Intraspecific Variation in the Acoustic Signals of Birds and One Species of Frog: Implications for the Acoustic Identification of Individuals

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy from the University of Adelaide

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BSc (Hons)

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University library, being available for loan and photocopying.

Daniel James Rogers, 1 February 2002

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This thesis is dedicted to the memory of my grandfather, Jim Hume, who passed away during its creation.

Abstract

The ability to identify individual animals within species is now an important tool in ecological research, and can assist in obtaining knowledge regarding the demographics, movement patterns and behavioural ecology of animal populations. Current techniques used to identify individual animals generally require each individual to be captured and artificially marked in some manner. These have the potential to significantly influence the behaviour of target individuals. Such impacts are important, both from the perspective of the welfare of the animals, and for the validity of the data being collected.

While the effects of capture and marking can be determined experimentally, non-invasive alternatives for identification exist. These alternatives are largely based upon intraspecific variation in some feature. For example, phenotypic variation in some features are often used to discriminate between individuals in a non-invasive manner, such as variation in the patterns of tigers and giraffe. Many species of animal use acoustic cues to discriminate between and recognise conspecific individuals, such as mates, territorial neighbours or kin. Such systems of recognition require that the acoustic signals of such species possess individually-distinct acoustic cues. These cues have been used by a number of investigators to demonstrate the potential for identifying and discriminating between individuals of certain species acoustically. The broad objective of this thesis is to investigate patterns of intraspecific variation in the acoustic signals of a range of vocal animal species, with the ultimate objective of demonstrating vocal individuality in these species, in a manner that allows for the practical identification of individuals acoustically.

The results of vocal individuality presented in this thesis focus on two methods of quantitative song analysis, discriminant function analysis and cross-correlation analysis. The majority of studies to date concerned with the acoustic identification of individuals have presented results using discriminant function analysis, as this multivariate technique is well suited to investigating patterns of variation both within and between individuals. However, the principle disadvantage of discriminant function analysis is its inability to identify new individuals, and therefore its limited application for use in surveys of animal populations. Cross-correlation analysis, however, allows for the comparison of as little as two acoustic recordings, and is therefore potentially more applicable as a survey tool, provided that vocal individuality can be demonstrated with this method.

While this thesis aims to demonstrate vocal individuality in a broad range of vocal species, the results focus on two species: Bibron's Toadlet *Pseudophryne bibronii* and Rufous Bristlebird *Dasyornis broadbenti*. *Pseudophryne bibronii* is a small Australian anuran species, in which the male commonly uses two distinct call types. Calls of *P. bibronii* were collected from 50 different individuals over three breeding seasons. Comprehensive analyses of both call types suggest that, across the three breeding seasons, the calls of *P. bibronii* varied as much intra-individually as between individuals, largely as a result of intra-individual variation between different nights. Although vocal individuality was demonstrated within the timeframe of single nights, such a system of acoustic identification of individuals does not provide any extra benefit from the current methods used to survey anuran populations. These attempts to demonstrate vocal individuality in *P. bibronii* are, however, the first for an anuran species, and the potential for vocal individuality still exists in other anurans, such as those for which individual acoustic recognition has been demonstrated.

Intraspecific variation in the songs of *Dasyornis broadbenti* were analysed across a variety of both temporal and geographic scales. Studies of small focal groups of individuals demonstrated that both males and females possessed repertoires of multiple distinct song types, a proportion of which were common with the song types of their immediate territorial neighbours. The system of acoustic identification of individuals demonstrated for *D. broadbenti* is based upon this phenomenon of shared song types, with different individuals being compared initially through the analysis and comparison of these shared song types. When the shared songs of different individuals were compared using both discriminant function analysis and cross-correlation analysis, high levels of vocal individuality were demonstrated for the songs of both sexes, amongst the focal group of 12 individual bristlebirds. However, such vocal individuality was not found between syllable types that were classified as belonging to the same type of syllable qualitatively. Vocal individuality in *D. broadbenti* was therefore limited to the comparison of common song types. Although these common song types were more likely to be encountered between territorial neighbours, common song types were also encountered between individuals whose territories were separated by distances of up to 37.7km within continuous populations. Although comparing common song types to identify individuals acoustically limits the effectiveness of this method in *D. broadbenti*, the prevalence of these common song types, coupled with high levels of identification accuracy, still make acoustic identification of individuals in this species a potentially viable method.

In addition to investigating patterns of intraspecific variation in the songs of *D. broadbenti* within continuous populations, patterns of song variation between isolated populations were also investigated. As the remaining populations of *D. broadbenti* have become fragmented through habitat clearance, the potential exists for the songs of these populations to diverge at rates that are greater than would be expected by the distances that separate them. Analyses of the songs collected from seven isolated populations suggest that the songs of different isolated populations differ from one another more than the songs of different individuals within continuous populations, although such patterns of song variation may have simply resulted from the distance that separated these populations, rather than isolation *per se*. Furthermore, song analyses support recent revisions of the distribution of the two extant subspecies of *Dasyornis broadbenti*, with songs collected from the two subspecies differing significantly in the syllabic structure of two song components, and also differing in temporal and spectral structure. Such analyses, therefore, did not provide conclusive evidence that isolation of bird populations through habitat clearance can influence patterns of song divergence, although this study did demonstrate how the collection of songs and other behavioural information can be useful in subspecific taxonomic investigations.

In order to demonstrate the extensive nature of vocal individuality amongst avian species, investigations of intraspecific song variation were made for three species in addition to *D. broadbenti*. These three species were Willie Wagtail *Rhipidura leucophrys*, South-eastern Red-tailed Black Cockatoo *Calyptorhyncus banksii graptogyne* and Sacred Kingfisher *Todiramphus sanctus*. *Calyptorhyncus banksii graptogyne* and *T. sanctus* possess a small number of distinct call types that are universal to all individuals in a similar manner to *P. bibronii*, and patterns of vocal individuality were investigated by comparing these common call types between individuals. Call individuality was demonstrated for both of these taxa, although the number of individuals for which data were presented in these studies was limited to a few individuals; five males in the case of *C. b. graptogyne*, and three in the case of *T. sanctus*. *Rhipidura leucophrys* presents the results of tests for vocal individuality in a species with song repertoires, in addition to *D. broadbenti*. Patterns of song variation for *R. leucophrys*, however, were slightly different to those for *D. broadbenti*, with repertoire sizes ranging from two to six distinct song types per individual. Furthermore, rates of song sharing between individuals were found to be relatively low compared to *D. broadbenti*. In addition, individual Willie Wagtails cycle through the song types in their repertoire in relatively quick succession, and complete repertoires can thus be obtained during single recording sessions. In addition, in cases where common song types were encountered, quantitative comparisons of these songs again demonstrated vocal individuality for this species. For this species, therefore,

acoustic identification of individuals is possible firstly through the visual identification of unique song types, and, in cases where song types are shared by more than one individual, the quantitative comparison of these shared songs.

Although vocal individuality was demonstrated for *D. broadbenti*, the results of cross-correlation analyses have the potential to be influenced by differences in recording conditions, rather than real variation in vocalisations. Experiments were conducted in order to determine the influence of environmental degradation of *D. broadbenti* songs on the accuracy of cross-correlation analyses used to correctly identify individuals acoustically. Synthetic songs were played from a loudspeaker that was placed at either ground level, or 2m height, and re-recorded from four distances away from the speaker, with the final distance being 100m away from the speaker. Both distance between source and receiver, and source height, significantly influenced song attenuation, measured as the sound pressure level of the received song. In addition, distance and height also influenced cross-correlation comparisons, both between undegraded songs and degraded songs, and between pairs of degraded songs recorded at different heights and distances. Such analyses suggested, however, that while the height of the source, and the distance between the source and the receiver both significantly influenced sound attenuation and perceived song structure, such degradation was unlikely to result in inaccurate identification of individuals when using cross-correlation analysis.

Vocal individuality, therefore, appears to be widespread, at least amongst avian species, and such individuality has the potential to be used to identify and monitor individuals acoustically, using cross-correlation analysis. However, pilot studies must be conducted for each species, both to determine the threshold values required for cross-correlation analysis, and to determine the singing behaviour of the species. The studies presented in this thesis highlight the need for these pilot studies, as the method used to identify individuals acoustically varied between the species for which data were presented. Nevertheless, the acoustic identification of individuals can be a potentially useful tool in the study of avian biology.

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Chapter 1 General Introduction

1.1 The Importance of Individual Identification to Biologists

Early works of zoological research provided a wealth of descriptive information about the natural history of animals, and are regarded as critical precursors to our current understanding of natural history. However, by the early 20th century, this “descriptive phase of natural history” (Delany 1978), based upon general and short-term descriptive observations, was becoming superceded by the more analytical and quantitative sciences of ecology and ethology. With the increasing complexity of these new sciences came a necessary requirement for accurate identification of individual animals within target populations, in order to answer the fundamental questions posed by these new sciences.

As a result, identification of individual animals is now used widely in ecological and behavioural research on animals. Accurate descriptions of ecological and behavioural processes depend upon identifying and monitoring individual animals through time. The ability to identify individual animals also improves the quality and validity of ecological data, and intensive studies based upon a number of identifiable individuals allow for the validity of results obtained from more extensive studies to be tested. Population surveys, especially of mobile species, suffer from the ambiguity of counting individuals more than once if the identity of these individuals is unknown; thus individual identification can strengthen the results of censuses (Baker 1998). The identification and monitoring of individuals can also be used to obtain information regarding the demography of animal populations, including longevity, survivorship, recruitment and densities (Sagar *et al.* 2000). In addition, behavioural information can be obtained regarding the origin, destination and route of animal migrations (Nicholls *et al.* 1995), as well as information regarding habitat use, home range and territory sizes, and patterns of dispersal (Mizutani and Jewell 1998). Identification of individuals in animal populations can also assist with a wide range of ethological studies, such as those regarding the nature of social and breeding systems (Miskelly 1999). The identification of animal individuals has also proven useful in the study and management of captive animals, with identification now a necessary requirement of zoo animal husbandry with the advent of breeding and animal exchange programs (Ashton 1978). However, captive breeding is certainly not the only field in which individual identification can play a role in conservation of biological diversity, with much of the data generated using individual identification in field studies being critical to the effective management of endangered species, and the successful execution of other biological conservation programs.

1.2 Current standard techniques used by biologists to identify individuals

The necessity for individual identification in many studies has resulted in the development of an enormous diversity of identification techniques that reflect the diversity of organisms for which identification techniques are required. The majority of such techniques involve artificially marking each individual in an individually-distinct manner that allow subsequent re-identification by researchers. While a large number of techniques exist that are species-specific, most of the standard identification techniques are generally used for the study of many different species within much broader taxonomic groupings.

1.2.1 Amphibians

The artificial marking of amphibians for individual identification presents a number of unique problems, as some features unique to anurans, such as a lack of taggable appendages, the mucous nature and frequent shedding of their skin, their powers of regeneration, and their relatively small size, mean that general marking techniques cannot be applied to this group (Nace 1982). As a result, many of the techniques used to identify individuals in other taxa are generally unsuitable for the identification of amphibian individuals. A number of techniques have thus been developed solely for the use of marking and identifying amphibians, although some techniques are equally useful for identifying reptile or mammal individuals.

Until recently, the most common technique used to discriminate between amphibian conspecifics was toe-clipping, which involves removing different combinations of toes from captured individuals. While the technique has the potential to identify a large number of individuals (up to 736; Donnelly *et al.* 1994b), ethical and welfare, as well as scientific considerations, have raised concerns about its use. Such concerns are warranted, with negative impacts of toe-clipping on survival having been demonstrated in at least one species of anuran (Clarke 1972), although data presented for non-anuran species do not generally demonstrate an effect (Fairley 1982, Korn 1987, Paulissen and Meyer 2000).

As a result of these reservations, alternative techniques have been developed which still aim to overcome the unique problems inherent in the artificial marking of amphibians for individual identification. Such techniques include freeze branding (Daugherty 1976, Bull *et al.* 1983), chemical branding (Thomas 1975), waistbanding (Rice and Taylor 1993), attachment of reflective tape (Robertson 1984b) and flourescent marking (Ireland 1991). However, most of these techniques still require some form of superficial damage to the animal, and they all require each animal to be captured and recaptured for identification. At this stage, no technique for marking and identifying anuran amphibians has yet become useful enough, such that its implementation is universal.

Many anuran species, however, possess natural skin markings that are individually-distinct, in a similar way to human fingerprints. Herpetologists have taken advantage of this skin pattern individuality as a method of identifying individual anurans that eliminates the need to artificially mark each individual (Hagstrom 1973, Loafman 1991, Doody 1995, Mitchell 2001). While the use of distinct skin patterns in identification is less invasive, and eliminates the associated effects of marking, the technique still requires the capture and recapture of each individual in a population for identification to take place.

1.2.2 Birds

Amongst ornithologists, the most common identification method involves the use of identification rings placed around the tarsus (Spencer 1978). There are a number of variations on this technique. Most tarsal bands used are metal, with some identifying information, such as a serial number, engraved upon the band. The use of numbered bands requires each individual to be captured in order to fit the band, and recaptured for subsequent identification. However, metal bands are often used in association with unique combinations of coloured plastic bands, such that identification can be made from a distance following the initial band installation. Although the use of colour bands still requires an initial capture of each individual, subsequent remote identifications eliminate the requirement of recapture.

While tarsal bands remain the most common technique used to identify avian individuals, a number of less common techniques have been developed, largely for species in which the use of tarsal bands is impractical. One of the more common of these alternative techniques is the patagial wing tag (Hester 1963), which is used in cases where it may be difficult or impossible to see the legs of birds, such as with raptors, waterfowl and many parrots (Bibby *et al.* 1993). The patagial tag consists of a plastic or metal tag pinned to the wing by a pin through the bird's patagium. Individuals are usually distinguished by the colour of the tag, although different letters, numbers and symbols are also used (Hester 1963). As with the use of coloured tarsal bands, the use of patagial tags requires a single, initial capture to fit the tag; subsequent identifications can be achieved visually.

Other less common techniques used specifically to mark individual birds include plumage dyes (Patterson 1978), neck collars, nasal saddles and leg flags (Bibby *et al.* 1993). These less common techniques tend to be developed with the specific requirements of target species in mind.

1.2.3 General techniques

As with the techniques described above, individual identification techniques in other groups of animals generally tend to work within the restrictions of the study species. Some techniques, such as toe-clipping have been applied successfully to a wider range of organisms, such as mammals (Twigg 1978) and reptiles (Swingland 1978), as well as amphibians (Donnelly *et al.* 1994b). Another extremely effective technique used in monitoring the movements of individual animals is radio-tracking, which involves attaching a radio transmitter to the study animal, and relocating the animal at regular intervals by receiving the radio frequency emitted by the attached transmitter (Kenward 1987). This technique has proven extremely valuable in studying many animal species, from a wide range of taxa (Marquiss and Newton 1981, Smith *et al.* 1993, Mizutani and Jewell 1998). The technique has also evolved somewhat to include remote tracking by satellites (Nicholls *et al.* 1995, Verlinden and Gavor 1998).

While the techniques used to identify individuals vary according to the study organisms, some generalities can be applied. Primarily, all of the identification techniques described thus far require at least the initial capture of each individual in the target population for successful identification to occur, while mark-recapture techniques require subsequent recaptures for ongoing identification. In addition to the requirement of capture, many of the techniques also require that each individual is marked artificially in some way that distinguishes it from conspecifics. The potential impacts that capture and artificial marking have on wild animals and populations is discussed below.

1.3 Potential and actual effects of standard marking techniques on the behaviour of target individuals

In order for a method of individual identification to be useful, a number of well-defined criteria must be met (Daugherty 1976, Delany 1978, Bibby *et al.* 1993). Identification techniques should primarily have no influence on the behaviour or ecology of the target animals. Techniques should, therefore, not increase the risk of predation, or have the potential to affect social or reproductive behaviours. Psychological stress should also be minimized, in order to reduce secondary stress-induced effects on survival or behaviour. In addition, the method employed to capture and mark each individual should not influence the likelihood of recapture. These factors are important not only in terms of the welfare of the individuals under scrutiny, but are also important if the identification technique has the potential to influence the ecological or behavioural characters which are being measured, thereby altering the results of the research. Individual identification techniques must also provide unequivocal identification of all individuals in the study population, for the duration of the study. This usually, but not always, requires the discriminating character to be permanent.

There is, however, considerable evidence that many standard identification techniques fail to meet at least one of these criteria. For example, many of the more commonly used techniques to individually identify birds have been shown to impact upon the behaviour and ecology of target individuals. Coloured tarsal bands, used extensively in behavioural studies of birds, have been shown in some cases to influence the social biology of target species. The best studied example of this phenomenon involves the zebra finch *Taeniopygia guttata*. The colour of the bands used in this species has been shown to influence mate choice behaviour, by altering the attractiveness of male birds to females. Female zebra finch, for example, preferentially mated with birds that were banded with pink or red bands, over those with green bands (Burley *et al.* 1982). Collins and ten Cate (1996) suggested that red coloured bands reinforced the visual cues naturally used by females in mate choice. Subsequent studies have also shown that females prefer males with symmetric colour bands (Waas and Wordsworth 1999), and young birds chose song tutors based upon band colour (Pearson *et al.* 1999). Such observations are not restricted to zebra finches, however, with colour bands also showing an influence on the behavioural ecology of bluethroat *Luscinia svecica* (Fiske and Amundsen 1997, Johnsen *et al.* 1997; but see Johnsen *et al.* 2000), and red-winged blackbirds *Agelaius phoeniceus* (Metz and Weatherhead 1991, but see Weatherhead *et al.* 1991).

Alternatives to tarsal banding have also received some attention. There is increasing evidence that patagial tags increase mortality of tagged individuals, when compared to individuals identified with tarsal bands alone (Howe 1980, Saunders 1988). Birds marked with patagial tags are thought to be at an increased risk of predation, due to an 'oddity factor' (Saunders 1988), where predators single out unusual individuals from a flock. Alternatively, patagial tags may influence the aerodynamics or mechanics of bird flight (Rowley and Saunders 1980). Some authors also suggest that if patagial tags are to be used in identification, individuals identified in this manner should not be used to estimate survival rates (Rowley and Saunders 1980, Saunders 1988), and such tags should not be used at all in the study of sensitive or endangered species unless there is a strong case for their use, and no alternatives exist (Saunders 1988).

While radio-tags and collars have proven extremely useful for monitoring individuals, a number of studies have shown that they may influence the behaviour and fitness of tagged animals. In a study of sharp-tailed grouse *Tympanuchus phasianellus* Marks and Marks (1987) found that, of 37 birds which had radio-collars attached, none were relocated the following year; this compared to four of nine birds for which colour-bands were used as the sole means of re-identification. The authors attributed this difference primarily to differences in rates of predation, as a result of the potentially increased conspicuousness of the grouse to avian predators, both visually and acoustically (Marks and Marks 1987). Similar effects on survival and reproduction have also been shown for spotted owls *Strix occidentalis* (Paton *et al.* 1991) and hen pheasants *Phasianus colchicus* (Warner and Etter 1983). However, other authors have found that the use of radio-tags bore no influence on the behaviour or ecology of tagged individuals (merlins (Sodhi *et al.* 1991); barn owls (Taylor 1991); guanaco (Bank *et al.* 2000); brush turkeys (Goth and Jones 2001); blue grouse (Hines and Zwickel 1985); wild turkey (Nenno and Healy 1979)). Even these authors make the point, however, that "the impact of radio transmitters on subjects should be studied to determine the reliability of the data collected and ensure the well-being of the study animals" (Sodhi, et al. 1991), and that such studies are lacking in most cases.

The examples above have shown that the method used to identify target individuals can potentially impact upon their survival and behaviour. However, the act of capture and handling may have as large an impact as the method of marking used. Mark-recapture studies of butterflies have shown that re-sighting rates of individuals caught and marked only once are significantly higher than those individuals recaptured a number of times (Morton 1984). Numerous studies of large mammals have shown an effect of handling (e.g. Byers 1997, but see Laurenson and Caro 1994, Ginsberg *et al.* 1995), which may be exacerbated by the necessary use of anaesthetic in potentially dangerous animals (Ramsay 1986, Alibhai *et al.* 2001).

1.4 Influence of recapture rate on the survival of small Australian passerines

In order to determine the impact of recapture rate on survival in small passerines, long-term banding data for Superb Fairy-Wrens *Malurus cyaneus* and Striated Thornbills *Acanthiza lineata*, collected between 1979 and 1999, were analysed in order to determine whether any correlative relationship existed between recapture rate and survival time. Analyses of these data revealed a relationship between the rate of recapture for each individual, and the estimated survival time of each individual, that suggested a negative impact of recapture on the survival of target individuals.

1.4.1 Methods

The banding data from which the following results were obtained were collected as part of a long-term banding study, aimed at investigating the population dynamics and seasonal movements of woodland bird species. The results presented here come from data collected at two sites, Cromer Conservation Park, and Hale Conservation Park, by David Paton, Tom Bradley and others. These two conservation parks are approximately 45km NE of Adelaide, with Cromer being located approximately 12km SSE of Hale. Both parks are dominated by Pink Gum *Eucalyptus fasciculosa* and Long-leaved Box *E. goniocalyx* woodland. Birds were captured using between 15 and 20 mist-nets each at Cromer and Hale, for 2 days per month per site. This banding regime was conducted between January 1983 and December 1987, with additional bird captures being made at less frequent intervals between 1979 and 1983, and 1987 and 1999.

From the available banding data, two bird species were chosen for analysis, the Superb Fairy-Wren *Malurus cyaneus*, and the Striated Thornbill *Acanthiza lineata*. Both of these species were chosen, as they share a number of characteristics that make them ideal for estimating survival rates. Both species are relatively long lived (Ford 1989, Rowley and Russell 1997), and as such it was possible to detect a difference in estimated survival time over the 10 years for which data were analysed. In addition, both species are sedentary (Ford 1989, Rowley and

Russell 1997), and therefore the subsequent absence of banded individuals from the data strongly implies the death of those individuals.

The data used for subsequent analyses were only taken from individuals who were last recaptured before October 1989. Any individuals recaptured after this date were not included in the analysis. Such exclusions were made in order to maximise the possibility that individuals included in the analyses were truly dead or missing, as these individuals were not encountered again for an additional 10 years despite continued trapping. In addition, only individuals that were initially captured as adult birds were included, to remove the effect of high mortality in juvenile birds. However, because individuals could not be aged once they were adults, it was impossible to discriminate between young and old adults, and therefore age-related mortality (post-juvenile) could not be accounted for.

Survival time was estimated as the difference (in days) between the date of last capture and the date of first capture for each individual. I was confident that this estimate provided a good relative estimate of minimum survival time, for the reasons explained above, although the potential for some individuals becoming 'trap-shy' could not be ruled out. Recapture rate was calculated as the number of times each individual was captured per month. This measure of recapture rate was an average, however, as for the period 1983-1987 trapping occurred on only 2 days per month.

1.4.2 Results

For Superb Fairy-Wrens, the estimated minimum survival time ranged from 28 days to 7.3 years (mean = 740 ± 51.3 (SE) days; $n = 128$), while recapture rate ranged from 0.03 captures/month to 3.3 captures/month (mean = 0.36 ± 0.04 (SE) captures/month; $n = 128$). For Striated Thornbills, the estimated time of survival ranged from 8 days to 12.8 years (mean = 1095 ± 69.5 (SE) days; $n = 143$), and recapture rate ranged from 0.03 to 7.6 captures/month (mean = 0.27 ± 0.06 (SE) captures/month; $n = 143$). Both minimum survival time and recapture rates did not differ between Hale Conservation Park and Cromer Conservation Park for Superb Fairy-Wrens (Wilcoxyn Tests; recapture rate: $Z = 1.51$; $p = 0.13$; survival: $Z = -0.67$; $p = 0.5$). While recapture rate did not differ between the two sites for Striated Thornbills, the estimated survival time of Striated Thornbills at Cromer Conservation Park was significantly greater than at Hale Conservation Park (Wilcoxyn Tests; recapture rate: Z =

0.66; $p = 0.51$; survival: $Z = -2.62$; $p = 0.009$). As such, the results of calculated correlations for Striated Thornbills are presented separately for each site.

For the 128 Superb Fairy-Wrens for which recapture data are presented, a negative power correlation existed between the rate of recapture and the estimated time of survival (Survival = 111 x (Recap. Rate)$^{-1.04}$; $r^2 = 0.692$; $p < 0.0001$; Figure 1.1). Similarly, a negative power correlation was also found between recapture rate and estimated survival for the 104 Striated Thornbills banded at Cromer Conservation Park (Survival = 155 x (Recap. Rate)$^{-0.907}$; $r^2 = 0.628$; $p < 0.0001$; Figure 1.2) and for the 39 Striated Thornbills banded at Hale Conservation Park (Survival = 82.1 x (Recap. Rate)$^{-1.1}$; $r^2 = 0.82$; $p < 0.0001$; Figure 1.3).

1.4.3 Discussion

The banding data for Superb Fairy-Wrens and Striated Thornbills presented in this section suggest a negative correlation between the rate of recapture and an estimate of survival time, estimated as the number of days between first and last capture for each individual. This correlation implies that the rate of recapture of individuals of these small bird species may impact upon the survival of these individuals, and subsequently the ecology of the target populations.

There are a number of possible causes for this suggested relationship between survival and recapture rate. The method of marking used may have had a negative impact upon the survival of the individual birds, as the metal tarsal band may have increased mortality due to predation, or reduced the efficiency of foraging in banded individuals. However, this was unlikely, as all individuals, independent of the rate at which they were recaptured, were marked in an identical fashion. A more probable explanation is that the acts of capture and handling resulted in the observed relationship, with individuals that were captured and handled more frequently surviving for a shorter time than those handled less frequently. Capture and handling can effect survival in a number of ways, most notably through capture myopathy (capture stress; Chalmers and Barrett 1982), which can result in loss of body mass (Kaufman and Kaufman 1994), or death to the individual (Marsh and Anderson 1983). In any case, the results presented here suggest that the act of capture and handling may have a strong influence on the ecology of target animals rather than the method used to mark them. As a result, the development and use of identification methods that eliminate both the need to

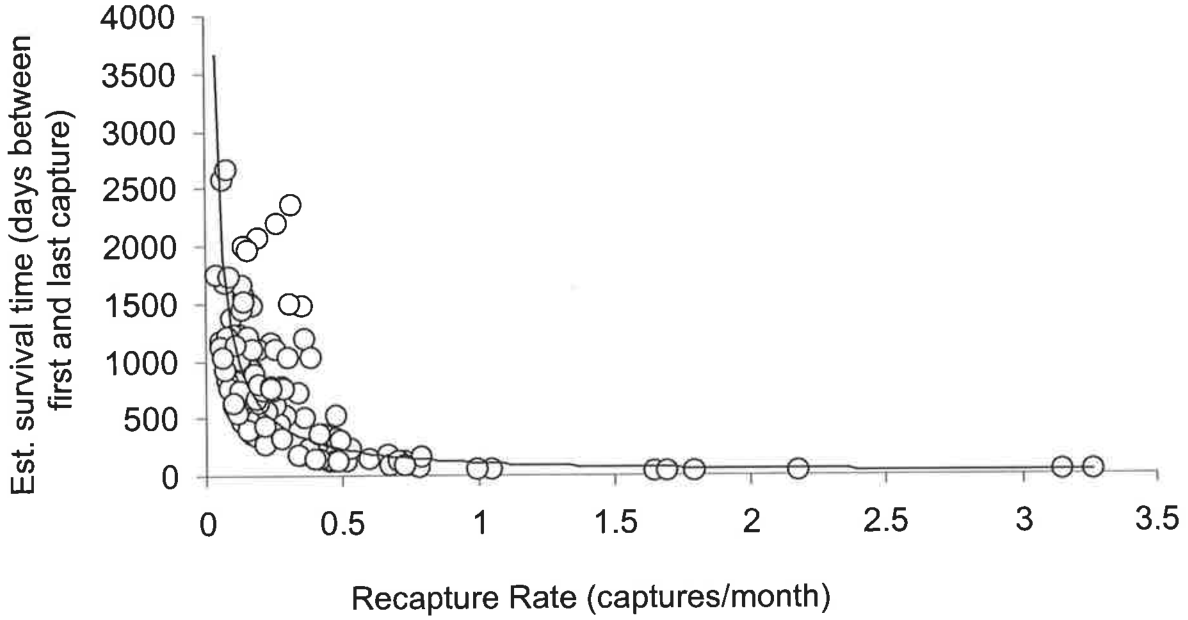


Figure 1.1. Estimated survival time aginst recapture rate for superb fairy-wren *Malurus cyaneus*. Data combined from Cromer Conservation Park and Hale Conservation Park, Mt. Lofty Ranges, South Australia. Relationship of curve: Survival = 111 x (Recapture Rate)$^{-1.04}$ ($r^2 = 0.692$).

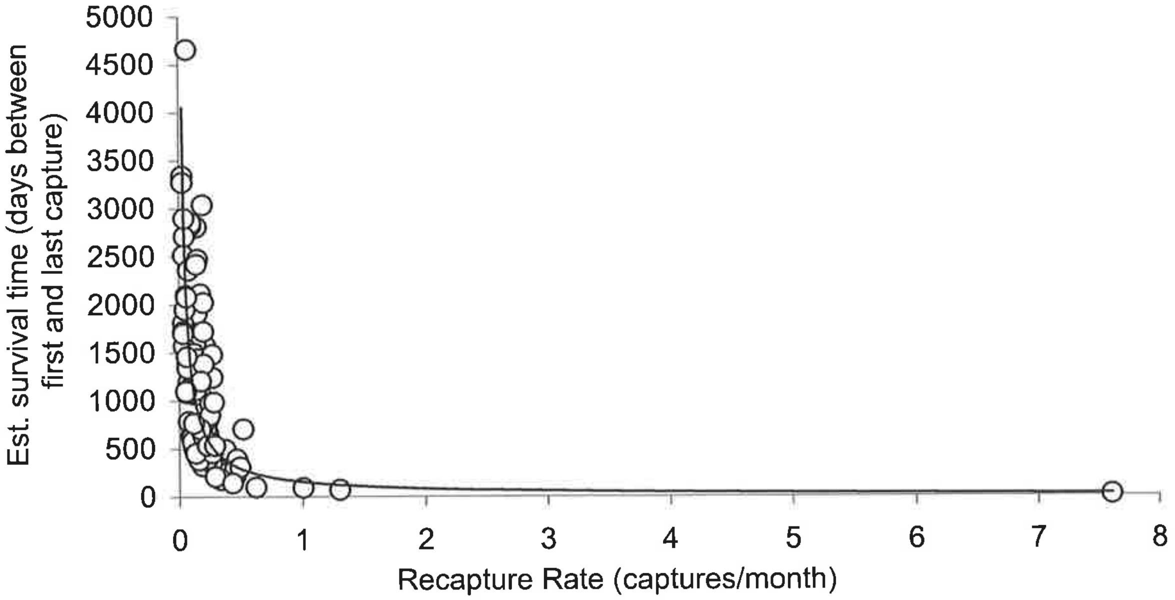


Figure 1.2. Estimated survival time against recapture rate for Striated Thornbill *Acanthiza lineata* at Cromer Conservation Park, Mt. Lofty Ranges, South Australia.
Relationship of curve: Survival = 155 x (Recapture Rate)$^{-0.907}$ ($r^2 = 0.628$).

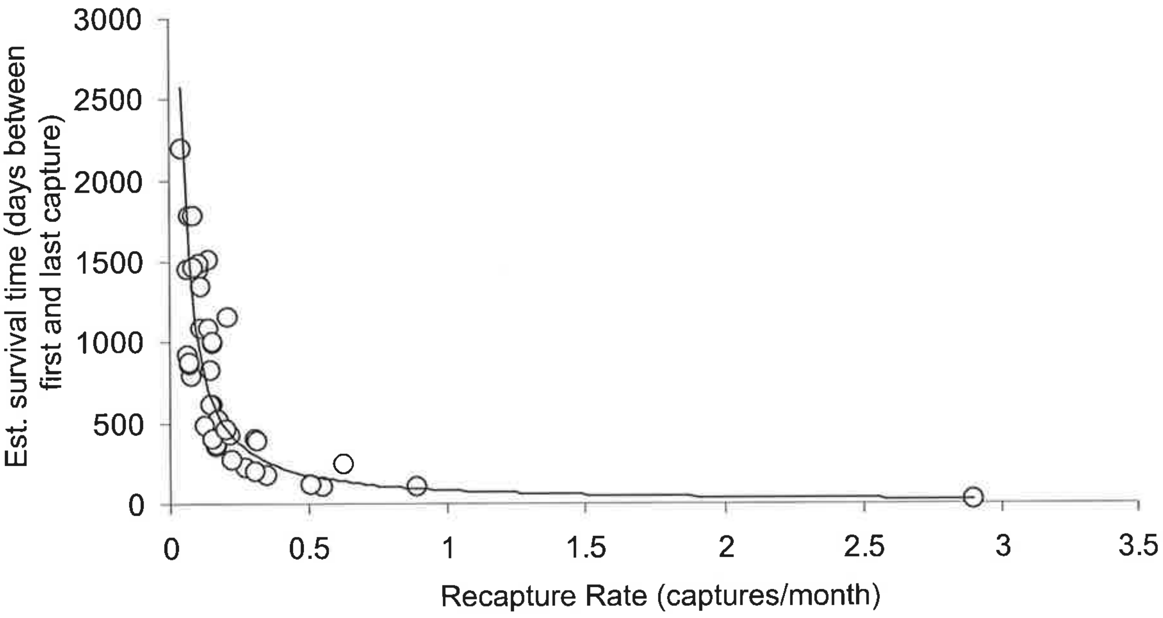


Figure 1.3. Estimated survival time against recapture rate for Striated Thornbill *Acanthiza lineata* at Hale Conservation Park, Mt. Lofty Ranges, South Australia.
Relationship of curve: Survival = 82.1 x (Recapture Rate)$^{-1.1}$ ($r^2 = 0.82$).

artificially mark, and capture target individuals, are required. However, to truly test the effects of capture and handling, one would need to follow the fate of individuals that were caught regularly with those that were not caught, an experiment that would require a non-invasive method of individual identification.

While the effects of standard methods of identificaton have been demonstrated in a number of cases, these effects are by no means universal for any of the commonly used techniques, with numerous studies demonstrating no effect. The equivocal nature of handling and marking effects thus highlights the need for pilot studies to be conducted for each case, before the identification technique can be used with confidence. However, the development of alternatives to artificially marking individuals are likely to eliminate these effects.

1.5 Non-invasive methods: the use of natural markings

Many animal species show intraspecific variation in the size, shape or markings of some features, which change relatively little – if at all – during each individual's lifetime. While the most widespread identification techniques require the capture and marking of target individuals, a number of examples exist where investigators have taken advantage of this natural variation between individuals, such that these individually-distinct markings can be used by biologists to accurately identify each individual.

