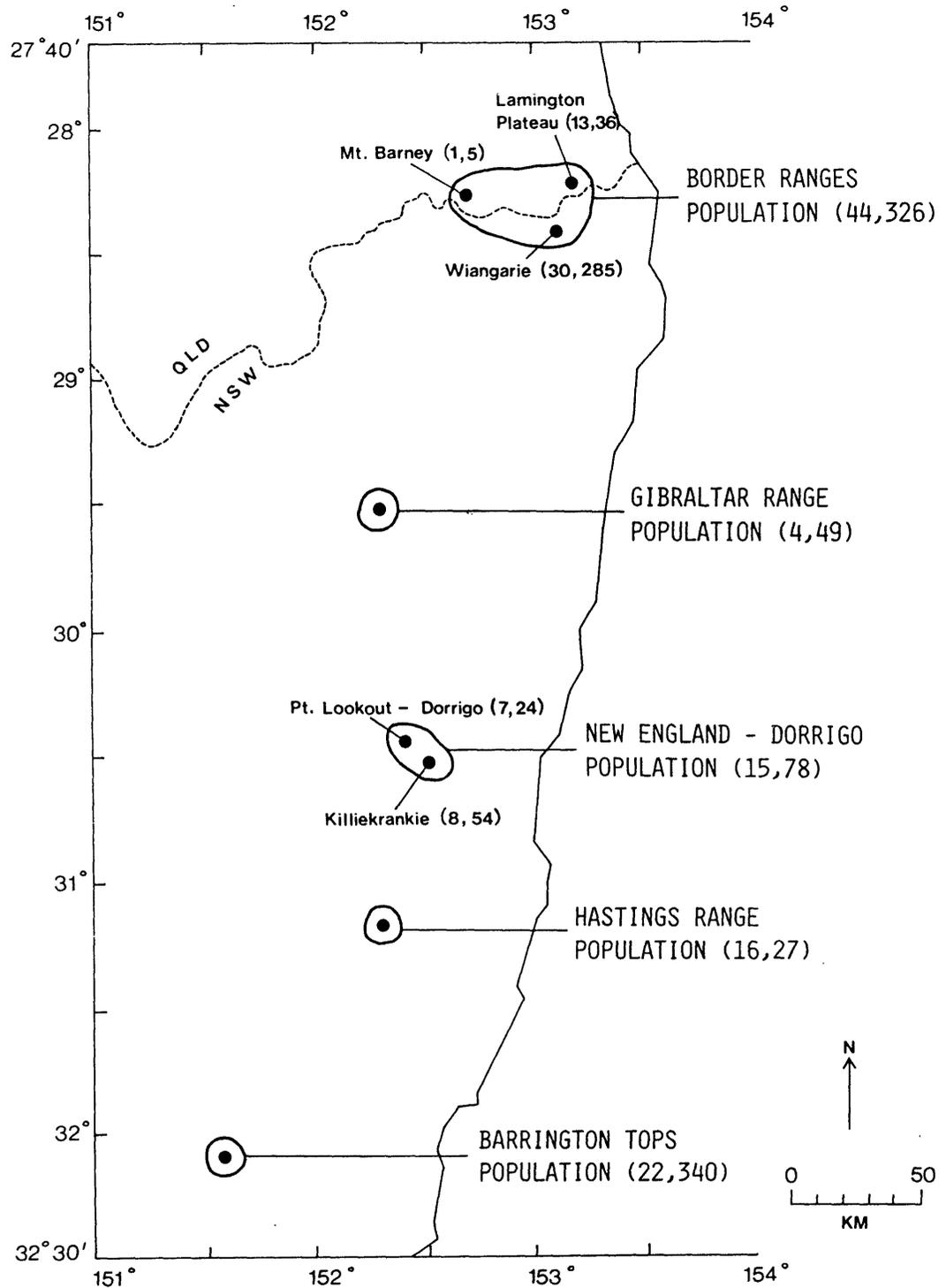


FIGURE 5.9. The grouping of study areas into "populations" for the purposes of analyzing geographical variation in song. Numbers in brackets indicate sample sizes; the first number indicates number of individuals sampled, while the second number indicates total number of song bouts sampled.

to ensure that the samples obtained from each population are representative. There are three main reasons why the song samples obtained in the present study might not be representative of the populations from which they were taken:

1. Song bouts sampled over a short time period from a particular individual may not be independent samples from the repertoire of that individual (Sokal and Rohlf 1969).
2. Songs sampled from a small number of individuals may not be representative of the total population if there is substantial individual variation.
3. Songs sampled from within a small area may not be representative of the total population if dialects exist within the population.

These three possibilities were investigated using the large samples from the Border Ranges and Barrington Tops populations (see Fig.5.9).

The existence of dependency between songs sampled from an individual over a short period of time was tested in the following way. From each of the two populations the seven individuals with the largest sample sizes were selected for analysis. From each individual's sample I extracted instances of "successive bouts". Successive bouts were defined as pairs of sampled bouts in which one bout directly followed another - i.e. the two bouts were known to have not been separated by a third bout of chipping. If successive bouts were not statistically independent events we would expect the song structure of the preceding and following bouts of the pair to be positively correlated. This was tested in each population by an analysis of covariance using the MANOVA program of the SPSS Statistical Package (Hull and Nie 1981). The dependent variable was the song component score (i.e. the score on the principal component described above) of the following bout of a successive pair, while the independent variables were the song score of the preceding bout and the individual from which the bouts were obtained. The analysis tested the correlation between preceding and following song scores within a population controlling for any differences between individuals. This relationship was not significant for either population (Border Ranges:  $F = 0.06$ ;  $df = 1,40$ ;  $p > 0.05$ . Barrington Tops:  $F = 3.73$ ;  $df = 1,68$ ;  $p > 0.05$ ).

Song differences between individuals within a population were tested by one-way analysis of variance using the SPSS ONEWAY program (Nie *et al.* 1975). All individuals with sample sizes of 8 bouts or more

were included in the analysis (15 individuals from the Border Ranges population and 13 individuals from the Barrington Tops population). Differences between individuals were not significant for either population (Border Ranges:  $F = 0.95$ ;  $df = 14,227$ ;  $p > 0.05$ . Barrington Tops:  $F = 1.46$ ;  $df = 12,284$ ;  $p > 0.05$ ).

This result suggests that dialects were probably absent within the Border Ranges and Barrington Tops populations. However, an analysis of variance is not an ideal way of testing for the existence of dialects because it does not take into consideration the spatial distribution of individuals. A different approach was therefore taken to specifically test for dialects. All individuals with sample sizes of 5 bouts or more were included in this analysis (23 individuals from the Border Ranges population and 20 individuals from the Barrington Tops population). The most popular approach to testing for the existence of dialects has been to plot some measure of song dissimilarity between two birds against the map distance separating those birds (e.g. Payne 1978; Payne and Budde 1979; Bradley 1981). Plots for the Border Ranges and Barrington Tops samples are presented in Fig.5.10. The measure of song dissimilarity used in these plots is the difference between the song scores of two individuals. Note that the difference in song between two birds does not appear to be correlated with the map distance separating those birds. However, as pointed out by Trainer (1983), the significance of these plots cannot be tested in the normal manner because the comparisons are not independent; each individual is compared to every other individual. Trainer has recommended the use of spatial autocorrelation analysis (Sokal and Oden 1978a, b) for testing this type of relationship. Spatial autocorrelation analysis tests whether the value of a variable at one location is dependent on its value at neighbouring locations. In the present study Moran's coefficient,  $I$ , was tested using a Gabriel-connected graph to define the pattern of geographical interactions (for details of this technique see Sokal and Oden 1978a). The autocorrelation was not significant for either the Border Ranges sample ( $I = -0.12$ ;  $p > 0.05$ ) or the Barrington Tops sample ( $I = -0.17$ ;  $p > 0.05$ ). These results suggest that dialects were not present within these two populations.

The general conclusion drawn from the above analyses is that relatively small samples of scrub-bird song, restricted in either space

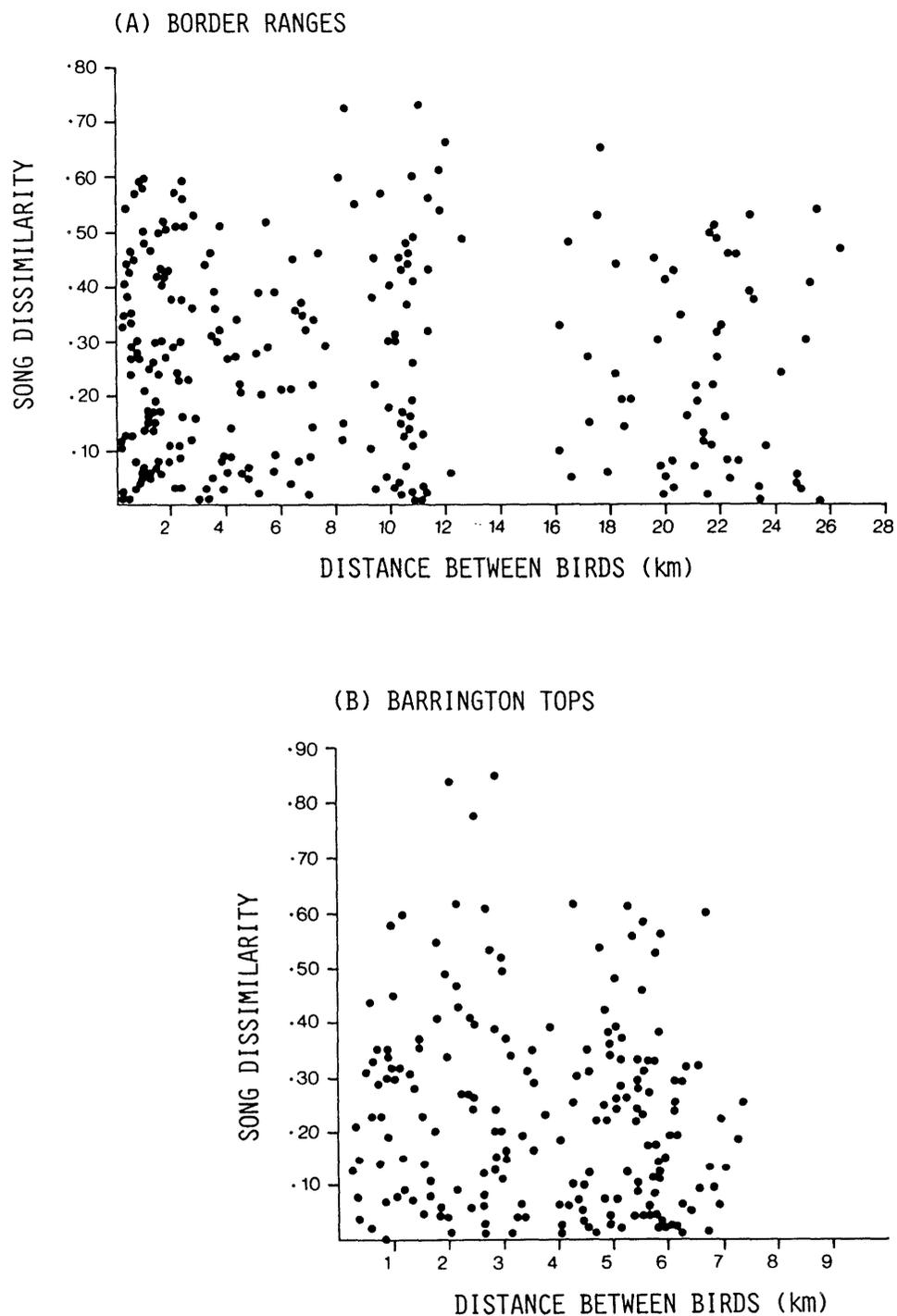


FIGURE 5.10. Song dissimilarity between two birds (difference in song scores) plotted against map distance separating those individuals.

or time, are nevertheless likely to be representative of the populations from which they were taken. It is therefore considered appropriate to include populations represented by relatively small samples in the following analysis of geographical variation (i.e. Gibraltar Range, New England-Dorrigo, and Hastings Range populations).

#### 5.4.1.3 Variation Between Populations

The analysis of geographical variation between populations essentially followed the rigid guidelines laid down by Gabriel and Sokal (1969). The approach involves an initial analysis of variance to test for homogeneity of a character throughout the entire region under consideration. If this overall analysis suggests that the character is not homogeneous throughout the region, the analysis proceeds to test for homogeneity within different combinations of populations using the sum of squares simultaneous test procedure (SS-STP). One modification of Gabriel and Sokal's approach has been necessary in the present analysis. Their method is well suited to an analysis of morphological variation in which a variable (e.g. wing length) is measured only once for each individual. However in the present study repeated samples of song were obtained from each individual. How do we compare populations in which the value for each individual is itself a mean estimated from a sample of values? This is an extremely common problem in research dealing with behavioural characters (e.g. behavioural comparisons between species, sex or habitats). Two poor solutions are to pool all values from all individuals within a population and compare these samples between populations, or to treat the mean for each individual as an accurate estimate of the true mean and compare these values between populations. A much better solution to the problem is to employ a "nested" analysis of variance (Falconer 1960; Sokal and Rohlf 1969). A nested analysis of variance can test whether the variation between populations is significantly greater than the variation between samples obtained from different individuals within each population. The following results are all based on nested analyses of variance conducted using the MANOVA program of the SPSS Statistical Package (Hull and Nie 1981).

The overall analysis strongly rejected the null hypothesis of homogeneity of song throughout the range of the Rufous Scrub-bird ( $F = 150.9$ ;  $df = 4,92$ ;  $p \ll 0.001$ ). This means that there were significant differences between populations. But which populations differed from which others? All combinations of populations were tested for homogeneity using the simultaneous test procedure (Gabriel and Sokal 1969; Sokal and Rohlf 1969). These tests revealed two distinct "groups" of populations (see Fig.5.11). The Border Ranges and Gibraltar Range populations did not differ significantly ( $p > 0.05$ ) thus forming a "northern group". The New England-Dorrigo, Hastings Range, and Barrington Tops populations did not differ significantly ( $p > 0.05$ ) thus forming a "southern group". Both populations in the northern group differed significantly from all populations in the southern group ( $p < 0.001$  for all combinations). The average song scores of the northern group were higher than those of the southern group (see Fig.5.11). This means that birds in the northern group tended to sing chipping phrases with more syllables, delivered more rapidly and less frequently inflected upward compared to birds in the southern group (see Fig.5.12).

#### 5.4.1.4 Variation in Relation to Environmental Factors

Could these population groupings reflect the influence of environmental factors on song rather than geographical variation per se? For example, song may vary with altitude and the differences between populations may be due simply to differences in altitude between the northern and southern populations. Alternatively, song may vary with time of year and the differences between populations may be due simply to differences in the time of year at which northern and southern populations were sampled. Possibilities such as these were investigated by an analysis of covariance using the SPSS MANOVA program (Hull and Nie 1981). The dependent variable was a song bout's component score while population was treated as a factor with five categories. The following variables were included as covariates (see Methods for description of each variable):

1. Habitat
2. Altitude
3. Month (treated as a third degree polynomial)
4. Time of day (treated as a third degree polynomial)

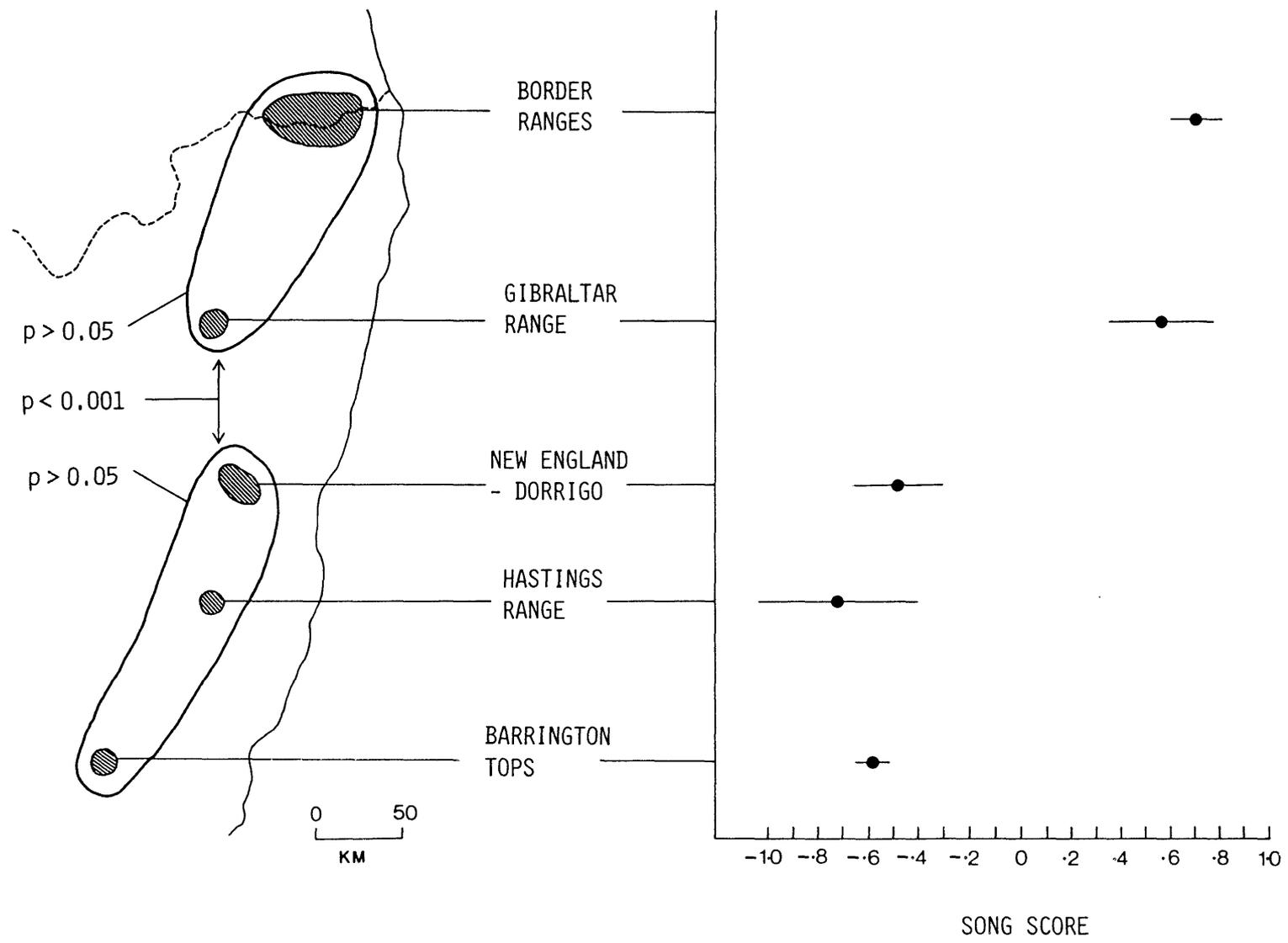


FIGURE 5.11. Results of SS-STP tests, testing for differences in song between populations. In the map on the left, heavy lines enclose subsets of populations that did not differ significantly ( $p > 0.05$ ). Mean song scores  $\pm$  95% confidence limits are shown on the right.

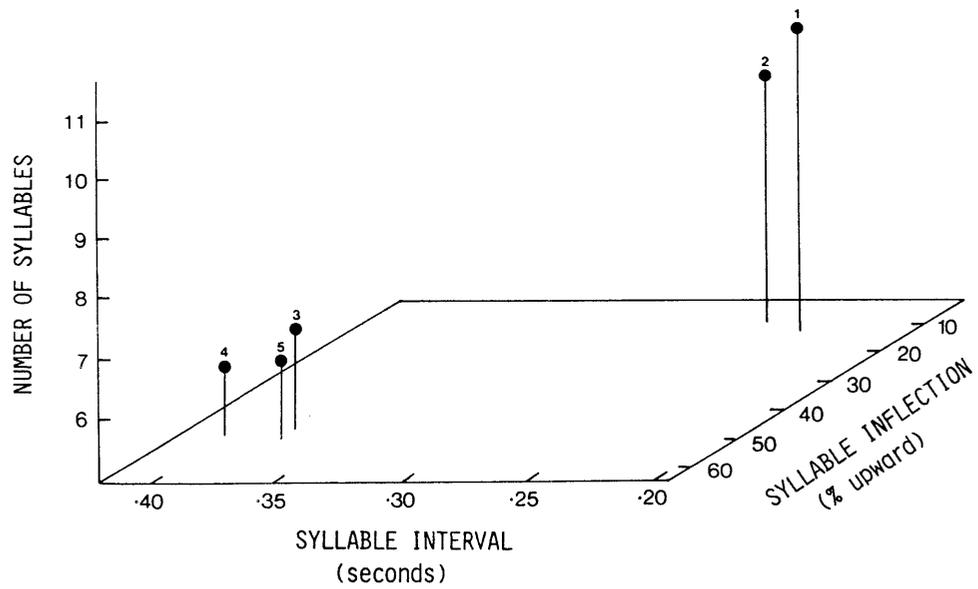


FIGURE 5.12. Trivariate means of song bouts from five populations (1 = Border Ranges, 2 = Gibraltar Range, 3 = New England-Dorrigo, 4 = Hastings Range, 5 = Barrington Tops).

5. Temperature
6. Relative humidity
7. Wind
8. Mist
9. Rain
10. Cloud

Only song bouts for which full environmental data had been collected were included in the analysis (636 bouts). The combined effect of the covariates on song, adjusting for the population factor, was not significant ( $F = 0.65$ ;  $df = 14, 617$ ;  $p > 0.05$ ). The effect of the population factor, adjusting for the covariates, was highly significant ( $F = 38.19$ ;  $df = 4, 617$ ;  $p < 0.001$ ). These results suggest that the observed differences between populations cannot be attributed to the direct influence of environmental factors.

The results of the above analysis do not preclude the possibility that environmental factors have shaped the evolution of song differences or similarities between populations. Habitat appears to be potentially the most important environmental factor influencing the evolution of bird song (Morton 1975; Nottebohm 1975; Bowman 1979; Hunter and Krebs 1979; Gish and Morton 1981; Wiley and Richards 1982). Scrub-birds within the northern group of populations most frequently occur within pure rainforest, whereas birds in the southern group are mostly found in ecotonal or open forest habitat (see Chapters 4 and 6). Of the 48 individuals sampled from the northern group, 85% occurred in pure rainforest while 15% occurred in ecotonal forest or open forest. Of the 53 sampled individuals from the southern group, only 17% occurred in rainforest while 83% occurred in ecotonal forest or open forest. The results of the analysis of covariance described above have already shown that habitat does not seem to have a direct influence on song; i.e. birds in different habitats within a single group of populations do not sing different songs, whereas birds in the same habitat within different populations groups do sing differently. This is illustrated in Fig.5.13. Despite the lack of direct correlation between habitat and song, it is still possible that differences in habitat between the northern and southern groups may have contributed to the evolution of different songs in these groups, and possibly to convergent or parallel evolution of songs between populations within each group. For example, the song of the northern group may have evolved to suit the rainforest habitat which at present supports most

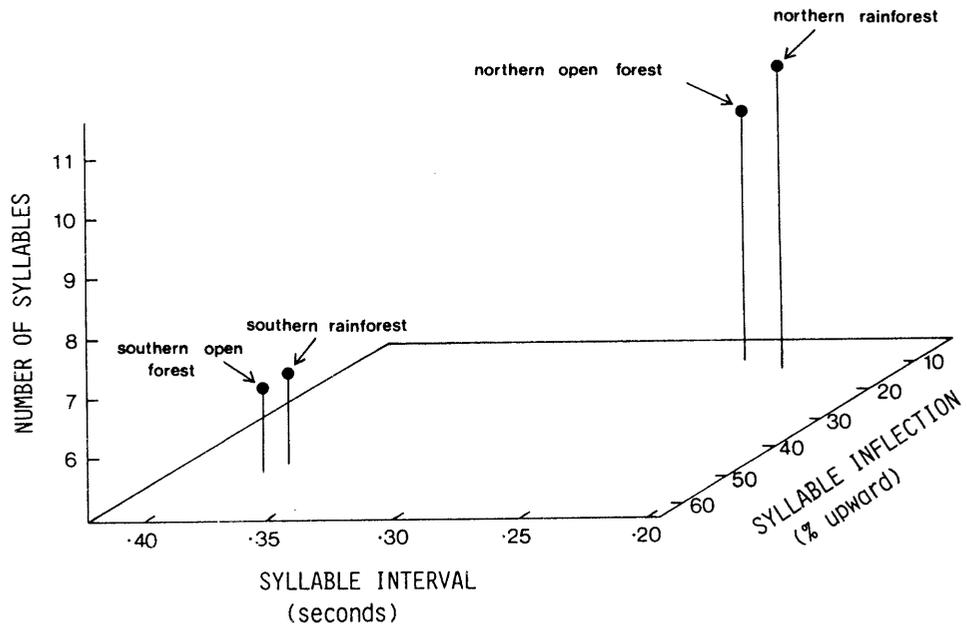


FIGURE 5.13. Trivariate means of song bouts grouped according to region and habitat type ("open forest" = combined open forest and ecotonal categories).

birds within that group, whereas the song of the southern group may have evolved to suit an ecotonal or open forest habitat. This hypothesis cannot be tested by comparing the songs of birds in different habitats within each group. The hypothesis does not predict that birds in different habitats within each group will have different songs, but rather that the song of each group has evolved to suit the habitat most commonly occupied by that group. One way of testing this hypothesis is to compare the observed differences in song characteristics between the two groups to predicted differences derived from previous research on the transmission of songs in different habitats (e.g. Morton 1975; Wiley and Richards 1982). This comparison will be made in the Discussion section of this chapter. Several of the predicted differences relate to the frequency structure of songs. For the purposes of the comparison we therefore need to know whether the songs of the northern group differ in frequency from those of the southern group.

The results of comparisons between the frequency structure of northern group songs and southern group songs are summarized in Table 5.2. The analysis included only those recordings for which distortion was judged to be minimal, and the distance between microphone and bird was less than 20 metres (31 bouts from the northern group and 40 bouts from the southern group). There was no significant difference in mean frequency between the two groups ( $t = 1.91$ ;  $df = 69$ ;  $p > 0.05$ ). The minimum frequency of northern songs was significantly lower than that of southern songs ( $t = 2.77$ ;  $df = 69$ ;  $p < 0.01$ ). The maximum frequency of northern songs was significantly higher than that of southern songs ( $t = 4.70$ ;  $df = 69$ ;  $p < 0.001$ ). The difference between the two groups can therefore be best expressed in terms of frequency range which was significantly greater in the northern group ( $t = 5.28$ ;  $df = 69$ ;  $p < 0.001$ ). Averaged frequency spectra for the two regions are presented in Fig.5.14.

TABLE 5.2

Means (and standard deviations) of frequency variables for song bouts from the northern and southern regions.

	Northern Region (n=31)	Southern Region (n=40)	t-value
Mean Frequency (kHz)	5.52 (.31)	5.39 (.30)	1.91
Minimum Frequency (kHz)	1.73 (.53)	2.05 (.43)	2.77**
Maximum Frequency (kHz)	7.00 (.34)	6.59 (.38)	4.70***
Frequency Range (kHz)	5.27 (.68)	4.54 (.48)	5.28***

\*\* p<0.01

\*\*\* p<0.001

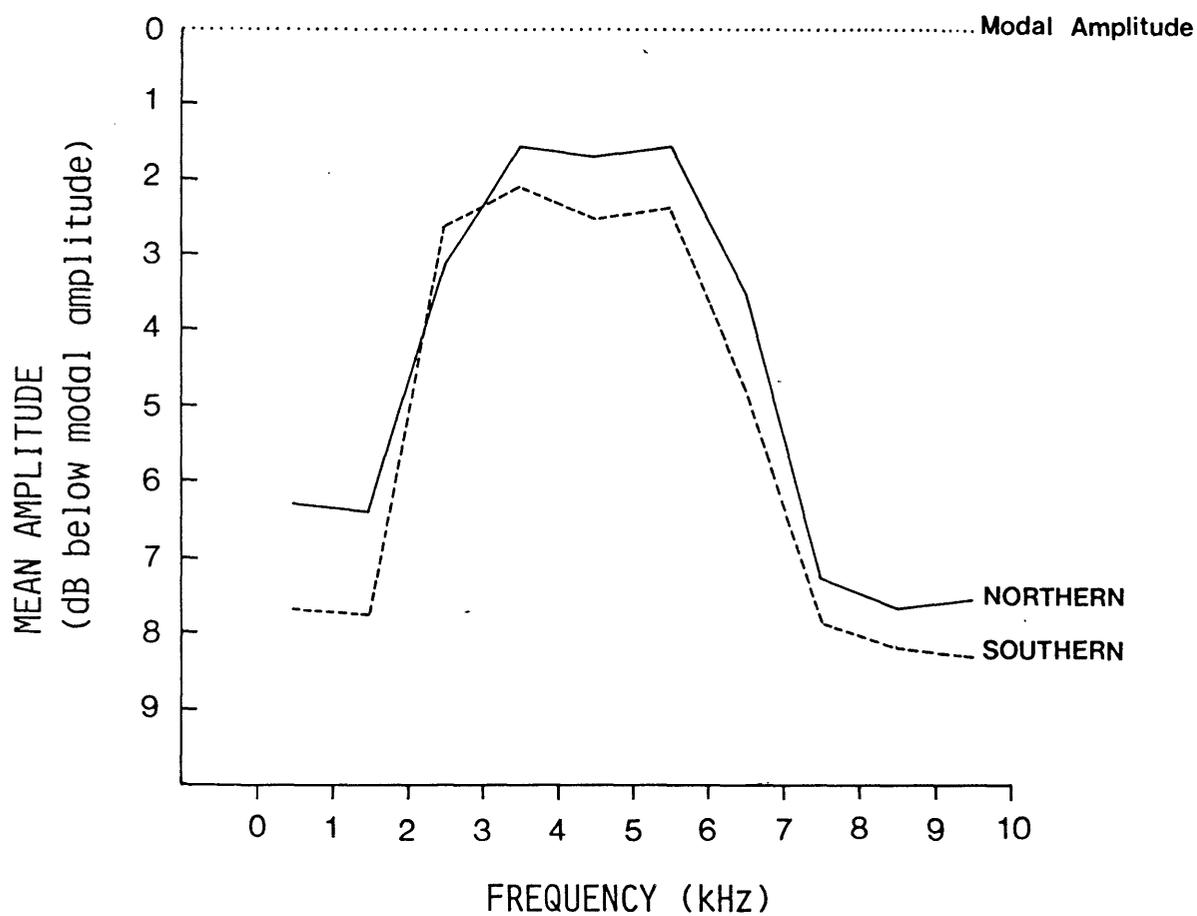


FIGURE 5.14. Sound frequency spectra averaged over all analyzed bouts from the northern region (n=31) and the southern region (n=40).

#### 5.4.2 MORPHOLOGY

Of the 34 specimens examined, 20 were labelled as males, 4 as females, 3 as either "♀(?)" or "said to be a ♀", and 3 as juveniles. The sex and age of the remaining 4 specimens were not stated. Comparison of the specimens of known sex and/or age suggested that these categories could be easily distinguished on the basis of morphological measurements and plumage characteristics (see Table 5.3 and Plate 5). Females could be distinguished from males by their shorter wings and tail. Juveniles could be distinguished from adults by their shorter bill. Based on the measurements of these known specimens, the 4 specimens of unknown sex and age all appeared to be adult males. All three specimens labelled as "♀(?)" or "said to be a ♀" also appeared to be males but were not included in the sample of known or assumed males analyzed below.

All of the female and juvenile specimens were collected from the northern group of populations and were therefore of little value to the analysis of geographical variation. The analysis was therefore confined to the 24 known or assumed male specimens. The localities from which these birds were sampled are depicted in Fig.5.15. Seven specimens were collected from within the region defined by the southern group of populations described above on the basis of song, while 17 specimens were collected from within the region defined by the northern group. A thorough examination of the specimens revealed no differences in plumage between the two regions (see Plate 6). The following were tested for each morphological variable:

1. The difference between specimens from the northern and southern regions using a t-test based on separate variance estimates (Nie *et al.* 1975).
2. The correlation between the variable and the latitude from which each specimen was collected using a regression analysis. This served as a test for clinal variation.
3. The difference between the northern and southern regions after adjusting for correlation with latitude, by means of an analysis of covariance using the BMDP1V program (Dixon 1981).

TABLE 5.3

Morphological measurements obtained from 34 Rufous Scrub-bird specimens. Mean and range (in brackets) are indicated for each category.

	Male	Female	Female(?)	Juvenile	Unknown Age and Sex
n =	20	4	3	3	3
Culmen	17.4 (16.1-18.2)	17.2 (16.5-17.6)	17.3 (16.9-17.8)	13.8 (13.2-14.9)	17.5 (17.4-17.6)
Tarsus	21.6 (19.8-23.0)	20.4 (20.0-20.7)	21.1 (20.9-21.5)	21.1 (20.5-22.0)	21.7 (20.7-22.4)
Wing	63.9 (59-69)	56.8 (56-57)	62.3 (60-64)	55.7 (51-62)	63.5 (62-65)
Tail	73.5 (69-80)	66.3 (63-68)	72.0 (70-73)	47.0 (34-66)	74.3 (72-76)

## PLATE 5

Series of Rufous Scrub-bird specimens demonstrating sex- and age-related plumage variation. Top to bottom: adult ♂, adult ♂, adult ♀, adult ♀, juvenile ♂, juvenile (unsexed), juvenile (unsexed).