Perhaps the most widespread use of natural markings in individual identification can be found in the study of cetaceans, where a number of different morphological features are used by biologists to discriminate between conspecifics (for a review of photo-identification in cetaceans, see Hammond *et al.* 1990). Natural variation in markings has also been used to monitor individual tigers *Panthera tigris*, using natural variation in stripe patterns (Karanth 1995, Karanth and Nichols 1998). The only limitation pointed out by the authors was its limited use in identifying and monitoring juveniles, largely due to their avoidance of camera boxes (Karanth and Nichols 1998). Tail patterns of cheetah have been used to identify individuals (Caro and Durant 1991). Variation in facial markings have been used with success in the monitoring of red-and-green macaw *Ara chloroptera* populations (Munn 1991), for example, while head patterns were used to identify and monitor individual osprey (Bretagnolle *et al.* 1994). Natural patterns have also been used effectively to identify amphibian individuals (Loafman 1991, Doody 1995, Mitchell 2001), although its use with amphibian species often requires capture and handling, due to their small size and cryptic nature.

Perhaps the greatest limitation with regard to the use of natural markings is the number of individuals that can be successfully identified. Although the number of individuals that are able to be identified is limited to some degree with the use of artificial marks, such limitations can be greater with the use of natural marks, as there is a risk that the natural patterns used for identification are duplicated as the size of the study population increases (Pennycuick 1978). However, such limitations can be effectively reduced with an appropriate choice of natural identification marking, in a number of ways. Generally, more complex markings will contain more identification information than less complex markings. Populations whose individuals can be successfully identified will increase where complex markings are used for identification (Pennycuick 1978). In addition, the number of individuals that can be identified is likely to increase in cases where the identification markings play a role in the social biology of the target species, and especially in cases where the markings are used by the animals themselves to discriminate between conspecifics. In such cases where individual recognition is important for the animals, there will be selective pressures for identification markings to be individually-distinct.

1.6 Individual recognition by animals, including acoustic recognition

A key to identifying the natural features that may be useful to biologists for individual identification may originate in the study of individual recognition in animals. Individual recognition is beneficial to animals in a variety of contexts. For territorial species, recognition of different territorial neighbours, as well as discrimination between neighbours and strangers, is critical for reducing physical territorial encounters, as known neighbours generally pose less of a threat to territory than unknown individuals (Yasukawa *et al.* 1982). Individual acoustic recognition has also been shown to occur between parents and offspring (Sieber 1985, Jouventin *et al.* 1999), group members (Boughman and Wilkinson 1998) and mates (Miller 1979, Robertson 1996).

Animals use a wide range of sensory cues in order to recognise and discriminate between conspecifics. Many of the phenotypic features highlighted in the previous section are used by animals as well as biologists, to visually discriminate between individuals, as is the case with sand lizards *Lacerta agilis* (Olsson 1994), crabs *Potamon fluviatile* (Vannini and Gheradi 1981) and iguana *Iguana iguana* (Phillips 1995).

Other sensory pathways are also used by animals to recognise conspecific individuals. Chemically-mediated recognition is a commonly employed communication pathway used to discriminate between individual giant panda (Swaisgood *et al.* 1999), deer (Lawson *et al.* 2000), kangaroo rats (Randall 1994, Murdock and Randall 2001), salamanders (Simon and Madison 1984, Anthony and Wicknick 1993), fish (Liley 1982) and capybara (Macdonald *et al.* 1985). McGregor and Westby (1992) have also shown that the electric signals of electric fish *Gymnotus carapo* are individually-distinct, and can be used by the fish to discriminate between conspecifics.

However, the sensory medium for which we have the most information with regard to individual recognition is acoustic communication. Amongst mammals, acoustically-mediated individual recognition has been demonstrated in primates (Cheney and Seyfarth 1982, Rendall *et al.* 1996), cetaceans (Sayigh *et al.* 1998), bats (Boughman 1997), felids (Grinnell *et al.* 1995), deer (Reby *et al.* 1998), rodents (Hare 1998, Jacobs and Kuiper 2000), elephants (McComb *et al.* 2000) and hyaena (Holekamp *et al.* 1999). Individual acoustic recognition has also been shown in two anuran species, the North American bullfrog *Rana catesbeiana* (Davis 1987), and the green frog *Rana clamitans* (Owen and Perrill 1998), and a number of fish species (e.g. Myrberg and Riggio 1985). However, the taxa for which we have the best knowledge with regard to acoustic individual recognition is birds.

Individual recognition through the acoustic pathway was identified in birds as early as 1908, where one of the functions of bird song was listed as “to proclaim an individual’s identity” (Craig 1908). However, quantitative evidence of individual recognition through song was not produced until the common availability of sound recording and playback, where experiments could be designed to test the use of acoustic cues in individual recognition. Subsequently, individual recognition by song has been quantitatively recognised in an enormous diversity of avian species, including many with song repertoires, and has been shown to play a role in all of the social contexts mentioned previously. Discrimination between territorial neighbours and strangers acoustically has been demonstrated for a wide variety of territorial passerine birds (Searcy *et al.* 1981, Stoddard *et al.* 1990, Brindley 1991, Galeotti and Pavan 1993), as well as acoustic discrimination between known territorial neighbours (Yasukawa, et al. 1982). Acoustic recognition also occurs between parents and young (Chaiken 1992, Leonard *et al.* 1997, Jouventin, et al. 1999) mates (Miller 1979, Robertson 1996) and family members (Price

1999). Individual acoustic recognition is also associated with certain ecological or environmental properties in birds, such as colonialism (for example, in seabirds Mathevon 1996, Jouventin, et al. 1999).

1.7 The use of individually-distinct acoustic signals for individual identification by biologists

The use of acoustic signals for individual recognition by animals thus appears to be widespread, especially amongst certain taxa, such as birds. As with other naturally-occurring features that are individually distinct, it may therefore be possible to use the individual features of an animal's acoustic signals to identify and monitor individuals in the field, as an alternative to techniques that require capture and artificial marking.

The concept of applying individually-distinct acoustic signals to the identification of individual animals was first suggested in 1924 (Saunders 1924), where a complementary alternative to bird banding was proposed:

> "individual variation in bird song is great enough so that it would seem possible, in some cases at least, to trace individual birds by the peculiarities of their songs"
>
> (Saunders 1924, p243)

As with demonstrations of individual acoustic recognition, critical analyses of acoustic identification only became possible with the invention of electronic sound recording devices, and modern sound analysis techniques, including sonographic analysis. Following the availability of such technologies, investigators, including wildlife managers, began to develop systems of individual identification based upon the vocal individuality. Such tools have been developed, or their potential exhibited, for American woodcock *Philohela minor* (Beightol and Samuel 1973), orange-crowned warbler *Vermivora celata* (Gilbert 1986), common loon *Gavia immer* (Miller 1988), bald eagle *Haliaeetus leucocephalus* (Eakle *et al.* 1989), wild turkey *Meleagris gallopavo* (Dahlquist *et al.* 1990), tawny owl *Strix aluco* (Galeotti and Pavan 1991), European bittern *Botaurus stellaris* (McGregor and Byle 1992, Gilbert and McGregor 1994), Japanese bush warbler *Cettia diphone* (Hamao 1993) peregrine falcon *Falco peregrinus* (Telford 1993), black-throated diver *Gavid arctica* (Gilbert and McGregor 1994) and corncrake *Crex crex* (Peake *et al.* 1998, Terry *et al.* 2001). In Australia, early attempts to quantify vocal individuality and develop acoustic census tools were conducted primarily by Denis Saunders and Ron Wooller, who found that the potential for vocal identification of individuals occurred in Sacred Kingfisher *Todiramphus sanctus* (Saunders and Wooller 1988), and also found quantitative evidence of vocal individuality in the Spinifexbird *Eremiornis carteri* (Wooller and Bradley 1981) and Australian Shelduck *Tadorna tadornoides* (Wooller *et al.* 1984). More recent studies have also shown that the surveys of the rare Christmas Island Hawk-Owl *Ninox natalis* are able to be conducted based upon vocal individuality (Hill and Lill 1998).

Studies to date, however, have been largely preliminary in nature, focussing on small numbers of individuals for which recordings were collected over limited time spans (Table 1.1). In order for future investigators to be confident with a system of acoustic identification, demonstrations of this system must contain information on larger numbers of individuals, recorded on multiple occasions over longer timeframes. Furthermore, the species for which acoustic identification has been demonstrated possess acoustic signals which are generally stereotypic in nature, in that a small number of different signals are used by all members of the population or species. However, many avian species possess repertoires of multiple song types that are not necessarily universal to all individuals in the species. One of the principal challenges to acoustic individual identification, therefore, is to investigate whether individuals of species with extensive song repertoires can also be identified through the analysis of acoustic signals, across multiple song types used by different individuals.

While the number of species for which individual identification using acoustic signals have been demonstrated is relatively small, two facts point to its more widespread potential. First, the taxonomic diversity of those species for which acoustic identification has been demonstrated suggests that such techniques may be useful in the study of a wider range of species, if closely related species to those already studied exhibit similar patterns of acoustic individuality. Second, and perhaps more importantly, the large number of species for which vocal individuality has been demonstrated, either through quantitative analysis of the acoustic signals (individuality of voice), or through playback experiments (individual recognition by conspecifics), strongly suggest that vocal individuality is indeed widespread amongst avian species. All that remains is for this observed vocal individuality to be applied to the identification of individual birds by biological investigators.

There is a critical difference between the use of visual and acoustic features for the identification of individual animals. While visual features are relatively invariant for each individual (for example, a tiger's stripes change little, if at all, during its lifetime), acoustic

Table 1.1 A list of the studies to date that have demonstrated vocal individuality, and applied such information to the acoustic identification of individuals. Optimally, a demonstration of acoustic identification should contain multiple acoustic recordings from a large number of individuals. In addition, the recordings should be collected over a long period of time, in order to demonstrate the consistency of vocal individuality over time. As can be seen, the studies to date only meet some these criteria in a few cases. Numbers of individuals followed by a question mark indicates cases where the proportion of individuals recorded on multiple occasions is unknown.

Species	# individuals (multiple recordings)	# individuals (single recordings)	timeframe of study	Reference
American Woodcock	0	36	~2 months	Beightol and Samuel (1973)
Orange-crowned Warbler	20?	0?	3 years	Gilbert (1986)
Common Loon	32?	0?	2 years	Miller (1988)
Bald Eagle	20	14	3 years	Eakle *et al.* (1989)
Wild Turkey	4	12	2 years	Dahlquist *et al.* (1990)
Tawny Owl	15	2	2 years	Galeotti and Pavan (1991)
European Bittern	5	0	1 month	McGregor and Byle (1992)
Japanese Bush Warbler	21?	0?	unknown	Hamao (1993)
Peregrine Falcon	17?	0?	3 years	Telford (1993)
Black-throated Diver	4	0	2 years	Gilbert and McGregor (1994)
Corncrake	7	9	2 years	Peake *et al.* (1998)
Sacred Kingfisher	8	26	2 years	Saunders and Wooller (1988)
Christmas Island Hawk-Owl	2	9	2 years	Hill (1998)

features vary significantly for an individual, depending upon the context of the vocalisation, the motivational status of the individual, and other factors, such as ambient temperature in anurans. As such, an understanding of how acoustic signals vary for each individual, as well as between individuals, is fundamental to the development of a system of identification based upon these acoustic features.

The objectives of this study are to investigate intra- and inter-individual variation in the acoustic signals of a range of animal species, with the ultimate objective being to use this information in the development of a system by which individuals of these species can be identified and monitored through the analysis of the individually-distinct components of their acoustic signals. The principle justification for this study is to increase the breadth of taxa for which acoustic identification techniques have been tested, as a way of highlighting to investigators the potentially extensive nature of acoustic identification. Should the results presented in this thesis demonstrate vocal individuality in a range of animal taxa, future investigators can predict with some confidence that a system of acoustic identification of individuals will be useful in their target organisms.

The animal species investigated in this thesis were chosen using a number of critical criteria. First, individuals of all of the species investigated are difficult to identify and monitor using conventional methods, as a result of their cryptic nature, threatened status, or morphological peculiarities (such as short legs precluding the use of colour bands). In addition, the species chosen represent a broad spectrum, both in terms of taxonomic diversity (anuran amphibians, as well as bird species representing four families), and diversity of acoustic signals, ranging from one or two simple call types (*Pseudophryne bibronii*; *Calyptorhyncus banksii*) to a repertoire of up to 30 complex song types, made up of an even greater diversity of song syllables (*Rhipidura leucophrys*; *Dasyornis broadbenti*). Both of these scales of diversity thus allow some generalisations to be made regarding vocal individuality in animals, and the potential for a system of individual identification based upon this individuality.

Chapter 2 Synopsis of General Methods

2.1 Introduction

The taxa for which results are presented in this thesis are necessarily diverse, both taxonomically, and with regard to their vocalisations and vocal behaviour. However, similar methods were used to record and analyse these vocalisations. This chapter presents the general methods used to record and analyse the vocalisations of the taxa discussed in subsequent chapters. More specific details of methods relevant to each of the taxa studied will are presented in the relevant chapters.

2.2 General Recording Methods

All recordings were made using one of the following alternative sets of equipment. The majority of recordings were made using a Sony DAT DC-8 Recording Walkman, with a Sennheiser ME-66 Directional Microphone. Additional recordings were also made using, a Sony WM-GX320 Recording Walkman, with a Sony ECM-MS907 Condenser Microphone. These analogue recording units were used predominantly to gather additional recordings from individuals of the two species that this thesis focuses on, *Pseudophryne bibronii* and *Dasyornis broadbenti*, as the efficiency of data collection was improved by the presence of a second recording unit in addition to the DAT recorder.

Recordings of the vocalisations of focal individuals were obtained opportunistically, taking advantage of temporal variations in vocal output, such as the dawn chorus of bird species. In general, however, it was necessary to monitor each individual or group of individuals for long periods, and gather recordings when possible.

2.3 Analysis

With regard to the intraspecific comparison of vocalisations, two methods of quantitative analysis were used. Both of these analytical techniques were necessary to gather the appropriate information required to determine the extent of intraspecific variation in the vocalisations of each taxa, and thus determine the potential for individual identification using these vocalisations. The complementary nature of the two analytical techniques is described in further detail below.

2.3.1 Feature Analysis and Discriminant Function Analysis

The first step taken to quantitatively determine the intraspecific variation and individuality of the vocalisations of each species was to measure a number of parameters that describe each vocalisation, and use these parameters to make both univariate and multivariate comparisons between the vocalisations of different conspecific individuals. In general, the parameters used to describe each vocalisation were chosen arbitrarily, although they describe a range of both temporal and spectral features of each vocalisation. The details of the parameters chosen are necessarily taxa-specific, and are thus described in more detail in the relevant chapters on each taxa.

The data generated from the measurement of these parameters were used to perform discriminant function analyses. Discriminant function analysis (DFA) allows researchers to investigate the differences between two or more groups of cases, with respect to several quantitative variables, by defining the multivariate variation that occurs both within and between the groups (Klecka 1980). In addition to statistically testing for differences between these groups, discriminant function analysis also allows for the *post-hoc* classification of each case. This *post-hoc* classification works by constructing a multivariate space that minimises the spatial overlap between the groups, as a way of maximising the proportion of cases that are correctly classified. The multivariate space of each group has a mean centroid, which has spatial coordinates that correspond to the mean values of each of the canonical functions used to construct the space. Each case is then classified as belonging to the group whose mean centroid the case is closest to. Because the original multivariate space was constructed in order to minimise group overlap, the proportion of cases classified to the correct group will be higher than if the space had been constructed randomly, with no prior knowledge of the group membership of each case. The construction of discriminant functions subsequently allows new cases to be classified to one of the groups upon which the original analysis was performed. In the case of investigating vocal individuality, each vocalisation is treated as a case, while each individual is treated as a group, for the purposes of these analyses. The discriminant function analysis thus has two main functions. DFA primarily provides some indication of the extent of individuality in the vocalisations of each animal taxa, by statistically testing whether the groups differ in multivariate space. In addition, DFA classifies each vocalisation to an individual, and subsequently calculates the proportion of vocalisations that are correctly classified, given some prior knowledge of the identity of the individuals from which the vocalisations were produced. DFA also provides an indication of which parameters are important in making the classifications (more specifically, which parameters are important in constructing the canonical functions), and are thus important in discriminating between individuals acoustically.

As the primary function of discriminant function analysis is to classify cases to groups based upon a number of variables, it appears to be an appropriate statistical tool for testing vocal individuality. Discriminant function analysis has thus been used extensively in other studies to demonstrate vocal individuality in a range of animal taxa, and, in a number of cases, to demonstrate the potential of acoustic signals as identification tools (eg. Galeotti and Pavan 1991, Naguib 2001). For the purposes of developing systems of vocal individual identification, however, discriminant function analysis is extremely limited in its potential as a census tool for wild populations of animals. The primary reason for this is that DFA does not allow for comparisons of the songs of new, unknown individuals, with those whose songs have been previously recorded and analysed, as new cases will simply be grouped with the known individual with the most similar songs to the new case. Therefore, while DFA has been shown to be extremely effective in discriminating between groups where the number of groups is already known (such as captive groups of animals, or between species), its use in censusing wild populations is obviously extremely limited.

2.3.2 Cross-Correlation Analysis

In order for a system of individual identification that is based on acoustic signals to be successful, investigators must be able to determine the identity of individuals immediately, through the recording and analysis of as little as two vocalisations. In addition, such a system should allow for the identification of new individuals, as well as the re-identification of previously encountered individuals.

One system of analysis that potentially allows for such identification is cross-correlation analysis. Cross-correlation analysis measures the similarity between two signals by calculating the proportion of sound energy that overlaps between the two signals at discrete time intervals (Clark *et al.* 1987). The two signals, represented as spectrograms, are shifted incrementally past one another along the time axis, and for each time interval, a cross-correlation coefficient is calculated. At the point at which the two signals obtain maximum similarity the peak correlation coefficient is obtained; this peak value is the one used to assess signal similarity. For the purposes of this thesis, this peak correlation coefficient has been given the abbreviation r_x.

The justification for using cross-correlation analysis to identify individuals is as follows. Investigators would be able to collect recordings of vocalisations from an animal population of interest, and then compare each pair of vocalisations using cross-correlation analysis. In cases where vocal individuality can be demonstrated, the r_x values calculated between songs produced by the same individual should be consistently higher than those calculated between songs from two different individuals. Figures 2.1 and 2.2 present examples of how r_x values might be distributed when calculated between the songs of different individuals, or the same individual, in cases where vocal individuality has been demonstrated. For the purposes of individual identification, the optimal distribution of r_x values is presented in Figure 2.1, where all r_x values produced intra-individually are higher than r_x values produced inter-individually. However, some overlap between the two classes of comparison may occur (Figure 2.2). With some prior knowledge of the optimal correlation threshold (r_x*) where maximum identification resolution is achieved (through the execution of pilot studies for the study taxa), calculated r_x values would immediately classify the two songs as being produced by the same individual, or two different individuals, depending on whether the values were greater or less than the r_x* value obtained. Where overlap does occur, pilot studies can also determine the degree of error one can expect. Subsequent recordings could then be compared with the existing library, to determine which of the known individuals produced the new song, or whether a previously unknown individual has been detected.

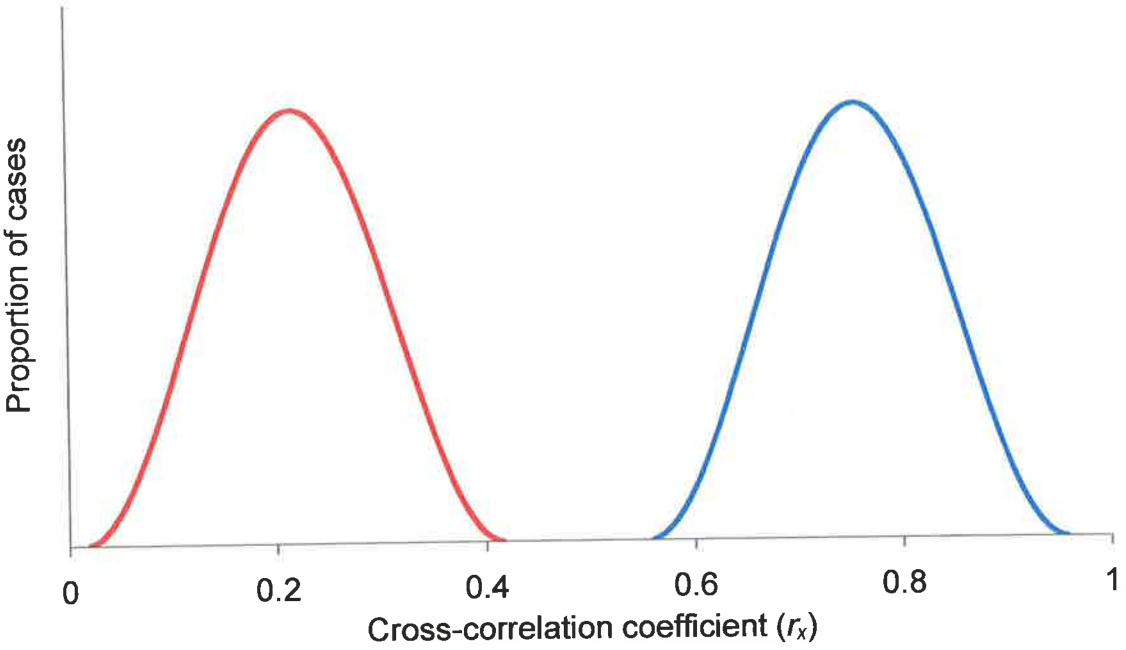


Figure 2.1 A hypothetical distribution of cross-correlation coefficients (r_x), calculated between the songs of the same individual (blue line) and between songs of different individuals (red line). For the purposes of acoustic identification of individuals, this presents an optimal example, with no overlap between the two classes of song comparison.

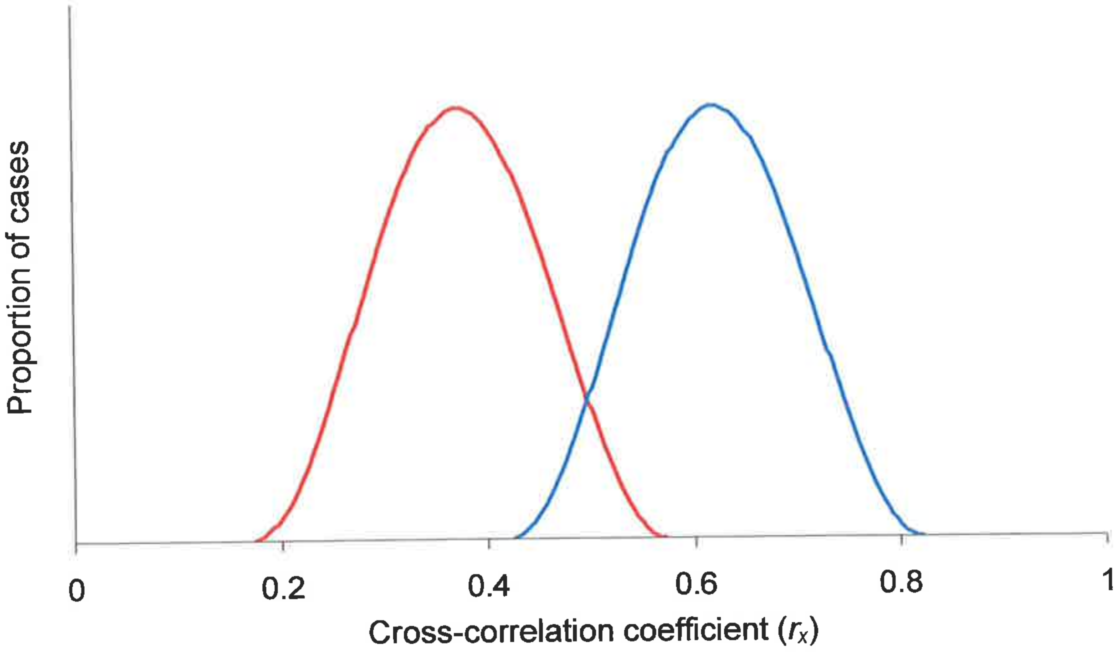


Figure 2.2 A hypothetical distribution of cross-correlation coefficients (r_x), calculated between the songs of the same individual (blue line) and between songs of different individuals (red line). The coefficients in this example are distributed sub-optimally for the purposes of individual identification, as overlap is present.

Cross-correlation thus has two principle advantages over multivariate statistical techniques such as DFA. First, standard multivariate techniques suffer from the bias of arbitrary parameter choice, with investigators preferentially choosing the sound information to be used to perform the analysis, leaving some information to be ignored. Cross-correlation analysis, however, compares the entire structure of two sounds, thereby eliminating any investigator bias by including all of the information available (Khanna *et al.* 1997). However. cross-correlation analysis is not completely free from investigator bias, as Khanna *et al.* (1997) demonstrated that the FFT (Fast-Fourier Transformation) lengths used to construct the spectrograms being compared can significantly influence the results of the analysis. In this thesis, all sonograms were constructed using the same FFT length of 256.

The second advantage that cross-correlation analysis has over multivariate analyses is more specific to its use in the acoustic identification of individuals. As discussed previously, multivariate analyses such as discriminant function analysis require that the identity of all individuals is known, and does not allow for the introduction and subsequent identification of previously unknown individuals. Such a system is therefore of extremely limited use to biological investigators, unless they are concerned with monitoring closed populations, such as captive populations. Cross-correlation analysis, however, does allow for the introduction of new individuals into a population, as the technique simply compares two signals and provides information on whether the two signals were produced by the same individual, or two different individuals. Comparing each new signal with a library of known signals thus allows investigators to decide whether the new signal was produced by an individual already represented in the library, or whether it was produced by a previously unknown individual.

Cross-correlation analysis has been used to assess the similarity of acoustic signals in a variety of contexts. For example, cross-correlation analysis has been used in studies of song development (Clark *et al.* 1987, Hile *et al.* 2000), song sharing (Gaunt *et al.* 1994) and song dialects (Latruffe *et al.* 2000). Of particular interest, however, is the use of cross-correlation analyses in assessments of vocal individuality. Dahlquist *et al.* (1990) used an automated version of cross-correlation to identify individual Wild Turkey *Meleagris gallopavo mexicana* through the comparison of the calls of different individuals, as a method of censusing turkey populations. Cross-correlation has also been used to demonstrate vocal individuality in European Bee-eaters *Merops apiaster* (Lessells *et al.* 1995), Fantailed Warblers *Cisticola juncidis* (McGregor *et al.* 1994, Terry *et al.* 2001) and European Bitterns *Botaurus stellaris* (Terry *et al.* 2001). However, the use of cross-correlation analysis in acoustic identification of individuals has yet to reach its full potential, especially with regard to the methodology highlighted above.

A number of authors have expressed reservations over the inappropriate use of cross-correlation analyses to compare acoustic signals. Principally, concerns have been raised regarding the use of cross-correlation to compare longer signals, or those with more than one continuous syllable (Khanna *et al.* 1997). For example, Specht (1998) suggested that similarities between signals would only be recognised when comparing signals with multiple syllables only if the distance between the syllables was identical. In testing the sensitivity of cross-correlation to variations in signal structure, (Khanna *et al.* 1997) concluded that the technique needs to be used with care when comparing animal vocalisations. The authors suggested that the scale of use should be limited to continuous syllables, "due to problems introduced by small variations in the time domain between notes and phrases within a vocalisation". Similar concerns have also been expressed about the impact of small variations in the spectral domain (Tchernichovski *et al.* 2000), such that a number of authors have suggested reducing the frequency resolution of spectrograms when they are to be compared using cross-correlation (Khanna *et al.* 1997, Tchernichovski *et al.* 2000). The work presented in this thesis has attempted to minimise the use of longer signals with cross-correlation analysis, by comparing song components or syllables, rather than whole songs. In addition, all signals were digitised using the same sampling frequency of 22 kHz. Although attempts were made in this thesis to minimise the concerns expressed by previous authors, when attempting to demonstrate vocal individuality, these small differences between signals may prove to be the very features that allow for individual acoustic identification.

All cross-correlation analyses conducted in this thesis used the Avisoft Correlator software package (Specht 2000). The algorithm used to calculate each cross-correlation coefficient (r_x) is:

$$r_x = \frac{\sum_x \sum_y ((a_{xy} - m_a) * (b_{xy} - m_b))}{\sqrt{\sum_x \sum_y (a_{xy} - m_a)^2 * \sum_x \sum_y (b_{xy} - m_b)^2}}$$

where m_a and m_b are the mean values of the spectrograms, and a_{xy} and b_{xy} are the intensities of the spectrogram points at the locations x,y (Specht 2000). Importantly, this method of calculating cross-correlation coefficients normalises the absolute amplitude of the two signals being compared (R. Specht pers. comm.). This means that the coefficient calculated between two signals is independent of any percieved differences in amplitude between the signals, as may result from differences in the distance between the source and receiver. Such independence is critical when comparing recordings obtained in a field situation, as it is extremely difficult to obtain such recordings under standard recording conditions. However, while the cross-correlation coefficients obtained are independent of absolute amplitude, variations in recording conditions can influence the structure of acoustic signals in other ways besides amplitude, such as changes in the percieved signal due to reflection and absorption of the signal trasmitted through the environment. The impacts of recording conditions on the percieved structure of acoustic signals are dealt with in Chapter 8.

The results of cross-correlation analyses in this thesis are expressed in two ways. First, r_x values between the songs of a single individual are compared statistically with r_x values produced between the songs of different individuals, using a t-test or non-parametric equivalent. This test was performed in order to determine whether intra-individual r_x are consistently higher than inter-individual r_x; that is, whether the songs of the same individual are more similar than the songs of different individuals. Second, the accuracy of identification using cross-correlation analysis was expressed as the maximum percentage of r_x that were correctly classified as having been produced by the comparison of songs intraindividually, or interspecifically, when a number of different songs were compared. This maximum percentage was obtained by determining the percentage of correctly classified r_x over the range of r_x produced by comparing all of the songs with each other separately. The correlation 'threshold' at which the peak accuracy occurred for each analysis is defined the peak correlation threshold (r_x*). For example, the peak percentage of correctly classified r_x from the data used to produce Figure 2.1 would be 100%, as there is no overlap between inter-individual r_x and intra-individual r_x. Furthermore, the peak correlation threshold (r_x*) for these data is between 0.42 and 0.56. For Figure 2.2, the peak percentage of correctly classifed r_x would be 72.8%, the reduction in accuracy due to the overlap between intra-individual and inter-individual r_x. This peak accuracy would occur at a r_x* of 0.5. For example, in Figure 2.1, 100% of r_x would be classified correctly if the correlation threshold were set at 0.5. However, if the correlation threshold were set at 0.2 in this example, 50% of the r_x values produced by interindividual comparisons would be classified as intraindividual, and therefore only 75% of the r_x values calculated would be identified correctly. The expressed value of peak accuracy is thus a reflection of the overlap of inter-individual and intra-individual r_x values, and, when used in conjunction with the peak correlation threshold value (r_x*), can be used to estimate the maximum accuracy (or, conversely, minimum error rate) one might expect from using cross-correlation to identify individuals acoustically, and at what r_x* value this level of accuracy is likely to occur.

Chapter 3 Intraspecific Variation in the Advertisement and Territorial Calls of *Pseudophryne bibronii*

3.1 Introduction

Intraspecific variation in the structure of anuran calls plays a significant role in the social biology of many species, and is influenced by a number of factors. Calls vary both within and between males due to environmental, morphological and social factors. For example, a significant factor relating to between-male variation in call structure is male body size, which primarily influences the dominant frequency of calls (Robertson 1986b, Wagner 1989b, Castellano and Giacoma 1998, Howard and Young 1998, Morrison *et al.* 2001). The relationship between body size and frequency is likely to be morphologically constrained, as the frequency of acoustic signals is directly linked to the mass of the vocal structures (Ryan 1991). However, this constraint placed upon call frequency allows it to play an important role in anuran social systems, by providing an honest signal of male size. Both conspecific females and other males are known to use this cue for size assessment. Female frogs may assess body size, and choose either larger mates (Ryan 1980), or mates that best match their own size (Robertson 1986a); (but see Morrison, et al. 2001 for evidence of selection for smaller males). Male frogs, on the other hand, use frequency as an assessment of body size in order to determine the probability of success in any physical competition for resources, such as territories (Wagner 1992). If a male can assess the size of a competitor prior to a physical battle, the likelihood of such battles actually taking place is reduced, thereby eliminating the associated costs and risks of such battles.

The most widely studied environmental factor that influences call structure is temperature. As anurans are ectothermic, physiological processes are influenced by ambient temperature. Such processes include some aspects of call structure, such as calling rate (Gerhardt 1991) and other temporal features of calls (Gerhardt and Mudry 1980). A complete review of the effects of temperature on anuran calls is dealt with in Section 3.3.5.

Social context also influences within-male call variation. In response to the calls of conspecifics, some species of frog alter their calling behaviour, either by switching from a mate attraction call to a distinct aggressive or territorial call (Robertson 1986b), or by altering the structure of the attraction call (Wells and Schwartz 1984). Social context also influences the dominant frequency of calls, with males of some species lowering the dominant frequency of calls in response to the calls of conspecifics (Wagner 1992). In many cases, responses to conspecific calls are graded, with increased threats resulting in a progressively increased aggressive structure to response calls (Wagner 1989a).

Such intraspecific variation in the structure of anuran calls plays an important role in anuran evolution, as this variation is used by females in mate choice (Lopez *et al.* 1988). In addition to size assessment, female preferences may favour calls that involve higher energy expenditure (Arak 1983, Sullivan 1983), which may be a signal of a male's relative fitness. Different components of anuran calls may also transmit different information such as species recognition (Gerhardt 1991), as well as signalling relative male fitness.

An additional role that intraspecific call variation plays in some anuran species is in cases of individual recognition, such as between territorial neighbours in species that maintain territories throughout a prolonged breeding season. Individual acoustic recognition has, however, only been identified in two anuran species. Owen and Perrill (1998) recently presented evidence that male green frogs *Rana clamitans* were able to discriminate between familiar and unfamiliar individuals on the basis of call, while Davis (1987) found that bullfrogs *Rana catesbeiana* possessed a system of acoustically-mediated neighbour recognition. In addition, recent evidence of long-term pair bonding in the spotted poison frog *Dendrobates vanzolinii* (Caldwell 1997) suggests that this frog species may possess the ability to recognise their mates acoustically, although vocal recognition has yet to be tested for this species. Although evidence for acoustic recognition in anurans principally stems from playback experiments (rather than quantitative analyses of anuran calls), the identification of acoustic recognition of individuals in these studies infers that the calls of some anuran species are individually distinct, and the potential may therefore exist for anuran individuals to be identified by biologists acoustically.

In order to monitor populations of animals effectively, the ability to identify individuals is often critical. Individual identification is required, for example, in order to accurately assess the size and distribution of a population, as well as measuring the survival, mortality and recruitment of its members (Donnelly *et al.* 1994a). Systems of individual identification should ideally allow permanent (or long-term) recognition of individuals, without influencing the behaviour or ecology of the animals in any way. The identification of amphibian individuals, however, presents a number of unique technical problems with regard to artificial identification marks. These include a lack of taggable appendages, the mucous nature and frequent shedding of their skin, their powers of regeneration, and their relatively small size

(Nace 1982). As a result, many of the techniques used to identify individuals in other taxa are generally unsuitable for the identification of amphibian individuals, and a number of techniques have thus been developed primarily for the use of marking and identifying amphibians. A review of standard identification techniques for amphibians is presented in Chapter 1.