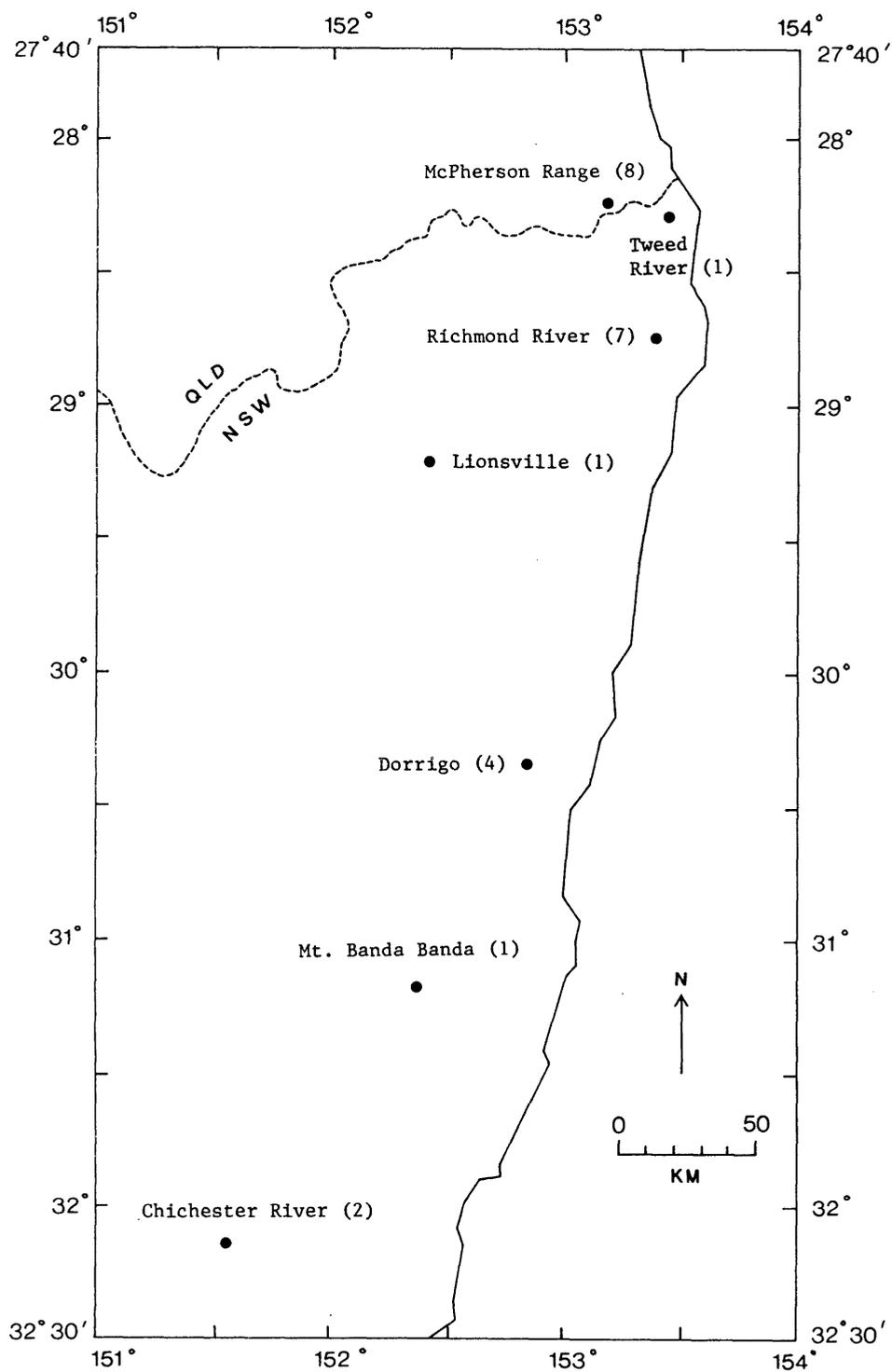


FIGURE 5.15. Localities of known or assumed male specimens used in the analysis of morphological variation. Numbers in brackets indicate sample sizes.

Tarsus length was the only variable yielding significant results ( $p < 0.05$ ) from these tests. The regression of tarsus length on latitude was significant ( $t = 3.77$ ;  $df = 22$ ;  $p < 0.01$ ), with length decreasing from north to south. The difference between regions after adjusting for this relationship was also significant ( $t = 2.09$ ;  $df = 22$ ;  $p < 0.05$ ). These results are clarified in Fig.5.16. Within both the northern and southern regions tarsus length varied clinally with latitude. However the regression lines fitting these two populations were significantly different (an analysis of covariance can be viewed as a test of the difference in elevation between two regression lines). The tarsus length of birds in the northern region was less than that predicted by the regression line fitting the southern region, while the tarsus length of birds in the southern region was greater than that predicted by the line fitting the northern population. This suggests that the regional factor has an effect on tarsus length over and above that explainable in terms of a latitudinal cline. This effect can be visualized by statistically adjusting the tarsus lengths of individuals to remove the influence of latitude (Dixon 1981). These adjusted lengths are plotted in Fig.5.16b.

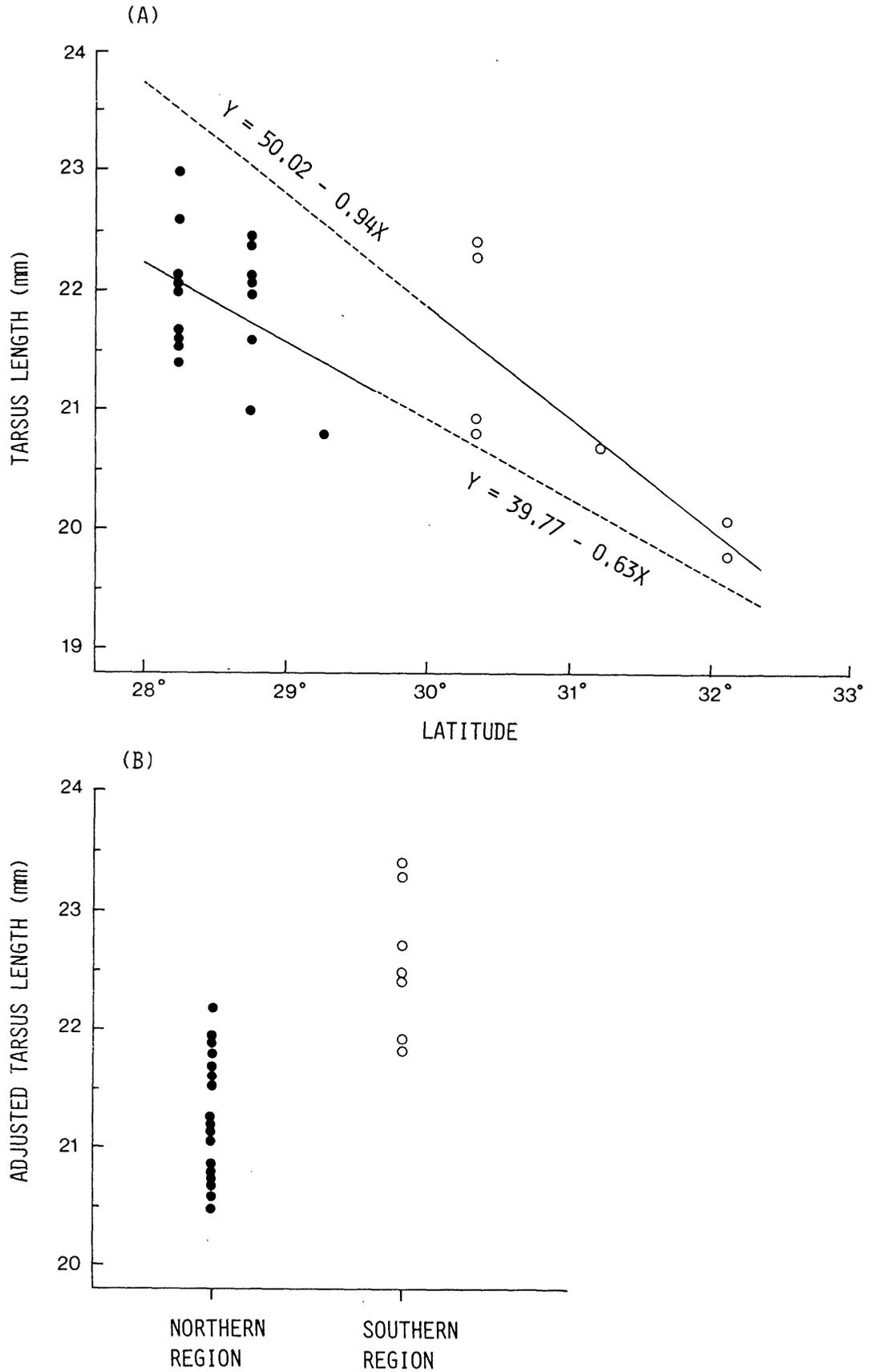


FIGURE 5.16. (A) Tarsus length plotted against latitude. Solid symbols represent specimens from the northern song region while open symbols represent specimens from the southern song region. Separate regression lines for the two regions are indicated.

(B) Tarsus length adjusted for the influence of latitude based on an analysis of covariance (latitude is held constant at its mean value).

## 5.5. DISCUSSION

Populations of the Rufous Scrub-bird have been shown to fall into two groups on the basis of song. Birds in the northern group sing chipping phrases with more syllables, delivered more rapidly and less frequently inflected upward compared to birds in the southern group. Should these two groups be regarded as subspecies in terms of the taxo-evolutionary subspecies concept? The following evidence supports the recognition of two subspecies:

1. There is an abrupt change from one song group to the other, rather than a gradation. Differences in song appear to have been acquired during allopatry. The possibility that the two groups represent a case of parapatric speciation seems unlikely because the Gibraltar Range and New England-Dorrigo populations are at present separated by a natural barrier of unsuitable habitat (see Chapter 6).
2. Song similarities between populations within each group are unlikely to have arisen by convergent or parallel evolution. Acoustic theory and results of previous studies (Morton 1975; Nottebohm 1975; Hunter and Krebs 1979; Gish and Morton 1981; Wiley and Richards 1982) predict that birds in dense habitat as opposed to open habitat should sing songs with: fewer syllables, more slowly delivered, a lower mean frequency, and a narrower frequency range. Yet scrub-birds in the northern group (mainly in dense rainforest) sing phrases with more syllables, more rapidly delivered, an equivalent mean frequency, but wider frequency range, compared to birds in the southern group (mainly in open forest).
3. Song differences are correlated with a regional shift in tarsus length. However, the latter is based on a very small sample of specimens and therefore requires confirmation. Tarsus length appears to vary clinally within each region (in accordance with Allen's rule), but these clines do not coincide, suggesting a shift in tarsus length during allopatry.

Despite the above evidence, I believe it would be premature to formally describe the two song groups as subspecies. Formal taxonomic revision of this species should await the results of further morphological and biochemical analysis (the latter is currently being planned in conjunction with the Australian Museum, W.E. Boles pers. comm.). However for the purposes of conservation it is important that the two groups should, for the time being, be regarded informally as subspecies (perhaps, at this stage, better referred to as "races"). This is the view adopted

throughout the remainder of this thesis. It should also be noted that the pattern of geographical variation described in this chapter does not conform with White's (1920) subspecific division. The subspecies *A.r.jacksoni* should no longer be considered valid.

The evolution of two races in the Rufous Scrub-bird is difficult to interpret on the basis of present habitat distribution. The habitat gap separating the Gibraltar Range and the New England-Dorrigo populations is not substantially wider than other habitat gaps in the species' range (see Figs.6.9 and 6.11 in Chapter 6). To interpret the present pattern of geographical variation in the Rufous Scrub-bird we need to look at past changes in habitat distribution. The following speculative reconstruction of events is based largely on palynological interpretations presented by Kershaw (1975, 1978, 1981), Bowler *et al.* (1976), Walker (1978), Galloway and Kemp (1981), Singh *et al.* (1981), Singh (1982), Sluiter and Kershaw (1982):

1. Robinson (1977) and Smith (1977) have argued that the primary habitat of scrub-birds was once *Nothofagus*-dominated rainforest, which was widespread throughout Australia between the Mid Eocene and the Early Miocene (Galloway and Kemp 1981). This hypothesis is supported by the close congruence of present distributional limits of *Nothofagus moorei* and *Atrichornis rufescens* (see Fig.5.17).
2. From the Mid Miocene onwards Australia's climate became drier culminating in a very dry period at the height of the last glacial, about 25,000-15,000 years BP. Rainfall during this period was lower than at any other time in the last 50,000 years, and areas of rainforest were largely replaced by open sclerophyllous vegetation (Kershaw 1981). During this period the distribution of *Nothofagus moorei* probably contracted to two main refugia. This is reflected in the present distribution of *N.moorei* as two isolated "core areas", one in the Border Ranges and the other extending from Dorrigo to Barrington Tops (see Fig.5.17). It is hypothesized that divergence within the Rufous Scrub-bird commenced during isolation in these two refugia.
3. From 10,000 years BP onwards rainfall increased allowing an expansion of rainforest which reached a peak 7,000-5,000 years BP (Kershaw 1981). It was possibly during this expansion that the Rufous Scrub-bird started utilizing habitats other than *Nothofagus*, such as other types of rainforest and adjacent wet sclerophyll forests. Scrub-birds from the Border Ranges probably dispersed south as far as Gibraltar

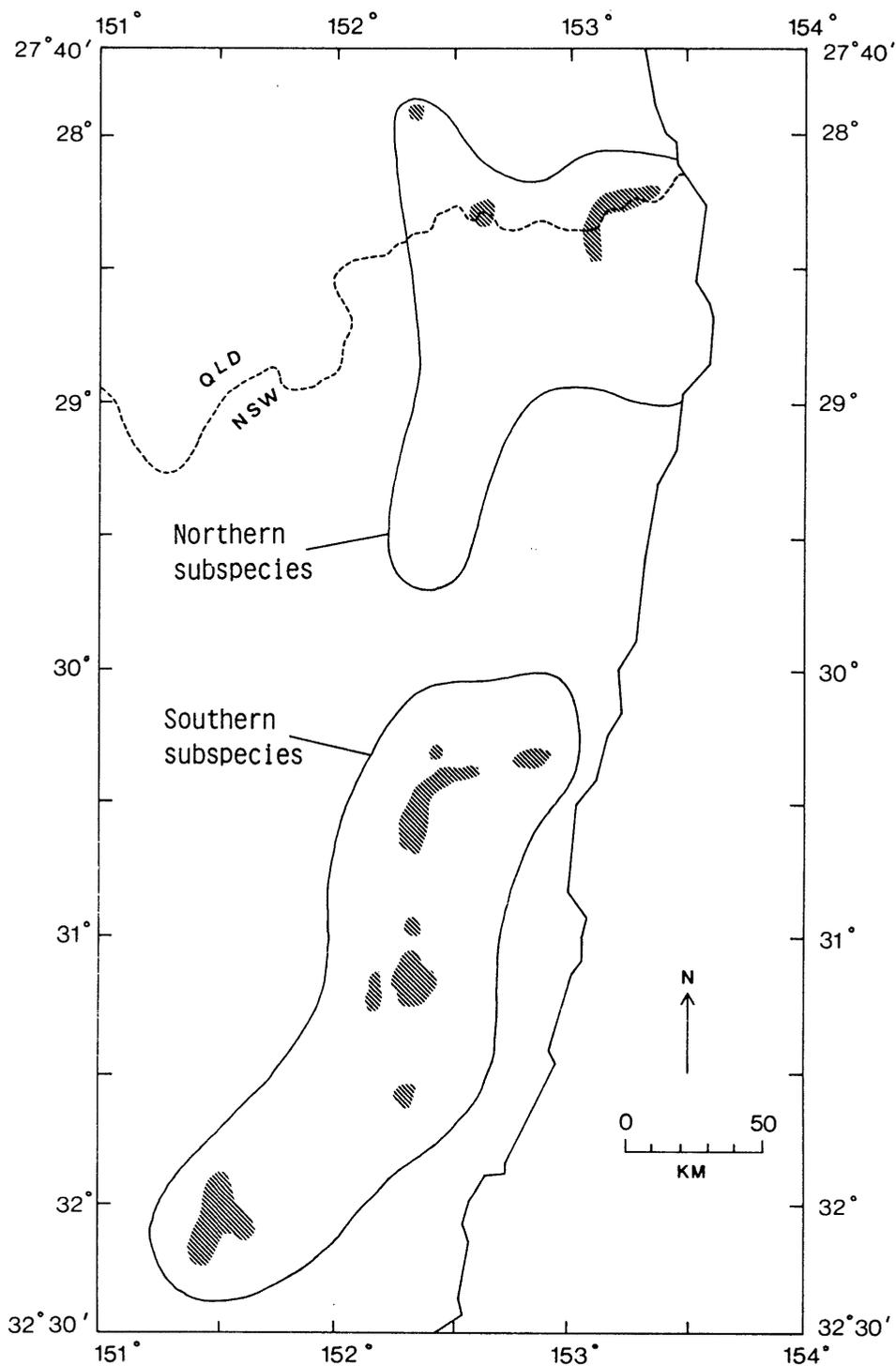


FIGURE 5.17. Approximate distribution of the two subspecies of the Rufous Scrub-bird in relation to the present distribution of *Nothofagus moorei* (shaded). The depicted distribution of the Rufous Scrub-bird is largely derived from detailed distribution maps presented in Chapter 6. The depicted distribution of *Nothofagus moorei* is based on Simpson (1976), Howard (1981), A.G. Floyd (pers. comm.), and personal observations.

Range (see Fig.5.17).

4. Between 3,000 BP and the present there has been a slight drop in rainfall. This, combined with the use of fire by aboriginal man, has resulted in fragmentation of what may have been more or less continuous tracts of rainforest facilitating the dispersal of the Rufous Scrub-bird (Kershaw 1981). The present highly fragmented distribution of the species is probably less than 2,000 years old.

The pattern of distribution displayed by the two races of the Rufous Scrub-bird does not conform with any of the general zoogeographical patterns of the Australian avifauna (Keast 1961, 1981; Kikkawa and Pearse 1969). This is probably because of the species' unusual habitat requirements and unusually limited powers of dispersal. Nevertheless, there is some congruency of the Rufous Scrub-bird pattern with patterns displayed by other pairs of taxa. One example occurs within the lyrebirds, which Robinson (1977) claims also evolved in *Nothofagus*-dominated forest, although they now occupy a variety of moist forests. The Albert Lyrebird *Menura alberti* occurs only in the Border Ranges and nearby areas, while the Superb Lyrebird *Menura novaehollandiae* occurs south from the Border Ranges (Morris *et al.* 1981). The lyrebirds may also have been affected, during the last glacial, by a dry barrier somewhere between the Border Ranges and the Dorrigo district. However in their case the southern form (*M.novaehollandiae*) has dispersed northwards to fill the gap following the return of more favourable conditions. Closer congruency exists with the pattern displayed by the frog genus *Philoria*. The ranges of *P.loveridgei* and *P.sphagnicolus* correspond closely with those of the two Rufous Scrub-bird races. *Philoria loveridgei* is known only from the Border Ranges and Gibraltar Range, while *P.sphagnicolus* occurs from the Dorrigo district south to Barrington Tops (Cogger 1975; Forestry Commission of New South Wales 1981; J.M. de Bavay pers. comm.). It is also interesting to note that the forest types occupied by *P.loveridgei* and *P.sphagnicolus* correspond closely with those occupied by the Rufous Scrub-bird. *Nothofagus*-dominated forest appears to have been the primary habitat of *Philoria loveridgei* and *P.sphagnicolus* although the species are now also found in other types of rainforest and adjacent wet sclerophyll forests (Cogger 1975; Forestry Commission of New South Wales 1981; J.M. de Bavay pers. comm.).

## CHAPTER 6

STATUS : A PRELIMINARY ASSESSMENT6.1. INTRODUCTION

In the General Introduction to this thesis I presented an operational definition of "status". The basic components of this definition were:

1. The "subspecies" is the most practical unit for the assessment of status. However, all other things being equal, a monotypic species should be given higher priority than a subspecies of a polytypic species.
2. The status of a species (or subspecies) is best measured in terms of the estimated time to extinction.
3. An assessment of status is primarily a prediction of future change in the total population size of a species.
4. A distinction should be made between "natural" and "man-made" factors underlying a species' status. All other things being equal, a naturally endangered species should be given lower priority than a species endangered primarily by human activity.

A preliminary assessment of the status of the Rufous Scrub-bird is presented below. This is based on the results of the exploratory survey (Chapter 2) interpreted within the context of the intensive research findings of Chapters 3, 4, and 5.

## 6.2. METHOD OF ANALYSIS

The sampling strategy used in the exploratory survey was neither random nor systematic (see Chapter 2). Sampling was biased towards areas where the Rufous Scrub-bird had been previously recorded or was considered likely to be recorded due to the presence of apparently suitable habitat. For this reason population size could not be estimated by direct extrapolation from densities recorded along survey routes (see Burnham *et al.* 1980). I therefore developed an indirect approach designed to alleviate the problems associated with sampling bias. This approach basically involved three steps:

1. Analysis of scrub-bird density in relation to broad-scale environmental factors (e.g. altitude, average rainfall, forest type).
2. Development of a model describing scrub-bird density in relation to these environmental factors.
3. Estimation of total population size based on this model and the distribution of different combinations of environmental factors throughout the range of the species.

A system of grid points was laid over the entire range of the Rufous Scrub-bird (see Figs.6.1 and 6.2). The grid system was based on latitude and longitude so as to allow future comparison with the results of other inventories such as the Australian Bird Atlas (Davies 1982). This system will also allow future workers to accurately locate areas delineated on the maps in this chapter. The main disadvantage of basing the grid on latitude and longitude was that the spacing of points varied latitudinally. However, this variation was slight, amounting to only a 2.9% north-south decrease in the area represented by each point. The variation was therefore ignored in all calculations described in this chapter. The area represented by each point was calculated as the average of values obtained at the northern and southern extremes of the grid. Data were collected for three sets of points (see Fig.6.2):

1. Coarse grid points. These were situated at the intersections of 5' lines running latitudinally and longitudinally. The total number of coarse grid points was 840 (see Fig.6.3).
2. Fine grid points. A fine grid point was sampled only if it fell within 200 metres of any route walked during the study. Fine grid points satisfying this requirement will be referred to as "surveyed grid points". Of the 6,720 fine grid points considered, 92 were

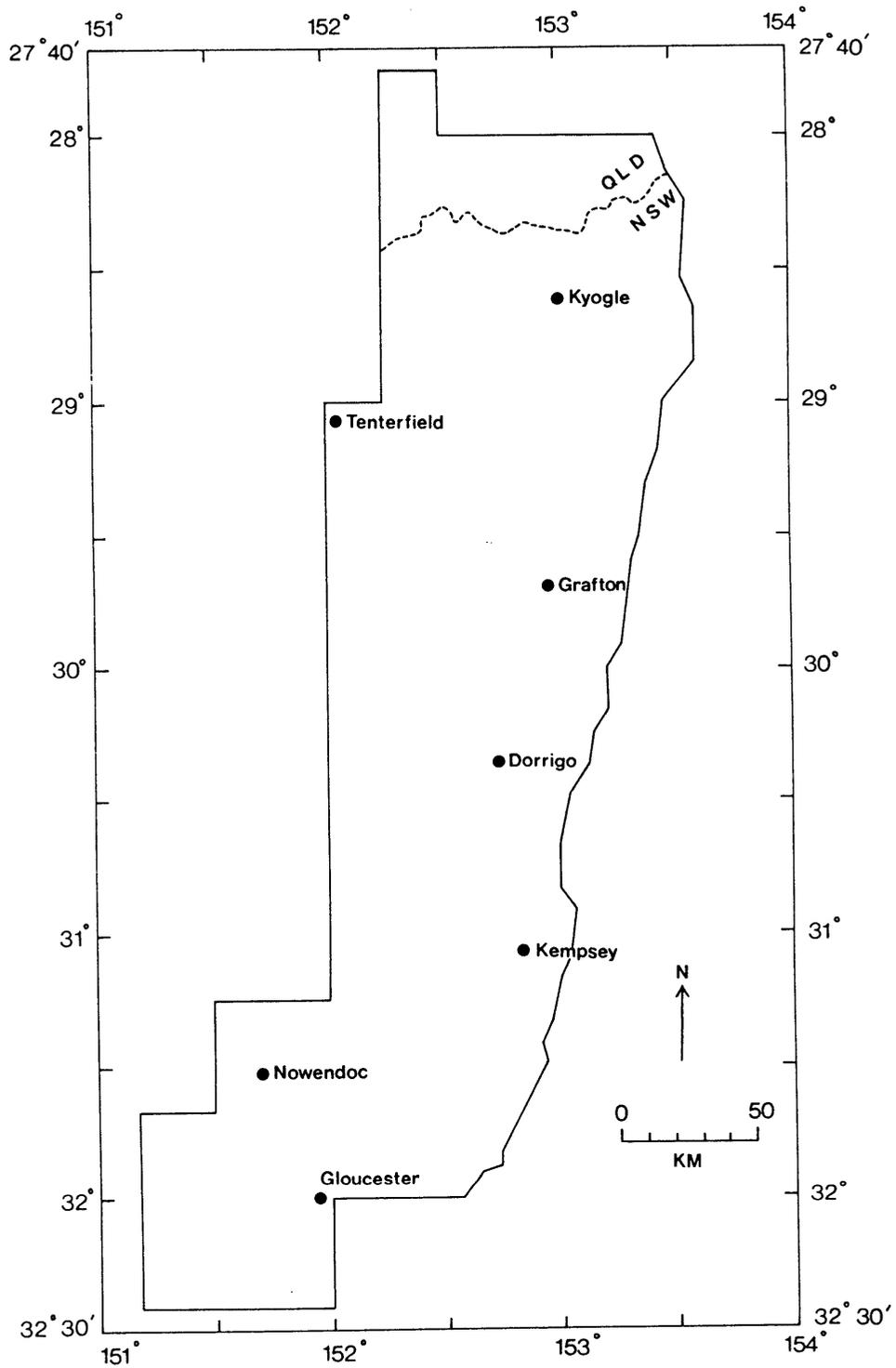
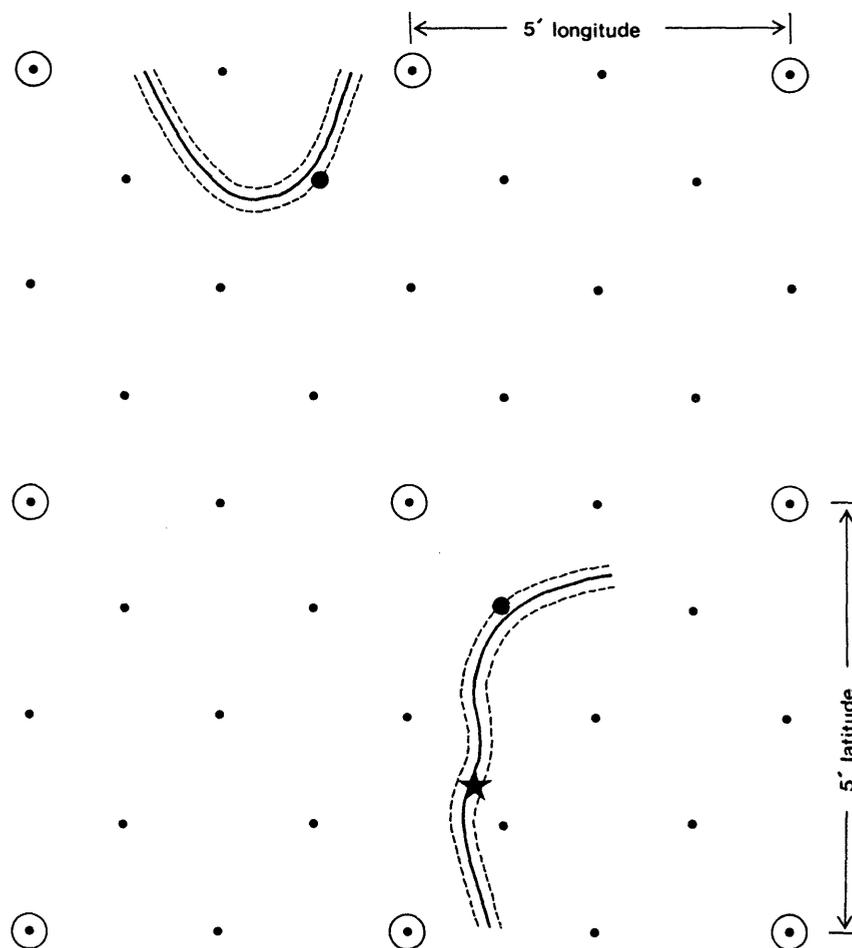


FIGURE 6.1. Boundary of the grid system used to analyze territory density in relation to environmental factors. (See Fig.6.2 for details on the layout of the grid.)



#### LEGEND

- = fine grid point
- ⊙ = coarse grid point (all coarse grid points were also included in fine grid point sample)
- = surveyed grid point
- ★ = scrub-bird point
- — — = walked route (dotted lines indicate 200m either side)

FIGURE 6.2. Layout of the grid system used to analyze territory density in relation to environmental factors. (See Fig.6.1 for details on the boundary of the grid.)

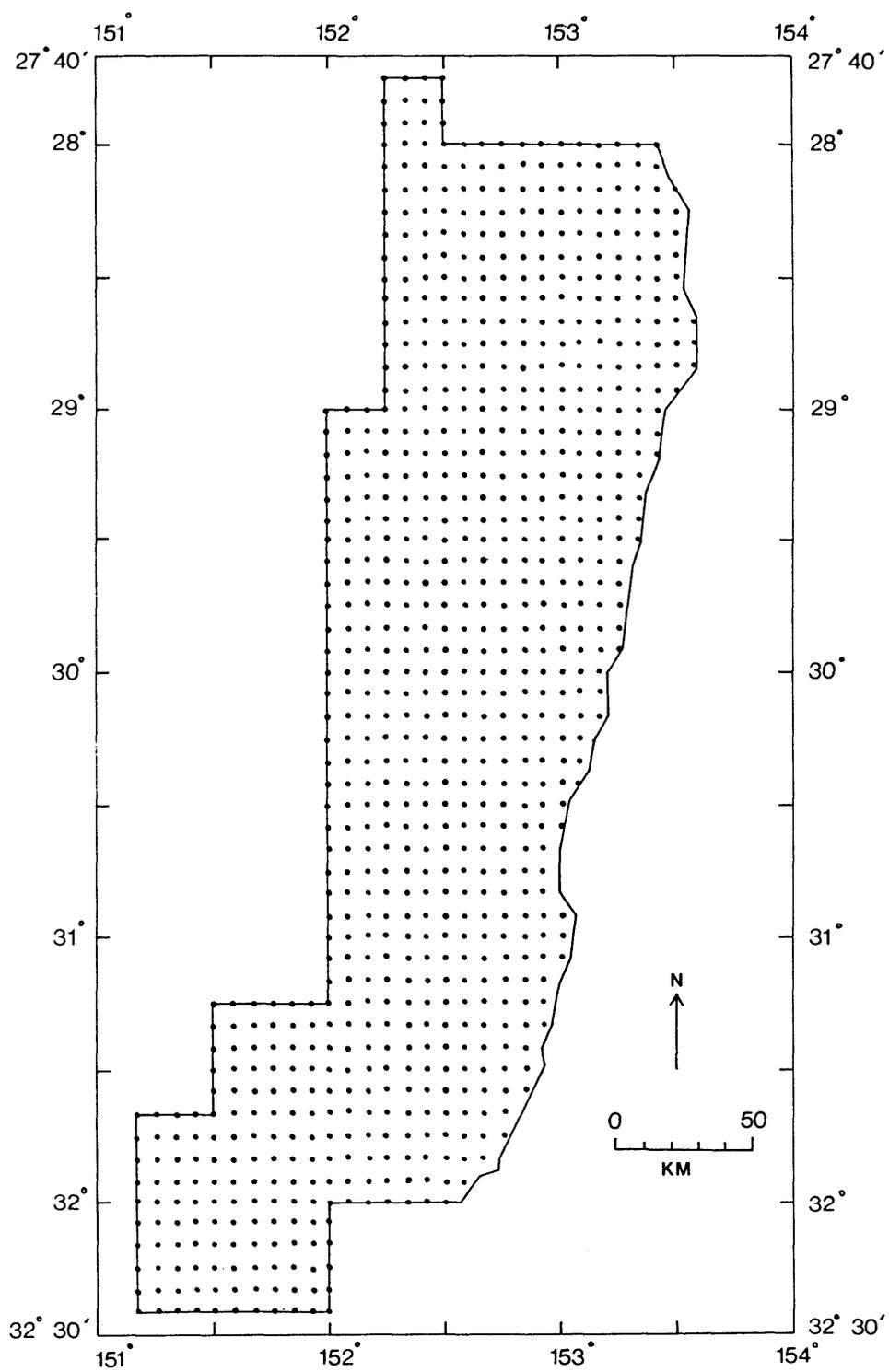


FIGURE 6.3. Distribution of coarse grid points.

surveyed grid points (see Fig.6.4).

3. Scrub-bird points. These were points at which a singing male scrub-bird was detected within 200 metres of a surveyed route during the first walk along that route. The total number of scrub-bird points was 104 (71 additional territories were discovered during replicate walks bringing the total number found during the study to 175).

The following variables were estimated for each of the points described above:

1. Altitude (to nearest 100 metres). Estimated from 1:25,000 and 1:100,000 topographic maps.
2. Average annual rainfall (mm). Reliable estimates of rainfall were not available for many of the points. This applied especially to points located long distances from the nearest settlement and at higher altitudes (most rainfall stations were located close to settlements at low altitudes). To overcome this problem I developed a three-dimensional trend surface model (Peikert 1962) describing rainfall variation throughout the area depicted in Fig.6.1. The three dimensions of the model were latitude, longitude, and altitude. The model was based on data from 177 rainfall stations situated within the area (Bureau of Meteorology 1977). The trend surface was fitted using the New Regression program of the SPSS Statistical Package (Hull and Nie 1981). The third-degree surface explained 77.3% of variation in average rainfall (the full model is included in Appendix B). The model was used to estimate average annual rainfall at each point on the basis of latitude, longitude, and altitude.
3. Average number of raindays per year. This was estimated in the manner described for average annual rainfall. The third-degree trend surface fitted to data from 177 rainfall stations explained 58.5% of variation in number of raindays (the full model is included in Appendix B). The model was used to estimate average number of raindays at each point on the basis of latitude, longitude, and altitude.
4. Clearing. The vegetation at each point was classified as either cleared or uncleared. This was based on vegetation data from 1:25,000 and 1:100,000 topographic maps, the FORINS forest type maps produced by the Forestry Commission of N.S.W. (Hoschke 1976; Hoschke and Squire 1976), and the Moreton Region Vegetation Map

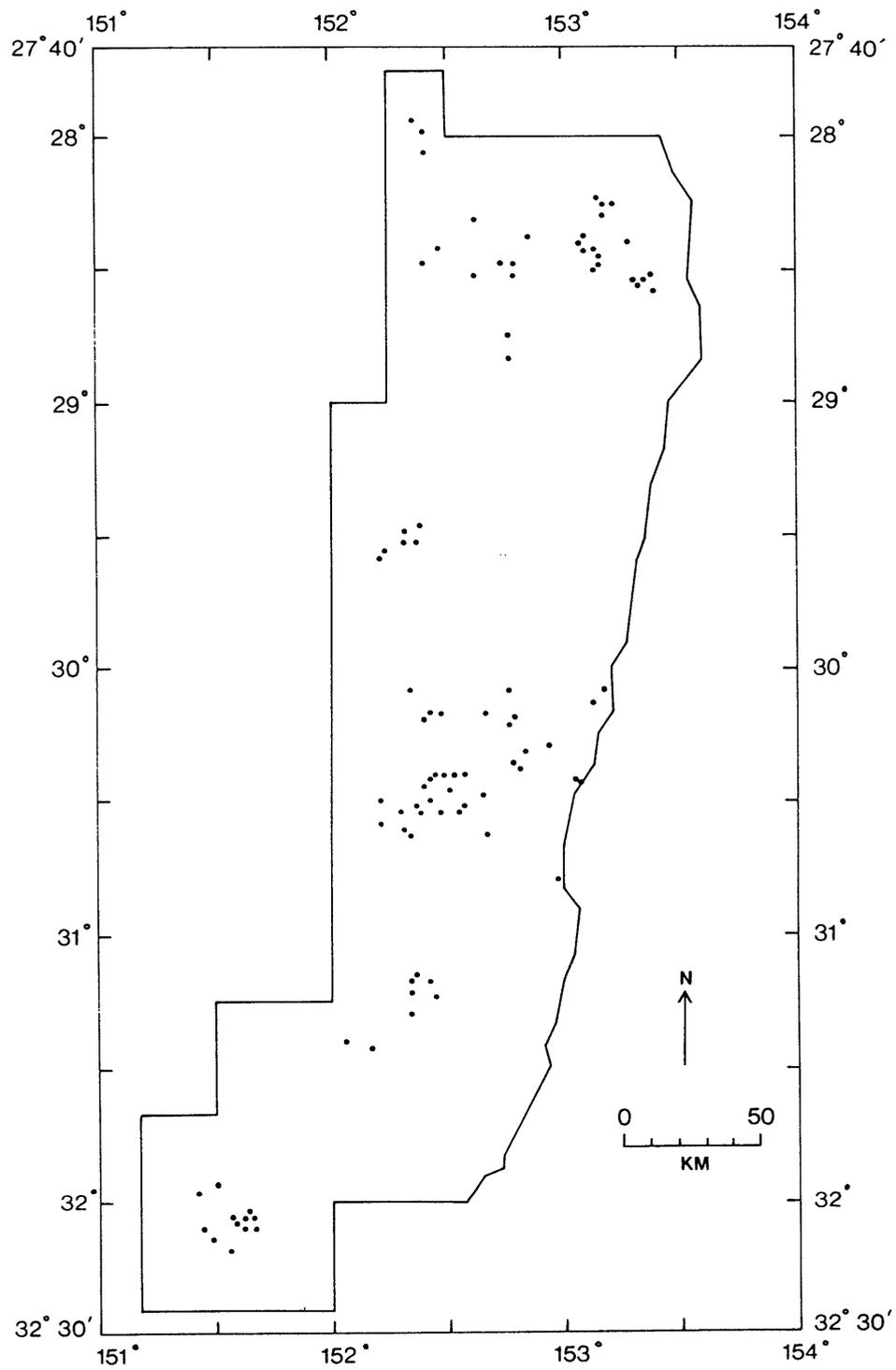


FIGURE 6.4. Distribution of surveyed grid points.