This study investigated patterns of intraspecific variation in the calls of Bibron's Toadlet *Pseudophryne bibronii*, both within and between individuals. The ultimate objective of this study was to determine whether the calls of *Pseudophryne bibronii* were individually distinct, and thus had the potential to be used to identify and monitor individual males in the field. While the possibility of using acoustic signals to identify and discriminate between individual anurans has previously been suggested (Baptista and Gaunt 1997), this is the first study to test whether such a system is actually feasible. In addition, the influence of temperature on call parameters and individual identification was also investigated.

3.2 Methods – animal, study site and recording techniques

Pseudophryne bibronii (Figure 3.1) is a small (30mm SVL) anuran species of the family Leptodactylidae, with a distribution extending from southeastern Queensland to southeastern South Australia (Cogger 2000). Males occupy territorial nests during the breeding season, and defend these nests acoustically (Woodruff 1972). Nests are usually found in shallow depressions under leaf litter or at the base of grass tussocks, or inside burrows angled into the banks of creeks. Three call types have been identified for the species (Pengilley 1971): an advertisement call, a territorial call (or 'threat' call), and a courtship call. Of the three call types, courtship calls were not encountered during the present study. The mean call rate of *P. bibronii* is five calls per minute (N. Mitchell, pers. comm.); the start and end of each call could therefore be easily distinguished from those of subsequent calls, as the mean call length was 0.25s.

The location of the study population of *Pseudophryne bibronii* was Watts Gully, Mt. Crawford Forest (34°45'S, 130°53'E), 40km north-east of Adelaide, South Australia. The study site consisted of open forest dominated by *Eucalyptus* spp., with a relatively open understorey dominated by *Xanthorrhoea semiplana* (Specht 1972).

Figure 3.1 *Pseudophryne bibronii* with eggs (Cogger 2000).

Frog calls were recorded with sound recording equipment as described in Chapter 2. Once an individual male was located by its vocalisations, approximately 10 calls were recorded from a distance of approximately 50cm. Following recording, the individual was removed from its burrow, and identified independently using individually-distinct ventral patterns, by comparing the ventral pattern of the individual with an identikit of photographs of previously identified individuals (Figure 3.2). The individual was then returned to its burrow, the position of which was marked with a peg and flagging tape, such that re-identification and recording of each individual was possible.

Recordings were made from the 11 to 27 May 1998, 6 April to 17 May 1999, and 5 April to 12 May 2000. In total, 968 advertisement calls from 50 individual males, and 374 territorial calls from 42 males were recorded over the three seasons of the study (see Table 3.1 for number of calls and males recorded in each season).

3.3 Feature Analyses of Calls

3.3.1 Measurement of Call Parameters

Following recording, calls were converted to digital format and stored on an IBM Pentium 350 MHz personal computer. Each call was subsequently analysed using Avisoft Pro SASLab software Version 3.5b (Specht 1998).

Twenty-one call parameters were measured to describe each advertisement call (Figure 3.3), describing both the temporal and spectral characteristics of each call. Fourteen of these parameters were measured directly using Avisoft, with a further seven parameters being derived from these fourteen (pulse rate of components 1 and 2, frequency spread of components 1 and 2, total length, total pulse number and total pulse rate). Eight parameters were measured to describe each territorial call (Figure 3.4). While most of the parameters used to describe each call are self-explanatory, a number require description. The 25% and 75% quartiles describe the frequencies at which the lower 25% and upper 75% of the sound energy are distributed. Frequency spread is the difference between these two measures, and provides an indication of the frequency range that the sound energy is spread over. Complete descriptions of all call parameters are presented in Appendix A.

Figure 3.2 Examples of the ventral markings of *Pseudophryne bibronii*, highlighting the individuality of the markings. Such individuality was used in this study to independently identify each individual whose songs were recorded.

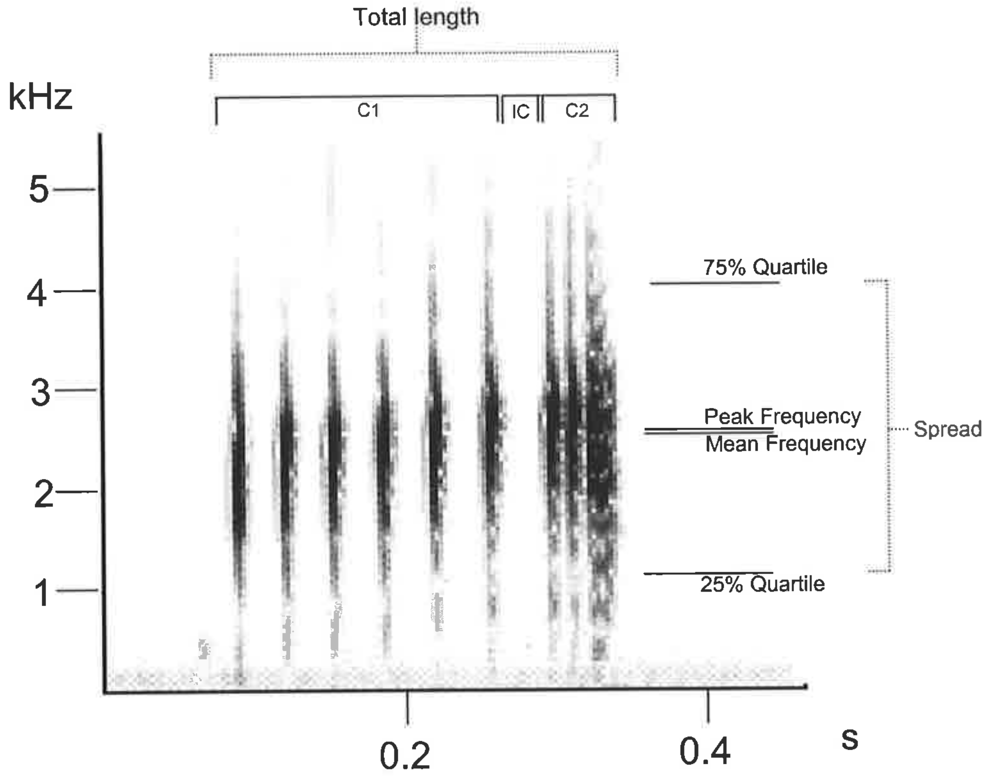


Figure 3.3 The advertisement call of *Pseudophryne bibronii*. C1 - call component 1; C2 - call component 2; IC - length between the 2 components. See Appendix A for detailed descriptions of call parameters.

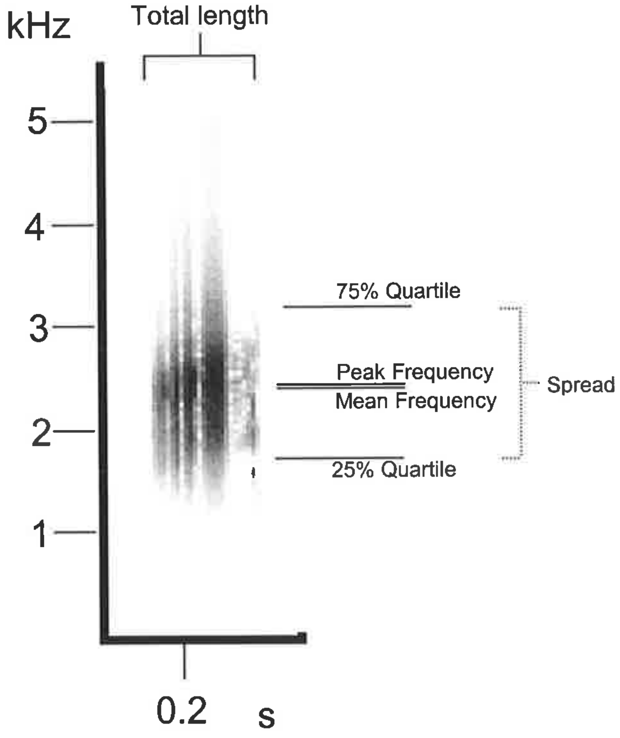


Figure 3.4 The territorial call of *Pseudophryne bibronii*. See Appendix A for detailed descriptions of call parameters.

Table 3.1 Number of individual males and calls sampled in each of the three recording seasons for *P. bibronii* advertisement and territorial calls.

	1998		1999		2000		# males recorded in multiple years	
	# males	# calls	# males	# calls	# males	# calls	2 years	3 years
Advertisement calls	15	103	27	366	28	499	8	1
Territorial calls	8	35	20	188	23	131		

Temporal call features were measured using Avisoft's oscillogram window, while spectral features were measured using both power spectrums and spectrograms (sampling frequency: 22.05 kHz; FFT length: 256; temporal resolution = 0.058ms; spectral resolution = 77 Hz). Due to variable recording conditions and distances, amplitude characteristics were not used for analysis.

3.3.2 Feature Analysis: Variation Between Calls of the Same Individual and Calls of Different Individuals, Across Different Temporal Scales.

3.3.2.1 Methods

Call variation was measured from the feature data collected by calculating coefficients of variation for each of the parameters used to describe the calls. Coefficients of variation provide a useful measure of variation, as they are a proportional measurement, and thus variation can be directly compared between parameters which differ in scale or measurement units. The following comparisons were made to calculate coefficients of variation: between all of the calls of the same individual; between the calls of all different individuals; between the calls of the same individual on a single night; between the calls of different individuals on a single night; and between the calls of the same individual on different nights. As fewer recordings were made of territorial calls, comparisons were not made between territorial calls of the same individual on different nights.

For the purposes of comparing variation between these different groupings, mean coefficients of variation represent the mean of the coefficients of variation calculated for each of the 21 parameters that describe each advertisement call and eight parameters that describe each territorial call.

3.3.2.2 Results

Advertisement Calls

For advertisement calls, a significant difference existed between the coefficients of variation calculated for the six call groupings (1-Way ANOVA on log-transformed data: $F_{5,120} = 3.659$; $p = 0.004$). However, a Tukey-Kramer HSD test revealed that significant differences were only found between the coefficients of varation calculated for single males on a single night and single males on different nights, and for single males on a single night and different males overall (Figure 3.5). The calculated coefficients of variation also suggest that the smallest variation between calls occurs between the calls of a single individual given on a single night. In addition, no difference was found between the coefficients of variation calculated between all of the calls of individual males, and all different males, suggesting that, over the three years of the study, the advertisement calls of *P. bibronii* vary as much between the calls of a single individual, as between different individuals.

Territorial Calls

For territorial calls, a significant difference existed between the coefficients of variation calculated for the four call groupings (1-Way ANOVA; $F_{3,32} = 4.44$; $p = 0.02$). Tukey-Kramer HSD test revealed, however, that this difference was due solely to the difference between the coefficients of variation calculated between the calls of single individuals on single nights, and between all individuals (Figure 3.6). As with advertisement calls, therefore, no difference was found between the coefficients of variation calculated between all of the territorial calls of individual males, and between all different males.

Comparisons between Advertisement Calls and Territorial Calls

Territorial and advertisement calls appear to vary between individuals in a similar way, both within and between individuals (Figure 3.7). For coefficients of variation calculated within individuals, no significant difference was found between the coefficients of variation calculated for advertisement calls and those calculated for territorial calls (t-test = 0.15; df = 27; $p = 0.89$). Similarly, no difference was detected between the coefficients of variation between the advertisement calls of all individuals and the territorial calls of all individuals (t-test = 1.8; df = 27; $p = 0.08$).

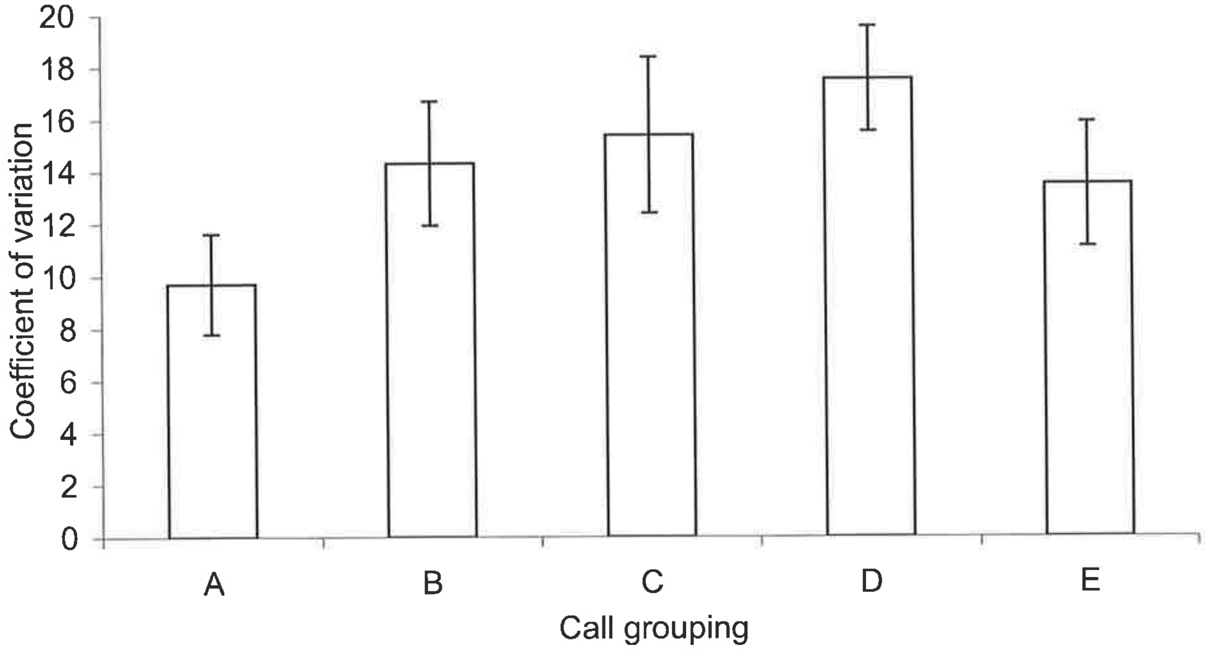


Figure 3.5 Mean (±s.e.) values for coefficients of variation between the calls of different groups of the advertisement calls of *Pseudophryne bibronii*, calculated as the mean of the CV values calculated for the 21 call parameters measured. Coefficients of variation were calculated between calls within the following groups: A - within males on a single night; B - between males on a single night; C - within males between nights; D - between males (overall); E - within males (overall). Sample sizes for each group was 21, and was equal to the number of parameters measured.

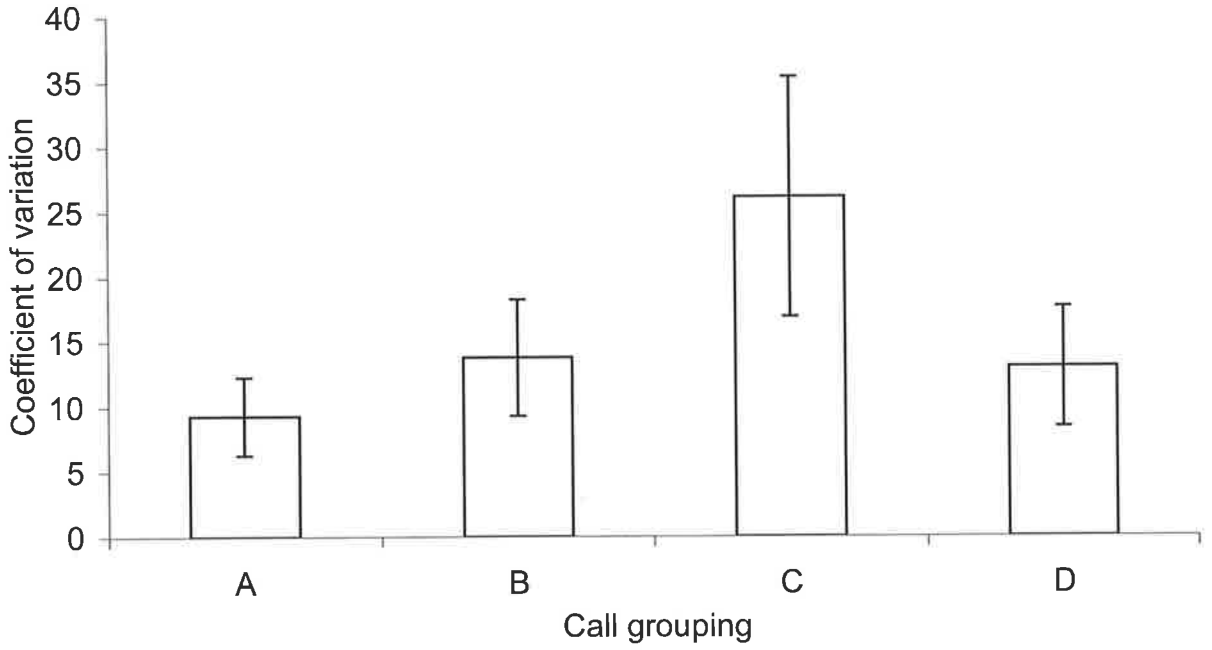


Figure 3.6 Mean (±s.e.) values for coefficients of variation between the calls of different groups of the territorial calls of *Pseudophryne bibronii*, calculated as the mean of the CV values calculated for the 21 call parameters measured. Coefficients of variation were calculated between calls within the following groups: A - within males on a single night; B - between males on a single night; C - between males (overall); D - within males (overall). Sample sizes for each group was 8, and were equal to the number of parameters measured.

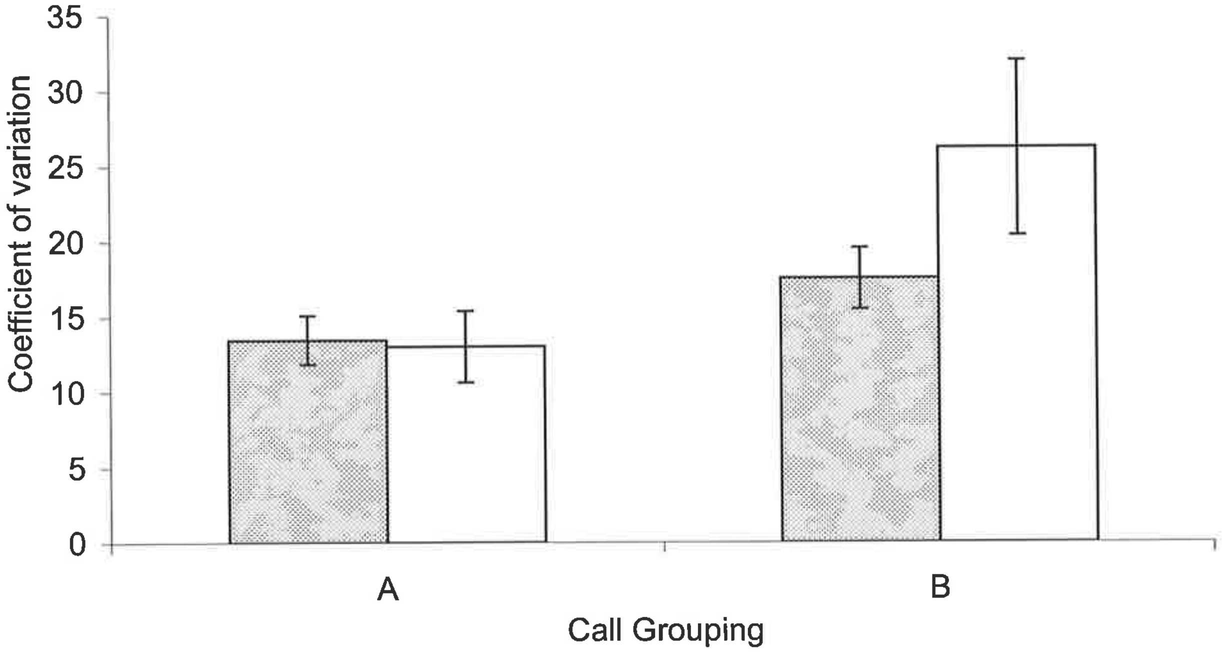


Figure 3.7 Comparison of coefficients of variation for advertisement calls (hashed bars) and territorial calls (open bars) of *Pseudophryne bibronii*, calculated both within individuals (overall) (A), and between individuals (overall) (B). Sample sizes were 21 for A, and 8 for B, and were equal to the number of parameters measured.

3.3.2.3 Discussion

The results of these analyses show that, over three years, the advertisement calls of *Pseudophryne bibronii* vary as much for each individual as they do between individuals. This suggests that there is little potential for identifying and monitoring individuals of *P. bibronii* acoustically, at least over a number of breeding seasons.

Why would the calls of individuals vary so dramatically over time, across different nights and seasons? The calls of a number of anuran species have been shown to be influenced strongly by a number of factors, including body condition and size (Gerhardt 1982), motivation (Gerhardt 1991), and temperature (see Section 3.3.5), and all of these factors were likely to be significant in determining the patterns of call variation exhibited here.

While long-term identification and monitoring of individual *P. bibronii* appears unlikely from these results, single-night censuses appear to have greater potential. Coefficients of variation for individual males on a single night were relatively low, both in comparison to the calls within males between nights, and, more importantly, in comparison to the calls of different males on a single night. Thus, from analyses of coefficients of variation, the calls of *P. bibronii* vary more between individuals than between the calls of each individual on a single night, an important and necessary precondition of individual identification (Saunders 1924). At a practical level, however, acoustic identification of individuals at the scale of single nights may not be any more useful than current survey techniques, based upon the number of calling males.

The final observation to be taken from these analyses is the fact that territorial calls appear to vary in much the same way as advertisement calls, both between individuals and between the calls of single individuals. At this stage, therefore, both call types have the same potential as tools for individual identification, although the relative prevalence in the use of each call type would indicate, from a practical perpsective, that advertisement calls may be more useful, as they would be easier to collect in sample sizes.

3.3.3 Variation in Call Features: Implications for Their Importance in Individual Discrimination

How different features of anuran calls vary within males has been demonstrated to have a significant influence on how females select for those preferences, and has subsequently shown the role that these parameters play in species recognition and mate choice. Gerhardt (1991) identified two groups of call features within the advertisement calls of three North American hylids: 'static' properties, which vary very little within males, and 'dynamic' properties, which vary considerably. This study, and subsequent investigations (eg. Castellano and Giacoma 1998) demonstrated that the two classes of call property are selected by females in different ways, with dynamic properties being selected in a strongly directional manner, while selection for static properties approaches the mean for the population. As a result, Gerhardt (1991) suggested that these static properties are likely to be used in species recognition by females, while dynamic properties are more likely to be indicators of male fitness.

As coefficients of variation were calculated for each call parameter, it was possible to use these calculations to compare the variation within each parameter, both within and between individuals, and thus identify the static and dynamic acoustic properties of *P. bibronii* calls. These analyses also provide some indication of the importance of each call feature to the vocal individuality *P. bibronii*.

3.3.3.1 Methods

For each of the 21 call parameters measured to describe each advertisement call and eight parameters measured to describe each territorial call, coefficients of variation were calculated between the calls of each individual, and between the calls of all different individuals. These calculations were then used to determine how each call parameter varies both within and between individuals.

In order to determine which parameters may be useful in discriminating between males acoustically, the ratio of intra-male variation to inter-male variation was also calculated for each call parameter, using the following equation:

$$CV_R = \frac{CV_{INTRA}}{CV_{INTER}}$$

where CV_R is the ratio of intra-individual call variation to inter-individual call variation; CV_{INTRA} is the mean coefficient of variation calculated between the calls of individual frogs, and CV_{INTER} is the mean coefficient of variation calculated between the calls of different individuals. This ratio calculation provides an indication of the value that each parameter will have in discriminating between individuals acoustically, as such discrimination is based upon the assumption that variation between individuals is consistently greater than variation within individuals. Parameters with low CV_R values are therefore more likely to be important in discriminating between individual males acoustically, than parameters with a high CV_R value.

3.3.3.2 Results

Advertisement Calls

The coefficients of variation for each of the 21 call parameters measured are given in Table 3.2, along with the CV_R values for each parameter, in ranked ascending order of CV_R. Within-male variation was lowest for spectral parameters, and highest for temporal parameters. While the least variant intra-individual parameters were generally spectral (e.g. mean frequency of second component, overall peak frequency), the parameters that produced the lowest CV_R values were temporal call parameters (e.g. number of pulses in the first component, total number of pulses, total length).

Territorial Calls

The results of the calculation of CV_R for the territorial calls of *P. bibronii* are presented in Table 3.3, again in ascending order. As with the parameters measured to describe advertisement calls, the parameters with the lowest CV_R values tend to be temporal call features, although the least variant parameters tend to be spectral features. In the case of territorial calls, however, this trend is less evident.

3.3.3.3 Discussion

Analyses of coefficients of variation for each parameter used to describe the calls of *P. bibronii* shows that the spectral features of these calls tend to vary less than the temporal features of the calls, both within and between individuals. If we expect that much of the

Table 3.2 Coefficients of variation for each parameter measured to describe the advertisement calls of *P. bibronii*, measuring both intra-male and inter-male variation. The ratio of intra-male to inter-male variation (CV_R) is a measure of the potential importance that the parameter plays in individual discrimination (see text for details). Abbreviations for each parameter are as follows: P#1 - number of pulses in first component; P# - total number of pulses; M(75)1 - frequency of 75% quartile of first component; LGTH - total length; PRATE - overall pulse rate; SPREAD1 - frequency spread of first component; P#2 - number of pulses in second component; LGTH1 - length of first component; SPREAD2 - frequency spread of second component; PRATE1 - pulse rate of first component; M(75)2 - frequency of 75% quartile of second component; MEAN1 - mean frequency of first component; PEAKF - overall peak frequency; PRATE2 - pulse rate of the first component; PEAKF1 - peak frequency of first component; M(25)2 - frequency of 25% quartile of second component; MEAN2 - mean frequency of second component; PEAKF2 - peak frequency of second component; LGTH2 - length of second component; ICL - length of time between components. Letters in parentheses following each parameter indicate whether the parameter is temporal (T) or spectral (S) in nature.

Call Parameter	CV_{INTRA}	CV_{INTER}	CV_R
P#1 (T)	16.74	32.48	0.516
P# (T)	10.89	18.03	0.604
M(75)1 (S)	8.46	13.15	0.643
LGTH (T)	11.33	17.38	0.652
PRATE (T)	12.52	19.15	0.654
SPREAD1 (S)	12.33	18.32	0.673
P#2 (T)	15.18	21.71	0.699
LGTH1 (T)	20.5	28.79	0.712
SPREAD2 (S)	29.61	40.82	0.726
PRATE1 (T)	12.5	16.65	0.750
M(75)2 (S)	11.26	14.97	0.752
MEAN1 (S)	4.32	5.28	0.818
PEAKF (S)	5.4	6.47	0.835
PRATE2 (T)	16.32	19.38	0.842
M(25)2 (S)	8.57	10.04	0.854
MEANF2 (S)	8.67	10.15	0.854
PEAKF1 (S)	6.02	7.00	0.860
M(25)1 (S)	13.01	14.81	0.878
PEAKF2 (S)	6.48	6.27	1.033
LGTH2 (T)	19.21	17.91	1.073
ICL (T)	33.66	28.97	1.162

Table 3.3 Coefficients of variation for each parameter measured to describe the territorial calls of *P. bibronii*, measuring both intra-male and inter-male variation. The ratio of intra-male to inter-male variation (CV_R) is a measure of the potential importance that the parameter plays in individual discrimination (see text for details). LGTH - call length; M75 - frequency of 75% quartile; SPREAD - frequency spread; P# - number of pulses; M25 - frequency of 25% quartile; PRATE - pulse rate; PEAKF - peak frequency; MEANF - mean frequency. Letters in parentheses indicate whether the parameter is temporal (T) or spectral (S) in nature.

Call Parameter	CV_{INTRA}	CV_{INTER}	CV_R
LGTH (T)	17.60	48.39	0.364
M75 (S)	9.89	21.14	0.468
SPREAD (S)	21.45	43.76	0.490
P# (T)	18.94	38.58	0.491
M25 (S)	10.12	16.63	0.608
PRATE (T)	17.61	28.38	0.620
PEAKF (S)	4.45	6.64	0.671
MEANF (S)	4.21	5.56	0.757

variation between calls is a result of changes in environmental conditions such as temperature, this result is as expected, as previous studies (e.g. Gayou 1984) have shown that such spectral features are little influenced by changes in temperature.

Previous work on within-male call variation in anurans has found that dominant frequency and pulse rate are the least variant ('static') properties of calls, while pulse number, call length and call rate are the most variant ('dynamic') properties (Gerhardt 1991, Castellano and Giacoma 1998). Defining the call properties of *P. bibronii* as static or dynamic is difficult from the present analyses, as the coefficients of variation calculated for the parameters measured cannot easily be grouped into parameters with low variation, versus parameters with high variation. However, the least variant properties of *P. bibronii* calls were shown to be spectral properties, while the most variant properties were generally related to call length. These results generally agree with previous studies (Gerhardt 1991), with the notable exception of pulse rate, which exhibited moderately high within-male variation for both call types (Table 3.2 and 3.3). As with the results of other studies on other anuran species, spectral features of the calls of *P. bibronii* may therefore play a role in species recognition, while the energetically expensive properties of call length and pulse number may be used by females to assess the relative fitness of males. However, the spectral features measured in this study also had the highest CV_R values, indicating that spectral properties of calls play a less important role in vocal individuality than temporal properties. Therefore, it appears that the least variable call properties, which are those that are likely to be important in species recognition, are those that are also likely to be less important in conveying identity information.

Such patterns of call variation, however, are not unexpected. While the spectral parameters of frog calls are generally not influenced by temperature, how frogs percieve the spectral properties of calls is influenced by temperature (Gerhardt 1978). Temporal properties, on the other hand, are influenced by temperature in much the same way as the perception of temporal properties, a phenonemon known as temperature coupling (Gerhardt 1978). From the frogs' perspective, therefore, temporal features do not vary with temperature, as their perception of temporal call properties is changing with temperature in parallel. As the same match does not occur for spectral call properties, this suggests that temporal properties may be more useful in conveying information that is important to the frogs' communication system, which may include individual identity information.

3.3.4 Discriminant Function Analyses

Calculations of coefficients of variation provide some indication of how the calls of *P. bibronii* vary across various temporal scales, both within and between individuals. The use of coefficients of variation, however, is limited by the fact that each parameter used to describe the call is analysed separately, with no appreciation for the relationship between call parameters, and how these relationships may influence our understanding of song variation within and between individuals. The use of discriminant function analyses (DFAs) overcome this restriction to some degree, through the construction of discriminant functions that take into account variation in all of the call parameters, and the relationships between the parameters. Discriminant function analysis also provides an estimate of individual discrimination based on the parameters used to describe the calls, as well as a determination of which parameters are useful in discriminating between individuals. A complete introduction to discriminant function analysis, and further justification for its application to individual identification, has been provided in Chapter 2.

3.3.4.1 Methods

The call data analysed in previous sections were used to perform discriminant function analyses, the general methods for which are described in Chapter 2. As outlined in Section 3.3.2.2, the parameters used to describe the advertisement calls of *P. bibronii* were ranked in order of CV_R, a measure of each parameter's individual discriminating potential. In order to determine the number of parameters that maximise the resolution of individual discrimination, call parameters were added sequentially, in ascending order of CV_R, to discriminant function analyses, with the proportion of calls correctly classified calculated after the addition of each new parameter for each subsequent analysis. A maximum of 17 parameters were added to the final DFA for advertisement calls, as four parameters (number of pulses in second component, 25% quartile of second component, 25% quartile of first component, and time between components) were excluded due to their high correlation (r>0.8) with other parameters. A maximum of seven parameters were used to construct the final DFA for territorial calls, with one parameter (25% quartile) being excluded.

For all discriminant function analyses, classification results are presented for the library of calls used to construct the discriminant functions. As a result, classification results presented are likely to be higher than if a new library of calls was subsequently analysed, with the identity of calling individuals unknown for the new library.

3.3.4.2 Results

Advertisement Calls

The proportion of calls that were correctly classified, as related to the number of parameters used to construct each DFA, are presented in Figure 3.8. The proportion of calls correctly classified continued to be improved with the addition of call parameters to each DFA up until all 17 parameters were added, with the exception of the addition of the ninth parameter (pulse rate of the first component). The maximum proportion of calls correctly classified was thus obtained by using all of the parameters available (not including the four excluded due to high inter-parameter correlations), except the pulse rate of the first component. The DFA constructed using these parameters classified 56.9% of advertisement calls to the correct male. The advertisement calls of *Pseudophryne bibronii* differed significantly between individuals (Wilk's $\lambda = 8.43 \times 10^{-4}$; $F_{833,11968} = 9.1$; $p < 0.0001$).

Table 3.4 shows the relative importance of each call parameter to each canonical variable, and the contribution that each canonical variable makes to the overall analysis. While 16 canonical variables were constructed in this analysis, no significant difference between individuals was found after the exclusion of the first 14 canonical variables, and greater than 95% of the variation between individuals was explained by the first 11 canonical variables. Therefore only the first 11 canonical variables are presented in Table 3.4.

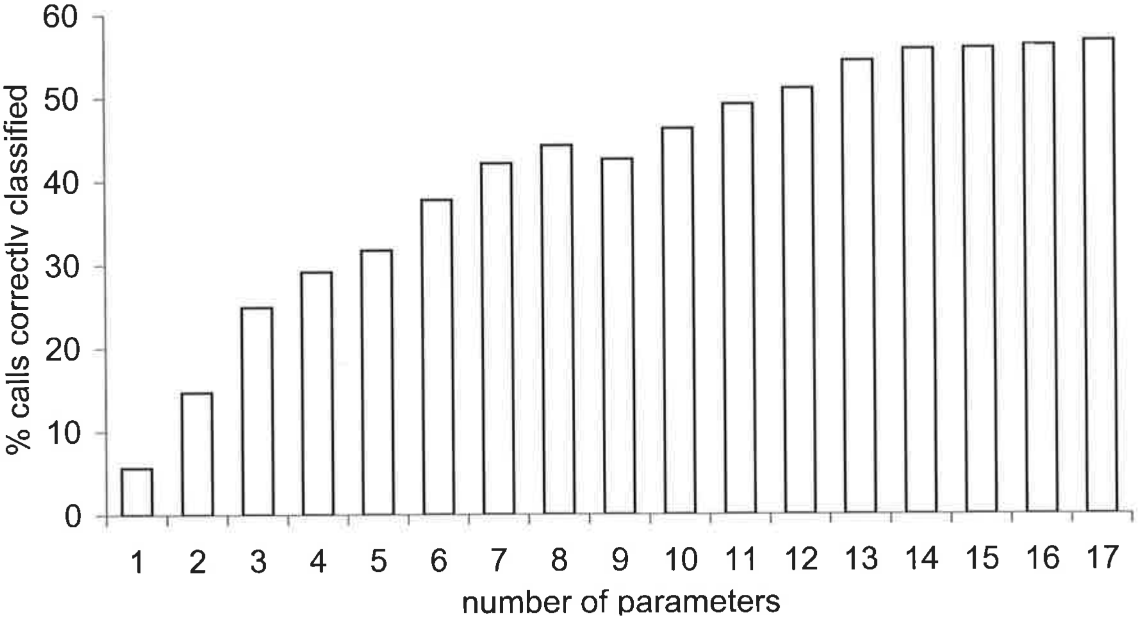


Figure 3.8 Percentage of advertisement calls of *P. bibronii* correctly classified using discriminant function analysis, as a function of the number of call parameters used to perform the analysis.