Series produced by the Queensland Department of Primary Industries (McDonald and Whiteman 1979).

5. Rainforest proximity. The distance from each point to the nearest patch of rainforest was rated on a 5-point scale: 0 = point located in rainforest; 1 = not in rainforest but less than 200 metres from nearest patch; 2 = 200 to 500m; 3 = 500 to 2,000m; 4 = greater than 2,000m. This information was obtained from the "New South Wales Rainforest Inventory, 1981" 1:25,000 maps produced by the Forestry Commission of N.S.W. (Pople and Cowley 1981), FORINS forest type maps, the Moreton Region Vegetation Map Series, and 1:25,000 forestry maps produced by the Queensland Department of Forestry. If a point was in cleared vegetation, rainforest proximity prior to clearing was estimated on the basis of nearby uncleared vegetation patterns.
6. Rainforest extent. The area of rainforest within a 4km radius circle centred at each point was estimated on a 5-point scale: 0 = no rainforest; 1 = 25% of vegetation within the circle was rainforest; 2 = 50%; 3 = 75%; 4 = 100%. If a point was in cleared vegetation, rainforest extent prior to clearing was estimated on the basis of nearby uncleared vegetation patterns.
7. Rainforest buffering. The degree of protection from fire afforded by surrounding rainforest was assessed using four lines, 2km in length, radiating out from each point (the lines were directed due north, south, east, and west). A count was made of the number of lines intercepted by rainforest (range 0 to 4). If a point was in cleared vegetation, rainforest buffering prior to clearing was estimated on the basis of nearby uncleared vegetation patterns.
8. Land tenure. Each point was classified into one of the following tenure classes:
  - (a) National Park or Nature Reserve other than those areas in Class (b).
  - (b) State Forest revoked for reservation as National Park or Nature Reserve as a result of the recent "Forestry Revocation and National Parks Reservation Act, 1983, No. 37" in New South Wales (Department of Environment and Planning 1983).
  - (c) State Forest Flora Reserves and Forest Preserves.
  - (d) State Forest and other Crown-timber land, except those areas in Class (c).
  - (e) Other, including freehold land, leasehold land, and vacant and reserved Crown land.

9. Subspecies. Each point was classified as falling within either the region occupied by the northern subspecies or the region occupied by the southern subspecies (see Chapter 5). The boundary between these two regions was defined as longitude 29°50' S situated approximately midway between the Gibraltar Range and New England-Dorrigo populations.
10. Detectability (recorded only for surveyed grid points). This was the average probability of detecting a male scrub-bird anywhere within 200m of a walked route, estimated from the logistic regression model developed in Chapter 3. Time of year and forest type were estimated from field notes and vegetation maps (see above). Weather variables were not recorded during most of the survey, and were therefore treated as constants (set at the mean values obtained during the intensive surveys at Wiangarie and Barrington Tops described in Chapter 3).

The first step of the analysis involved analyzing and modelling the relationship between scrub-bird density and the environmental factors described above. The basic estimator of density used (or assumed) in the analysis was:

$$\text{Density of scrub-bird territories} = \frac{N_t}{N_s \times A_s \times \bar{P}}$$

where  $N_t$  = number of territories detected (i.e. number of scrub-bird points).

$N_s$  = number of surveyed grid points.

$A_s$  = area represented by each surveyed grid point. (this is a constant determined by the spacing of points; for a discussion of the principles of this aspect of grid sampling see Hoschke and Squire 1976).

$\bar{P}$  = probability of detection averaged over all surveyed grid points.

Due to computational limitations, the statistical technique used to analyze the significance of relationships between scrub-bird density and environmental factors differed from that used to model these relationships. The former was accomplished using multiple linear regression analysis. Surveyed grid points and scrub-bird points were used in the analysis giving a total sample size of 196 points. The

dependent variable was coded as 0 for surveyed grid points and 1 for scrub-bird points. The analysis was therefore equivalent to a two-group discriminant function analysis (see Cavallaro *et al.* 1981). The regression approach was used in favour of a discriminant analysis to allow flexibility in the stepwise handling of dummy variables. The analysis was conducted using the New Regression program of the SPSS Statistical Package (Hull and Nie 1981). To adjust for variation in detectability the data from surveyed grid points were weighted as follows:

$$\text{Case weight} = \frac{P}{\bar{P}}$$

where P = the estimated probability of detection associated with a particular surveyed grid point.

$\bar{P}$  = average probability of detection for all surveyed grid points.

Weighting of points was achieved using the SPSS "case weight" facility (Nie *et al.* 1975). By weighting points in the above manner, grid points sampled under conditions of high detectability were given more weight than points sampled under conditions of low detectability, without changing the total sample size or the degrees of freedom for significance tests. The null hypothesis tested by the regression analysis was that the sample of scrub-bird points did not differ significantly from the weighted sample of surveyed grid points, in terms of any of the independent environmental variables. The analysis therefore essentially tested the relationships between scrub-bird density and the independent variables. The independent variables considered in the analysis were altitude, average annual rainfall, average raindays, rainforest proximity, rainforest extent, rainforest buffering, land tenure, and subspecies. All of the independent variables except for altitude, annual rainfall, and number of raindays, were treated as categorical variables and were handled by conversion to dummy variables (see Nie *et al.* 1975). Preliminary analyses were made to check for nonlinearity and for interactions between the independent variables. In the final analysis a backward elimination procedure was used to remove variables that did not make a significant contribution ( $p < 0.05$ ) over and above that of the other variables in the equation (see Hull and Nie 1981). Variables remaining after backward elimination were included in the model of scrub-bird density described below.

A logistic regression model (Fienberg 1980; Engelman 1981) was used to describe variation in scrub-bird density in terms of environmental factors. The model was fitted by the maximum likelihood method using the BMDPLR program (Engelman 1981). The dependent variable of the logistic regression was the proportion of all points (i.e. scrub-bird points and surveyed grid points combined) that were scrub-bird points. Because the analysis could only handle integer case weights, the weights described above were multiplied by 20 and rounded off to the nearest integer (all scrub-bird points were assigned an unweighted value of 20). The form of the logistic regression equation was:

$$Y = \frac{e^x}{1 + e^x}$$

where  $Y$  = the proportion of points that were scrub-bird points.

$x$  = a multiple regression equation of the usual form (see Chapter 3).

Values of  $Y$  were transformed to predicted territory densities in the following manner:

$$\text{Density of scrub-bird territories} = \frac{Y}{(1-Y) \times A_s \times \bar{P}}$$

where  $A_s$  = area represented by each surveyed grid point (a constant)

$\bar{P}$  = probability of detection averaged over all surveyed grid points (a constant).

Estimates of population size were obtained by applying the model to data obtained at the coarse grid points. The number of territories within a specified area enclosing  $n$  coarse grid points was estimated as:

$$\text{Number of territories} = \Sigma(D_i \times A_c)$$

where  $D_i$  = estimated density of territories at coarse grid point  $i$ .

$A_c$  = area represented by each coarse grid point (a constant).

Predicted territory densities at the coarse grid points were also used to plot maps displaying contours of scrub-bird density. These maps were prepared using the MAP-79 computer mapping system (Balía 1982) and were plotted on a Zeta 3600 drum plotter.

### 6.3. RESULTS AND DISCUSSION

#### 6.3.1. PRESENT DISTRIBUTION AND ABUNDANCE

Results of the multiple regression analysis of scrub-bird density in relation to environmental and other factors are summarized in Table 6.1. Four variables were retained in the regression equation following backward elimination of non-significant variables. These significant variables were altitude, average annual rainfall, rainforest proximity, and rainforest buffering. It should be noted that the correlation of each of these variables with scrub-bird density was significant even after controlling for the other variables. For example, scrub-bird density was significantly correlated with altitude after controlling for correlations with average annual rainfall, rainforest proximity, and rainforest buffering. The distribution of surveyed grid points and scrub-bird points in relation to each of the four significant variables is depicted in Figs.6.5 and 6.6. Conditions associated with a high density of territories were high altitude, high rainfall, close proximity to rainforest, and extensive buffering by surrounding rainforest. Variables that were not significantly correlated with scrub-bird density after controlling for the other variables were number of raindays, rainforest extent, land tenure, and subspecies. Preliminary analyses also failed to reveal any significant interaction between subspecies and the other independent variables. This suggests that the relationship between territory density and environmental factors does not differ significantly between the northern and southern subspecies. The reasons underlying the significance or nonsignificance of the independent variables will be discussed later in the chapter.

The four significant variables from the linear regression analysis were used as independent variables in a logistic regression model describing variation in scrub-bird density. The fitted model was as follows:

TABLE 6.1

Significant variables retained in the multiple regression relating territory density to environmental factors.

Variable	d.f.	F
1. Altitude	1 , 184	31.9***
2. Average annual rainfall	1 , 184	25.4***
3. Rainforest buffering (4 dummy variables)	4 , 184	7.8***
4. Rainforest proximity (4 dummy variables)	4 , 184	4.6**
Total Regression	10 , 184	23.5***

\*\*  $p < 0.01$

\*\*\*  $p < 0.001$

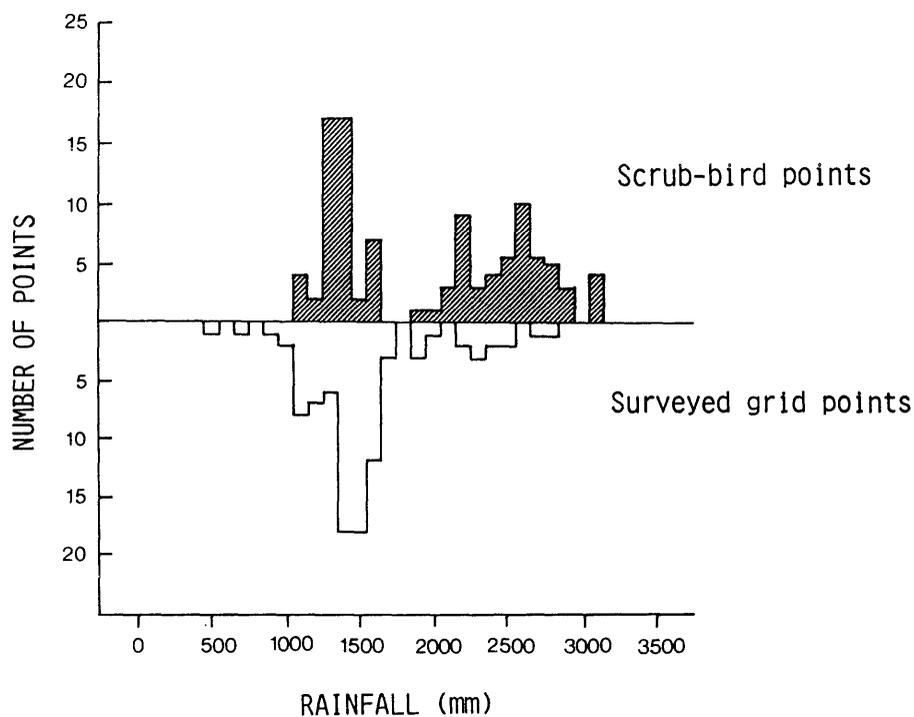
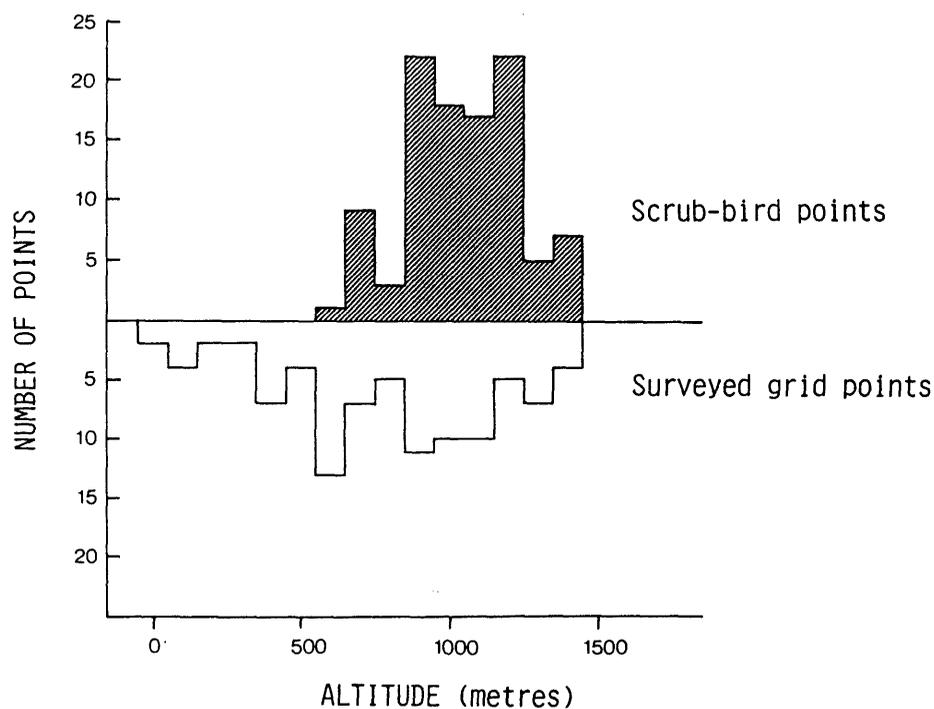


FIGURE 6.5. Distribution of scrub-bird points and surveyed grid points in relation to altitude and average rainfall. The surveyed grid points are weighted to compensate for variation in detectability (see text). No adjustment is made for other independent variables (i.e. the data depict univariate relationships).

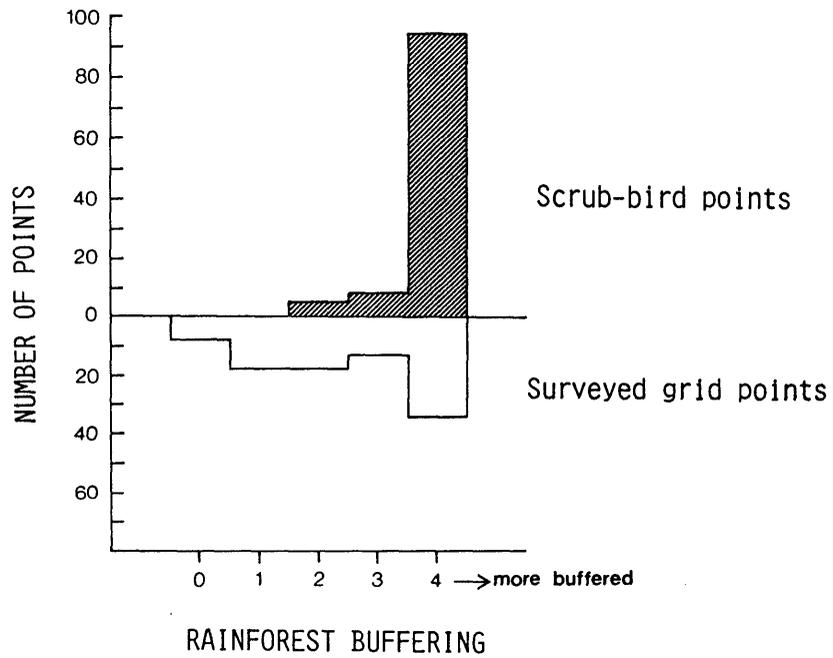
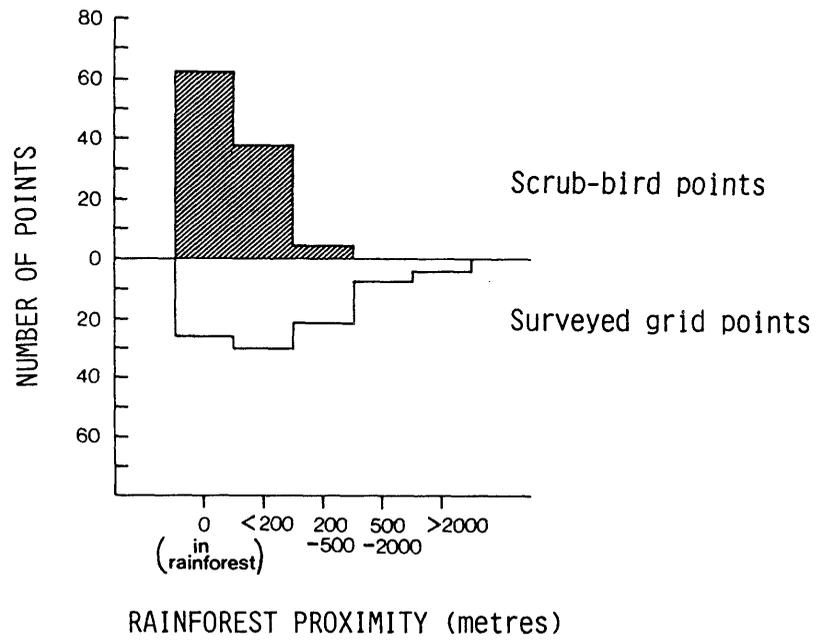


FIGURE 6.6. Distribution of scrub-bird points and surveyed grid points in relation to rainforest proximity and rainforest buffering. The surveyed grid points are weighted to compensate for variation in detectability (see text). No adjustment is made for other independent variables (i.e. the data depict univariate relationships).

$$\text{Scrub-bird density (territories per km}^2\text{)} = \frac{Y}{3.79 (1-Y)}$$

$$\text{where } Y = \frac{e^x}{1 + e^x}$$

$$\begin{aligned} \text{where } x = & -7.78 - 7.76 (\text{ALT1}) - 1.30 (\text{ALT2}) + \\ & 2.56 (\text{ALT3}) + 3.25 (\text{ALT4}) - 1.74 (\text{AV1}) - \\ & 0.54 (\text{AV2}) + 0.73 (\text{AV3}) + 0.82 (\text{AV4}) + \\ & 1.59 (\text{RP1}) + 3.01 (\text{RP2}) + 2.12 (\text{RP3}) - \\ & 3.78 (\text{RP4}) - 3.91 (\text{RB1}) + 1.66 (\text{RB2}) + \\ & 2.56 (\text{RB3}) + 4.20 (\text{RB4}) \end{aligned}$$

where ALT1, ALT2 etc. are dummy variables assigned a value of 1 if the following conditions are satisfied and 0 if the following conditions are not satisfied:

ALT1	:	Altitude <350m	
ALT2	:	Altitude 350 - 650m	
ALT3	:	Altitude 650 - 950m	
ALT4	:	Altitude >950m	
AV1	:	Average rainfall <1150mm	
AV2	:	Average rainfall 1150 - 1650mm	
AV3	:	Average rainfall 1650 - 2150mm	
AV4	:	Average rainfall >2150mm	
RP1	:	Rainforest proximity 0m (in rainforest)	
RP2	:	Rainforest proximity >0m and <200m	
RP3	:	Rainforest proximity 200m - 500m	
RP4	:	Rainforest proximity >500m	
RB1	:	Rainforest buffering 0 or 1	see methods
RB2	:	Rainforest buffering 2	section for
RB3	:	Rainforest buffering 3	definition
RB4	:	Rainforest buffering 4	of ratings

Predicted relationships between territory density and each environmental variable are presented in Figs.6.7 and 6.8. Predicted territory densities are tabulated in Appendix C.

Present population sizes were calculated by estimating the density of territories for each uncleared coarse grid point using the above model (assuming a density of zero for cleared points). The estimated total population sizes were :

Northern subspecies	:	731 territories
Southern subspecies	:	1,722 territories
Total for species	:	2,453 territories

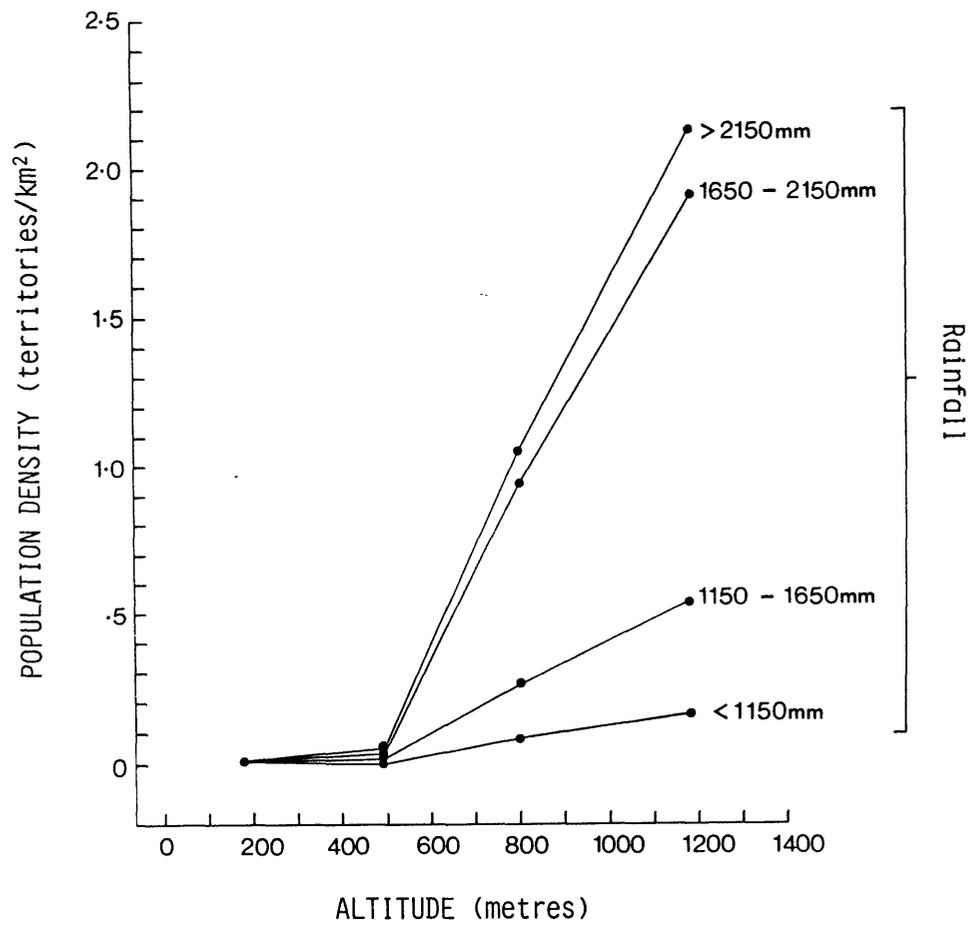


FIGURE 6.7. Population density in relation to altitude and rainfall, as predicted by logistic regression model. All estimates are for rainforest.

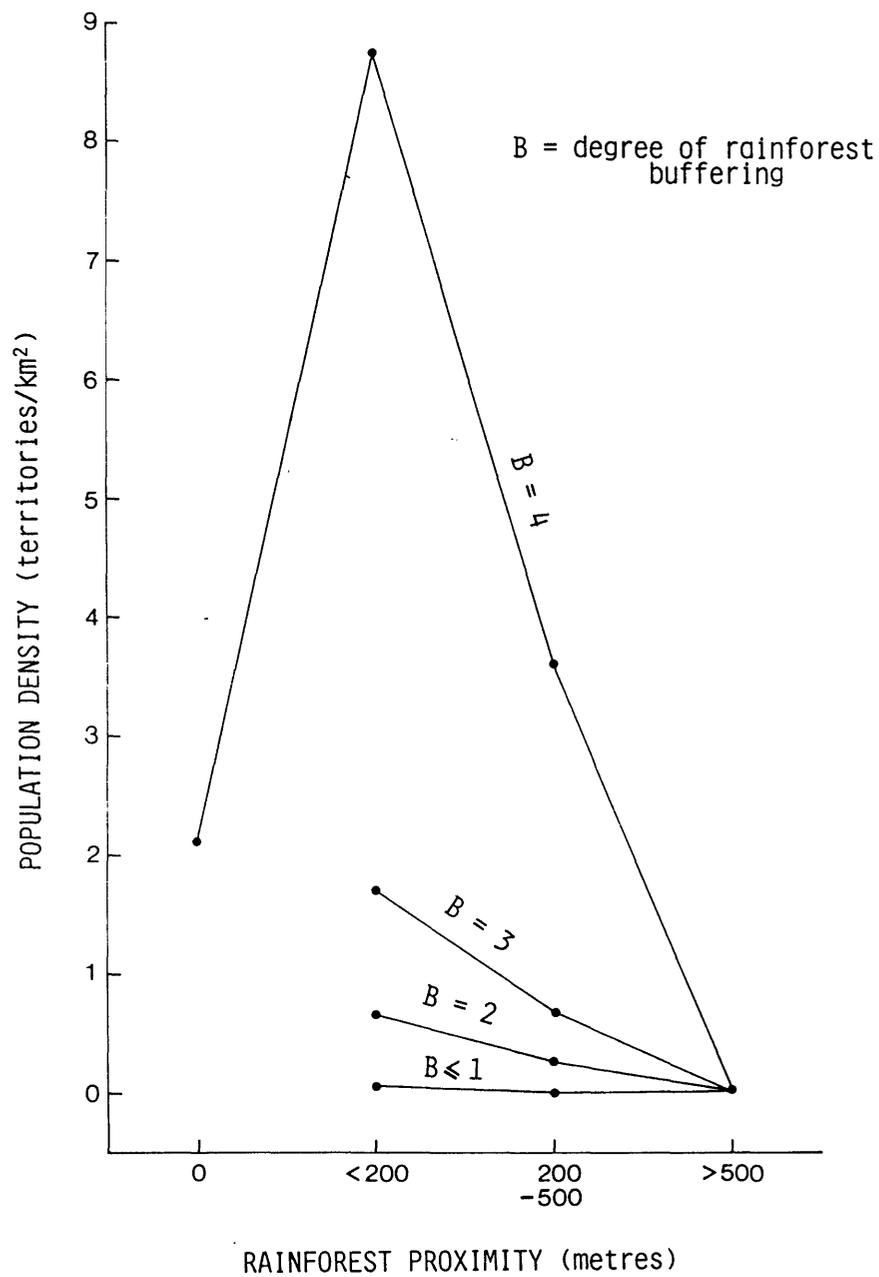


FIGURE 6.8. Population density in relation to rainforest proximity and rainforest buffering, as predicted by logistic regression model. Altitude is held constant at 1200m and rainfall is held constant at 2200mm.

Confidence limits could not be assigned to these estimates as the magnitude of error involved in each step of the calculations was unknown. These population sizes should therefore be regarded as "best available estimates" of unknown reliability.

The predicted 0.5 territories per km<sup>2</sup> contour is plotted in Fig.6.9. This provides an indication of the present distribution of the Rufous Scrub-bird. It should be kept in mind that the accuracy of this and other maps presented in this chapter is limited by the coarseness of the sampling grid involved and by the assumption that territories are evenly distributed throughout areas of similar habitat.

### 6.3.2 PAST CHANGES IN DISTRIBUTION AND ABUNDANCE

#### 6.3.2.1 Before European Settlement

Changes in the abundance of the Rufous Scrub-bird prior to European settlement most likely resulted from changes in three factors:

1. Rainfall. This would have influenced the availability of suitable habitat both directly (see above analysis), and indirectly through its effect on rainforest distribution.
2. Extent of rainforest (see above analysis).
3. Fire frequency. Fire would have indirectly influenced habitat availability by regulating the distribution of rainforest. In addition, fire probably had a direct influence on the suitability of habitat in areas of open sclerophyll forest. At present, scrub-bird territories in open forest are confined to areas more or less surrounded by patches of rainforest (see above analysis). The most reasonable explanation for this association is that the rainforest affords protection from fire. It seems likely that territories are restricted to areas of low fire frequency. Within the range of the Rufous Scrub-bird, a low fire frequency also promotes the development of wide ecotones between rainforest and open forest (Turner 1976; Webb and Tracey 1981; Smith and Guyer 1983). The "mixed forest" (open forest canopy with rainforest understorey; see Ashton 1981) occurring in these ecotones frequently supports habitat suitable for the Rufous Scrub-bird (see Chapter 4 and Appendix D). The influence of fire is discussed in greater detail later in this chapter.

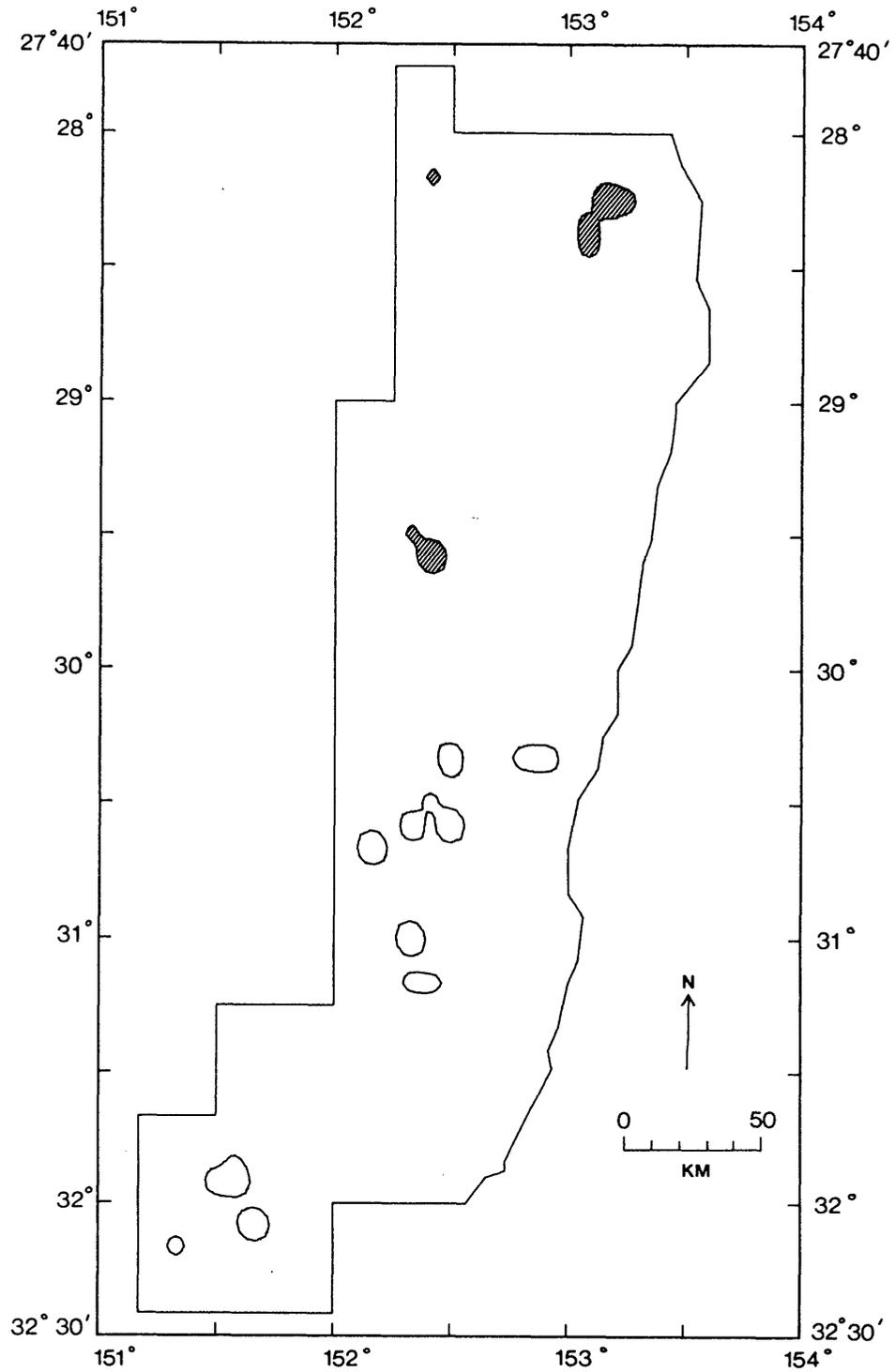


FIGURE 6.9. Present distribution of the Rufous Scrub-bird predicted by logistic regression model. The areas shown are those predicted to support a scrub-bird density of greater than 0.5 territories per  $\text{km}^2$ . Shaded areas represent the northern subspecies while unshaded areas represent the southern subspecies.

Changes in abundance of the Rufous Scrub-bird during the 100,000 years prior to European settlement were assessed on the basis of various reconstructions of rainfall, rainforest extent, and fire frequency (Kershaw 1975, 1978, 1981; Bowler *et al.* 1976; Walker 1978; Galloway and Kemp 1981; Singh *et al.* 1981; Singh 1982). Special emphasis was placed on the palynological data from Lynch's Crater (Kershaw 1981) and Lake George (Singh *et al.* 1981), because these are in closest proximity to the present range of the Rufous Scrub-bird. Lynch's Crater is located within rainforest on the Atherton Tableland (approx. 17°S 146°E). Lake George is located within open woodland near Canberra (approx. 35°S 149°E). General trends in rainfall, rainforest extent, and fire frequency are summarized diagrammatically in Fig.6.10. Inferred changes in scrub-bird abundance are also shown. Points of special interest are:

1. At the height of the last glacial (about 25,000 - 15,000 years BP.) the total population size of the Rufous Scrub-bird was probably much less than at the time of European settlement, and perhaps even less than at present. Rainfall was lower than at any other time in the last 50,000 years, and areas of rainforest were largely replaced by open vegetation (Kershaw 1981). The favourability of conditions for the Rufous Scrub-bird was probably further lowered through the use of fire by aboriginal man. It was probably during this period that the species was split into two geographical populations and commenced subspeciation (see Chapter 5).
2. The favourability of conditions increased after the last glacial, reaching a peak between 7,000 and 5,000 years BP. Scrub-bird abundance probably increased during this period.
3. Reductions in rainfall and rainforest over the last few thousand years suggest that the abundance of the Rufous Scrub-bird was probably declining gradually at the time of European settlement.

#### 6.3.2.2 After European Settlement

The logistic regression model of scrub-bird density was used to estimate total population sizes at the time of European settlement. The estimation was based on four assumptions:

1. That, prior to clearing, forest that is now cleared supported the same density of scrub-bird territories as equivalent uncleared forest.