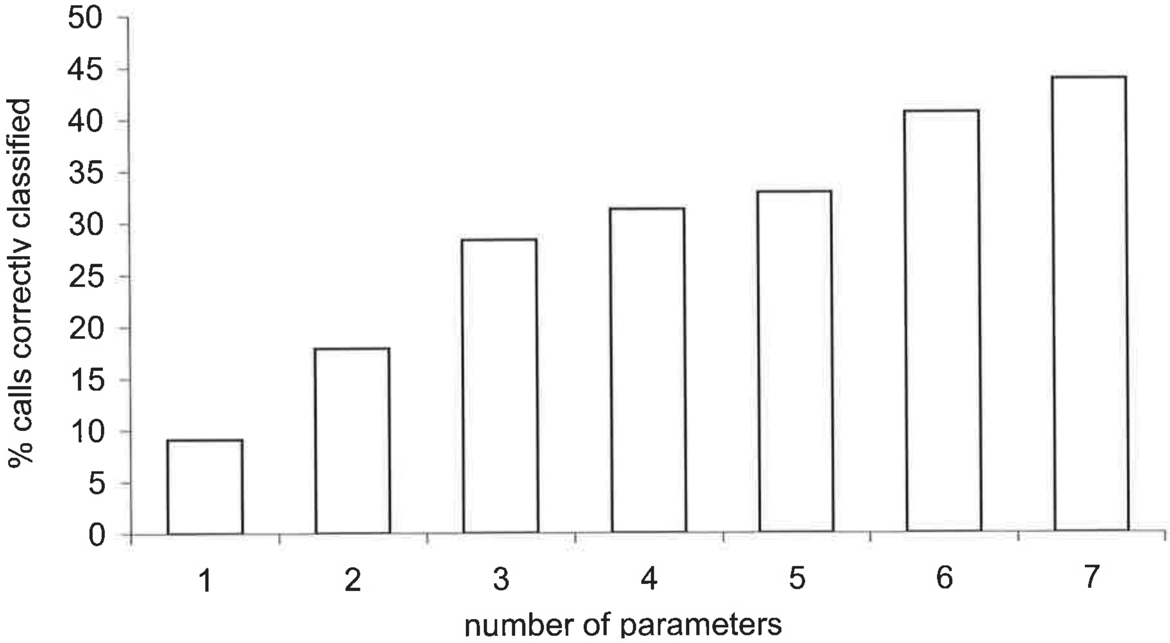


Figure 3.9 Percentage of territorial calls of *P. bibronii* correctly classified using discriminant function analysis, as a function of the number of call parameters used to perform the analysis.

Table 3.4 Canonical variable coefficients for each parameter measured to perform a discriminant function analysis on all advertisement calls of *P. bibronii*. Coefficients in bold are those with values greater than one. Cum. Prop. indicates the cumulative proportion of the variation in the analysis explained by each canonical variable. See Table 3.2 caption for parameter abbreviations. Letters in parentheses following each parameter indicate whether the parameter is temporal (T) or spectral (S) in nature.

	Can. Var. 1	Can. Var. 2	Can. Var. 3	Can. Var. 4	Can. Var. 5	Can. Var. 6	Can. Var. 7	Can. Var. 8	Can. Var. 9	Can. Var. 10	Can. Var. 11
P#1 (T)	**-1.07**	0.55	-0.01	-0.52	0.09	0.25	-0.35	**-1.80**	-0.37	-0.98	-0.71
M(75)1 (S)	**2.30**	-0.72	**-1.37**	0.06	**2.58**	**2.98**	**3.30**	**2.71**	**-2.16**	-0.44	0.59
P# (T)	0.13	-0.70	0.92	-0.86	**-1.64**	-0.32	**1.82**	**1.89**	**-1.32**	**1.50**	0.27
SPREAD2 (S)	0.35	0.26	-0.08	-0.44	0.27	0.07	0.18	**3.00**	0.12	0.49	**-1.80**
PEAKF1 (S)	0.23	0.01	-0.19	-0.07	-0.15	-0.24	0.26	-0.29	-0.48	-0.32	-0.19
LGTH1 (T)	0.22	-0.61	**-1.18**	0.43	0.66	**-1.80**	**1.59**	**1.02**	**1.96**	-0.65	0.87
SPREAD1 (S)	**-1.82**	0.50	0.74	-0.45	**-2.78**	**-2.80**	**-3.25**	**-3.00**	**1.83**	0.38	-0.49
PRATE2 (T)	0.20	-0.87	0.12	0.00	**1.25**	-0.22	-0.64	**-2.02**	0.14	-0.40	**-1.02**
PRATE (T)	-0.47	0.58	**-1.70**	**1.15**	0.63	0.95	**-1.97**	0.72	**1.10**	**-1.17**	0.67
LGTH (T)	0.05	**1.06**	-0.72	**1.13**	**1.26**	**2.51**	**-3.38**	-0.15	-0.27	0.54	-0.27
MEAN2 (S)	-0.08	0.08	-0.39	-0.38	0.21	-0.40	-0.46	0.30	-0.15	0.71	0.39
MEAN1 (S)	-0.20	0.60	0.18	0.58	-0.82	-0.53	-0.66	-0.60	**1.13**	0.16	-0.73
LGTH2 (T)	-0.19	-0.86	-0.46	-0.27	0.63	-0.88	0.07	**-2.00**	**1.16**	-0.73	-0.60
M(75)2 (S)	-0.18	-0.18	0.38	-0.21	0.11	0.04	-0.11	**-2.66**	-0.10	-0.98	**1.78**
PEAKF2 (S)	-0.06	-0.04	0.01	0.09	-0.03	-0.14	-0.33	0.29	-0.21	0.09	-0.19
PEAKF (S)	-0.07	0.16	-0.13	0.20	0.14	-0.20	0.03	0.32	0.07	-0.05	-0.24
Cum.Prop	**0.26**	**0.41**	**0.54**	**0.64**	**0.71**	**0.78**	**0.82**	**0.86**	**0.90**	**0.93**	**0.95**

The relative importance a parameter plays to each canonical variable can be assessed by its coefficient for each variable. For each canonical variable, higher value coefficients (independent of whether the coefficient is positive or negative) indicate a more important role in the construction of the variable. For the first 11 canonical variables, assessments of these coefficients suggests that temporal call features tended to play a more important role in the construction of the canonical variables, and thus in discriminanting between individuals, than spectral features. However, one spectral feature played an important role in the contruction of the discriminant functions (75% quartile of the first component). This call parameter was also the spectral call feature with the lowest CV_R value in Section 3.3.3. The observations here therefore agree with the conclusions drawn from analyses of coefficients of variation described in Section 3.33.

Territorial Calls

The proportion of territorial calls that were assigned to the correct male, as related to the number of call parameters used to construct each DFA, is presented in Figure 3.9. As with advertisement calls, the proportion of calls classified correctly generally continues to increase with the addition of call parameters until all seven parameters are used to construct the final DFA. For this final DFA, 43.9% of calls were attributed to the correct male. As with advertisement calls, territorial calls differed significantly between individuals (Wilk's $\lambda = 6.07 \times 10^{-3}$; $F_{287,2265} = 8.63$; $p < 0.0001$).

Comparison Between Call Types

A chi-squared test was performed between the maximum proportion of calls that were correctly classified calls for advertisement and territorial calls, to determine whether the difference in call classification accuracy between the call types was statistically significant. This test indeed revealed that a significantly higher proportion of advertisement calls (0.57) than territorial calls (0.44) were classified correctly ($\chi^2 = 13.22$; $p = 0.0003$).

3.3.4.3 Discriminant Function Analyses – Single Night Comparisons

While the potential for long-term monitoring of individual *P. bibronii* appears limited, analyses of coefficients of variation suggest that the calls of *P. bibronii* may be used to conduct single-night surveys of individuals. As such, DFAs were performed on the call data for each recording night separately, for those nights where the calls of at least three different males were recorded.

Advertisement Calls

Over the three recording seasons, three or more males were recorded on 17 separate nights. The number of males recorded on these nights ranged from 3 to 12 (mean = 6.8 ± 0.64). The results of discriminant function analyses performed on the call data for each of the 17 nights are summarised in Table 3.5. Discrimination of individuals on the basis of the call parameters measured was high for all of the 17 nights; 100% of calls were correctly classified on 14 of the 17 nights, including one night where calls of 10 different individuals were recorded. In addition, advertisement calls differed significantly between individuals on all of the 17 nights analysed. These results suggest that the potential exists for populations to be censused on single nights, using calls for the identification and discrimination of individuals.

Territorial Calls

Territorial calls were recorded from three or more males on a single night on nine separate nights, with the number of males recorded ranging from three to nine individuals ($X = 5.0$ males ± 0.78). Results for discriminant function analyses performed on the territorial call data from these nine nights are summarised in Table 3.6. The proportion of calls that were assigned to the correct male ranged between 58.5% and 100%, with 100% of calls being correctly classified on four of the nine nights. As with advertisement calls, territorial calls differed significantly between individuals on all of the nine nights analysed.

3.3.4.4 Discriminant Function Analyses Between Nights, Using Call Data Averaged Within Each Call String

Because male *P. bibronii* are generally well spaced geographically during the breeding season, each of the calls recorded in a string of calls can safely be assigned to the same individual. A call string is simply defined here as a sequence of calls given by a single individual, in which no two calls are separated by an extended period of silence. Whereas call strings can be separated by many minutes, the calls within call strings tend to be separated by a maximum of 20 seconds. It may therefore be possible to improve our accuracy of identification by averaging the data generated for each of the call features measured, for the

Table 3.5 Results of discriminant function analyses performed on advertisement call data analysed separately for each recording night (minimum 3 individuals recorded).

Date	# males	# calls	# parameters	p	% correct
11/5/98	6	34	15	<0.0001	100
14/5/98	5	28	11	<0.0001	100
18/5/98	5	38	9	<0.0001	100
6/4/99	3	25	6	<0.0001	100
10/4/99	7	73	16	<0.0001	91.8
20/4/99	7	24	12	<0.0001	100
12/5/99	5	27	11	<0.0001	100
20/5/99	10	67	15	<0.0001	100
5/4/00	9	64	16	<0.0001	100
6/4/00	10	100	17	<0.0001	99.0
11/4/00	6	57	16	<0.0001	100
12/4/00	3	19	11	<0.0001	100
16/4/00	12	101	15	<0.0001	99.0
17/4/00	10	52	15	<0.0001	100
19/4/00	7	36	11	<0.0001	100
24/4/00	6	32	15	<0.0001	100
5/5/00	4	16	9	<0.0001	100

Table 3.6 Results of discriminant function analyses performed on territorial call data analysed separately for each recording night (minimum 3 individuals recorded).

Date	# males	# calls	# parameters	p	% correct
6/4/99	4	19	2	<0.0001	68.4
10/4/99	7	69	6	<0.0001	89.9
19/4/99	4	20	4	<0.0001	100
20/4/99	3	17	1	.0245	58.5
12/5/99	4	15	5	<0.0001	100
5/4/00	3	16	6	<0.0001	100
6/4/00	3	8	4	<0.0001	100
16/4/00	9	26	5	<0.0001	92.3
17/4/00	8	53	7	<0.0001	83.0

calls in each of these strings. If we then compared call strings rather than individual calls, intra-individual call variation may be reduced, as we have eliminated variation between calls in the same call string.

For the purposes of this comparison, individual males were included only if at least two different call strings were recorded for that male. Under this condition, 770 advertisement calls were included in the analysis, from 29 individuals. These 770 calls were taken from 110 call strings, the mean values of which were calculated for each call parameter. These mean values were then compared with the values obtained for the 770 calls, using discriminant function analysis. As with the calculation of coefficients of variation (Section 3.3.2), comparisons between call strings for single males was not possible for territorial calls, due to a lack of appropriate data.

When the 770 calls were treated as independent units for analysis, DFA classified 57.5% to the correct male, with the calls being significantly different between individuals (Wilk's $\lambda = 0.004$; $F_{476,10628} = 10.46$; $p < 0.0001$). When the mean values for each of the 110 call strings were used to construct the DFA, 64.5% of calls were correctly classified. Call strings also differed significantly between individuals (Wilk's $\lambda = 0.0012$; $F_{364,859} = 1.79$; $p < 0.0001$). No significant difference was detected between the proportion of calls classified to the correct male, and the proportion of call strings classified correctly ($\chi^2 = 1.95$; $p = 0.163$).

3.3.4.5 Discriminant Function Analyses – Discussion

Over the three years of this study, discriminant function analyses demonstrated that while the calls of different individuals were significantly different from one another, a relatively low proportion of calls were classified to the correct individual, for both territorial and advertisement calls, especially considering the *post hoc* nature of the classification process (see Chapter 2). With regard to long-term monitoring of individual *P. bibronii*, the use of acoustic identification appears to have little potential.

However, discriminant function analyses also revealed that relatively high percentages of calls were classified correctly for surveys conducted on single nights, which suggests that, while long-term acoustic monitoring of individuals appears unlikely, one-off acoustic censuses of *P. bibronii* populations has definite potential.

From a practical perspective, however, our apparent ability to identify individuals acoustically on single nights is not likely to improve upon the accuracy of current survey methods. This is especially true of species such as *Pseudophryne bibronii*, in which individuals are generally well-spaced, and do not move large distances within the space of a single night. At this scale, therefore, simply counting the number of calling males at different locations is likely to provide as good an estimate of population size and density as attempting to identify individuals through the analysis of their calls.

In some respects, the results of discriminant function analyses presented here contradict those presented for analyses of coefficients of variation. The results of Section 3.3.2 suggest that both advertisement and territorial calls have the same potential as cues for individual identification, although the fact that advertisement calls are used more regularly by *P. bibronii* means that these calls could be collected more efficiently. However, results of discriminant function analyses presented in this section demonstrate that, based upon the parameters used to construct the DFAs, a significantly higher proportion of advertisement calls are correctly classified than territorial calls, both overall, and for single-night analyses. These results suggest that the advertisement calls of *P. bibronii* should be used exclusively for the identification of individual males.

Why do the two analyses present apparently contradictory findings? The primary reason for this difference is likely to be the parameters that were used to construct the discriminant function analyses for each call type. For the advertisement call DFA, 17 call parameters were used, while only seven were used to construct the territorial call DFA. While increasing the amount of information used to construct a discriminant function analysis does not necessarily improve the discriminating resolution of the analysis, in the case of this study, increasing the number of parameters improved the proportion of calls correctly classified, for both call types. The strong difference in call classification between the two call types is therefore likely to be a result of the amount of information used to perform the analyses. This suggests that in cases where an equal amount of information is used for the analysis of each call type (as occurs with cross-correlation analyses), similar identification accuracies may result.

The results of discriminant function analyses performed for call data collected on single nights supports the results of analyses of coefficients of variation, with a high proportion of advertisement calls correctly classified for all recording nights. Again, therefore, the potential for discriminating between individual *P. bibronii* on the basis of their advertisement calls appears to be limited to surveys conducted on individual nights. While it may be possible to achieve a useful degree of accuracy when conducting these single night surveys, such surveys are limited in their usefulness with regard to monitoring the demographic features of populations of *P. bibronii*, as they exclude the ability to monitor individuals over time. Furthermore, similar survey results are likely to be produced by simply counting the number of calling males on a given night, as would result from the analysis and classification of calls to individuals statistically.

From a practical perspective, our ability to monitor individuals over longer periods of time may be improved by averaging the call data collected from each call string. However, DFA revealed that there was no difference in the proportion of call strings correctly classified, compared to the proportion of calls correctly classified. Therefore, despite reducing intra-individual variation by averaging the calls in call strings, our identification accuracy is not significantly improved. Such a result, however, is not surprising when we consider that the majority of intra-individual call variation results from variation between nights, with the calls within call strings varying very little.

3.3.5 Effects of Temperature on Call Variation

The results presented so far have demonstrated that the advertisement and territorial calls of *P. bibronii* exhibit variation both within and between individuals, with the greatest intra-male variation occurring between nights.

Why do the calls of individual males vary temporally? There is evidence that the calls of anurans vary due to a number of factors, such as temperature, body size, and social context, all of which are likely to act in concert, and exert different influences on different properties of the calls.

In this section of the thesis, I have concentrated on the influence of temperature on the structure of *P. bibronii* calls. The effects of temperature on the structure of anuran calls is well documented, with strong evidence suggesting that temporal properties such as pulse rate are strongly influenced by temperature, whereas spectral features are not. As these temporal properties were shown to have the most potential as cues in conveying individual identification information, I wished to determine whether within-male variation was reduced when the effects of temperature were taken into account, and whether this improved our ability to discriminate between individuals acoustically.

3.3.5.1 Methods

For the 1999 and 2000 recording seasons, temperature data were recorded immediately after each sound recording. Air temperature was measured using a Micronta indoor/outdoor thermometer, calibrated against a standard thermometer. Whilst cloacal temperature is regarded as the most appropriate measure when determining the effects of temperature on frog calls (Gayou 1984), the objective of this study was to provide a non-invasive technique of individual identification, which included measurements of temperature.

Correlations were conducted between each of the 17 advertisement call parameters used to construct the discriminant function analyses and temperature, and the seven territorial call parameters and temperature. Where a significant relationship existed between a call parameter and temperature, the data for that parameter were corrected to 10°C, using the equation:

$$\mathrm{CD}_{10} = \mathrm{CD}_{\mathrm{amb.}} - (\mathrm{T}_{\mathrm{amb.}} - 10) \times b$$

where CD_{10} is the data corrected to 10°C for each call parameter, $\mathrm{CD}_{\mathrm{amb.}}$ is the uncorrected data for each call parameter, $\mathrm{T}_{\mathrm{amb.}}$ is the temperature at the time of recording, and b is the slope of the relationship between the call parameter and temperature (Platz and Forester 1988). The relationship between the data collected at ambient temperature and temperature-corrected data is therefore dependent on the relatonship between the call parameter and temperature, as expressed in this equation by b.

Coefficients of variation were calculated between all calls of the same individual, between all individuals, and between calls of the same individual recorded on different nights, for both uncorrected data, and data corrected to a temperature of 10°C. DFAs, grouping calls to individual males, were also carried out on both the uncorrected and corrected call data, in order to determine if individual discrimination can be improved by removing the effects of temperature. As with the analyses of coefficients of variation described in Section 3.3.2, comparisons between nights for single individuals could not be made with territorial call data, due to insufficient recordings.

3.3.5.2 Results

Advertisement Calls

Over the two seasons for which temperatures were recorded, 694 calls from 45 males were used to determine the effects of temperature on call variation. The temperatures recorded over these two seasons ranged from 6.6°C to 19.2°C.

Of the 17 call parameters used to describe each advertisement call, 10 exhibited significant relationships with temperature (Table 3.7). Seven of these 10 parameters described temporal features of the calls, which is a greater proportion than what would be expected by chance (Fisher Exact Test; $p = 0.04$). Temperature, therefore, had a greater effect on the temporal features of the advertisement calls of *P. bibronii* than on their spectral features.

Coefficients of variation were not significantly different between uncorrected data and data corrected for temperature, for any of the three groups of calls compared (Figure 3.10). In addition, the DFAs performed on both the corrected and uncorrected data resulted in similar proportions of calls being assigned to the correct male (uncorrected data: 69.6%; temperature-corrected data: 71.2%; $\chi^2 = 0.418$; $p = 0.518$).

Territorial Calls

248 calls from 34 individuals were used to determine the effect of temperature on variation in the territorial calls of *P. bibronii*. These calls were recorded at temperatures that ranged from 6.2°C to 19.2°C.

Only two of the seven call parameters used to describe territorial calls exhibited significant correlations with temperature; total call length, and pulse rate (Table 3.8). Both of these parameters described were temporal call features (of the three temporal features measured), while none of the four spectral features were influenced by temperature. This again shows that temperature tends to have an impact on the temporal features of anuran calls, rather than the spectral features.

As with advertisement calls, variation between territorial calls did not appear to be influenced by temperature, either within or between individuals (Figure 3.11). In addition, temperature

Table 3.7 Observed relationships between ambient temperature and the parameters measured to describe the advertisement calls of *P. bibronii*. * - significant at 0.05. ** - significant at 0.001. + - y: call parameter; x: temperature (°C). See Table 3.2 Legend for parameter abbreviations. Letters in parentheses indicate whether the parameter was temporal (T) or spectral (S) in nature.

Call Parameter	r^2	Relationship⁺
P#1 (T)	-0.18**	y = 8.2 - 0.14x
P# (T)	-0.07	-
M(75)1 (S)	-0.06	-
LGTH (T)	-0.53**	y = 0.36 - 0.01x
PRATE (T)	0.47**	y = 34.3 + 3.7x
SPREAD1 (S)	-0.07	-
LGTH1 (T)	-0.41**	y = 0.25 - 0.01x
SPREAD2 (S)	-0.17**	y = 2271 - 76.9x
PRATE1 (T)	0.48**	y = 23.8 + 1.9x
M(75)2 (S)	-0.16**	y = 4054 - 61.6x
MEAN2 (S)	-0.03	-
PEAKF (S)	0.04	-
PRATE2 (T)	0.36**	y = 141.5 + 7.1x
MEAN1 (S)	0.11*	y = 2415 + 6.5x
PEAKF1 (S)	0.02	-
PEAKF2 (S)	0.05	-
LGTH2 (T)	-0.30*	y = 0.07 - 0.001x

Table 3.8 Observed relationships between ambient temperature and the parameters measured to describe the territorial calls of *P. bibronii*. * - significant at 0.05. ** - significant at 0.001. + - y: call parameter; x: temperature (°C). See Table 3.3 Legend for parameter abbrevations. Letters in parentheses indicate whether the parameter was temporal (T) or spectral (S) in nature.

Call Parameter	r^2	Relationship⁺
LGTH (T)	-0.15*	y = 0.42 - 0.007x
M(75) (S)	-0.09	-
SPREAD (S)	-0.10	-
P# (T)	0.07	-
PRATE (T)	0.25**	y = 51.4 + 4.42x
PEAKF (S)	0.01	-
MEANF (S)	0.06	-

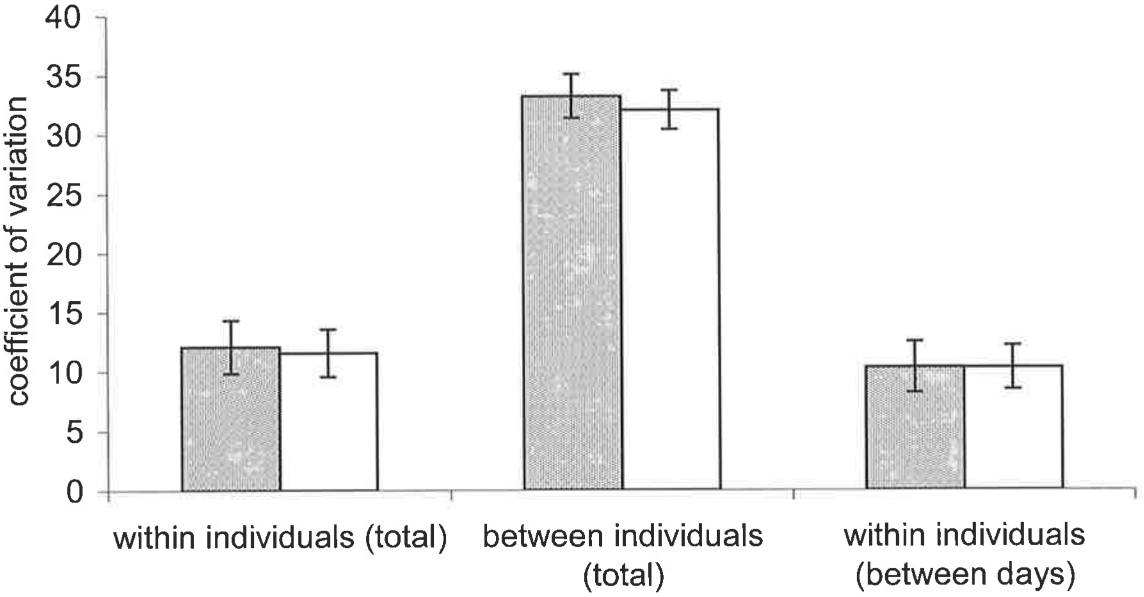


Figure 3.10 Coefficients of variation (CVs) calculated for call data variation exhibited between the advertisement calls of each individual, the calls of all individuals, and the calls of each individual on different nights, for raw call data (stippled columns) and call data corrected to a temperature of 10°C (see text). Sample size for each group is 21, the number of parameters measured.

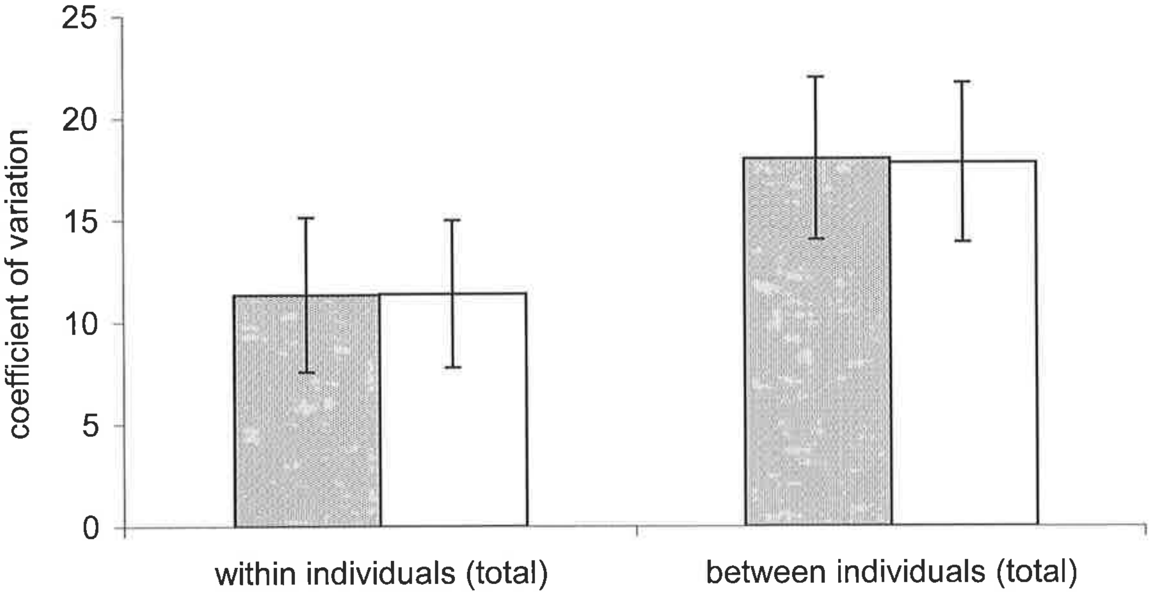


Figure 3.11 Coefficients of variation (CVs) calculated for call data variation exhibited between the territorial calls of each individual and the calls of all individuals, and the calls of each individual on different nights, for raw call data (stippled columns) and call data corrected to a temperature of 10°C (see text). Sample size for each group is 8, the number of parameters measured.

had no effect on the proportion of territorial calls that were assigned to the correct male using DFA; 49.2% of calls were correctly classified for both uncorrected calls and calls where the data had been corrected to 10°C.

3.3.5.3 Discussion

This present study has demonstrated that the parameters of *P. bibronii* calls most strongly influenced by temperature are those that describe temporal features of the calls, while the spectral features of these calls generally vary independently of air temperature. This general conclusion is supported by the results of previous studies concerning the effects of temperature on anuran calls. For example, in a study regarding reproductive isolating mechanisms between two sympatric species of *Scaphiopus* toads, (Forester 1973) investigated the effects of temperature on a number of call parameters. Both pulse rate and call length were found to be temperature dependent, while dominant frequency was not influenced by temperature. However, (Forester 1973) also demonstrated that the number of pulses was not influenced by temperature, thus implying that the observed effect of temperature on pulse rate stems from changes in call length with temperature, rather than changes in pulse number. The results presented in this thesis agree with this observation, with the total number of pulses in the calls of *P. bibronii* being independent of temperature for both advertisement and territorial calls.

Similar results were also found for *Hyla versicolor* (Gayou 1984), where all five temporal call parameters measured exhibited significant relationships with temperature, while dominant frequency (the sole spectral parameter measured) did not appear to be influenced by body temperature. However, (Gayou 1984) also found that the number of pulses in a call varied with temperature, an observation that was not found in this present study of *P. bibronii*, or in the study conducted by (Forester 1973).

In a study concerning speciation of *Microhyla* species, (Blair 1958) found that dominant frequency was significantly correlated with temperature for both the species examined. However, (Blair 1958) did not attempt to correlate any temporal call features with temperature, and dominant frequency was the only spectral feature measured.

The significance of temperature to the structure of anuran calls can only be addressed with certainty by measuring the temperature of the calling apparatus, rather than the temperature of the calling environment. (Gayou 1984) highlighted a number of problems with previous studies concerning the effects of temperature on anuran call structure. The author was principally concerned with inconsistencies in the method used to measure temperature, and demonstrated that a difference of "up to" 4°C can be found between air temperature and cloacal temperature. Air temperature was measured in this present study, since the broader objectives of the study called for methods of call recording and temperature measurement that did not require handling or other disruptions to the study organisms. While this methodological compromise may have led to inaccurate observations with regard to the relationship between temperature and call structure, the fact that similar patterns of call variation with temperature were found in this study to previous studies – including those that measured body temperature – suggests that the patterns observed here at least broadly reflect the impact that temperature has on call structure in *P. bibronii*.

The results presented here support the general suggestion that the temporal features of anuran calls are most strongly influenced by temperature, while spectral features generally vary independently of temperature. Of interest is the fact that the call parameters most influenced by temperature, were also the most variable, as suggested by analyses of coefficients of variation (Section 3.3.3). This observation agrees with the results of (Gerhardt 1991), who found that 'dynamic' parameters, such as call rate and call duration, changed significantly with temperature, while 'static' parameters, such as dominant frequency and pulse rate, did not. This study has shown that, in general, temporal parameters are the most variable, both within and between males, and that these parameters are generally those that are most influenced by temperature.

With regard to discriminating between individuals acoustically, these results suggest that the relatively invariant spectral parameters may be more useful in successful identification over time than temporal parameters, in contrast to analyses of coefficients of variation (Section 3.3.3). However, coefficients of variation were not significantly reduced when the effects of temperature were removed, nor were the classification results of discriminant function analyses significantly improved. Other factors than temperature, therefore, appear to be influencing the structural variability of the calls of *P. bibronii*, especially between calling nights.

What other factors are likely to influence the patterns of within-male call variation demonstrated in this study? Body mass and condition have been shown to influence call structure, through changes in the mass and tension of the calling apparatus (Wagner 1989b).

(Robertson 1986b) demonstrated that the body mass of *Uperoleia rugosa* changed during the breeding season, in a way that was dependent upon the status of the male. Calling territorial males, for example, lost body weight while maintaining territories, which had a subsequent impact upon the structure of the call of these individuals. Call features related to body weight, therefore, have the potential to change over time. However, such changes are likely to vary between individuals, as reductions in body weight are related to calling effort (both through the energetic cost of calling, and the time spent calling rather than foraging), while non-calling males possess the potential to actually increase in weight (Robertson 1986b).

Social conditions also have the potential to influence the structure of anuran calls. The advertisement calls of a number of species change in response to the calls of conspecifics (Wells and Schwartz 1984, Wagner 1989b, Howard and Young 1998), primarily through immediately lowering the dominant frequency of calls. However, this system of 'graded' aggressive responses to conspecifics (Wagner 1989b) is unlikely to occur in *P. bibronii*, as they possess an alternative call type with which to respond to an increased competitive threat by conspecific males. Therefore, rather than altering the structure of advertisement calls in response to competitive threats, male *P. bibronii* are more likely to simply switch call types (see also (Robertson 1984a).

Understanding the underlying causes for within-male call variation would thus appear to require information regarding the body mass and condition of calling males, as well as information on caller densities and social context. Future studies investigating these aspects of *P. bibronii* behaviour would, therefore, contribute to our understanding of the function of call variation in the social biology of this species.

3.3.6 Feature Analysis - Discussion

The preceding analyses of intraspecific variation in the calls of *Pseudophryne bibronii* provide us with some impression of vocal individuality in this anuran species, and the potential for acoustic identification of individuals over various time scales. In summary, these analyses demonstrate that, while *P. bibronii* exhibits vocal individuality, the potential of vocal individuality as identification tools may be limited to censuses conducted within the confines of a single night.

The primary reason for this observed pattern is the variation found between the calls of individuals recorded on different nights. One possible explanation for this observed pattern of call variation is temporal or seasonal variations in the calling environment, and its subsequent effect on call structure. Temperature, however, did not have a large effect on the proportion of calls which were correctly classified using DFA. Other environmental, behavioural or physiological changes may account for the observed patterns of call variation between nights.

3.4 Cross-correlation Analysis

3.4.1 Introduction

From the results discussed previously in this chapter, the calls of *P. bibronii* do not vary significantly more between individuals than between calls of each individual separately, suggesting that their use in individual identification would be limited or impossible. However, intra-individual variation was largely due to variation between calls recorded on different nights, and the calls of each individual recorded on a single night varied little, compared to inter-individual variation on single nights. While long-term monitoring of individuals using acoustics appears unlikely, the identification of individuals on a single night does appear to have some potential, which may thus lead to the development of single-night surveys of *P. bibronii*, with the use of acoustic signals.

As discussed in Chapter 2, the use of discriminant function analysis allows us to determine the level of acoustic individuality in the calls of *P. bibronii*; it does not, however, result in the development of a system of acoustic identification of individuals that can be readily used by biological investigators. The use of the cross-correlation method, however, brings us a step closer to a readily available system of acoustic identification. The justification and merits for using cross-correlation analysis have been discussed more fully in Chapter 2.

While the use of cross-correlation analysis has received criticism, their use has been generally accepted as being best suited for the analysis of pulsatile acoustic signals, such as cricket and frog calls (Baptista and Gaunt 1997). This section thus presents the results of cross-correlation analyses performed on the calls of individuals recorded on single nights.

3.4.2 Methods

The general methodology of cross-correlation analysis used throughout this thesis is described in Chapter 2. For the purposes of this chapter, cross-correlation analyses were performed between the calls recorded on a single night (see Section 3.3.4.3), for each night where the calls of three or more individuals were recorded, as previous analyses have suggested that vocal identification of individuals appears restricted in its usefulness to the identification of individuals on single nights. As described in Chapter 2, cross-correlation analysis compares the complete structure of two signals, and provides a correlation coefficient (r_x), a measure of similarity between the two signals. Identification accuracy can thus be expressed as the proportion of r_x values that are correctly classified as having compared two calls of the same individual, or two calls of two different individuals.

3.4.3 Results

As with other cross-correlation analyses presented in this thesis, the results of cross-correlation analyses performed on the calls of *P. bibronii* are presented as the maximum percentage of r_x values that are correctly classified as being produced by the same individual or two different individuals, at the optimal correlation threshold (r_x*). A graphical example of how the percentage of correctly classified calls changed with the correlation threshold for the calls of *P. bibronii* is given in Figure 3.12.