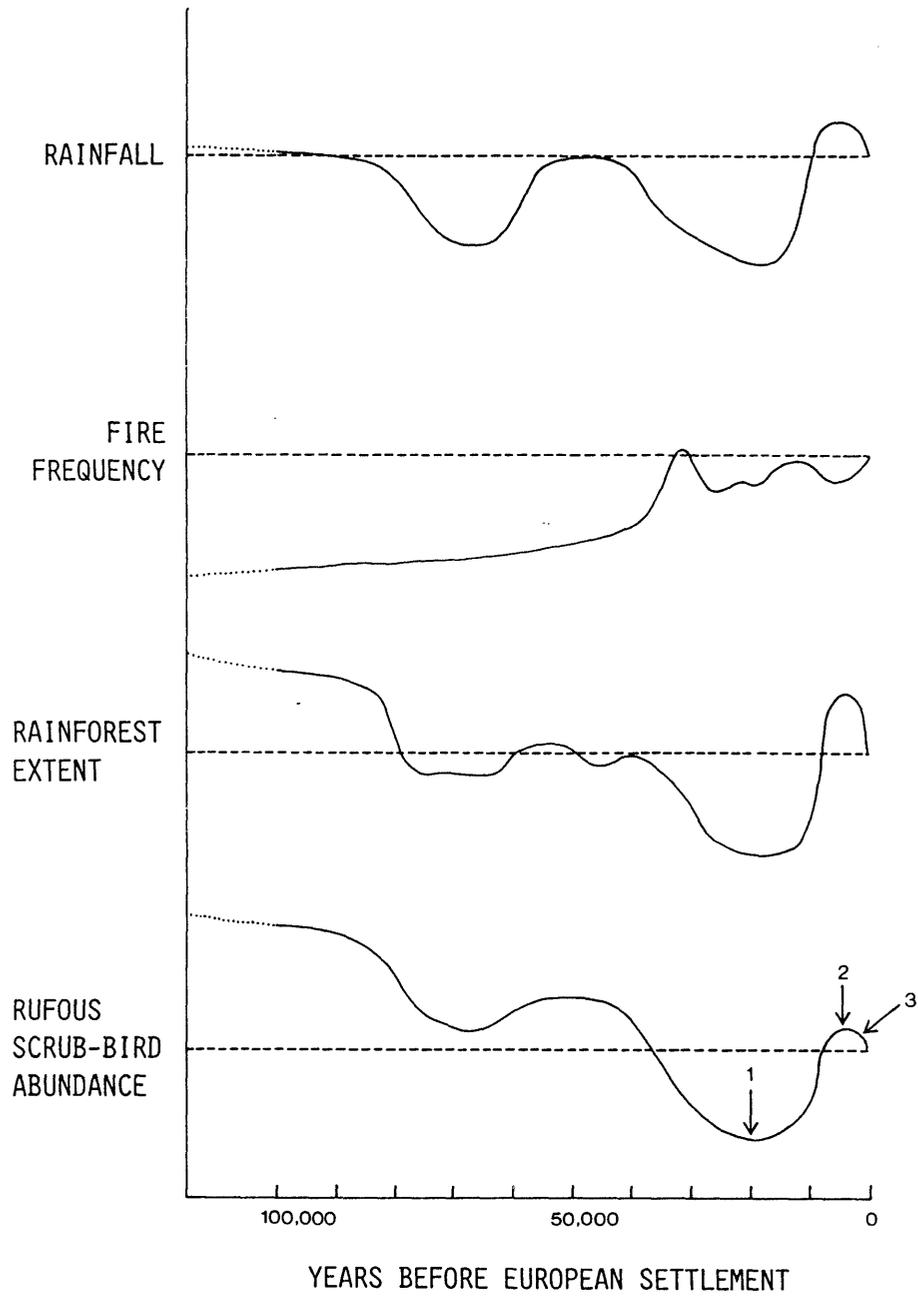


FIGURE 6.10. Diagrammatic reconstruction of changes in rainfall, fire frequency, rainforest extent, and Rufous Scrub-bird abundance during 100,000 years prior to European settlement.

2. That there was no relationship between scrub-bird density and altitude at the time of European settlement. The records of early collectors reviewed by Chisholm (1951) suggest that the density of territories in the "Big Scrub", an area of lowland rainforest virtually at sea-level, was at least as great as that presently found only at higher altitudes. Possible reasons for this recent altitudinal retreat are discussed later in the chapter.
3. That forest management practices within uncleared forest have had little influence on scrub-bird density. No significant relationship between territory density and land tenure was found in the multiple regression analysis described earlier (see Table 6.1). Of particular interest is the fact that territory density did not differ significantly between National Park and State Forest, after controlling for all other variables. The management of State Forests for timber production appears to have had little influence on scrub-bird density. This has probably resulted from a balancing of effects rather than from an absence of effect per se. For example, the beneficial influence of selective logging on habitat suitability in rainforest has probably been balanced by the detrimental influence of logging in open forest, and by the loss of existing territories during logging operations (see Chapter 4). The effects of forest management practices are discussed in greater detail later in the chapter.
4. That no other factors have influenced scrub-bird abundance since European settlement. The validity of this assumption is not known. If any such factors exist, they are most likely to have had a negative influence on abundance. The following estimates should therefore be regarded as conservative.

Population sizes at the time of European settlement were calculated by estimating the density of territories for both cleared (prior to clearing) and uncleared coarse grid points using the logistic regression model. In order to remove the influence of altitude from the calculations, each point was assigned a constant altitude of 1200 metres. The estimated total population sizes were:

Northern subspecies :	4,794 territories
Southern subspecies :	7,117 territories
Total for species :	11,911 territories

The predicted 0.5 territories per km<sup>2</sup> contour at the time of European settlement is plotted in Fig.6.11. The estimated changes in abundance since European settlement are summarized in Fig.6.12.

The present and past distributions of the Rufous Scrub-bird predicted by the logistic regression model (Figs.6.9 and 6.11) correspond closely with the species' recorded distribution depicted in Fig.6.13. Of particular interest is the fact that the model has correctly predicted scrub-bird presence and recent extinctions in areas that were not visited during the present study (i.e. data for these areas were not used to derive the model), but have been visited by reliable independent observers. A good example is the Lionsville-Washpool area (29°15' S, 152°25' E). Ramsay (1919) recorded the Rufous Scrub-bird here in 1918. Although the area was not visited as part of the present study, recent faunal surveys by other workers have failed to locate the species, suggesting that local extinction may have occurred (G. Holmes pers.comm.). The model predicted that scrub-birds would have been present in this area at the time of European settlement but were now likely to be extinct, probably as a result of altitudinal retreat (the area remains uncleared). It is also interesting to note that the patchiness of the recorded distribution of the species (Fig.6.13) is not simply an artefact of patchy observer effort. The model suggests that the distribution of the Rufous Scrub-bird has in reality been patchy, even at the time of European settlement (Figs.6.9 and 6.11).

### 6.3.3 FUTURE CHANGES IN DISTRIBUTION AND ABUNDANCE

It is very difficult to predict future changes in the abundance of the Rufous Scrub-bird. The simplest approach would be to extrapolate linearly from past trends in abundance (see Fig.6.12). This approach assumes that past trends have actually been linear and that the factors responsible for those trends will continue operating at unchanged levels causing a steady ongoing decline. Unfortunately neither of these assumptions are likely to be valid in the case of the Rufous Scrub-bird. Factors potentially complicating a simple linear extrapolation include the following:

1. The rate of clearing of scrub-bird habitat has slowed down over the last few decades. The logistic regression model of scrub-bird

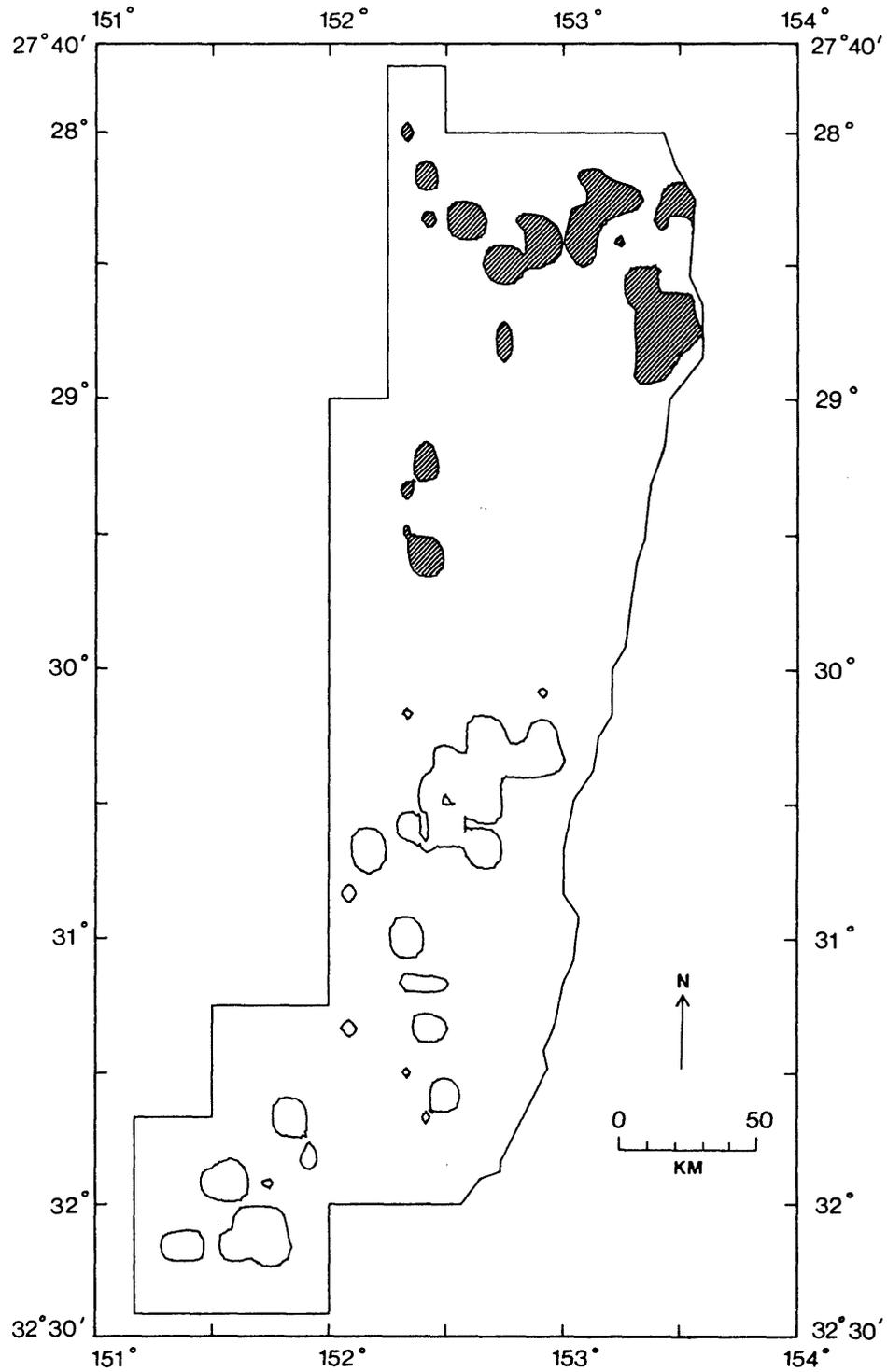


FIGURE 6.11. Distribution of the Rufous Scrub-bird at the time of European settlement, predicted by logistic regression model. The areas shown are those predicted to support a scrub-bird density of greater than 0.5 territories per  $\text{km}^2$ . Shaded areas represent the northern subspecies while unshaded areas represent the southern subspecies.

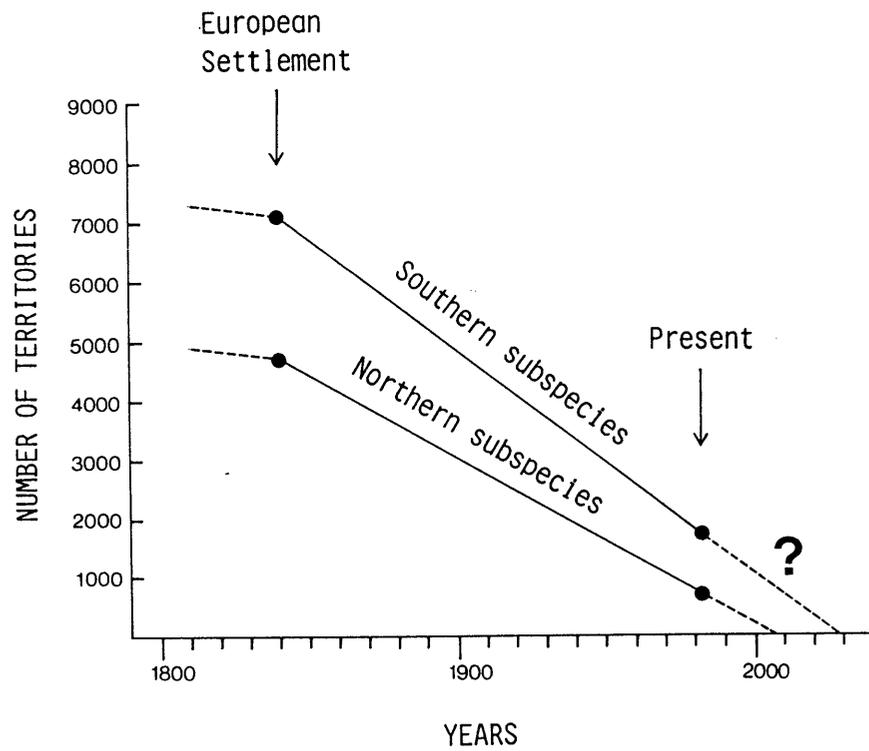


FIGURE 6.12. Total abundance of Rufous Scrub-bird territories at the time of European settlement and at present, as predicted by logistic regression model (see text for details).



density was used to estimate present numbers of territories occurring in different land tenure classes. These results are summarized in Table 6.2. Most territories are now either fully protected from clear-felling in National Parks and Nature Reserves (35.8%) or semi-protected in State Forests (54.3%).

2. Although forest management practices (i.e. selective logging, prescribed burning) appear to have had little net influence on scrub-bird abundance in the past, this could change if management practices alter or if present practices have long term effects not yet apparent. In the past there seems to have been a rough balance between the beneficial and detrimental effects of management practices. Changes in forest management policy could affect this balance. For example, the "rainforest policy" recently implemented in New South Wales (Dept. of Environment and Planning 1983) will reduce logging of rainforest while increasing logging of hardwood forest (i.e. open forest). In Chapter 4 it was shown that logging in these two forest types has different effects on the suitability of habitat for the Rufous Scrub-bird. The beneficial effects of selective logging in rainforest may in the future be outweighed by the detrimental effects of logging in open forest.

The potential influence of fire management on the Rufous Scrub-bird seems to have been underestimated by previous authors (e.g. Smith 1977; King 1981). This is probably because the species has been regarded as occurring mostly in rainforest. However, the results presented in Table 6.2 suggest that about 66.3% of all Rufous Scrub-bird territories occur in open forest, Territories in open forest are mostly confined to localities buffered from fire by surrounding patches of rainforest (see Table 6.1 and Fig.6.8). Fire probably affects scrub-birds both directly by destroying the occupants of existing territories, and indirectly through its influence on habitat suitability. Both of these effects need to be considered in order to assess the overall influence of any particular fire regime. Destruction of existing territories will obviously be greater in a regime of high fire frequency (or intensity) compared to a regime of low fire frequency. The long-term effects of fire on habitat suitability are more difficult to ascertain. Research on the Noisy Scrub-bird in Western Australia has suggested that burning at intervals of less than 3 to 5 years may not allow regeneration of suitable habitat, whereas burning at intervals greater than 30 years may

TABLE 6.2

Estimated numbers of Rufous Scrub-bird territories occurring in different habitat types and land tenure classes. Estimates were derived using the logistic regression model described in the text.

## (a) Northern Subspecies

	Old National Park*	New National Park#	State Forest §	Other	Total
Rainforest	272	92	21	64	449 (61.4%)
Open Forest	83	3	194	2	282 (38.6%)
Total	355 (48.6%)	95 (13.0%)	215 (29.4%)	66 (9.0%)	731

## (b) Southern Subspecies

	Old National Park	New National Park	State Forest	Other	Total
Rainforest	70	207	79	21	377 (21.9%)
Open Forest	144	8	1038	155	1345 (78.1%)
Total	214 (12.4%)	215 (12.5%)	1117 (64.9%)	176 (10.2%)	1722

## (c) Total for Species

	Old National Park	New National Park	State Forest	Other	Total
Rainforest	342	299	100	85	826 (33.7%)
Open Forest	227	11	1232	157	1627 (66.3%)
Total	569 (23.2%)	310 (12.6%)	1332 (54.3%)	242 (9.9%)	2453

\* National Parks and Nature Reserves dedicated before "N.S.W. Government Rainforest Policy" decision (1982)

# National Parks and Nature Reserves dedicated in "N.S.W. Government Rainforest Policy" decision (1982)

§ Including Forest Preserves and Flora Reserves

allow successional changes to render areas unsuitable for that species (Smith 1977). The relationship between fire frequency and habitat suitability is probably similar for the Rufous Scrub-bird, although details concerning optimal burning intervals are yet to be established. At Barrington Tops, habitat suitability 10 months after prescribed burning was observed to be extremely low in terms of cover density, leaf litter volume, and humidity at ground level. At the other end of the successional scale, eucalypt forest adjacent to rainforest within the range of the Rufous Scrub-bird tends to develop into rainforest if fire is excluded for a long period (Turner 1976; Webb and Tracey 1981; Smith and Guyer 1983). Habitat suitability probably declines during the later stages of this transition due to a reduction in ground cover density. The suitability of habitat apparently reaches a peak at an intermediate seral stage, known as "mixed forest" (Ashton 1981), consisting of a eucalypt open forest canopy with a rainforest understorey. Mixed forest at the ecotone between rainforest and open forest supports a higher density of the Rufous Scrub-bird than either pure rainforest or pure open forest (see Chapter 4, Appendix D, and Fig.6.8). Fire regimes promoting the development of a sharp boundary between rainforest and open forest, with little intervening mixed forest, are likely to have a detrimental influence on the species. The optimal fire regime for ensuring long term habitat suitability would be one that maintained maximum availability of mixed forest. Detailed information concerning the influence of fire management on vegetation in areas occupied by the Rufous Scrub-bird is not yet available (see Turner 1976; Smith and Guyer 1983). Further research is needed to determine the long term influence of fire frequency and intensity on habitat suitability.

3. The "altitudinal retreat" described earlier in this chapter has been a major cause of population decline in the Rufous Scrub-bird. This is illustrated by the following estimates of total population size for the species obtained using the logistic regression model (see also Fig.6.14):

- (a) At the time of European settlement : 11,911 territories
- (b) After habitat clearance but  
    assuming no altitudinal retreat : 9,535 territories
- (c) After both habitat clearance and  
    altitudinal retreat : 2,453 territories

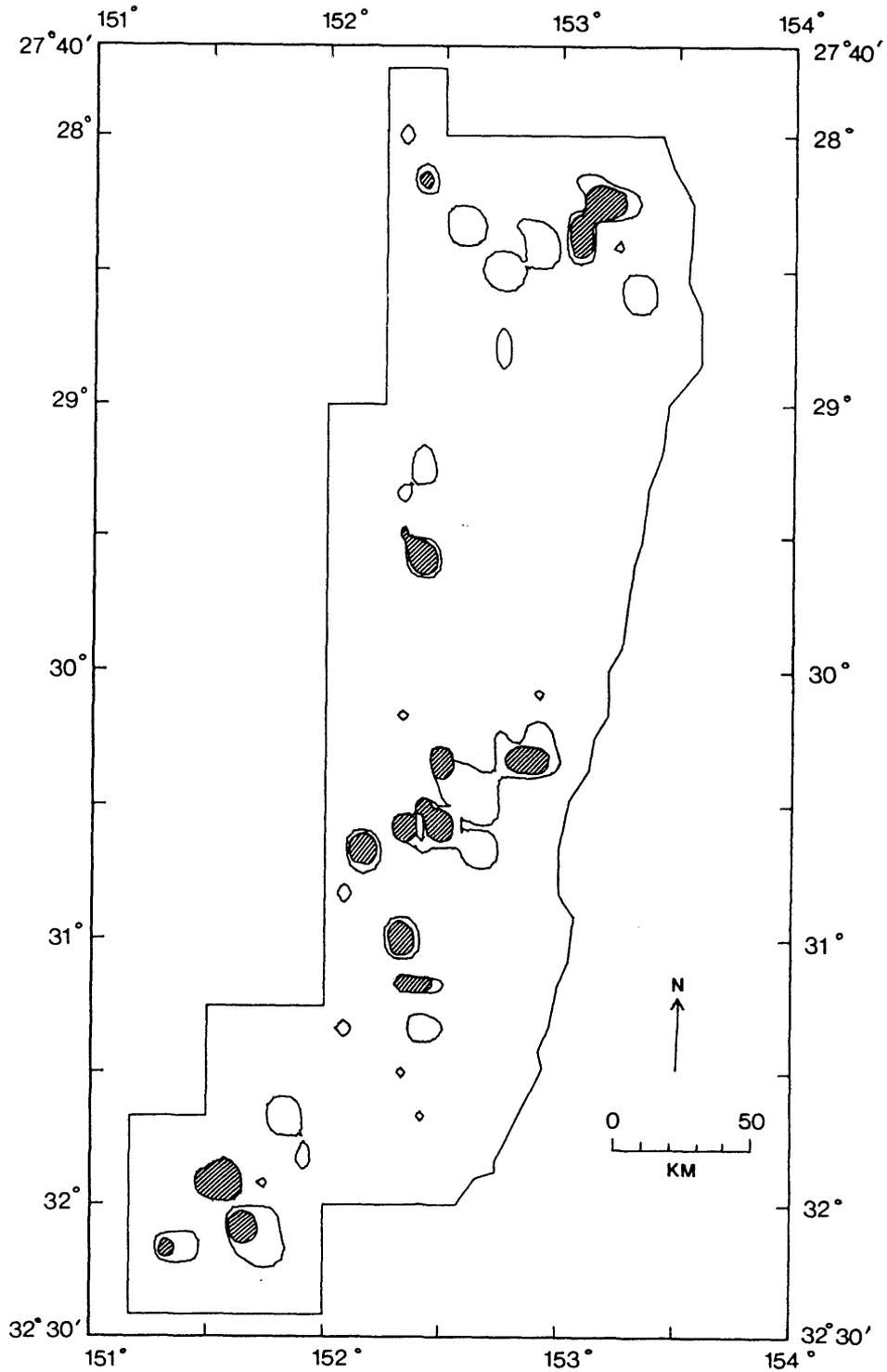


FIGURE 6.14. Present distribution of the Rufous Scrub-bird (shaded areas) compared to expected distribution assuming habitat clearance but no "altitudinal retreat". The areas shown are those predicted by the logistic regression model to support a scrub-bird density of greater than 0.5 territories per  $\text{km}^2$ .

Will this altitudinal retreat continue or will the lower altitudinal limit of the species remain at its present position? The answer to this question will depend largely on the cause of the retreat which is at present unknown. It seems unlikely that habitat clearance has been a direct cause. The regression analysis presented earlier in this chapter (see Table 6.1) suggests that territory density is significantly correlated with altitude even after controlling for other associated variables (i.e. rainfall, rainforest proximity, rainforest buffering). In other words, the Rufous Scrub-bird is absent at lower altitudes even in areas that may otherwise be suitable for the species. Good examples of this phenomenon occur in Lamington National Park, Wiangarie State Forest, and New England National Park. Although reserves support substantial areas of apparently suitable habitat at low altitudes (<600m), surrounded by large areas of uncleared forest, scrub-birds are found only at higher altitudes. Other possible causes of the altitudinal retreat include introduced predators and introduced disease. The former seems improbable because the three most likely predators - Feral Cat *Felis catus*, Fox *Vulpes vulpes*, and Black Rat *Rattus rattus* - all occur at both high altitudes and low altitudes and two (Fox and Black Rat) do not penetrate far into densely forested areas (Watts 1983; Coman 1983; Jones 1983). The best documented case of introduced disease affecting the altitudinal distribution of birds is that of mosquito-borne diseases in Hawaii, especially on the island of Maui (Warner 1968; Halliday 1978; King 1981). Following the introduction of the Night Mosquito in 1826 several birds became extinct while others became confined to altitudes above about 600m where the mosquito could not survive. If the altitudinal retreat of the Rufous Scrub-bird were caused by an introduced disease we would expect other species to display a similar phenomenon. It seems unlikely that such a disease would be specific to one species alone. There is no evidence of altitudinal retreat in any other species within the range of the Rufous Scrub-bird, suggesting that introduced disease is an improbable cause. Further research is needed to determine whether the altitudinal retreat is continuing thereby confining the species to progressively higher altitudes, and if so, the cause of this retreat.

4. The abundance of the Rufous Scrub-bird may in the future be influenced by factors other than those discussed above. In particular, the species may face problems associated with the small size and isolation of populations. The distribution of the Rufous Scrub-bird was probably

already fragmented at the time of European settlement (see Fig.6.11). The effects of habitat clearance and altitudinal retreat have enhanced this fragmentation; populations are now even smaller and more isolated from one another (see Fig.6.9). Because of the species' apparently limited powers of dispersal and the unsuitability of intervening habitat, the local extinction of a population is unlikely to be rectified by immigration from other populations. Even if systematic pressures such as habitat clearance are removed, the total population size of the Rufous Scrub-bird may still continue to decline as a result of stochastic extinction of small isolated populations. Bunnell (1978) and Shaffer (1981) have reviewed the many causes of stochastic extinction in small populations. These include genetic factors (e.g. inbreeding), demographic factors (e.g. chance events in the survival and reproduction success of individuals), and environmental factors (e.g. fires, droughts etc.). It is difficult to predict the likelihood of stochastic extinction of present scrub-bird populations. Further data would be needed in order to utilize predictive models such as those discussed in the General Introduction of this thesis. The theory of island biogeography predicts that extinction is most likely to occur in the smallest and most isolated populations (MacArthur and Wilson 1967; Bunnell 1978; Wilcox 1980). Observations made during the present study suggest that some small isolated populations of the Rufous Scrub-bird may have already become extinct despite habitat reservation. Marshall (1935) recorded two male scrub-birds on Mount Warning ( $28^{\circ}24'S$ ,  $153^{\circ}17'E$ ) in 1933. These were located at an altitude of approximately 900m. Three visits to the general area described by Marshall during the present study failed to locate the species, although areas of suitable habitat were observed. Mount Warning is now reserved as a National Park but is more or less surrounded by cleared farmland. Four visits to the Cunningham's Gap-Mt. Mistake area ( $28^{\circ}2'S$ ,  $152^{\circ}22'E$ ) also failed to locate the Rufous Scrub-bird despite the existence of earlier records (Chisholm 1960; Storr 1973; M.T. Goddard pers. comm.), and the presence of suitable high altitude habitat. This area represents the northern extreme of the species' recorded distribution and is separated from the remainder of the Border Ranges complex by a series of low saddles supporting dry open forest.

The general conclusion drawn from the above discussion is that the status of the Rufous Scrub-bird must at this stage be regarded as uncertain. This uncertainty can only be reduced by future monitoring of changes in abundance. Detailed guidelines for population monitoring are presented in the following chapter.

## CHAPTER 7

GENERAL CONCLUSIONS AND RECOMMENDATIONS

1. Two races of the Rufous Scrub-bird (see Chapter 5) warrant at least informal recognition for the purposes of conservation. The northern race extends from the Border Ranges to Gibraltar Range, while the southern race extends from the Dorrigo area to Barrington Tops. Different conservation strategies may be required for the two races because the northern race occurs mostly in pure rainforest (61.4% of territories) whereas the southern race occurs mostly in open forest adjacent to rainforest (78.1% of territories). Further research is needed to determine whether the two races should be formally described as subspecies.

2. The abundance of the Rufous Scrub-bird has probably declined greatly since European settlement (see Chapter 6). The species' total population is at present estimated to be about 2,400 territories compared to an estimated 11,900 territories at the time of European settlement. Future changes in abundance are difficult to predict. Although approximately 90% of remaining scrub-bird habitat is now at least semi-protected from clearing, the decline in abundance may continue as a result of other factors. The three most potentially important factors are (a) the upward retreat of the species' lower altitudinal limit, shown in Chapter 6 to be independent of changes in habitat availability, (b) the long-term influence of forest management practices, especially in open forest habitat, and (c) stochastic extinction of small and isolated populations. Until the influence of these factors is revealed by future monitoring of changes in abundance (see below), the status of the Rufous Scrub-bird must be regarded as uncertain. Nevertheless, I recommend that the bird's listing in the ICBP Red Data Book (King 1981) should be changed from "rare" to "vulnerable". The vulnerable category is defined by the International Union for Conservation of Nature and Natural Resources (King 1981) as including:

"Taxa believed likely to move into the endangered category in the near future if the causal factors continue operating. Included are taxa of which most or all the populations are decreasing because of overexploitation, extensive destruction of habitat or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security is not yet assured; and taxa with populations that are still sizeable but are under threat from serious adverse factors throughout their range."

The Rufous Scrub-bird falls into this category as a taxon "with populations that have been seriously depleted and whose ultimate security is not yet assured".

3. Active management (e.g. captive breeding) is not required at present. Instead I recommend implementation of the following measures (described in detail below): (a) exclusion of disturbance from known territories, (b) research on the long-term effects of forest management practices, and most importantly (c) monitoring of changes in abundance.

4. Exclusion of disturbance from known territories. The immediate effects of fire and logging on territory occupants are likely to be deleterious, regardless of any long term influence that these factors may have on habitat suitability. The Forestry Commission of New South Wales has already introduced a policy excluding all known territories in State Forest from future logging (R.A. Curtin pers. comm.). In some areas, the Forestry Commission of N.S.W and the National Parks and Wildlife Service of N.S.W. have undertaken to also exclude fire from known territories (K. Carter pers. comm.; D. Hardman pers. comm.; G. Roberts pers. comm.). The Forestry Commission at present retains a "20 ha unlogged circle" (a radius of 250 metres) around each known territory. This policy should perhaps be reviewed in the light of the home range results presented in Chapter 4. These results suggest that, allowing for some error in the estimation of territory centres, the unlogged circle radius could be safely lowered to 200 metres thereby reducing the excluded area to about 13 ha. The effectiveness of the Forestry Commission's policy will be determined largely by the efficiency with which territories can be located. The efficiency of searching for territories could be maximized by adopting the following procedure:

(a) Establish a system of grid points over maps of the area of interest (e.g. a proposed logging area). Estimate territory density for each grid point using Appendix C and information derived from topographic maps, forest type maps, and aerial photographs (if reliable rainfall estimates are not available, this information can be derived from the model presented in Appendix B). Use grid point estimates to map areas of potentially high scrub-bird density. It should be noted that the density values tabulated in Appendix C are point estimates and can therefore be applied to a grid of any dimensions. This flexibility will allow grid spacing to be varied according to

availability of time and financial resources.

- (b) Search the mapped areas of potentially high scrub-bird density under conditions of high detectability, as determined from Appendix A. Searches should obviously be conducted by people familiar with scrub-bird vocalizations. Both the location of any detected males, and the distribution of suitable habitat (see Table 4.5) should be noted.
- (c) If time permits, subsequent visits should concentrate on areas of apparently suitable habitat in which birds were not detected during the first search, and on mapping additional locations for previously detected individuals, thereby allowing more accurate assessment of territory centres.

5. Research on the long term effects of forest management practices. Emphasis should be placed on researching the effects of different logging and fire regimes in open forest (at present supporting about 66% of all territories). The future influence of these factors in rainforest will be minor due to the New South Wales Government's recently introduced "rainforest policy" restricting future logging (Dept. of Environment and Planning 1983), and the low probability of fire entering rainforest habitat (Catling and Newsome 1981; Webb 1981; Smith and Guyer 1983). In order to determine the overall influence of forest management practices, the research in open forest needs to consider both immediate effects on the occupants of existing territories and long term effects on habitat suitability. The habitat results presented in Chapter 4 can be used as a basis for assessing changes in habitat suitability.

6. Monitoring of changes in abundance. This should be given higher priority than the other recommendations presented above. Population monitoring will provide vital information on changes in abundance, thereby enabling accurate assessment of status. The frequency and intensity of future surveys will obviously be governed by the availability of resources. The guidelines presented below are therefore intended to allow a considerable degree of flexibility in survey design. It is recommended that an estimate of total population size should be obtained not less than once every 10 years. The accuracy and precision of these estimates can be maximized by adopting the following procedure:

- (a) Establish a system of grid points over the entire range of the Rufous Scrub-bird. While the 5' coarse grid system described in Chapter 6 can be used as a guide, a finer grid (2' or even 1') would

be desirable. Predict territory density for each grid point using Appendix C and information derived from topographic maps, forest type maps, and aerial photographs (estimates of average annual rainfall can be derived from the model presented in Appendix B). Points falling in cleared vegetation are assigned a density of zero. Use predicted grid point densities to map areas potentially supporting the Rufous Scrub-bird. The 0.5 territories per km<sup>2</sup> contour employed in Chapter 6 could be used to delimit such areas. These mapped areas will make up the "total survey area".

- (b) Randomly select sections (e.g. 3km) of road, fire trail, or walking trail located within the total survey area to be used as transects. This could perhaps be achieved using a sample of points distributed randomly throughout the area. The nearest section of trail to each point could be selected as a transect. The number of transect sections required to achieve a specified precision for the total estimate should be assessed from the size of the total survey area, expected average detectability associated with each transect (Appendix A), and the rough preliminary estimates of total population size derived in Chapter 6 (a method for calculating the precision of abundance estimates is presented in Chapter 3).
- (c) Survey each selected transect section at a walking speed of approximately 2.5km per hour, counting all singing males heard within 100 metres either side of the transect. In order to maximize the accuracy and precision of estimates, the survey should be conducted by people highly familiar with scrub-bird vocalizations, and preferably under conditions of high detectability (Appendix A). Time of year, weather, and forest type should be recorded to allow probabilities of detection to be estimated from Appendix A.
- (d) Total population size can be estimated as follows:

$$\text{Total number of territories} = \frac{n A_t}{\bar{P} A_s}$$

where  $n$  = the total number of singing males counted during the survey.

$\bar{P}$  = the probability of detecting a territorial male anywhere within 100m either side of the transect, averaged over all transect sections (see Appendix A).

$A_t$  = total survey area (in units of horizontal map area).

$A_s$  = sampled area; calculated as combined length of transect sections (in units of horizontal map length) multiplied by transect width (i.e. 200m). This serves as an adequate estimate of sampled area even if transects are not straight.

A method for calculating approximate confidence limits for estimates of abundance is described in Chapter 3.

- (e) Recording of supplementary information during surveys will facilitate identification of the causes underlying any detected trends in abundance. The following should be recorded for each transect section: habitat suitability (see Table 4.5), altitude, and location in relation to mapped areas potentially supporting the Rufous Scrub-bird (see (a) above). Analysis of territory density in relation to these factors will help to determine the influence of detrimental processes such as "altitudinal retreat" and stochastic extinction of small isolated populations (see Chapter 6).

A practical example of the planning, implementation, and interpretation of a small scale Rufous Scrub-bird survey is included in Appendix D (the report of a survey along the northwestern boundary of New England National Park contracted by the National Parks and Wildlife Service of New South Wales).

The recommendations presented above will be described in greater detail in a separate report to be submitted to the National Parks and Wildlife Service of New South Wales.