Advertisement calls

The results of cross-correlation analyses conducted on the advertisement calls recorded on single nights are summarised in Table 3.9. The peak percentage of r_x values that were classified correctly on these nights ranged from 71.7% to 90.8% (mean = 83.1 ± 2.2%), at r_x* values that ranged from 0.65 to 0.9 (mean = 0.75 ± 0.01). Calculated intra-individual r_x were significantly higher than inter-individual r_x for seven of the nine nights for which analyses were conducted (Table 3.9).

Territorial Calls

The results for cross-correlation analyses conducted on the territorial calls recorded on single nights are summarised in Table 3.10. The peak percentage of r_x values that were classified

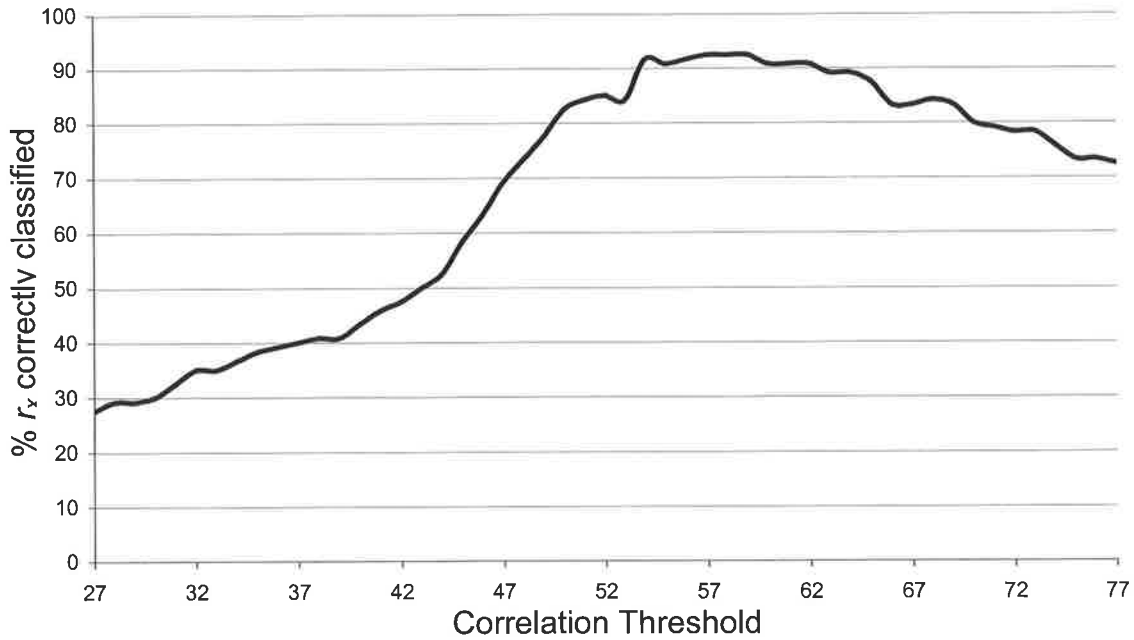


Figure 3.12 Example of the impact of correlation threshold (r_x*) upon the percentage of r_x values calculated for the calls of *P. bibronii* that were classified correctly as having been produced intra- or inter-individually. Example taken from advertisement call data recorded on 12 May 1999, based upon 5 individuals and 30 calls.

Table 3.9 Results of Cross-correlation analyses performed on the advertisement calls of *P. bibronii*. Analyses were conducted separately for each recording night. * - parametric t-test on log-transformed data; ** - Kruskal-Wallis test; otherwise parametric t-test on untransformed data.

Date	# males	# calls	peak % correct	r_x*	mean intra r_x (±s.e.)	mean inter r_x (±s.e.)	p (intra v inter)
11/5/98	6	34	82.46	0.67,0.68	0.58 (±0.009)	0.49 (±0.004)	<0.0001**
14/5/98	5	29	81.77	0.72,0.73	0.62 (±0.013)	0.56 (±0.005)	<0.0001
18/5/98	5	30	74.02	0.71,0.74-0.78	0.51 (±0.011)	0.49 (±0.005)	0.087*
6/4/99	4	25	71.67	0.68-0.69,0.72-0.75, 0.84,0.90	0.51 (±0.01)	0.46 (±0.006)	<0.0001*
10/4/99	7	73	83.49	0.72,0.73	0.56 (±0.005)	0.51 (±0.002)	<0.0001
20/4/99	7	18	89.54	0.69-0.70	0.45 (±0.02)	0.44 (±0.007)	0.61**
12/5/99	5	30	85.52	0.65-0.68	0.61 (±0.009)	0.51 (±0.004)	<0.0001*
20/5/99	10	67	90.82	0.80,0.83-0.86	0.59 (±0.007)	0.51 (±0.002)	<0.0001**
5/4/00	9	64	88.84	0.82,0.85-0.86	0.58 (±0.007)	0.54 (±0.002)	<0.0001*

Table 3.10 Results of Cross-crrelation aalyses performed on the territorial calls of *P. bibronii*. Analyses were conducted separately for each recording night. * - parametric t-test on log-transformed data; ** - Kruskal-Wallis test; otherwise parametric t-test on untransformed data.

Date	# males	# calls	peak % correct	r_x*	mean intra r_x (±s.e.)	mean inter r_x (±s.e.)	p (intra v inter)
6/4/99	4	19	76.61	0.58	0.52 (± 0.014)	0.48 (± 0.007)	0.002**
10/4/99	9	71	81.61	0.75	0.55 (± 0.006)	0.50 (± 0.003)	<0.0001**
19/4/99	5	21	78.57	0.61	0.62 (± 0.009)	0.54 (± 0.005)	<0.0001**
20/4/99	3	16	72.5	0.59-0.62	0.52 (± 0.014)	0.48 (± 0.009)	0.003*
12/5/99	5	16	92.5	0.57-0.59	0.66 (± 0.012)	0.45 (± 0.009)	<0.0001
20/5/99	6	10	91.11	0.81-0.85	0.72 (± 0.038)	0.64 (± 0.010)	0.016
5/4/00	5	18	87.58	0.64-0.67	0.71 (± 0.013)	0.56 (± 0.006)	<0.0001
16/4/00	8	24	89.13	0.76,0.78-0.81	0.69 (± 0.010)	0.57 (± 0.006)	<0.0001

correctly for these nights ranged from 72.5% to 92.5% (mean = 83.7 ± 2.6 %), at r_x* values that ranged from 0.7 to 0.86 (mean = 0.77 ± 0.01). Calculated intra-individual r_x were significantly greater than inter-individual r_x for all eight nights for which analyses were conducted (Table 3.10).

Comparison between Call Types

The percentages of calls correctly classified on single nights using cross-correlation analyses were statistically compared between the two call types. No significant difference was detected between the percentage of advertisement calls correctly classified on single nights, and the percentage of territorial calls correctly classified on single nights (t-test = 0.17; df = 15; p = 0.87).

3.4.4 Discussion

For surveys conducted on single nights, cross-correlation analyses achieved relatively high levels of identification accuracy, although the accuracy achieved was never perfect (100% of r_x values correctly classified). As discussed elsewhere in this thesis, the error rate observed when using cross-correlation analysis must be weighed against the potential benefits of acoustic identification by each individual investigator when determining the objectives of their study.

3.5 General Discussion and Conclusions

The analyses presented here generally compare a small number of individual males on any given night (between 3 and 10). Although investigators may wish to be able to identify a greater number of individuals, acoustic identification may still be useful, in that it has the potential to confirm the results of more extensive surveys in a non-invasive manner, providing a 'control' against which the effects of capture, handling and marking can be compared. Alternatively, many surveys of frog populations currently use counts of the number of calling males to estimate population size, with the principal assumption being that the number of calling males accurately reflects population size. Intensive studies using calls to identify small groups of individuals can be used to test this assumption, by obtaining accurate measures of male density at a local scale, and the relationship between calling activity and number of individuals.

In addition, many species of frog have become so severely fragmented that populations may not number much greater than 10 individuals in any case. For example, populations of both Corroboree Frog *Pseudophryne corroboree*, and Red-crowned Toadlet *Pseudophryne australis* contain many isolated breeding groups that number ten or less individuals (Osborne 1989)(K. Thumm pers. comm.). While the presence of these isolated populations is a concern for the conservation of these species, it does allow for high levels of acoustic identification accuracy within these populations, using cross-correlation analyses on the calls of different individuals.

While the use acoustic signals for individual identification has potential over single nights, the premise of using calls for population surveys of anurans is hampered by a number of difficulties associated with the biology of the taxa in general. Primarily, such a system could only be used to identify and monitor the males in a population, as the males of most anuran species are the only sex to call. Even within males, a certain proportion of the population (often called 'satellite' males) do not call during part or all of the breeding season, relying on alternative strategies to acquire mating opportunities (Arak 1988). In addition to females, therefore, these non-calling males would not be included in any survey based upon acoustic identification of individuals.

Such drawbacks of acoustic identification in anurans appear serious. However, what must be taken into account is the fact that current survey techniques - including those that rely on mark-recapture - are biased towards counting calling males in any case, as they are the easiest group for investigators to locate. While such biases are more extreme with the exclusive use of acoustic identification, again such negative biases need to be weighed against the negative impacts of capture and marking.

Cross-correlation analyses revealed that both call types exhibited similar levels of vocal individuality, and thus have similar potentials to be used to census individuals. While the use of territorial calls may provide an equivalent level of identification accuracy to advertisement calls for this species, the equivalent resolution may have to be weighed against the practicalities of collecting appropriate numbers of call recordings for individual identification. Calls in this present study were recorded opportunistically, in association with other studies investigating the biology of *P. bibronii* ((Mitchell 2001). Using this opportunistic recording method, approximately three times as many advertisement calls were obtained than territorial calls (968 advertisement calls versus 374 territorial calls), a direct indication of their use by the frogs. Increasing the number of calls recorded certainly has the potential to improve the accuracy of individual identification, simply as a function of identification certainty. Therefore, from a practical perpective, surveys of calling males may be easier to perform with the use of advertisement calls rather than territorial calls.

In summary, variation in the calls of *Pseudophryne bibronii* was found both within and between individuals, and varied across a range of temporal scales. As a result of significantly greater variation between nights and within individuals than within nights between individuals, the potential for identifying individuals based upon their acoustic signals is limited to surveys conducted on single nights. While this eliminates the possibility of monitoring individuals and populations over longer time periods, single-night surveys can be used to test the assumptions of surveys that use traditional identification techniques. The limitations of the acoustic identification technique described here should thus be weighed against the potentially negative impacts that such standard techniques (as outlined in Chapter 1) have upon study populations. Such assessments are likely to be context-specific, and need to be made by investigators on a case by case basis.

Chapter 4 The Singing Behaviour of *Dasyornis broadbenti*

4.1 Introduction

Song repertoires, where individual animals regularly use more than one song type, are prevalent among oscine birds, and thus the evolution of song repertoires has received considerable attention (see Kroodsma and Byers 1991 for a review). The most widely accepted explanation for the evolution of song repertoires is that they have evolved largely as a result of sexual selection, and that the unit of selection is primarily the number of different song types in an individual's repertoire (Searcy and Andersson 1986, Kroodsma and Byers 1991). In this case, the nature of the songs themselves has less bearing on an individual's fitness; it is the diversity of songs that an individual uses that is most critical. There is indirect evidence that larger repertoire sizes do indeed increase fitness (e.g. McGregor *et al.* 1981, Catchpole 1986), although evidence to date is largely correlative in nature, and is often confounded with other factors, such as territory quality and experience (Yasukawa *et al.* 1980, Cosens and Sealy 1986). In any case, this general explanation leads to the suggestion that the song types that make up an individual's repertoire are functionally interchangeable.

In some cases, however, the different song types that make up a repertoire have distinct functions, or are used in specific behavioural interactions. One example is song sharing, where a proportion of the song types in a bird's repertoire are shared with its territorial neighbours. Song sharing has been correlated with aspects of male fitness in two species (Payne *et al.* 1988, Beecher *et al.* 2000, Wilson *et al.* 2000; but see Grant 1984), and primarily plays a role in territorial interactions between neighbours. Neighbouring birds use shared song types during song contests, by either replying to a singing bird with the same song type (song-type matching; Armstrong 1963), or by replying with a song type that is different from the initiating song, but that is present in the repertoires of both of the territorial individuals (repertoire matching; Beecher *et al.* 1996). In both cases, the use of matched songs in territorial contests reduces the need to escalate these contests into physical battles, thus minimising the energetic cost and risk of injury that such escalations incur (Krebs *et al.* 1981). In addition to these benefits to intrasexual interactions, song sharing may also be used as a cue for mate choice by females, as the level of song sharing is indicative of the length of territory tenure, and thus the ability of males to obtain and maintain territories (Hill *et al.* 1999).

Assessing the function of song sharing in avian social behaviour has been assisted by the correlation of certain ecological and social factors with the extent of song sharing. Of particular interest has been the correlation between patterns of movement and song sharing, where nomadism and migratory populations have lower rates of song sharing than sedentary populations, or those migratory populations that regularly return to the same breeding territories (Beecher *et al.* 1994). Such patterns have now been shown for a number of avian species (eg. McGregor and Krebs 1989, Beecher, et al. 1994). The strongest evidence, however, comes from the study of different populations of the same species that exhibit different movement patterns, such as Rufous-sided Towhees (Ewert and Kroodsma 1994), Sedge Wrens (Kroodsma *et al.* 1999a, Kroodsma *et al.* 1999b) and Song Sparrows (Kramer and Lemon 1983, Beecher *et al.* 1994, Nielsen and Vehrencamp 1995). In these species, sedentary populations exhibit significantly higher rates of song sharing than migratory or nomadic populations of the same species. The relationship between movements and song sharing is far from resolved, with different, closely related populations of song sparrows exhibiting similar rates of song sharing, independent of the nature of their dispersal patterns (Hill *et al.* 1999). Further information regarding song sharing in other taxa is therefore required to improve our understanding of this apparent relationship.

This chapter investigates rates of song sharing in the Rufous Bristlebird *Dasyornis broadbenti*, a southern Australian species for which there is evidence of strong sedentary behaviour (Table 4.1 and Table 4.2). Rufous Bristlebirds form long term pair bonds, and while the boundaries of territories may fluctuate seasonally, the relative positions of territorial neighbours generally remains constant over a number of years. As such, territorial neighbourhoods are relatively stable, and bristlebirds are therefore expected to exhibit high levels of song sharing. In addition, I report on the estimated repertoire size for the Rufous Bristlebird, as well as observations on song-type matching and repertoire matching.

4.2 Methods

Recordings of Rufous Bristlebirds were made at the Coorong National Park, South Australia, approximately 12 km south-east of the township of Salt Creek (139°41'E, 36°13'S). This site is close to the western end of the distribution of the species, and is within the distribution of the western subspecies of the rufous bristlebird *Dasyornis broadbenti broadbenti*. The site consists of coastal heath vegetation (Specht 1972), dominated by coastal beard heath *Leucopogon parviflorus*, coastal wattle *Acacia longifolia* and coastal daisy *Olearia axillaris*.

Table 4.1 Capture and recapture locations for adult rufous bristlebirds, for individuals recaptured at least once, and initially caught as adults (to preclude possible effects of juvenile dispersal). All individuals were caught between January 1995 and December 1998. *n* is the number of times each individual was captured (standard errors not given for individuals caught twice only)(Paton and Seymour, unpubl. data).

Bird ID	*n*	Time interval between first and last capture (days)	Maximum distance travelled (m)	Mean (± se) time (days) between captures	Mean (± se) distance (m) moved between captures
1	2	1106	700	1106	700
2	3	635	10	318 (±143)	5 (±5)
3	5	1064	100	266 (±138)	76 (±14)
4	3	715	20	358 (±26)	23 (±13)
5	2	516	2251	516	2251
6	3	441	60	221 (±220)	127 (±29)
7	3	489	420	245 (±228)	221 (±201)
8	3	333	0	167 (±111)	0 (±0)
9	2	149	231	149	231
10	2	51	10	51	10
11	2	78	0	78	0

Table 4.2 Results of radiotracking data collected on six adult rufous bristlebirds, again highlighting the sedentary nature of this taxa (Paton and Seymour, unpubl. data).

Bird ID	# dates located	tracking period (days)	maximum N-S distance travelled (m)	maximum E-W distance travelled (m)
1	6	18	130	110
2	20	70	390	240
3	4	5	230	160
4	13	54	80	70
5	12	25	140	130
6	3	3	100	130

Recordings of Rufous Bristlebird songs were made with a Sony DAT Walkman TCD-D8 and Sennheiser ME-66 directional microphone. Subsequent analyses of recordings were done using Avisoft SAS-Lab (Specht 1998). Each song was converted into a sonogram (Sampling Frequency = 22 kHz) for visual analysis and song type classification. Song types were classified only when all three song components matched (Figure 4.1), as the song types used by bristlebirds are extremely stereotypic, with complete song components rarely found in more than one song type (e.g. Figure 4.2).

In order to measure repertoire size and the extent of song sharing in male and female bristlebirds, recordings were made of the songs produced by a small focal group of bristlebirds, comprising six pairs of territory-holding birds. While most of these individuals were colour banded as part of previous studies (Seymour and Paton 2000), the cryptic nature of the species largely excluded the use of these bands for identification in this study. As such, individuals were generally identified by mapping the territorial boundaries of each pair, through the identification of singing locations, as well as through occasional opportunistic colour band sightings. All of the focal individuals formed a territorial neighbourhood; that is, the territories of focal individuals were a maximum of one territory-width from the territories of all other focal birds. Recordings that could not be confidently assigned to a pair were excluded from all analyses; however, only 5% of all song recordings were unable to be assigned to a focal individual. Repertoire size was taken as the number of song types recorded for each individual. The rate of song sharing was calculated using the method of McGregor and Krebs (1982); overall, the proportion of song types shared was equivalent to the average number of song types shared between each pair of neighbours, divided by the average number of song types recorded for each individual. Recordings were made between 24 August and 3 September 1999, and 24 August and 6 September 2000.

4.3 Results

4.3.1 Song Description and Singing Behaviour

The rufous bristlebird song is sexually dimorphic, with the members of breeding pairs often singing antiphonally (Seymour and Paton 2000) . Male and female song types differ markedly in structure. The different songs (often termed ‘A’ and ‘B’ songs) of some antiphonal Australian bird species do not necessarily represent male and female songs, as is the case with

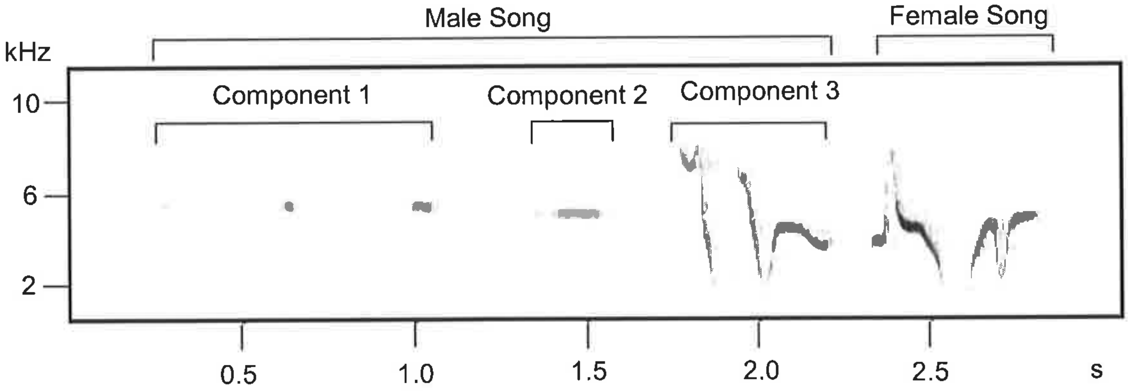


Figure 4.1 Sonogram of rufous bristlebird song, showing the male and female songs, and the components of the male song. This sonogram also provides an example of a pair of bristlebirds singing antiphonally.

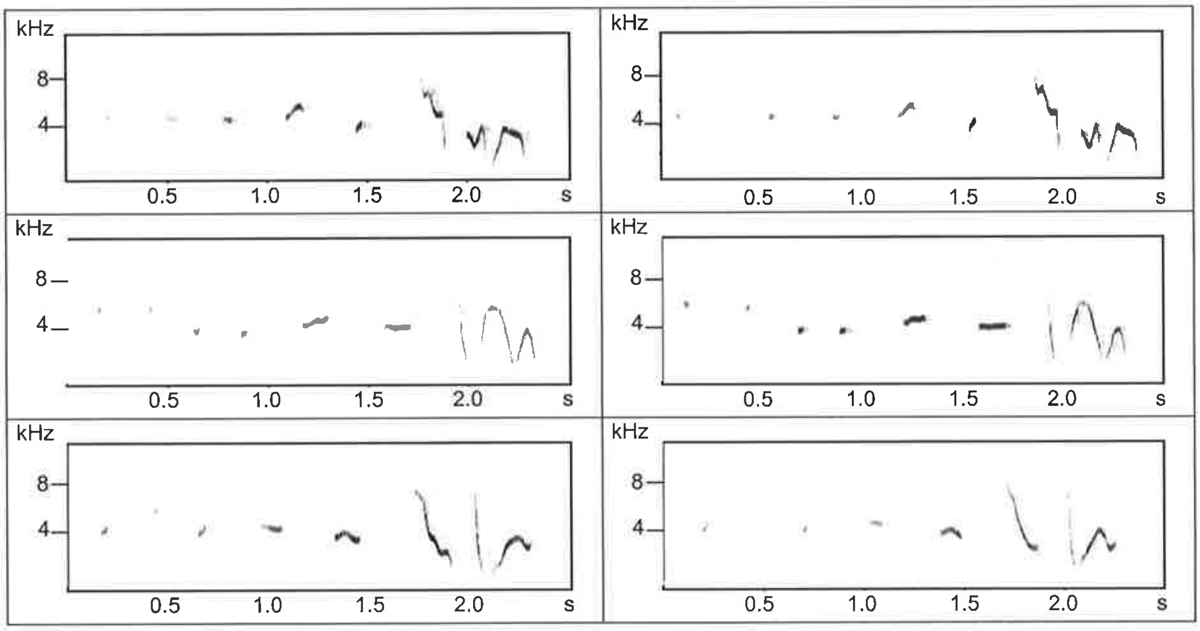


Figure 4.2 Sonograms of several song types used by male rufous bristlebirds at the Coorong, South Australia. The three sonograms on the left are three different song types from the same individual, while the three sonograms on the right are the same song types as the ones on the left, but sung by three different individuals. Each horizontal pair of sonograms thus represents a single song type, sung by two different males.

Western Whipbirds (Smith 1991), and Eastern Bristlebirds (Baker 1998), with the two classes of song often being interchangeable between the sexes (Baker 1998). However, the little evidence available for *Dasyornis broadbenti* suggests that these different songs can be assigned to the two sexes with confidence for this species (Seymour and Paton 2000). The male song consists of three components, each of which is made up of a number of syllables (Figure 4.1). The first is a series of short, simple notes, which either remain at the same frequency, or alternate between two frequencies. The second component, which may be absent, is a series of one to three notes which, while still relatively simple in structure, are generally longer than the notes of the first component. The final component is a series of three notes, which are complex relative to the first two components, and vary rapidly in frequency. The female song broadly resembles the final component of the male song (Figure 4.1), although no female songs in this study were identical in structure to the final component of male songs. The definition of these components, however, was performed purely from a song structure perspective; that is, the three song components only differ in their structure. The identification of these components should not, therefore, be interpreted in a way that suggests either independent song functions for each of the components, or that the components are learnt by males independently.

Rufous bristlebirds rarely switched song types within a single continuous period of singing; that is, continuous singing events rarely contained more than one song bout. Of the 266 recordings of singing males, a song type switch was observed on only two occasions. For females, song type switches were observed on five occasions from the 110 continuous singing periods recorded. Both male and female bristlebirds, therefore, generally used the same song type throughout a continuous bout of singing.

4.3.2 Repertoire Size

In 1999, song recordings were made of 6 focal pairs of Rufous Bristlebirds. In 2000, song recordings were made of 4 of the focal pairs recorded in 1999. 50 different song types were recorded for male bristlebirds, and 19 different song types for female birds. In 1999, 38 male song types were recorded, while 29 of these were also recorded in 2000, plus an additional 12 song types unrecorded in 1999. In 1999, 17 female song types were recorded, 13 of which were common with song types recorded in 2000. An additional five female song types were recorded in 2000 but not 1999. Because of the extremely cryptic nature of bristlebirds, intensive studies of more individuals was difficult. Although a limited number of song recordings were collected from other individuals outside of this focal neighbourhood (see Section 4.3.5 and Chapters 5 and 6), these recordings were not extensive enough to obtain accurate measures of repertoire size.

While I could not be certain that all song types were recorded for each individual, cumulative plots of the number of song types recorded against the number of song bouts recorded suggested that the repertoire sizes observed approached the actual repertoire size for these birds, and that any unrecorded song types were rarely used (eg. Figures 4.3 and 4.4). Observed repertoire sizes for male rufous bristlebirds ranged between 29 and 32 song types for the four birds recorded over the two years of the study (mean = 30.5 ± 0.65). Female repertoire sizes ranged from 12 to 14 for the four birds recorded (mean = 13.5 ± 0.96). Repertoire size differed significantly between the two sexes (t-test = 14.7; df = 6; $p < 0.0001$).

4.3.3 Extent of song sharing

Song sharing was extensive between neighbouring bristlebirds. The proportion of song types shared between pairs of close neighbouring male bristlebirds ranged between 60.0 % and 71.2 % of song types (mean = 64.5 % ± 0.02; $n = 6$), while female bristlebirds shared between 50.0 % and 73.3 % of song types (mean = 58.9 % ± 0.04; $n = 6$).

If song sharing between neighbours were significant in conveying important information, one might expect that shared song types would be used in preference to unique song types. Male rufous bristlebirds in this study preferentially use song types shared with their neighbours, over song types unique to their repertoire (Figure 4.5; $\chi^2 = 17.93$; $p < 0.0001$). Female bristlebirds also appear to preferentially use shared song types (Figure 4.6; $\chi^2 = 5.76$; $p = 0.016$). The probability of randomly encountering a song type shared between neighbours, therefore, ranged from 67.9 % to 79.4 % ($X = 75.2 \pm 0.02$ %) for male birds, and between 67.7 % and 73.4 % ($X = 70.0 \pm 0.01$ %) for female birds. The probability of encountering a shared song type was significantly greater than the proportion of song types shared for male birds (t-test = 4.56; df = 10; $p = 0.001$), and female birds (t-test = 3.05; df = 10; $p = 0.012$).

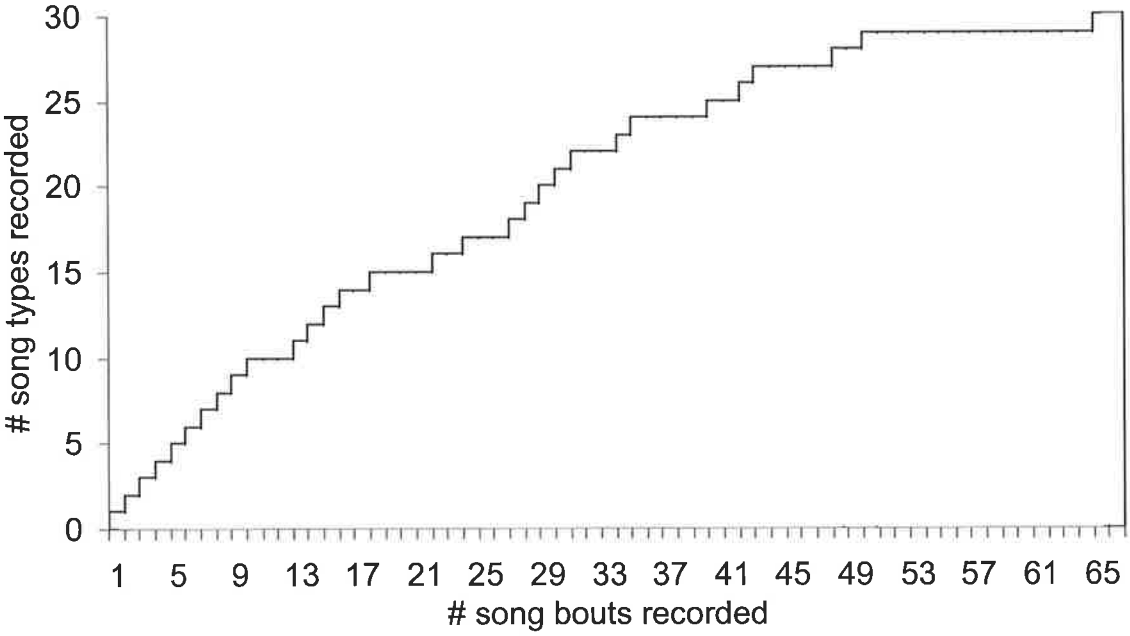


Figure 4.3 Example of a cumulative plot of the number of song types recorded as a function of the number of song bouts recorded for a male rufous bristlebird

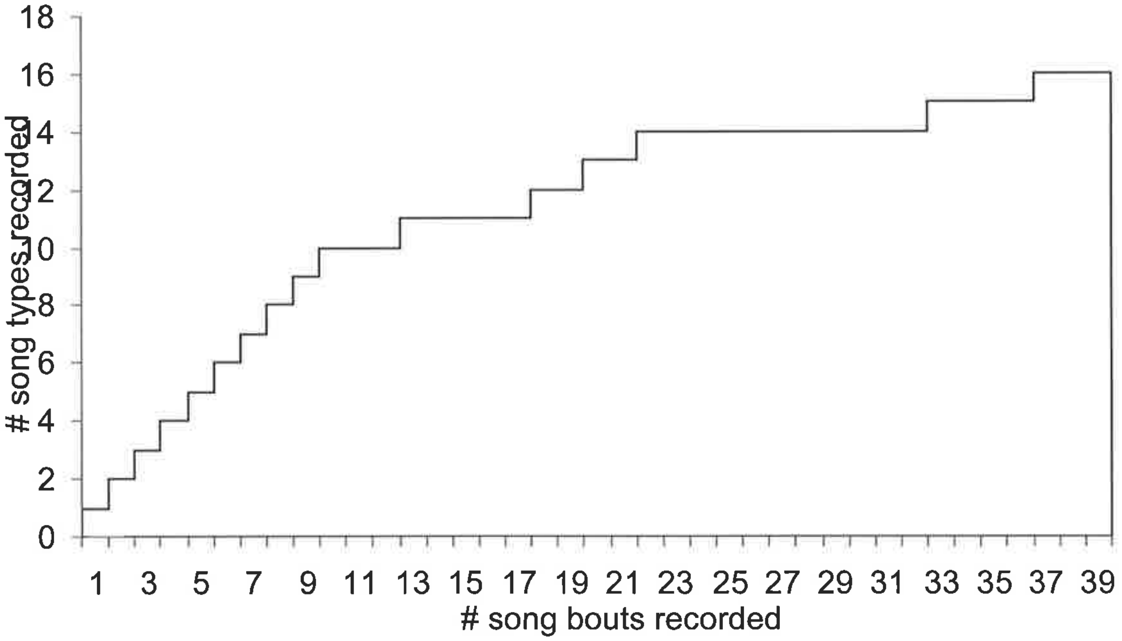


Figure 4.4 Example of a cumulative plot of the number of song types recorded as a function of the number of song bouts recorded for a female rufous bristlebird

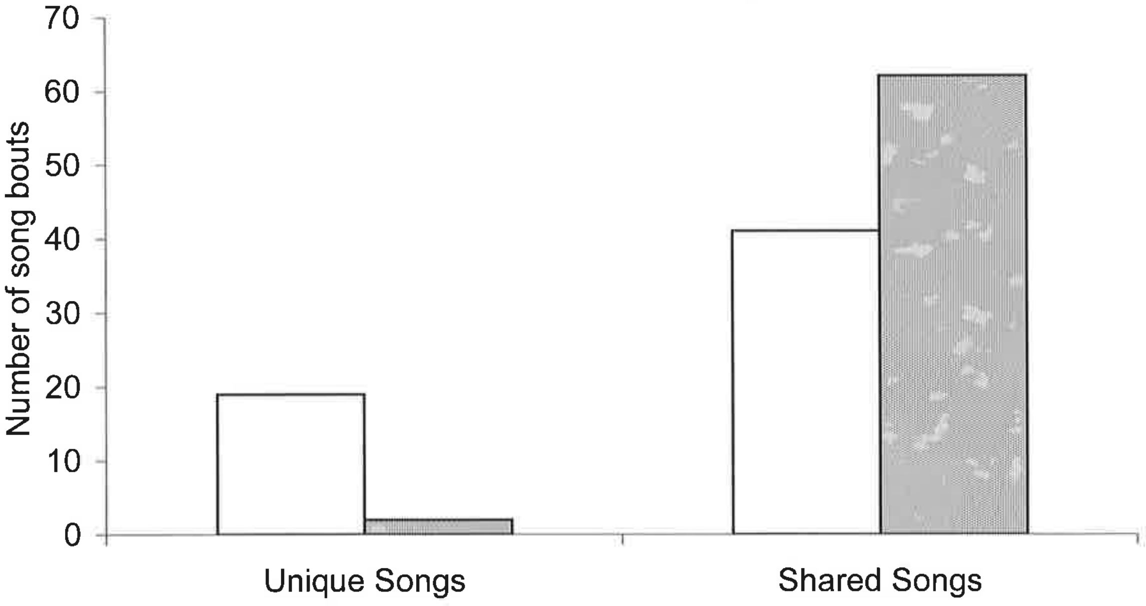


Figure 4.5 Number of male song types recorded once only (open bars), and more than once (hashed bars), for song types unique to one individual and song types shared by two or more territorial neighbours

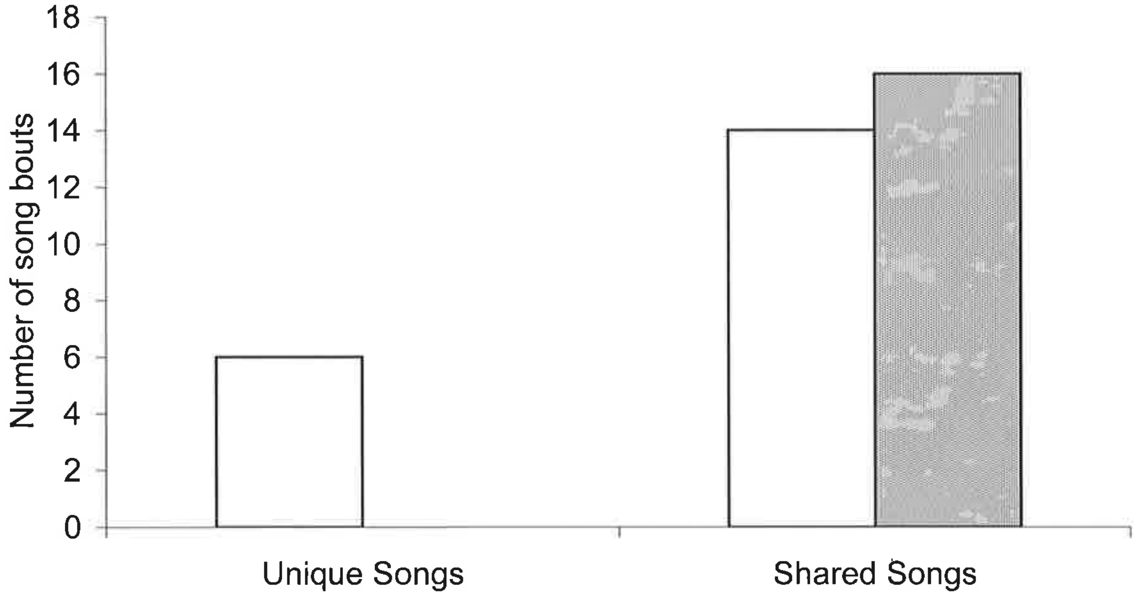


Figure 4.6 Number of female song types recorded once only (open bars), and more than once (hashed bars), for song types unique to one individual and song types shared by two or more territorial neighbours

4.3.4 Type Matching

Song-type matching between neighbouring rufous bristlebirds was recorded on a number of occasions. Song contests here were defined as vocal interactions between two birds of the same sex, identified as such when two birds of the same sex were singing at the same time, in close proximity (e.g. near a territorial boundary). Of the 15 song contests recorded between focal males, song-type matching occurred on 4 occasions, which was significantly greater than would be expected by chance (binomial test; observed = 26.7%; expected = 4.3%; $p <$ 0.004). Repertoire matching was also prevalent; focal birds used a song type from a neighbour's repertoire when interacting with that neighbour on 12 of 15 occasions. However, due to the high degree of song sharing between neighbouring males, this level of repertoire matching was not significantly greater than expected by chance (binomial test; observed = 80%; expected = 59.9%; $p = 0.09$). Rates of song- and repertoire-matching were not estimated for female birds, as they were never observed initiating or participating in territorial song contests during this study.

4.3.5 Extensive song type comparisons

Although song sharing was found to be high between neighbouring individuals in this study, a territorial function for song sharing cannot be presumed unless one can demonstrate that such song sharing is higher between neighbours than between any pair of birds in a population. In order to test whether song sharing between neighbours is greater than song sharing throughout a population, the song types recorded from the eight birds that form the focus of this study were compared with song types recorded opportunistically at Tea-Tree Crossing, located approximately 7.5 km north-west of the site where the eight focal birds were located, but still within the same continuous population. If song sharing between neighbours was no greater than between birds within the population as a whole, the probability of recording a song type that was common between the focal birds and birds recorded at Tea-Tree Crossing would be equal to the probability of detecting a shared song type within the focal neighbourhood (ie 75.2% for males and 70.0% for females).

Overall, 20 male bristlebird song bouts, and 10 female bristlebird song bouts were recorded from Tea-Tree Crossing, comprising 16 male song types and nine female song types. Of the 16 male song types recorded, six were also found amongst the repertoires of the four focal male birds (37.5 %), while three of the nine female song types were also found amongst the repertoires of the four focal female birds (33.3 %). While song types used by the eight focal individuals were also used by bristlebirds at Tea-Tree Crossing, the proportion of shared song types detected between these two sites was less than what would be expected if rates of song sharing were as high between these sites as between territorial neighbours within sites.

4.4 Discussion

Amongst the most detailed studies of song sharing, a general pattern has emerged that suggests a link between sedentary behaviour and higher levels of song sharing between territorial neighbours. This chapter provides more support for this relationship, with the sedentary rufous bristlebird exhibiting levels of song sharing that ranged from 42% to 69% between territorial neighbours. These results are comparable to levels of song sharing in other sedentary populations and species (24% to 71%), which are generally (although not always) higher than the rates found in populations that exhibit unpredictable migratory or nomadic patterns of movement (4% to 34%; Ewert and Kroodsma 1994, Hill *et al.* 1999, Kroodsma *et al.* 1999a, Kroodsma *et al.* 1999b).

Rufous bristlebirds in this study were observed to preferentially song-type match with neighbours, but did not repertoire match more than expected by chance. These results contradict the results of previous studies, which have generally found that territorial individuals will song-type match to strangers (Falls 1985), and preferentially repertoire match with known territorial neighbours (Beecher *et al.* 1996). Rufous bristlebirds on the Coorong breed from August to October (Pizzey and Knight 1999), so this study was therefore conducted at the beginning of each breeding season. Although bristlebird neighbourhoods tend to be stable over long periods of time (based upon banding and tracking data; see Tables 4.1 and 4.2), territorial interactions are likely to be almost absent during the late Autumn and Winter. As such, territorial individuals may have to re-establish territorial boundaries at the beginning of each breeding season, and re-evaluate the identity and status of their territorial neighbours. These activities may require an initially higher level of antagonism between neighbours, resulting in higher levels of song-type matching, and reduced repertoire matching. This trend may reverse later in the breeding season, once relationships between territorial neighbours are re-established.

With regard to testing hypotheses concerning ecological correlates of song sharing, the strongest conclusions can be drawn from comparisons between closely related species, or subspecific taxa of the same species, as such comparisons limit potentially confounding phylogenetic factors. The majority of such studies have thus compared sedentary populations of a species with nomadic populations of the same species, or closely related species. Such comparisons, however, are not possible for rufous bristlebirds. Ecological studies of the eastern subspecies of rufous bristlebird (*D. b. caryochrous*) suggest that this subspecies is also sedentary (B. Wilson pers. comm.), and at an interspecific level, all three species of bristlebird (*D. broadbenti*, *D. longirostris* and *D. brachypterus*) are considered sedentary in nature (Baker 1998, Garnett and Crowley 2000, Seymour and Paton 2000). While these observations eliminate the possibility of comparing nomadic populations of bristlebird with the sedentary populations presented in this study, they still allow for future comparisons of song sharing between sedentary populations and species, which are presumably genetically as well as geographically distinct. Closely related populations of song sparrow have been shown to exhibit similar levels of song sharing, despite differing in their movement behaviours (Hill *et al.* 1999). Comparing the results of this study with the extent of song sharing in *D. b. caryochrous* and other *Dasyornis* species would provide us with a test for the opposite effect: genetically distinct populations with the same apparent patterns of movement and dispersal. Such tests may thus assist in separating the effects of genetics and phylogenetics from the perceived relationship between residency and song sharing.

Despite being an analysis of song sharing in a single species, this study provides another example of the relationship between patterns of movement and rates of song sharing in avian species with song repertoires. How, then, does song sharing develop in rufous bristlebirds? For other sedentary bird taxa, two models of song development have been proposed. The first suggests that birds develop their song repertoires prior to dispersal, learning songs from adult tutors, including their parents and parents' territorial neighbours (Cunningham and Baker 1983). Subsequently, birds do not disperse far from their natal territories, and form territories that may share boundaries with their parents and other tutors. An alternative model suggests that birds do not develop their song repertoires until after they have dispersed from their natal territory, and song types are learnt from territory-holding birds in post-dispersal neighbourhoods (Payne 1981). Seymour and Paton (2000) found that dispersing rufous bristlebirds were less than 15 months old, with some birds dispersing prior to six months of age. In addition, at least some individuals disperse considerable distances from their natal territories (Seymour and Paton 2000). Although behavioural and ecological information is sorely lacking in this species, these observations do suggest that, unless bristlebirds develop their song repertoires at an early age, they are likely to learn songs from neighbours in their post-dispersal neighbourhood. However, it is still difficult to assess the significance of each of the described models to the development of song sharing in the rufous bristlebird, as we still do not know at what age bristlebirds develop their song repertoires. With the use of captive reared birds, experiments could be designed to improve our understanding of song development in this species, and of the proximate mechanisms of song sharing in general. Such studies, however, would have to be coupled with more extensive studies regarding dispersal in *Dasyornis broadbenti.*

In conclusion, the evidence presented here suggests that male and female rufous bristlebirds each share a considerable proportion of their song repertoires with immediate neighbours, a suggestion which, considering the sedentary nature of the species, is expected. In addition, while the use of some song types extended beyond immediate territorial neighbourhoods, sharing between neighbours is higher than between non-neighbours. This information can thus be used to design methods of determining the level of song individuality exhibited by members of the species, and subsequent identification of individual birds by biologists. Such ideas will developed more extensively in Chapter 5.

Chapter 5 Vocal Individuality in *Dasyornis broadbenti*

5.1 Introduction

"There is a peculiar virtue in the music of elusive birds"

Aldo Leopold, 'A Sand County Almanac'

The identification of individuals has probably received the greatest attention amongst ornithologists, with individual identification yielding important information regarding the ecology and behaviour of bird populations. For example, information regarding the identity of individuals in study populations has resulted in significant advances in our understanding of avian demographics (eg. Payne and Payne 1990) and movement patterns (Nicholls *et al.* 1995). As a result of this extensive interest in avian ecology at an individual level, as well as the fact that the majority of avian species are particularly vocal, the development of acoustic identification techniques has largely focussed on bird species.

Acoustic identification of individuals has been attempted to varying degrees in a number of bird species. The earliest authors of acoustic identification research were general in nature, focussing on species that particularly interested the investigators for reasons independent of their vocal behaviour, such as endangered species conservation (Gilbert 1986, Saunders and Wooller 1988). More recent studies have suggested that, in addition to the general benefits of acoustic identification outlined in Chapter 1, a particular suite of species may especially benefit from the development of such techniques. For example, the study of such species may benefit from the development of non-invasive identification techniques (including acoustic identification) because they are threatened with extinction, and thus capture is especially risky (Gilbert and McGregor 1994). More particularly, the development of acoustic identification techniques would be especially suitable for the study of species that are normally difficult to identify and monitor visually, such as nocturnal species, or those species that are cryptic and/or dwell in dense habitat (Peake *et al.* 1998). In Australia, a suite of bird species exist that are extremely difficult to observe visually, but, conversely, are also extremely vocal. A system of individual identification based upon acoustic signals would be of particular advantage for the study of this suite of species, especially considering that many of these cryptic, vocal species are nationally or regionally threatened (Garnett and Crowley 2000).

Dasyornis broadbenti is a shy and cryptic species of terrestrial bird, that generally dwells in moderately dense coastal heath that has variously been described as "thick coastal scrub" (Smith 1977), "closed coastal scrub" (Peter 1999) and "dense coastal heath" (Morcombe 1986). Essentially, the optimal habitat for *D. broadbenti* contains a heath understorey in which the vegetation is of a relatively high density. As a result of its cryptic behaviour and dense habitat, *D. broadbenti* is considered a difficult species to observe in the field (Peter 1999), a fact that is reflected in the extremely limited knowledge available regarding the behaviour and ecology of the species.

Conversely, rufous bristlebirds are also well known for their vocal nature, such that many surveys and observations of the species have been conducted by initially locating individuals by their voice (Blakers *et al.* 1984). These aspects of the species' ecology have been known for some time, with most reports regarding the biology of *D. broadbenti* discussing these particular aspects. For example, Ross (1911) wrote:

> "I spent the whole of the next day in that gully, but I had to return to the township in the evening without having caught a glimpse of a Bristle-Bird, although…I heard birds and followed the calls through the scrubs several times." (Ross 1911, p120)

Even the most recent published literature concur with these observations:

> "Bristlebirds are shy and cryptic, and inhabit dense vegetation. However, although difficult to see, rufous bristlebirds are easily located, even when among dense vegetation, by following their loud and characteristic calls" (Peter 1999, p10)

The general behaviour and ecology of *D. broadbenti* thus appear to make the species an ideal candidate for acoustic identification, both because it is a particularly difficult species to observe visually, and because its vocalisations are particularly easy to record and analyse. In addition, *D. broadbenti* is a species of some conservation concern, with the species as a whole being recently listed as Near Threatened (Garnett and Crowley 2000). The eastern subspecies, *D. b. caryochrous*, is listed as Vulnerable in the 2000 Action Plan for Australian Birds (Garnett and Crowley 2000), and is listed as threatened on Schedule 2 of the Flora and Fauna Guarantee Act, Victoria (1988). While the Coorong subspecies *D. b. broadbenti* was listed as of Least Concern (Garnett and Crowley 2000), its extremely limited range and apparent inability to disperse through inhospitable habitat suggest that the species as a whole should be treated with caution, a suggestion highlighted by the apparent extinction of the western subspecies *D. b. litoralis*. Again, techniques used to monitor such species should limit or eliminate potential impacts, such as those that may potentially arise as a result of capture, handling and marking.

While the potential for acoustic identification of individuals has been shown for a range of vocal species, one of the greatest challenges to the technique is the development of an acoustic identification system for species with extensive song repertoires. The majority of species for which acoustic identification has been demonstrated use only one or two simple types of song, making direct comparisons between individuals relatively easy. Comparing the songs of species with complex song repertoires of many song types poses a number of challenges, especially in cases where the signal types are not universal to all of the individuals in a population. Overcoming these challenges is important, as acoustic identification should allow for the comparison of songs both within and between individuals, independent of the song type that is encountered by the investigator. For example, acoustic identification requires a system that is able to re-identify each individual even in cases where the song used for re-identification is a different song type to the song that the individual was originally identified with.

As described in Chapter 4, the singing behaviour of *D. broadbenti* allows for the testing of these ideas, as male and female *D. broadbenti* have song repertoires of up to 32 and 14 different song types respectively, of which a proportion are shared between individuals in the population, especially territorial neighbours. As a result, comparisons between the common songs of different individuals can be made, as well as comparisons between song types, both within and between individuals. The broad objectives of this chapter, therefore, are twofold. First, I wished to test whether shared song types can be used to discriminate between individual rufous bristlebirds of both sexes. Second, I wished to test whether song features that are common to a number of song types can also be used to discriminate between individuals, thus allowing individual identification across multiple song types.

5.2 Methods – Recording

The field site, and methods for recording analysing songs are described in Chapters 2 and 4. Recordings of twelve individuals (six male, six female) were obtained in 1999, while four of these six pairs were re-recorded in 2000. These four pairs that were recorded over two years were the four for which repertoire size was obtained in Chapter 4. The number of separate recordings obtained for each individual ranged from 8 to 88 for male birds ($X = 46.3 \pm 12.9$), and from 4 to 39 for female birds ($X = 19.8 \pm 5.4$).

In addition to the twelve individuals for which extensive recordings were obtained, additional songs were recorded from approximately 16 other individuals, within the same continuous linear population, including the individuals recorded at Tea-Tree Crossing whose songs were described briefly in Chapter 4. Each of these individuals were generally recorded on only one occasion. As these individuals were not monitored as intensively as the focal individuals, their identity could not always be independently assessed. As a result, the songs of these additional individuals were only compared with the songs of the focal individuals, and each other, following the demonstration of vocal individuality amongst the focal individuals (see Section 5.6).

5.3 Comparison of Shared Song Types

As individuals within bristlebird populations share many of the song types in their repertoire, these shared song types provided an initial method of comparing the songs of different individuals, and as such, a way of assessing vocal individuality. In this case, the comparison of shared song types for *D. broadbenti* is equivalent to the comparison of common call types (advertisement or territorial calls) in *P. bibronii*, although the number of different signal types in *D. broadbenti* is obviously much greater. As with other assessments of vocal individuality presented in this thesis, songs were first compared using discriminant function analysis (DFA), in order to make a preliminary assessment of vocal individuality for subsequent cross-correlation analyses.

5.3.1 Discriminant Function Analysis

5.3.1.1 Methods

For the purposes of comparing shared song types between different individuals, a number of song parameters were chosen to describe each song type. As the structure of male and female songs are fundamentally different, the method of describing the songs of males and females was also different.

As described in Chapter 4, the songs of male rufous bristlebirds are composed of three distinct components (see Figure 4.1), and the parameters chosen for the DFAs reflect this. Each of the syllables of a song was described using nine parameters, six of which describe spectral features of the song, and three of which describe temporal features. The number of syllables in the third component of male bristlebird songs remained remarkably consistent within the Coorong population upon which this study is based, both between individuals and song types (see descriptions of songs in Chapter 4), although the number syllables in the first component varied significantly, and was dependent on whether the beginning of each song was recorded. Any observed variation in the first component may therefore have been a reflection of the song recording, rather than the song itself. As such, only the final two syllables of the first component were analysed, to eliminate these potential recording effects. Thus for each song, six syllables were described (two from component 1; one from component 2 and three from component 3). The nine parameters used to describe each of these syllables were: syllable length, minimum frequency, time (from beginning of syllable) at which minimum frequency occurred, maximum frequency, time at which maximum frequency occurred, frequency range, frequency at beginning of syllable, frequency at end of syllable, and mean frequency change (the average change in frequency over the length of the syllable, calculated as the difference between the frequency at the end of the syllable and the frequency at the start of the syllable, divided by the length of the syllable). In addition to these parameters, five extra parameters were used to describe the length of time between syllables, and six parameters used to describe features of the entire song, such as total song length, overall minimum and maximum frequencies and overall frequency range, and where these frequencies occurred in the song. In total, 65 parameters were used to describe each male rufous bristlebird song.

As has already been suggested, the female song of the rufous bristlebird essentially resembles the final component of the male song (Figure 4.1), although a number of female song types were comprised of only two syllables. As such, the same parameters used to describe this final component of the male song were also used to describe the female song. Female songs were thus generally described by measuring 35 parameters, except in cases where the song type was comprised of two syllables, where 25 parameters were used.

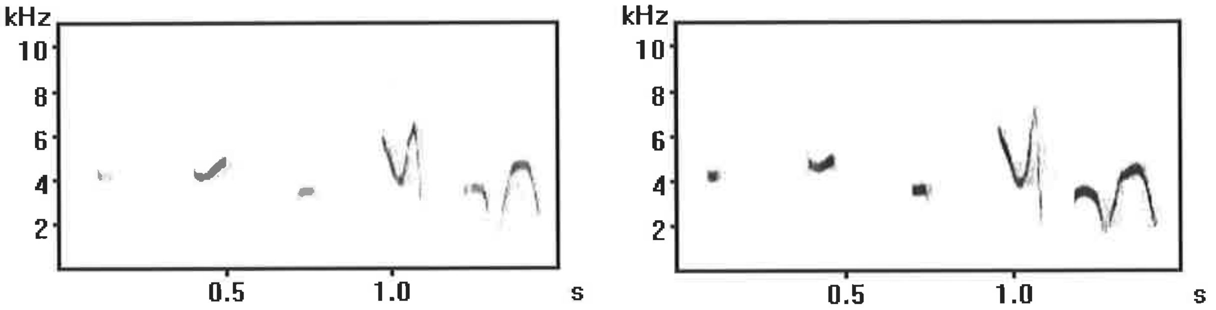
Based on these parameters, a DFA was performed on each song type, grouped by individual. However, for all analyses, a large number of parameters were excluded due to a high level of parameter redundancy. A parameter was thus excluded from analyses if the correlation coefficient between it and another parameter was greater than 0.8. The mean number of parameters used to construct the discriminant functions on male songs was therefore only 10.0 (± 5.73) for the analyses of the total song, 9.5 (± 3.9) for the analyses of the first two components combined, and 9.0 (± 4.5) for the analyses of the final component. On average, 8.0 (± 5.3) parameters were used to construct the DFA performed on female songs.

In addition to analysing each entire song, DFAs were also performed separately on the first two components of the male song combined, and the final component of the male song, in order to assess the importance of each of these components to the discrimination of individual male rufous bristlebirds acoustically.

DFAs were only performed on songs recorded in 1999, as a way of making a preliminary assessment of vocal individuality.

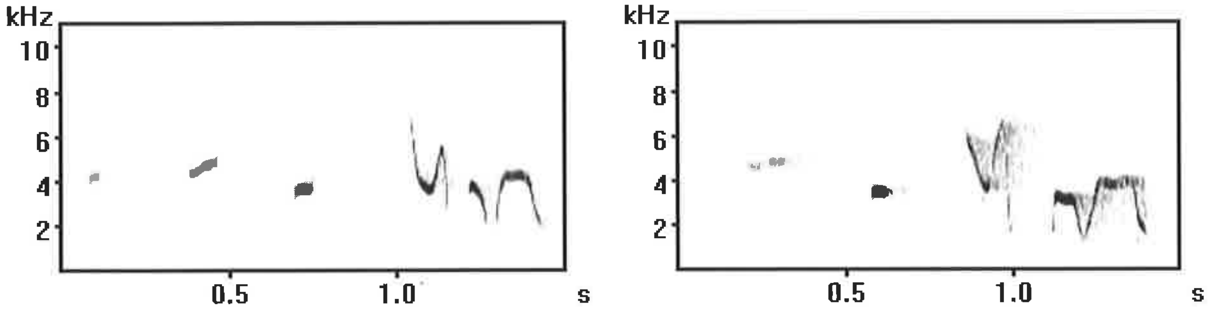
5.3.1.2 Results

In 1999, 20 different song types were recorded for more than one male individual, for the six focal males observed in this study (see Chapter 4 for detailed results of song sharing). Sonographic examples of each of these 20 song types are presented in Appendix B. The results of the DFAs performed on each of song type are summarised in Table 5.1. The DFAs reveal that, while neighbouring individuals use a proportion of the same song types, these shared song types differ significantly between these individuals. An example of how shared song types differ between individuals is presented in Figure 5.1. All song types exhibited a significant difference between individuals in structure, based upon the parameters used to describe the song. When the entire song is used to discriminate between individuals, 100% of the songs were classified to the correct individual for 19 of the 20 song types analysed, with the final song type classifying 82.8% of songs correctly. Overall, a mean of 99.1 (±9.9) % of songs were classified to the correct individual, for the 20 song types analysed (Table 5.1). However, a similar result was obtained when only the final component was used to perform each analysis (mean = 98.3 ± 1.2%; Table 5.2), or when the syllables of the first two components alone were used to perform the analysis (mean = 98.8 ± 0.67%; Table 5.3). No significant difference was detected between the proportion of songs classified correctly between these three analyses (Kruskal-Wallis Test; Z = 1.14; df = 2; $p = 0.56$).



Male 4, recorded 29 August 1999

Male 2, recorded 24 August 1999



Male 3, recorded 26 August 1999

Male 6, recorded 29 August 1999

Figure 5.1 Example sonograms of the same song type being sung by four different male rufous bristlebirds, highlighting the variation that occurs between individuals using the same song type. Example taken from male song type G, recorded in 1999.

Table 5.1 Summary of results of discriminant function analyses performed on the shared songs of male Rufous Bristlebirds in 1999, for the total song. See Appendix B for the structure of these song types.

Song Type	# birds	# songs	Wilks λ	F	p	% correct
B	3	27	8.3×10^{-4}	18.9	<0.0001	100
G	4	29	1.0×10^{-8}	173.4	<0.0001	100
H	2	32	1.1×10^{-1}	14.4	<0.0001	100
K	3	22	3.3×10^{-4}	13.7	<0.0001	100
R	4	20	9.8×10^{-5}	9.4	<0.0001	100
S	4	27	3.3×10^{-4}	10.9	<0.0001	100
E	2	9	1.2×10^{-1}	22.7	0.002	100
N	2	8	3.8×10^{-2}	33.5	0.003	100
O	2	13	9.7×10^{-3}	51.2	0.0009	100
Q	2	32	1.7×10^{-2}	32.2	<0.0001	100
T	3	11	4.9×10^{-3}	16.7	0.0001	100
V	2	9	5.7×10^{-3}	520.2	<0.0001	100
X	2	39	3.4×10^{-3}	399.3	<0.0001	100
W	2	20	7.2×10^{-3}	124.6	<0.0001	100
Y	3	33	4.1×10^{-3}	9.2	<0.0001	100
Z	2	23	2.9×10^{-2}	39.8	<0.0001	100
AB	2	29	7.7×10^{-1}	3.9	0.033	82.8
AE	2	17	1.5×10^{-2}	87.4	<0.0001	100
AF	2	22	1.5×10^{-1}	10.7	0.0001	100
AK	2	20	5.6×10^{-2}	23.3	<0.0001	100

Table 5.2 Summary of results of discriminant function analyses performed on the shared songs of male Rufous Bristlebirds in 1999, for the parameters of the third component only.

Song Type	# birds	# songs	Wilks λ	F	p	% correct
B	3	28	8.0×10^{-4}	34.3	<0.0001	100
G	4	31	1.5×10^{-6}	78.7	<0.0001	100
H	2	35	3.1×10^{-1}	7.4	<0.0001	100
K	3	33	1.4×10^{-3}	40.6	<0.0001	100
R	4	20	1.0×10^{-6}	110.1	<0.0001	100
S	4	34	4.9×10^{-4}	14.7	<0.0001	100
E	3	11	1.8×10^{-6}	374.5	<0.0001	100
N	2	8	4.4×10^{-2}	53.9	0.0004	100
O	2	19	7.1×10^{-5}	5424	<0.0001	100
Q	2	37	8.5×10^{-2}	15.1	<0.0001	100
T	3	11	7.5×10^{-5}	143.1	<0.0001	100
V	2	9	4.2×10^{-4}	2396	<0.0001	100
X	2	39	8.2×10^{-3}	206.9	<0.0001	100
W	2	21	5.5×10^{-2}	51.5	<0.0001	100
Y	3	36	1.1×10^{-1}	6.4	<0.0001	94.4
Z	2	23	5.2×10^{-2}	26.1	<0.0001	100
AB	2	42	8.5×10^{-1}	3.4	0.042	76.2
AE	2	18	1.5×10^{-2}	92.9	<0.0001	100
AF	2	23	4.6×10^{-1}	5.4	0.005	95.7
AK	2	20	1.1×10^{-2}	51.3	<0.0001	100

Table 5.3 Summary of results of discriminant function analyses performed on the shared songs of male rufous bristlebirds in 1999, for the first two components of the song only.

Song Type	# birds	# songs	Wilks λ	F	p	% correct
B	3	27	2.2×10^{-2}	4.5	0.0003	100
G	4	29	3.7×10^{-3}	6.6	<0.0001	100
H	2	32	2.3×10^{-1}	6.1	0.0003	100
K	3	22	6.9×10^{-4}	30.3	<0.0001	100
R	4	20	7.3×10^{-5}	13.5	<0.0001	100
S	4	27	1.6×10^{-2}	6.1	<0.0001	92.6
E	2	9	2.9×10^{-2}	19.8	0.017	100
N	2	8	4.2×10^{-2}	57.3	0.0004	100
O	2	13	9.3×10^{-4}	358.4	0.0002	100
Q	2	32	2.4×10^{-1}	6.7	0.0001	93.8
T	3	11	7.5×10^{-3}	8.4	0.003	100
V	2	9	4.2×10^{-4}	2395	<0.0001	100
X	2	39	1.7×10^{-2}	143.7	<0.0001	100
W	2	20	2.6×10^{-2}	26.8	<0.0001	100
Y	3	33	1.2×10^{-2}	7.5	<0.0001	100
Z	2	23	9.2×10^{-3}	50.3	<0.0001	100
AB	2	29	6.0×10^{-1}	3.0	0.031	89.7
AE	2	17	2.2×10^{-2}	43.6	<0.0001	100
AF	2	22	1.1×10^{-1}	13.3	<0.0001	100
AK	2	20	9.3×10^{-3}	38.0	0.0004	100

The six focal female birds monitored in 1999 shared six song types between at least two neighbours, sonograms of which are presented in Appendix B. The results of the DFAs performed on these song types are summarised in Table 5.4. Again, a significant difference was found between the songs of individual females using the same song types. In addition, 100% of songs were attributed to the correct individual for five out of the six song types, with 96.6% of songs being correctly attributed for the other song type (X = 99.4 ± 0.6%).

5.3.2 Potential Identification Analyses

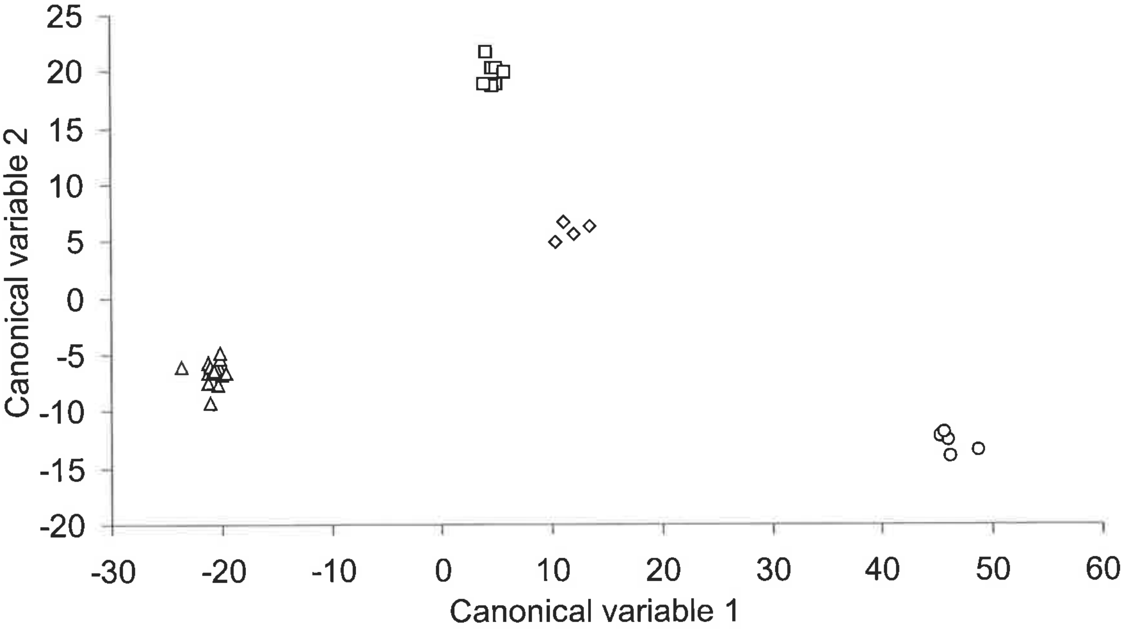
In general, therefore, the results of the DFAs performed strongly suggest that the shared song types of Rufous Bristlebirds exhibit vocal individuality. If a large proportion of this pattern can be explained by the first two canonical functions of each DFA, it is possible to construct 2-dimensional scatter-plots, which provide some graphical indication of the degree of separation in acoustic space between the songs of different individuals using the same song type. Two examples of these are presented in Figure 5.2. As can be seen, for a number of these shared song types, songs used by a single individual generally group together, while those of different individuals are well separated. Based on these graphical representations, it was possible to estimate the number of individuals that could be potentially identified acoustically, based on each shared song type. This was achieved by measuring the total area of 'acoustic space' (based on the scatter-plot produced by the first two canonical

Table 5.4 Summary of results of discriminant function analyses performed on shared female song types of the rufous bristlebird, for the total song. See Appendix B for the structure of these song types.

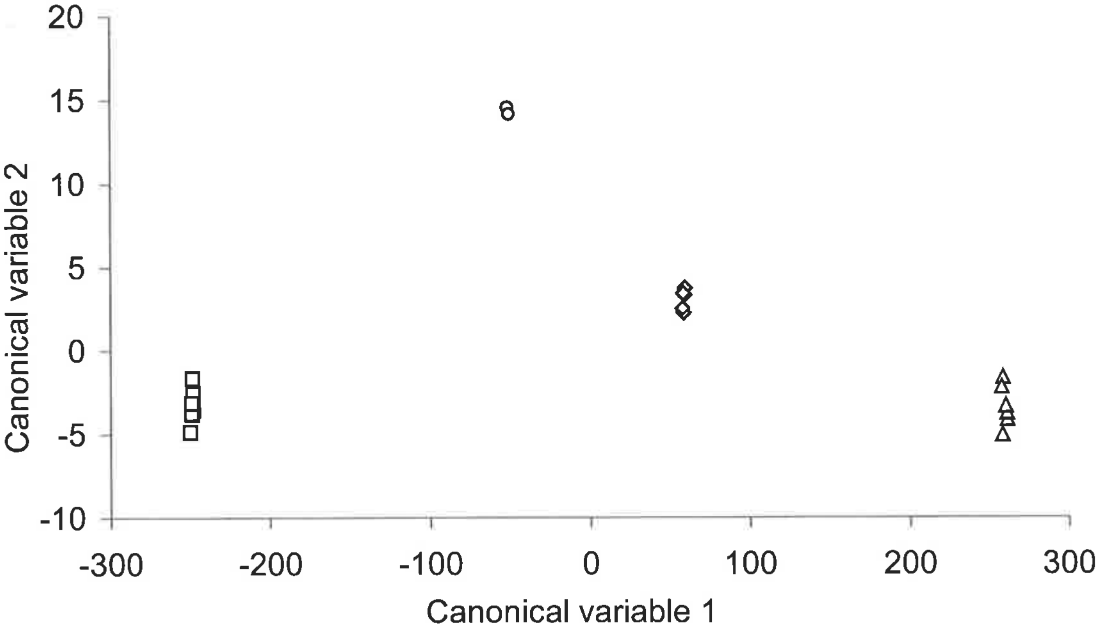
Song Type	# birds	# songs	Wilks λ	F	p	% correct
E	2	40	3.25×10^{-2}	31.32	<0.0001	100
F	3	15	4.63×10^{-4}	53.07	<0.0001	100
G	2	17	3.05×10^{-2}	69.96	<0.0001	100
H	6	29	4.58×10^{-5}	6.265	<0.0001	96.55
I	3	36	3.46×10^{-3}	52.01	<0.0001	100
J	2	31	6.6×10^{-2}	38.77	<0.0001	100

functions) that a particular song type covered for all of the recorded individuals, and measuring the acoustic space taken up by the songs of each individual. Estimates of the number of potential individuals that could be successfully discriminated were calculated by dividing the total acoustic space that a song type covered for all recorded individuals, by the maximum acoustic space that the songs of a single recorded individual covered (see Figure 5.3 for graphical explanation of this method). The total acoustic space for the recorded individuals represents the minimum acoustic space for that song type in a population, as any new individuals recorded can only increase the area that a song type covers, although intra-individual song variation may also increase with the addition of new individuals. Given that estimates were calculated using the maximum observed acoustic space that the songs of a single individual covered, these estimates of population size that can be potentially identified acoustically represent a relatively conservative estimate. Such estimates were only calculated for song types that were used by at least three individuals, and where at least 95% of the variation was explained by the first two canonical functions used to construct the scatter-plots. Based on these restrictions, estimates were made for 7 of the 20 male song types, and three of the six female song types. Potential identification analyses were performed both for the total song type, and for the third component, and first two components, separately, as was done with DFAs.

For the seven male song types for which estimates were made, the distribution of songs in the acoustic space of the song types suggests that between 6 and 423 individuals ($X = 77.0 \pm 58.3$) can potentially be identified acoustically, the potential number of individuals depending upon the song type (Table 5.5). In addition, potential identification analyses supported the importance of the final song component to individual identification (Table 5.5), although again no significant difference was detected between the potential population sizes calculated for each of the song components alone, versus the entire song (Kruskal-Wallis Test: $Z = 3.14$; $df = 2$; $p = 0.21$). For the three female song types for which estimates were made, the number

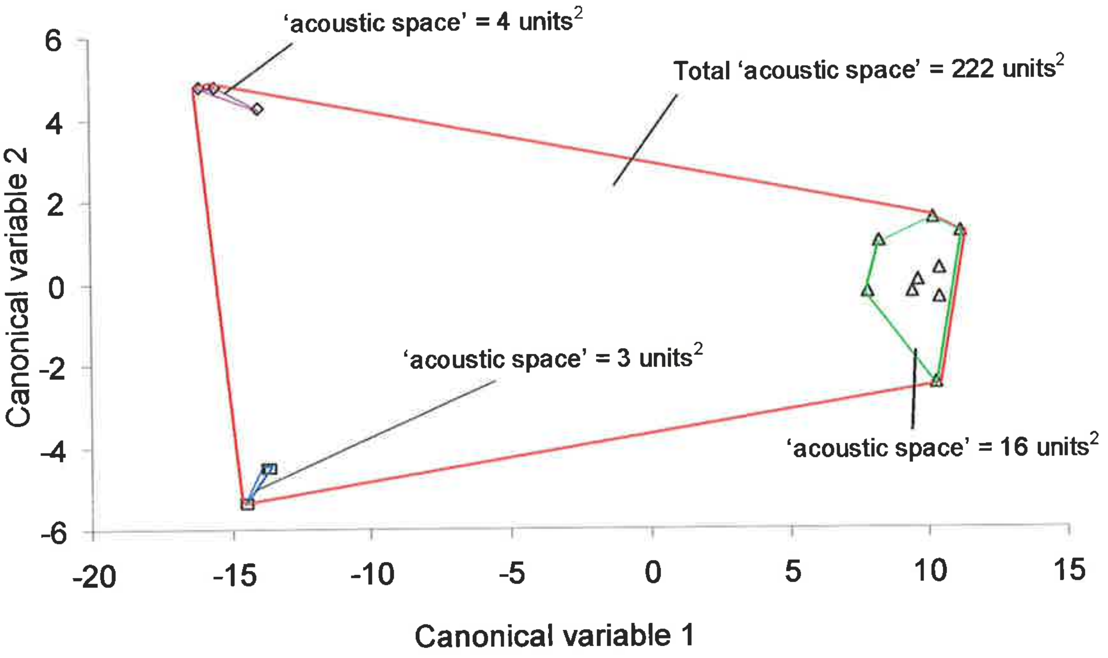


a. Male song type G, third component



b. Male song type R, third component

Figure 5.2 Examples of the distribution of songs in two-dimensional 'acoustic' space, defined by the plot of scores of the first two canonical variables constructed by discriminant function analyses. Each point on each plot represents one song, while each different shape represents one individual. See Appendix B for the structure of song types.



Total 'acoustic space' = 222 units^2

Maximum 'acoustic space' / individual = 16 units^2

∴ Potential identifiable population size = $^{222}/_{16}$

= 13 indivduals (rounded down)

Figure 5.3 Graphical explanation of the method used to estimate population sizes that can potentially be identified acoustically using shared song types.

Table 5.5 Potential population sizes of male rufous bristlebirds that can be potentially discriminated acoustically, based upon the total song, the third component only, and the first two components only. See text for methodology of calculating potential population size. See Appendix B for structure of song types.

Song Type	Potential population size		
	Total song	Third component only	First two components only
B	15	11	5
G	71	195	5
K	9	14	16
R	423	18	21
S	8	12	2
T	6	32	7
Y	7	2	6

Table 5.6 Potential population sizes of female rufous bristlebirds that can be potentially discriminated acoustically, based upon the total song. See text for methodology of calculating potential population size. See Appendix B for structure of song types.

Song Type	Potential population size (total song)
F	13
H	12
I	9

of individuals which can potentially be identified acoustically ranged from 9 to 13 ($X = 11.3 \pm 1.2$; Table 5.6).

5.3.3 Cross-Correlation Analysis

The results of discriminant function analyses performed on songs recorded in 1999 suggest that the shared song types used by both male and female Rufous Bristlebirds exhibited a high degree of vocal individuality. At the level of shared song type, therefore, it may be possible for investigators to identify individual bristlebirds acoustically, by comparing the same song type between individuals. However, as outlined in Chapter 2, discriminant function analyses have extremely limited potential as tools of acoustic identification, primarily due to their inability to allow for the identification of previously unknown individuals. As a result of the promising results of discriminant function analyses, cross-correlation analyses were thus performed on the same songs recorded in 1999, as well as songs recorded in 2000, to determine whether cross-correlation can be used to discriminate between known bristlebird individuals acoustically, as well as identify previously unknown individuals.

5.3.3.1 Methods

The general method for conducting cross-correlation analyses on acoustic signals of different individuals is described in Chapter 2. For male bristlebirds, cross-correlation analyses were only conducted on the final component of the song, as a number of investigators have suggested that the use of cross-correlation analyses be limited to comparisons between single syllables, or song components of limited duration (Khanna, et al. 1997, Tchernichovski, et al. 2000). The superior quality and consistency of recordings of the third component warranted their use over other song components. As suggested in Chapter 2, recording quality may significantly influence the results of cross-correlation analyses. In addition, the DFAs described in this chapter suggest that the success of individual discrimination using shared song types is not significantly greater for the entire song as compared to the final component only.

For the purposes of this section, cross-correlation analyses were only conducted on song types recorded for three or more individuals in one year. In 1999 cross-correlation analyses were performed for nine male song types, and four female song types, while in 2000, cross-correlation analyses were performed for 18 male song types and three female song types.

As with other cross-correlation analyses presented in this thesis, the results of cross-correlation analyses performed on Rufous Bristlebird songs are presented as the maximum percentage of cross-correlation coefficients (r_x) that are correctly classified as having been produced by comparing two songs of the same individual, or two different individuals, at a peak correlation threshold (r_x*). Graphical examples of how the percentage of correctly classified r_x values changes with r_x* for the songs of rufous bristlebirds are presented in Figure 5.4.

5.3.3.2 Results

Cross-correlation results for shared male song types are presented in Table 5.7. For male rufous bristlebirds in 1999, the peak identification accuracy for the nine song types analysed ranged from 76.7% to 100% (mean = 87.4 ± 2.8%). Peak identification accuracy was achieved at an r_x* that ranged from 0.15 to 0.68 (mean = 0.57 ± 0.01). r_x values calculated between songs of the same individual were significantly greater than r_x values calculated between songs of different individuals, for all nine song types (Table 5.7).

For male bristlebirds in 2000, peak identification accuracy ranged from 60.4% to 96.7% (mean = 82.1 ± 3.2 %), at an r_x* that ranged from 0.26 to 0.8 (mean = 0.6 ± 0.03). Intra-individual r_x values were significantly greater than inter-individual r_x values for all but two of the male song types analysed in 2000 (Table 5.7).

Cross correlation results for shared female song types are presented in Table 5.8. For female bristlebirds in 1999, peak identification accuracy for the four song types analysed ranged from 73.9% to 94.0% (mean = 89.4% ± 5.3%), at an r_x* that ranged from 0.31 to 0.59 (mean = 0.51 ± 0.03). r_x values calculated between the songs of the same individual were significantly greater than r_x values calculated between songs of different individuals for all four song types.

Only three female song types were analysed using cross-correlation analysis for recordings collected in 2000. For female bristlebirds in 2000, peak identification accuracy ranged from 78.7% to 87.9% (mean = 83.8 ± 2.7%), at an r_x* that ranged from 0.49 to 0.54 (mean = 0.51 ± 0.01). Again, intra-individual r_x values were significantly greater than inter-individual r_x values for all of the three female song types analysed in 2000 (Table 5.8).

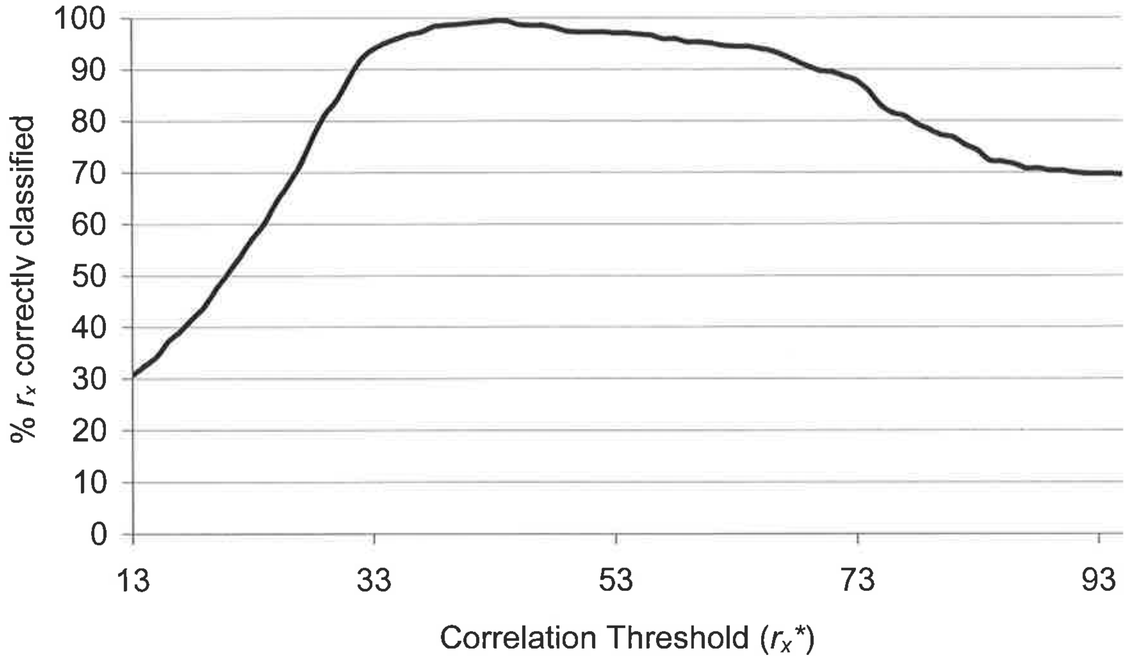


Figure 5.4 Example of the impact of correlation threshold (r_x* x 100) upon the percentage of r_x values classified correctly as having been produced intra- or inter-individually. If the correlation threshold is set too low, r_x values produced by comparing different individuals will be incorrectly classified as being produced by comparing songs of the same individual, whereas if r_x* is set too high r_x values produced by comparing songs of a single individual will be incorrectly classified as being produced by comparing the songs of two different individuals. Example taken from male song type G, 1999.

Table 5.7 Results of cross-correlation analyses performed on male shared song types. The p values are those produced from statistical tests comparing correlation coefficients (r_x) between songs of the same individual (intra), and correlation coefficients (r_x) between songs of different individuals (inter). * denotes non-parametric test. See Appendix B for structure of song types.

a. 1999

Song type	# males	# songs	#bouts/male	p (intra v inter)	% correct	peak threshold (r_x*)	% correct at r_x* of 0.6
B	3	28	1	<0.0001*	76.72	58	75.66
E	3	10	1.33	<0.0001*	100	51-61	100
G	4	31	1.25	<0.0001*	99.35	43-44	95.27
H	3	42	1.33	<0.0001*	77.35	56	75.84
K	4	27	1.25	<0.0001	91.45	74	60.4
R	4	22	1.5	<0.0001*	87.01	55	84.4
S	4	35	1.25	<0.0001*	84.87	65-66	82.18
T	3	11	1	<0.0001	85.46	43,51-58	78.18
Y	3	37	1.33	<0.0001*	83.93	72-73	65.92

b. 2000

Song type	# males	# songs	#bouts/male	p (intra v inter)	% correct	peak threshold (r_x*)	% correct at r_x*of 0.6
A	3	14	1.33	0.77*	60.44	69	39.56
B	4	25	1.50	<0.0001*	89	55	83.67
E	3	34	2.33	<0.0001	81.28	59,61	81.11
I	4	20	1.25	<0.0001*	96.67	59-60	96.67
K	4	46	2.50	<0.0001*	81.45	63	79.32
Q	4	41	1.50	<0.0001*	91.46	56	90.24
V	4	14	1.75	<0.0001*	90.11	56,64	88.89
Y	4	14	1.50	<0.0001	90.11	66	89.01
AK	4	41	3.00	<0.0001*	65.61	26	72.53
AC	3	23	1.67	<0.0001*	85.38	61-62	83.39
AN	3	23	2.33	<0.0001*	80.63	71-72	59.88
R	3	19	1.67	<0.0001*	90.06	59	60.08
C	4	24	1.50	<0.0001*	89	55	83.67
D	3	16	1.33	<0.0001*	80.88	70	63.24
M	3	14	1.00	<0.0001*	73.33	71,73	60
O	3	28	1.67	0.0525*	63.3	80	55.42
T	3	13	1.33	<0.0001*	84.62	71-73	79.12
W	3	30	1.67	<0.0001*	83.87	64	80

Table 5.8 Results of cross-correlation analyses performed on female shared song types. The p values are those produced from statistical tests comparing correlation coefficients between songs of the same individual (intra), and correlation coefficients between songs of different individuals. * denotes non-parametric test. See Appendix B for structure of song types.

a. 1999

Song type	# males	# songs	#bouts/ female	p (intra v inter)	% correct	peak threshold $(r_x{}^*)$	% correct at r_x* of 0.51
F	4	16	1.25	<0.0001	97.5	51-59	97.5
G	3	18	1.33	<0.0001	73.85	31	41.8
H	6	29	1.5	<0.0001*	92.36	55	92.12
I	3	35	1.33	<0.0001	93.95	35	71.26

b. 2000

Song type	# males	# songs	#bouts/ female	p (intra v inter)	% correct	peak threshold $(r_x{}^*)$	% correct at r_x* of 0.51
F	4	17	1.5	<0.0001	78.68	49-50	77.94
H	4	18	2	<0.0001*	84.97	52	84.31
I	3	23	1.67	<0.0001	87.87	54	83.67

Although high levels of identification accuracy were found for most song types recorded in the two years of analysis, some variation existed in the r_x* at which peak identification accuracy occured. A single r_x* that could be used for all of the shared song types encountered would make a system of acoustic identification in species with large song repertoires more practical, and simpler to use. As a result, the mean r_x* across all song types was calculated, to determine the r_x* that produces the best identification accuracy across all song types. This calculation was performed on male and female song types separately.

For male rufous bristlebirds, the r_x* that produced the best overall identification accuracy was at 0.6. At this r_x*, peak identification accuracy for each song type ranged from 39.6% to 100% ($X = 76.4 \pm 2.7\%$). This peak identification accuracy detected at an overall r_x* of 0.6 was significantly less than the mean peak identification accuracy detected for each song type separately ($X = 83.8 \pm 1.9\%$; t-test = 2.22; df = 52; $p = 0.031$; Figure 5.5). However, the impact of using this general correlation threshold was not great for many of the song types analysed (Table 5.7).

For female bristlebirds, the r_x* that produced the best overall identification accuracy was at 0.51. At this r_x*, peak identification accuracy ranged from 41.8% to 97.5% ($X = 78.4 \pm 6.9\%$; Table 5.8). No difference was detected between the mean identification accuracy calculated for all song types at an r_x* of 0.51, and the peak identification accuracy for each song type separately ($X = 87.0 \pm 3.2\%$; t-test = 1.135; df = 12; $p = 0.278$; Figure 5.6).

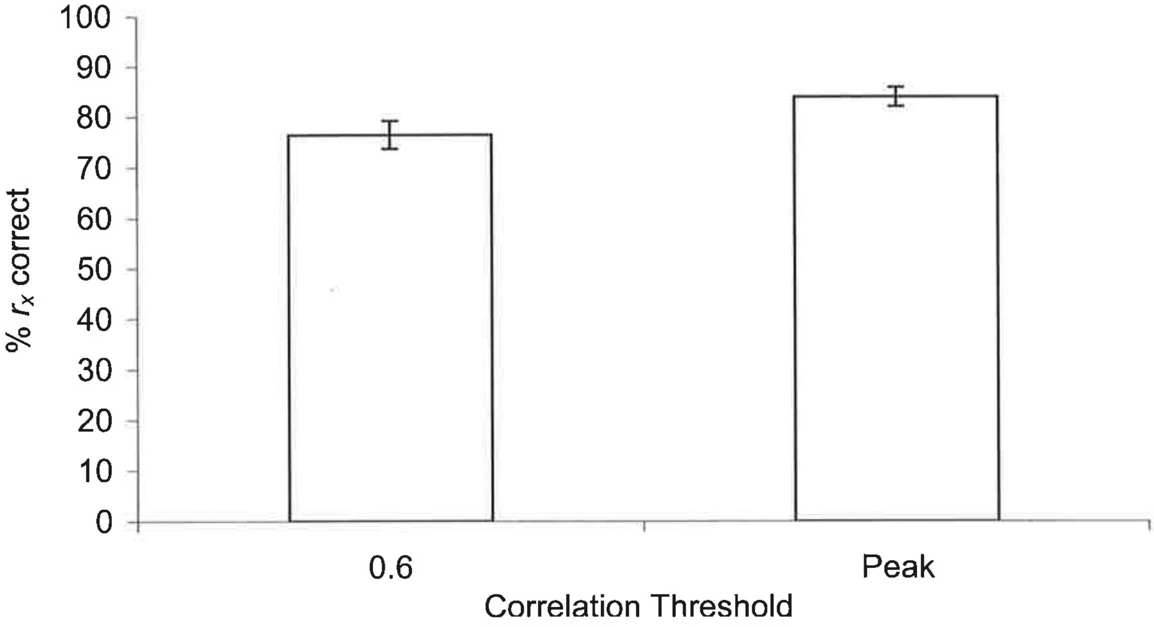


Figure 5.5 Percentage of r_x values correct at an r_x* of 0.6 for all song types, versus percentage of r_x correct at a r_x* for each song type, for shared male Rufous Bristlebird song types.

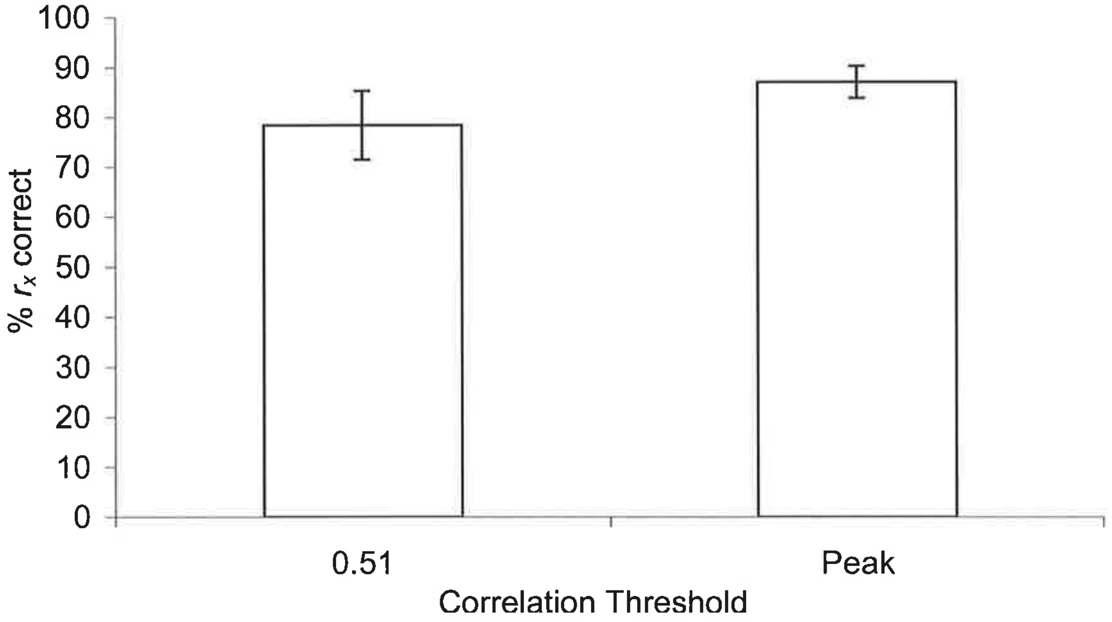


Figure 5.6 Percentage of r_x values correct at an r_x* of 0.51 for all song types, versus percentage of r_x values correct at an r_x* for each song type, for shared female rufous bristlebird song types.

5.3.3.3 Discussion

Despite the fact that, for the song types analysed, multiple recordings were made for most individuals, cross-correlation analyses were able to accurately discriminate between individuals based upon comparisons of shared song types between individuals. For all male song types, an average of 83.8% of r_x values calculated between two songs were classified correctly at an optimal r_x*, while for female song types, an average of 87.0% of r_x values were correct at each r_x*. When overall r_x* of 0.6 for male song types and 0.51 for female song types were used, this identification accuracy dropped to an average of 76.4% and 78.4%, respectively. However, this loss of accuracy must be measured against the benefits of using a universal r_x* value. While using the optimal r_x* for each song type does improve identification accuracy, it requires that a pilot study be conducted for each new song type encountered, in order to determine this optimal r_x*. The use of a universal r_x* for all song types means that future studies will be able to identify individuals with a known degree of accuracy, using shared song types not featured in this study. In any case, the degree of improved accuracy gained by using specific r_x* for each song type was not great for males, and was not significantly different for female song types.

Cross-correlation analysis, therefore, appears to be useful in identifying individual bristlebirds of both sexes, through the comparison of common song types. How useful this technique is will now largely depend on the prevalence of these common song types throughout a population. If, for example, song types are used amongst small neighbourhoods of birds, then the comparison of common song types for identification purposes would be limited to the comparison of these small groups of individuals. Song types found throughout populations or species, on the other hand, would allow these populations to be surveyed more extensively using these common song types.

5.4 Comparison of Common Song Features

The previous sections of this chapter have shown that the shared song types used by both male and female Rufous Bristlebirds were individually distinct, and had potential to be used for the identification of individual birds. However, the comparison of shared song types alone has a number of important restrictions. First, the songs of different individuals could only be compared if the individuals shared some proportion of their song repertoire; it would not be possible to compare two individuals who did not share any of the song types in their repertoire. For small and localised populations of *D. broadbenti*, such a limitation is generally not a problem, as neighbouring birds tend to share a high proportion of the song types in their repertoire (see Chapter 4). However, as will be discussed in Section 5.5, the probability of encountering a song type that is shared by two birds decreases with the distance between the two birds, and a system of individual identification based upon comparing shared song types would thus be most effective for localised populations.

Second, comparisons based upon shared song types do not allow for comparisons within or between individuals across different song types. If, for example, a particular song type was recorded, subsequent recordings would only be useful for identification purposes if they were the same song type as the original recording. Surveys based upon the comparison of common song types would thus run independently of each other; knowledge gained from the identification of individuals using one song type would not improve the results of surveys based upon other song types.

As a method of minimising the impacts of these limitations, the three syllables that comprise the third component of the male song of *D. broadbenti*, and the three syllables that comprise the female song, were treated as separate units for comparative analysis between individuals, and compared across multiple song types. As many of the syllable types were found in more than one song type, such comparisons may allow the songs of individual bristlebirds to be compared for identification purposes, both within and between different song types.

5.4.1 Discriminant Function Analysis

5.4.1.1 Methods

For all song types recorded and analysed in Section 5.3, the syllables of the third component of the male song and the syllables of the female song were grouped visually to syllable type. The nine song parameters measured for each syllable in Section 5.3 were subsequently used to perform discriminant function analyses on each syllable type. Two DFAs were performed for each syllable type; the first grouped each syllable by individual, and the second grouped each syllable by the song type from which it was derived. This second DFA was performed in order to determine the extent of variation between syllables that were visually classified as equivalent, but derived from different song types, as a way of assessing whether the same syllables from different song types can be used for individual identification.

5.4.1.2 Results

The 20 male song types recorded and analysed in Section 5.3 yielded a total of 35 syllable types. Of these syllable types, 16 were present in only one song type, and were thus excluded for the purposes of these analyses. With these 16 syllable types excluded, therefore, a total of 19 syllable types were analysed. Examples of these 19 syllable types are presented in Appendix C.

The results for discriminant function analyses performed on these 19 syllable types are summarised in Table 5.9. All syllables differed significantly between individuals, with the proportion syllables being classified to the correct individual ranging from 50% to 94.2% (mean = 74.2 ± 2.4%). However, when the same data were grouped by song type, the proportion of syllables classified to the correct song type ranged from 74% to 100% (mean = 92.5 ± 1.8%), and was significantly greater than when the syllables were grouped by individual (Wilcoxon test; Z = 4.48; df = 18; $p < 0.0001$).

The 18 female song types recorded and analysed in Section 5.3 yielded at total of 51 syllable types. However, the vast majority of these were unique to one song type; only three of these 51 syllables were in fact found in more than song type, and these three were only found in two different song types. The results of discriminant function analyses performed on these three syllable types are presented in Table 5.10. For the three syllable types analysed, syllables differed significantly both between individuals, and between song types. The proportion of syllables classified to the correct individual ranged from 75% to 100% (mean = 90.9 ± 7.97%), and this was not significantly different from the proportion of syllables classified to the correct song type (mean = 86.0 ± 5.5%; t-test = 0.503; df = 4; $p = 0.64$).

5.4.1.3 Discussion

The results presented for discriminant function analyses of common syllable types suggest two things. First, and most importantly for the purposes of this chapter, visually-classified syllable types do not appear to be useful with regard to discriminating between individuals,

Table 5.9 Summary of results of discriminant function analyses performed on parameters used to describe each of 19 syllable types derived from the third component of male rufous bristlebird songs, grouped by both individual, and song type from which the syllable was derived. See Appendix C for structure of syllable types.

Syllable Type	#songs	#individuals	By individual			#song types	By song type		
			Wilks λ	p	%correct		Wilks λ	p	%correct
1	119	5	0.269	<0.0001	68.91	7	0.005	<0.0001	86
2	86	5	0.047	<0.0001	79.07	5	0.007	<0.0001	88.37
3	24	3	0.169	<0.0001	83.33	2	0.456	<0.0001	91.67
4	79	4	0.209	<0.0001	67.089	3	0.010	<0.0001	93.86
5	45	6	0.061	<0.0001	71.11	3	0.351	<0.0001	82.22
6	31	4	0.159	<0.0001	67.74	3	0.012	<0.0001	100
7	60	4	0.088	<0.0001	83.33	3	0.022	<0.0001	95
21	92	5	0.061	<0.0001	75	6	0.001	<0.0001	94.57
24	58	4	0.489	<0.0001	50	3	0.125	<0.0001	81.03
32	68	5	0.012	<0.0001	80.882	4	0.000	<0.0001	100
8	138	6	0.117	<0.0001	76.81	5	0.007	<0.0001	85.51
23	93	5	0.033	<0.0001	84.95	3	0.004	<0.0001	100
25	54	4	0.113	<0.0001	83.019	2	0.079	<0.0001	98.11
27	49	4	0.477	0.0002	62.5	2	0.021	<0.0001	100
28	53	4	0.034	<0.0001	94.23	2	0.231	<0.0001	88.46
30	76	5	0.008	<0.0001	78.95	2	0.049	<0.0001	100
31	84	4	0.313	<0.0001	67.47	3	0.002	<0.0001	100
34	98	4	0.273	<0.0001	74.47	2	0.300	<0.0001	97.87
35	146	6	0.285	<0.0001	60.96	5	0.063	<0.0001	73.97

Table 5.10 Summary of results of discriminant function analyses performed on parameters used to describe each of three syllable types derived from female rufous bristlebird songs, grouped by both individual, and song type from which the syllable was derived. See Appendix C for structure of syllable types.

Syllable Type	#songs	#individuals	By individual			#song types	By song type		
			Wilks λ	p	%correct		Wilks λ	p	%correct
1	42	2	0.053	<0.0001	97.62	4	0.567	0.0007	85.71
2	60	2	0.127	<0.0001	75	6	0.588	0.0001	76.67
3	23	2	0.011	<0.0001	100	3	0.354	<0.0001	95.65

with an average of 74.2% of syllables for male songs being classified by DFA to the correct individual. Female syllable types exhibited slightly more individuality, with an average of 90.9% of syllables being classified to the correct individual, although the limited number of syllable types that were common to more than one song type severely restricts their potential as identification tools, in a manner which has greater usefulness than the comparison of shared song types. While the proportion of syllables correctly classified to individual is greater than expected by chance, observations from comparisons of shared song types suggest that even relatively high classification percentages do not directly translate into equivalent identification accuracies when using the directly applicable identification technique of cross-correlation analysis; that is, *post hoc* classification percentages using DFA tend to be inflated (as discussed in Chapter 2).

Second, the observation that the proportion of syllables classified to the correct song type was consistently higher than the proportion of syllables classified to the correct individual for male songs suggests that these syllables vary more between song types than between individuals. Such a suggestion is important for a number of reasons. It firstly suggests that the syllables that make up the songs of Rufous Bristlebirds are not structurally interchangeable; that is, song types are likely to be the basic unit of the bristlebird song repertoire, rather than syllable type. With regard to the use of shared syllables for individual identification, the results of analyses such as those presented here must be treated with caution, as patterns of inter-individual variation are likely to be confounded by patterns of inter-song type variation. The results of syllable classification to individuals, for example, may be inflated if the song type from which syllables are derived differ between individuals, and results are simply a reflection of variation between the song types used by each individual.

Due to the concerns outlined above with the use of visually classified syllable types for acoustic individual identification, I recommend that comparisons between individual bristlebirds be limited to shared song types. Although this limits the use of acoustic identification in species with extensive song repertoires, it does allow for the maintenance of the high levels of identification accuracy observed when using shared song types.

5.5 Distribution of Song Types Within a Continuous Population of *D. broadbenti*

The results presented so far in this chapter suggest that the comparison of common song types is the most appropriate method of identifying individual rufous bristlebirds by their songs. As suggested previously, using common song types to identify individual bristlebirds has potential limitations, that are largely dependent on the extent to which these common song types occur through a population. In order to assess the effectiveness of a system of individual identification based upon the comparison of common song types, this section of the thesis will determine how song types are distributed through a continuous population of rufous bristlebirds, as a way of determining the effectiveness of a system of acoustic identification that is based upon the comparison of these common song types between individuals.

5.5.1 Methods

Rufous bristlebird songs were recorded opportunistically along a continuous strip of appropriate habitat; the bristlebirds within this continuous habitat were called the Loop Road population, after the road that runs through, and parallel to, this population. Recorded songs were then compared visually, and grouped to song type. As suggested in Chapter 4, the songs of Rufous Bristlebirds are highly stereotypic within song types, and as such songs were only considered to be the same if all three of the components identified for male songs had the same structure. The population of Rufous Bristlebirds which this study focuses on is linear, with available habitat being a maximum of two territories wide along the majority of the site. Songs were compared between birds within this linear population by firstly segregating the site into 200m long sections, which approximates the size of a single bristlebird territory (Seymour and Paton 2000). Song comparisons between these 200m sections were conducted by comparing all of the songs recorded from the focal bristlebird group of Chapters 4 and 5 (subsequently referred to as 'focal songs'), with the songs recorded in each 200m section. This comparison was done as the song repertoires of these four focal pairs was well known, and song types encountered elsewhere that were not amongst the songs used by the focal birds could be reasonably assumed not to be used at all by these focal birds. The proportion of song types that were shared between each 200m section and the focal site was then related to the distance between each section and the focal site, as a way of determining how song-type sharing was affected by the distance between individuals.

5.5.2 Results

In total, 55 song types were compared between the focal study site and other sections of the population, with focal songs being encountered elsewhere in an additional 45 song recordings. For the 55 song types compared in this analysis, the number of sites where each song type was recorded ranged from one to seven (mean = 2.7 ± 0.22), with 41 of these 55 song types being recorded outside of the focal study site.

The proportion of focal songs that were also recorded at other sites is presented in Figure 5.7, as a function of distance from the focal site. As shown in Figure 5.7, song types common between the focal birds and other birds were recorded over large distances relative to the size of bristlebird territories. No significant relationship was detected between the proportion of focal song types common to other sites and distance from the focal site ($r^2 = 0.11$; $p = 0.77$).

For the 41 song types recorded outside of the focal site, the maximum distance separating the locations where common song types were recorded ranged from 200m (adjoining site within the population) to 7.8 km (mean = 2.9 ± 0.37 km). This maximum distance of 7.8 km is equal to the distance that separates the focal study site and Tea-Tree Crossing, as in Chapter 4. Of these 41 song types, 13 were only found in adjoining sites, as expected by the suggestion that neighbouring birds share song types. However, six song types were encountered at sites separated by the maximum distance of 7.8 km.

5.5.3 Discussion

Extensive recordings of bristlebird songs within the continuous Loop Road population suggest that many of the song types used by the focal individuals of this study are also used by a number of other individuals through the population, separated by a distance of at least 7.8km, the maximum distance between two sites sampled. While the probability of encountering a common song type is greatest between territorial neighbours (as suggested in Chapter 4), the more prevalent use of many song types between even widely separated individuals suggests that, at least with continuous populations, the use of common song types

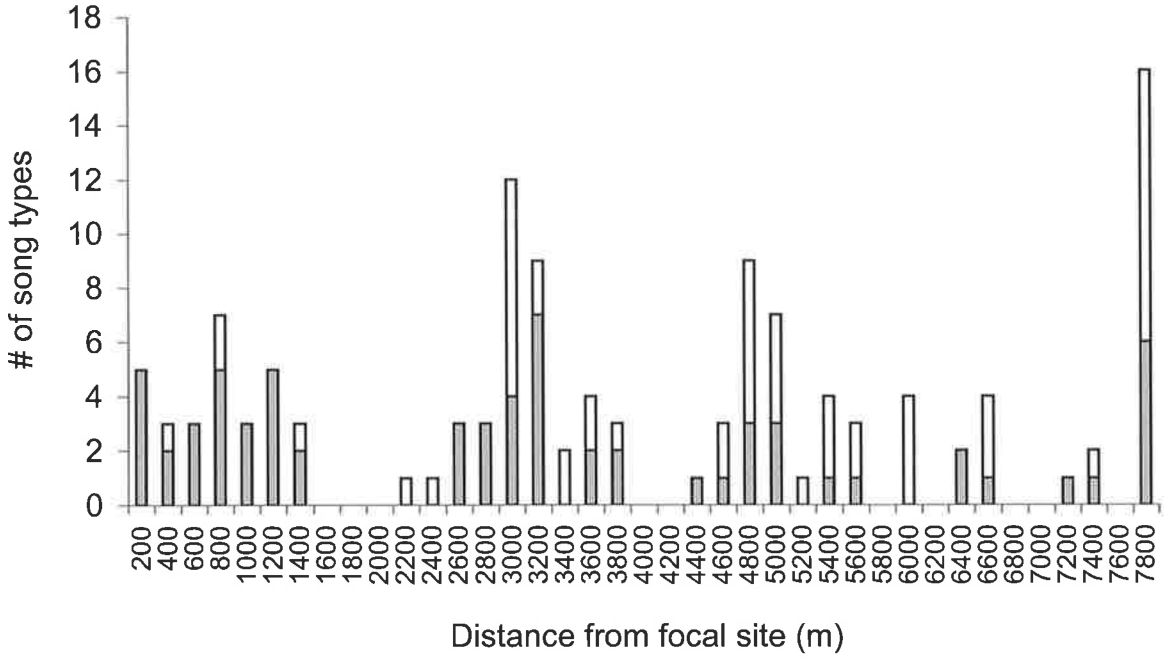


Figure 5.7 The proportion of male song types used by focal individuals encountered as a function of distance from the focal site. Hashed bars (▨) indicate the number of song types encountered that are common with those used by focal individuals; open bars (☐) are song types encountered that were not used by focal individuals. Distance categories with no songs were not sampled, as they generally contained inappropriate habitat for *D. broadbenti*.

in acoustic identification of individuals has some potential, with regard to comparing a large number of individuals using these common song types.

While the extensive use of some song types allows for the identification of individuals separated by relatively large distances, it still does not allow for the comparison of different song types within or between individuals. This restriction means that surveys of individual bristlebirds can only be conducted on individual song types, and re-identification can only be performed when the same song type is encountered. Such a limitation may be especially restricting for this species, considering the size of each individual's repertoire (see Chapter 4).

5.6 Using Song Individuality to Survey Populations of *D. broadbenti*: An Example

As an example of how acoustic identification can be used to conduct surveys and answer ecological questions, the technique was used to compare the songs of focal individuals with songs recorded at other, more extensive locations, as described in sections 5.2 and 5.5, as a way of determining whether songs recorded at different locations were produced by the same or different individuals. These comparisons were then used to subsequently identify the singers from these locations, to test whether the prevalence of common song types is due to different individuals using these same song types, or the same individuals moving large distances.

For the purposes of this survey, five song types were analysed using cross-correlation analysis. These five song types were chosen for two reasons: first, the identification accuracy of these song types using cross-correlation analysis, as determined in Section 5.3.3, was 80% or greater, and therefore one could be confident of using these song types to identify individual males. Second, each of the five song types was recorded over extensive distances (up to 7.8 km), which allows for tests of movements over longer distances than might be expected if rufous bristlebirds are in fact sedentary.

The shared songs recorded at each pair of sites were compared using cross-correlation analyses, as described above, to determine whether these shared song types were sung by the same, or different individuals, using an r_x* of 0.6. Identity was determined by calculating the proportion of r_x values that were below 0.6. If greater than 50% of r_x values between sites were below 0.6, the individuals recorded at the two sites were deemed to be two different individuals. However, if the majority of r_x values between sites were greater than 0.6, the two song recordings at the two different sites were deemed to be have been sung by the same individual.

Locations where each of the five song types were recorded, including the focal site, are shown in Figure 5.8. The results of the cross-correlation analyses are summarised in Table 5.11, and strongly suggest that all individuals recorded outside of the focal area are different individuals to the focal birds. r_x values between focal songs and songs recorded outside the focal area were all under the standard r_x* of 0.6. These results suggest that male rufous bristlebirds are sedentary, as no individual was ever re-recorded at a site greater than 200m from its original recording location, and that the extensive presence of common song types throughout this continuous bristlebird population is a result of many different individuals using the same song types, rather than a small number of individuals moving extensive distances.

Such a result is what we would expect, from the limited information that is available regarding movements in rufous bristlebirds (see Tables 4.1 and 4.2). Bristlebirds are thought to be mobile only when they disperse from their natal territory; following the establishment of a breeding territory, adult bristlebirds tend to remain on that territory throughout the year. The observation in this study that the extensive use of common song types is not due to large-scale movements of individuals thus supports arguments for the sedentary nature of the species.

5.7 General Discussion and Conclusions

The results presented in this chapter suggest that it may be possible for investigators to identify individual rufous bristlebirds of both sexes, through the analysis and comparison of song types that are common to more than one individual. Furthermore, the prevalence of many song types throughout continuous populations of rufous bristlebird suggests that the comparison of such common song types may be used to identify a number of individuals within these populations.

Restricting comparisons between individuals to common song types obviously limits to what extent investigators can use this acoustic identification technique to identify individual bristlebirds in the field. This restriction limits the effectiveness of acoustic identification in two ways. First, discrimination between individuals can only occur if they share a proportion of the song types in their song repertoire, and that these shared song types are encountered

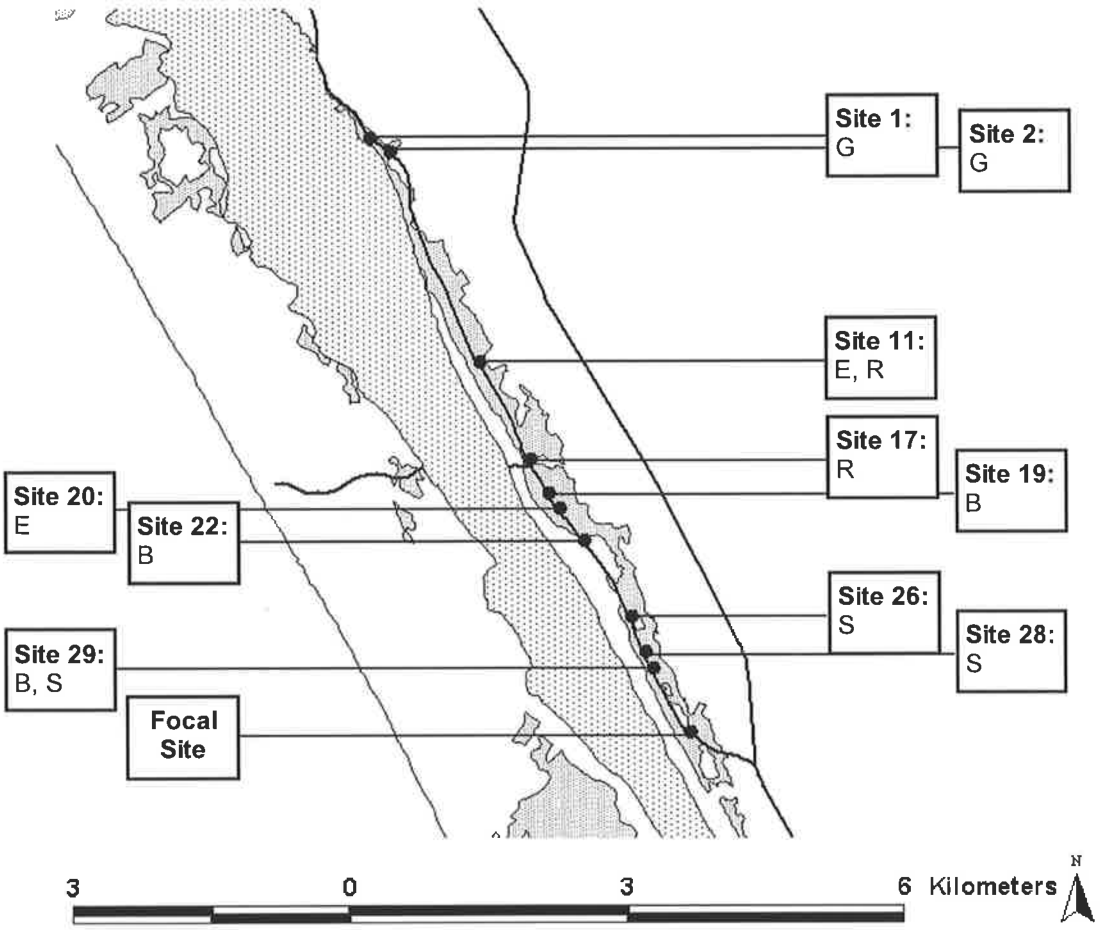


Figure 5.8 Map of Loop Road, Coorong National Park, highlighting sites for which common song types were compared in Section 5.6. Closed stippled areas are areas of optimal habitat for *D. broadbenti*; open stippled area is the Coorong lagoon. Common song types located at each site are listed (all song types listed were found at the Focal Site).

Table 5.11 Results of cross-correlation analyses performed between songs of focal individuals and songs of unknown individuals at other sites. The number of sites includes the focal site. * denotes that the individuals recorded at the two sites were either the same individual (S) or two different individuals (D).

a. Song type E

# sites	focal site v site 11		focal site v site 20		site 20 v site 11	
	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*
3	100	D	100	D	100	D

b. Song type G

# sites	focal site v site 1		focal site v site 2		site 2 v site 1	
	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*
3	100	D	100	D	100	D

c. Song type R

# sites	focal site v site 11		focal site v site 17		site 17 v site 11	
	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*
3	100	D	100	D	100	D

d. Song type S

# sites	focal site v site 26		focal site v site 28		focal site v site 29		site 26 v site 28		site 26 v site 29		site 28 v site 29	
	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*
4	100	D	100	D	100	D	100	D	100	D	95	D

e. Song type B

# sites	focal site v site 19		focal site v site 22		focal site v site 29		site 19 v site 22		site 19 v site 29		site 22 v site 29	
	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*	%<0.6	ID*
4	100	D	100	D	100	D	100	D	100	D	100	D

regularly enough for such comparisons to be useful. However, such limitations may not be significantly restrictive in the case of *D. broadbenti*, as many song types are used extensively throughout continuous populations (Section 5.5), and neighbouring birds, at least, appear to use shared song types more often than unique song types (Chapter 4), thus increasing the probability of encountering these common song types. Although acoustic identification through the comparison of common song types may not be as effective in *D. broadbenti* as in species which use one or two different song types, such a limitation does not make the technique prohibitively ineffective in this species.

The second limitation, however, does place some severe restrictions on the use of acoustic identification in this species, in that the comparison of common song types does not allow different song types to be compared within or between individuals. The consequence of this limitation is that any survey that uses acoustic identification of individuals for this species must be executed as a series of independent surveys, one for each different song type encountered. As a result, demographic information obtained using one song type for identification does not improve on information obtained using other song types. This restriction may be overcome if individual birds cycled through their song repertoire during a single bout of singing, and the data generated from surveys conducted using different song types would be additive. Such is not the case, however, for *D. broadbenti* (as demonstrated in Chapter 4), with individuals rarely singing more than a single song type during a continuous bout of singing. Investigators must, therefore, be aware of this limitation when using acoustic identification to conduct surveys in species with song repertoires. The restriction of comparing song types for identification must, however, be tested in other species with large repertoires, in order to test the effectiveness of comparing song features that are common to many song types for individual identification in these species.

Individual acoustic recognition has been demonstrated in a number of species that have extensive song repertoires (Kroodsma 1976, Stoddard *et al.* 1992); (Weary *et al.* 1992, Godard and Wiley 1995), but see (Godard 1993), despite suggestions that larger song repertoires may constrain recognition (Krebs and Kroodsma 1980). However, these studies do not imply that birds can discriminate between individuals by comparing song features that are common to all song types. The mechanism for individual recognition in species with large song repertoires appears to involve both comparisons within song types, and knowledge of the song repertoires of different individuals (Stoddard, et al. 1992). Current evidence, therefore, suggests that individuals of species with extensive song repertoires discriminate between conspecific individuals in much the same way as biological investigators can, as has been demonstrated in this chapter, primarily through within-song type comparisons, and not through the comparison of features that are common to all song types.

The functions of song for *D. broadbenti* remain unclear, although personal observations regarding the associated behaviours of singing suggest that song plays a dual role in this species: as a tool in territory defence and maintenance, and as a method of maintaining pair bonds between mated pairs. Preliminary attempts to investigate the functions of song in rufous bristlebirds were concerned with individual recognition, but were severely hampered by the cryptic nature of the species; essentially, behavioural responses to playback experiments were extremely difficult to quantify accurately. Nevertheless, these preliminary efforts did provide some evidence of the role of song in territory defence, with territorial individuals often reacting strongly to the playback of bristlebird songs within their territories. Such observations have also been noted by other authors (Morcombe 1986).

Acoustic identification of individuals in *D. broadbenti* is therefore a technique that can be used by investigators with some effectiveness, with the use of cross-correlation analyses allowing for the immediate identification of previously unknown individuals. Investigators must also be aware, however, of the limitations of the technique for this species, as identification only appears possible through the comparison of song types that are common between a number of individuals. The development of acoustic identification in other avian species with song repertoires, however, may find that these restrictions are limited to *D. broadbenti*, and that acoustic identification can be an effective tool in species with extensive song repertoires.

Chapter 6 Geographic Song Variation Within and Between Isolated Populations of the Rufous Bristlebird *Dasyornis broadbenti*

6.1 Introduction

The way in which the communication signals of animals vary geographically has received considerable attention, especially with regard to geographic variation in acoustic signals. This attention is understandable, given the suggestion that such variation in communication systems and other behaviours may be important in reproductive isolation (Mayr 1963). Such suggestions are also supported by empirical evidence, such as the observation that geographic call variation has been important in the speciation of Hawaiian crickets (Otte 1989).

Geographic variation in bird song has been explained by a number of mechanisms, which are not necessarily mutually exclusive. One suggestion is that variation in bird song structure between populations is a result of little more than random processes, as a result of events such as population bottlenecks (Thielcke 1969, Mirsky 1976, Wiens 1982). Such an explanation is especially important when considering insular populations, as bottlenecks and founder effects have been shown to impact upon such systems genetically, as well as culturally (Carson 1992).

In addition to these chance events, differences in the abiotic and biotic acoustic environment have the potential to result in variations in song structure between bird populations. There is considerable evidence that the physical structure of the habitat can influence sound transmission (Linskens *et al.* 1976, Cosens and Falls 1984), and that birds have evolved acoustic signals that are best adapted to their habitat (Morton 1975). Differences in the physical structure of the habitat could thus have a bearing on subsequent differences between populations in the structure of their songs (Kroodsma 1985).

However, the songs of birds tend to adapt to the overall sound environment in which they evolve, and biotic factors also play a role in their evolution. For bird songs, the most important biotic factor is the songs of other bird species, and songs and singing behaviour thus have adapted to minimise interference from the songs of other species (Bremond 1977, Miller 1982, Doutrelant and Lambrechts 2001). If avifaunal assemblages vary geographically, then the structure of the songs of the birds that make up the assemblages may also vary (Marler 1960). Again this may be especially important for insular populations, as smaller 'islands' will tend to have less species than larger 'islands'(MacArthur and Wilson 1967), and the songs of species inhabiting smaller islands may thus undergo a version of ecological release, where there is less selective pressure on songs to occupy tight areas in acoustic space (Marler 1960). Marler's hypothesis thus leads to the suggestion that species-specific, stereotypic songs will evolve in regions of high avifaunal diversity, whereas less distinct songs will be found in regions of lower diversity.

These propositions thus suggest that the songs of isolated populations have the potential to differ from one another more than might be expected solely from the distances that separate the populations. Such a suggestion is supported by empirical evidence for a number of species. (Kroodsma 1985) found that the songs of Bewick's wren *Thryomanes bewickii* differed more between an island population and a mainland population separated by 30 km, than between two mainland sites within a continuous population, separated by 150 km. (Mirsky 1976) found that the songs of Anna's hummingbirds *Calypte anna* and juncos *Junco hyemalis* also differed between island and mainland populations, to the point of supporting the proposal that the island population of juncos be given specific status. However, a number of people have also shown that little or no difference exists in the song of island and mainland populations of songbird, including house finch *Carpodacus mexicanus* (Bitterbaum and Baptista 1979) and chiffchaff *Phylloscopus collybita* (Thielcke 1969). Such patterns may at least partially depend upon whether regular movements between island and mainland populations occur.

Isolation of bird populations need not require such populations to be surrounded by ocean. Populations can become isolated when surrounded by any form of inhospitable habitat to the bird species in question. Fragmentation of habitat and subsequent isolation of populations can occur naturally, through such mechanisms as climate or geological changes, or anthropogenically, such as a result of the extensive vegetation clearance that has occurred throughout the world. As with song divergence between birds inhabiting oceanic islands, the potential thus exists for the songs of birds inhabiting fragmented habitats to diverge in a manner disproportionate to the distances between the populations. Indeed, such patterns have been found between populations of great tit *Parus major* isolated by barriers such as desert, mountains and savannah (Thielcke 1969), although populations of Lincoln's sparrow *Melospiza lincolnii* isolated by unsuitable habitat, such as pine forest, exhibited song variation that was no greater than expected by the distances between populations inhabiting continuous habitat (Cicero and Benowitz-Fredericks 2000). Recent work on altitudinal specialists of the wet tropics of Australia has also shown that isolation of populations through warming has resulted in the production of distinctly different songs by these different populations, to the point that individuals from one population often fail to recognise the songs of other populations as conspecific (D. Westcott, pers. comm.).

The analogy between oceanic islands and fragmented terrestrial habitat is now well recognised, to the point that island biogeography theory is now truly integrated into conservation theory, as "the remaining areas of more-or-less natural habitats become increasingly isolated within a sea of altered and generally inhospitable habitat; in short, they are habitat islands" (Whittaker 1998). In this chapter, therefore, I suggest that songs of bird populations that have become isolated through habitat clearance have the potential to diverge over time in ways not expected by the distances that separate these populations alone. (Thielcke 1969) found that populations of short-toed treecreeper *Certhia brachydactyla* in Spain exhibited significantly more song variation than populations from northern and central Europe, and suggested that such patterns were a result of the fragmentation of treecreeper habitat in southern Spain by timber plantations, citrus orchards and fields (Thielcke 1969). The history of habitat modification and fragmentation in Europe is obviously much older than that found in post-European Australia. Investigations into song variation between fragmented populations of Australian birds would thus be especially useful to understanding the impact of habitat clearance on the communication systems of animal populations, considering the relatively recent history of habitat alteration in this country.

The Rufous Bristlebird *Dasyornis broadbenti* provides a suitable model for the study of song divergence in anthropogenically isolated populations, as it is a terrestrial bird with poor flying ability, and is thus thought to be a poor disperser through inhospitable habitat. As such, the isolated populations discussed in this paper are thought to be truly isolated, with no exchange of individuals between these populations. As early as 1932, (Sutton 1932) suggested that "the chief call (in the Coorong) was quite different from that of the birds found near Robe". This paper therefore investigates patterns of song variation in the rufous bristlebird, both within continuous populations, and between populations that have been isolated through habitat clearance. Although some populations of *D. broadbenti* have become isolated as a result of 'natural' processes (such as changed in distribution as a result of climate change), such isolation has become exacerbated by anthropogenic factors, especially since the end of the Second World War (T. Croft, pers. comm.). In addition to testing the effects of anthropogenic isolation on song divergence, songs of the two extant subspecies of *Dasyornis broadbenti* were compared to determine whether song variation between the taxa supports their subspecific status.

6.2 Methods

6.2.1 Site locations and recording methods

Recordings of rufous bristlebird songs were obtained from seven sites within the Coorong National Park (COOR), representing sites within a continuous population, and six sites isolated from both the Coorong National Park, and each other. The seven sites sampled within the Coorong National Park were located at Jack Point (JP; 36°02'S 139°34'E), Salt Creek (SC, 36°07'S 139°38'E), Tea-Tree Crossing (TTX, 36°08'S 139°38'E), Loop Road South (LRS, 36°13'S 139°41'E), Chinaman Well (CW, 36°15'S 139°42'E), 42-Mile Crossing (42MX, 36°17'S 139°43'E) and 32-Mile Crossing (32MX, 36°23'S 139°46'E). The isolated sites were at the following locations: Butcher's Gap Conservation Park (BGCP, 36°53'S 139°48'E), Beachport Conservation Park (BPCP, 37°27'S 139°58'E), Canunda National Park (CAN, 37°42'S 140°16'E), a reserve close to the township of Portland (PTLD, 38°20'S 141°36'E), Port Campbell National Park (PCNP, 38°38'S 143°02'E), and within a coastal reserve near the township of Airey's Inlet (AIL, 38°27'S 144°06'E). The locations of each of these sites are shown in Figure 6.1. The Coorong National Park, Butcher's Gap Conservation Park, Beachport Conservation Park and Canunda National Park all lie within the range of the western subspecies *D. b. broadbenti*, while Pt. Campbell National Park and Airey's Inlet coastal reserve are within the range of the eastern subspecies *D. b. caryochrous* (Schodde and Mason 1999). The site at Portland lies between the two proposed subspecific boundaries, which is located either west of Portland at the mouth of the Glenelg River (eg. (Condon 1951), or is located east of Portland, "between east Portland Bay and Peterborough, Victoria." (Schodde and Mason 1999).

The majority of songs were recorded between 8 September and 22 September 2000, and between 7 October and 17 October 2001, using a Sony TC-D8 DAT-Recorder with a Sennheiser ME-66 directional microphone. Additional song recordings were provided by Harold Crouch, and taken from the Field Guide to Australian Bird Song tape series (BOC 1994). Only male songs were included in subsequent analyses, as inadequate samples of female songs were collected.

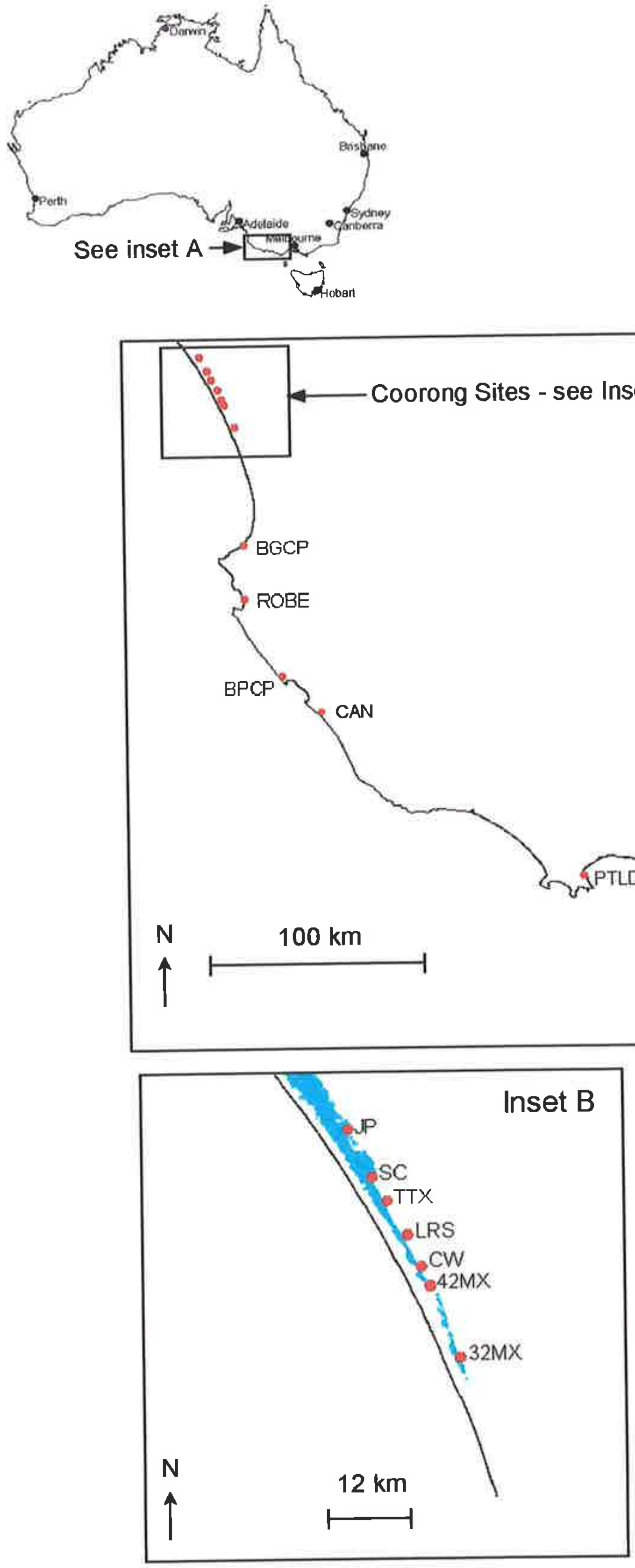


Figure 6.1 Maps showing location of sites sampled for recordings of *D. broadbenti* songs. Inset A: all sites; Inset B: Coorong sites. See text for site name abbreviations.

6.2.2 Song analyses

Following the acquisition of the song recordings, each recording was tranferred to a personal desktop computer and analysed using AviSoft SASLab Pro (Specht 1998). Each song recording was converted into a sonogram (Sampling Frequency: 22 kHz; FFT Length: 256) and subsequently inspected visually.

All song types were compared between sites to determine the proportion of song types that were common between sites within the same population, and between isolated populations. Additionally, three measures of song structure were quantified. As described in previous chapters, the male rufous bristlebird song is composed of three components (Figure 6.2), each of which was initially analysed separately for variation in syllabic and component structure. Songs were analysed in order to determine whether the syllables of the first component alternated in frequency or not. In addition, the presence or absence of the second component was determined, as well as the number of syllables in the final song component (e.g. Figure 6.3).

In addition to these visual comparisons, quantitative comparisons were performed between sites, based upon a number of temporal and spectral features of the songs. This second analysis complements the first, in that the first was aimed at determining structural variation among sites with respect to the syllabic structure of each song, whereas this second analysis was aimed at determining overall variation in song structure, with respect to variation in the spectral and temporal features of each song. The following parameters were measured to describe each song: the length of the first component, length of the second component, length of the third component, total length of the song, minimum frequency of the song, maximum frequency of the song, and frequency range (Figure 6.2). As with Chapter 5, only the final two syllables of the first component were included in these measurements and subsequent analyses, as the number of syllables in this component varied greatly, and partially depended on whether the start of each song was recorded.

Based upon these seven song parameters, song variation within and between populations was determined by performing a DFA (Statsoft 1995), grouped firstly by sites within the Coorong, and secondly by isolated sites. A final DFA was also performed on the same song data, grouped by subspecies.

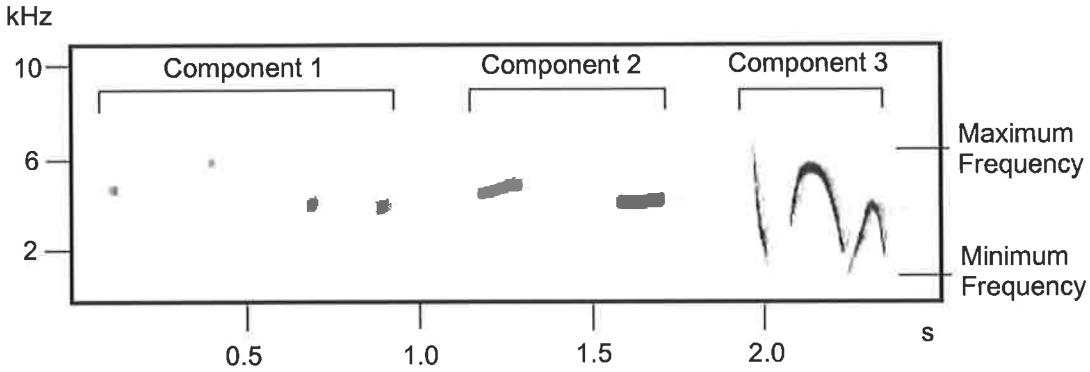


Figure 6.2 Sonogram of a typical male rufous bristlebird song, highlighting the components of the song and the parameters measured to describe each song.

6.3 Results

6.3.1 Extent of song type use

Song types recorded at more than one site within the Coorong National Park are presented in Table 6.1. Of the 36 song types recorded at the seven different sites, seven were found to occur at more than one site. Six of these seven song types were only common between adjoining sites (that is, sites separated by a maximum distance of 7.6 km), with two of 12 song types sampled common between Tea-tree Crossing (TTX) and Loop Road South (LRS). However, the seventh song type recorded in more than one Coorong site was recorded at the two Coorong sites separated by the greatest distance, Jack's Point and 32-Mile Crossing, separated by a distance of 37.7 km. While the probability of encountering identical song types generally appears to decline with distance (as suggested in chapters 4 and 5), identical song types can be encountered between sites separated by as much as 37.7 km.

While identical song types were recorded between sites within the continuous Coorong population of rufous bristlebird, no song type was recorded in more than one isolated site. The isolation of these sites may therefore act as a barrier to the exchange of song types, although such a suggestion can only be confirmed through more thorough and comprehensive sampling.

6.3.2 Aspects of song structure

In total, the number of song types recorded at each of the 13 sites sampled ranged from 4 to 49 ($X = 21.9 \pm 3.5$; $n = 13$). The number of different song types recorded at each of the 7 Coorong sites ranged from three to eight song types ($X = 5.1 \pm 0.74$; $n = 7$), while for the six isolated sites, between 4 and 13 song types were recorded ($X = 8.5 \pm 1.5$; $n = 6$).

There was little variation in the proportion of songs where the syllables of the first component alternated in frequency, for all sites. Within the Coorong, 66.7% of song types possessed monotonous first components. Although there was variation between Coorong sites in the proportion of monotonous first components, there was no trend between this variation and distance between sites (Figure 6.4). In addition, variation in the proportion of monotonous first components was not greater between isolated sites than that found between Coorong sites

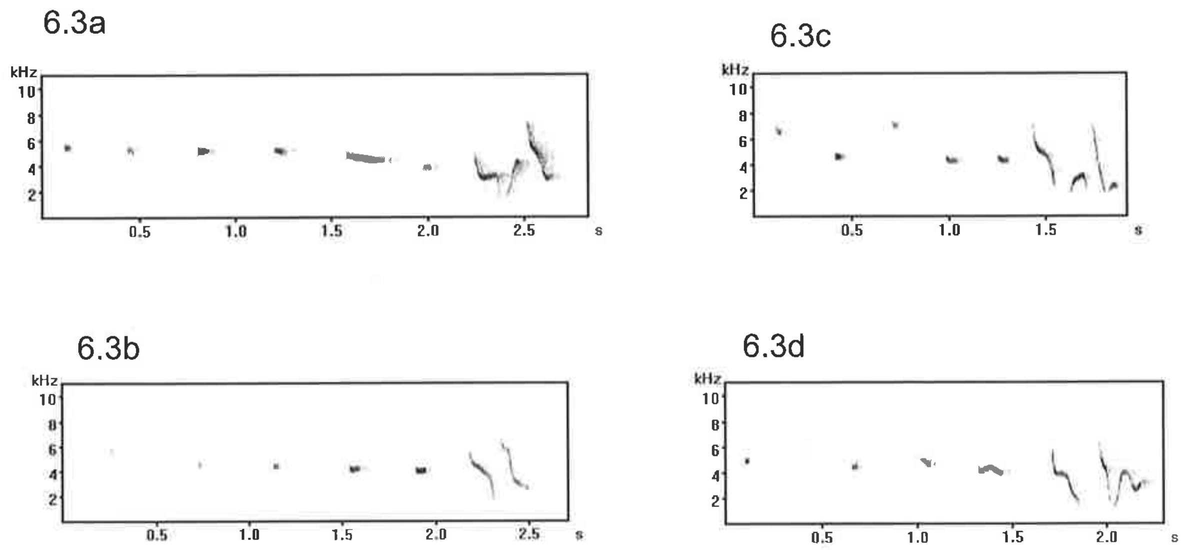


Figure 6.3 Example sonograms of the male songs of *Dasyornis broadbenti*, highlighting variation in the structure of the three song components analysed in this study. In the song depicted in 6.3a, the first component is monotonous, the second component is present, and the third component has three syllables. In the song depicted in 6.3b, the first component is monotonous, the second component is absent, and the third component has two syllables. In song 6.3c the first component alternates between two frequencies, the second component is absent and the third component has four syllables. Finally, in song 6.3d, the first component alternates between two frequencies, the second component is present and the third component has three syllables.

Table 6.1 Common song types recorded between sites within the Coorong National Park. The number in each cell is the number of song types shared between the two sites; numbers in brackets are the number of song types recorded at each site.

	JP (5)	**SC (3)**	**TTX (6)**	**LRS (8)**	**CW (7)**	**42MX (4)**	**32MX (3)**
JP (5)	-						
SC (3)	1	-					
TTX (6)	0	1	-				
LRS (8)	0	0	2	-			
CW (7)	0	0	0	1	-		
42MX (4)	0	0	0	0	1	-	
32MX (3)	1	0	0	0	0	0	-

(Figure 6.5). Therefore, this aspect of song structure does not appear to vary more between isolated populations than within continuous populations.

There was little variation in either the presence of the second component, or the number of syllables in the third component, between the seven Coorong sites. All song types recorded in the Coorong contained the second component (Figure 6.6), and only one song type in each of four sites had a final component consisting of two syllables; the remaining 31 song types contained three syllables in their final component. The proportion of final components that contained three syllables was thus consistently high for all of the five Coorong sites (Figure 6.8)

Variation in these song parameters was greater, however, between isolated sites. However, for these parameters, there was little divergence between sites where *D. b. broadbenti* is located according to (Schodde and Mason 1999), including the Coorong sites, and Portland. All songs recorded within sites of the western subspecies had high proportions of final components with three syllables (Figure 6.9). In addition, the presence of a second component was recorded in all song types of *D. b. broadbenti* (Figure 6.7), with the exception of a single song type recorded at Beachport.

These aspects of song structure for *D. b. caryochrous*, however, appear to have diverged strongly from those of *D. b. broadbenti*. Songs recorded at Pt. Campbell National Park and Airey's Inlet both had a low proportion of song types with the second component present (Figure 6.7), as well as lower proportions of song types with three syllables in the final component (Figure 6.9). The number of syllables in the final component for this subspecies appears to be more flexible than for *D. b. broadbenti*, with two song types recorded having four syllables, as well as four song types having two syllables (Figure 6.9). Chi-squared

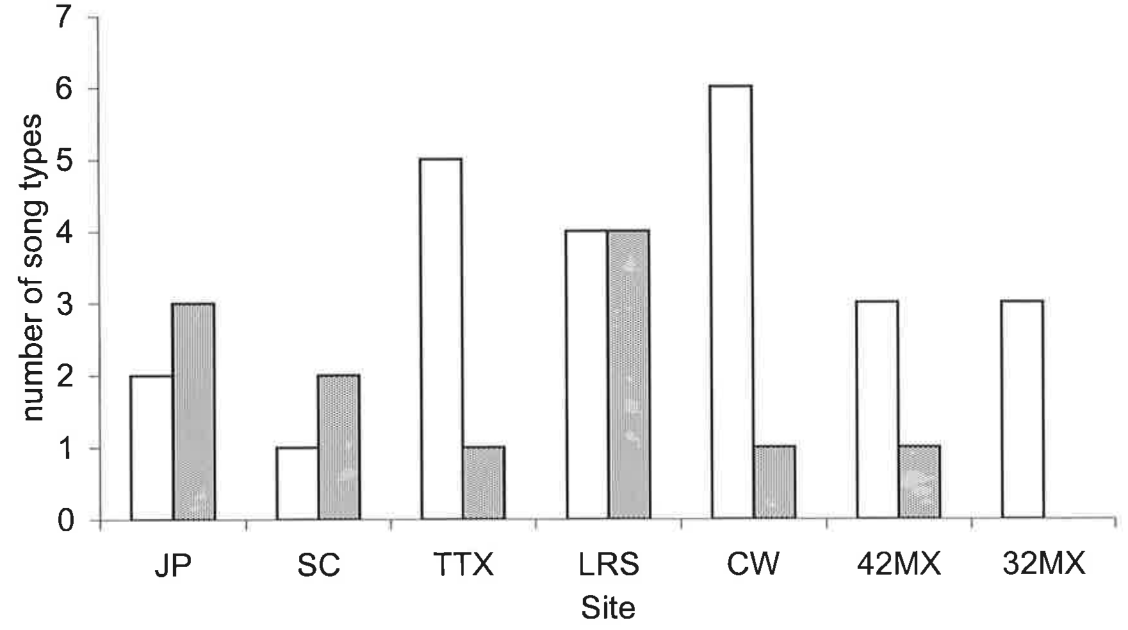


Figure 6.4 The number of song types recorded at each of seven sites within the Coorong National Park, whose first component syllables were monotonous (open bars), or alternated between two frequencies (stippled bars). Abbreviations for sites in text.

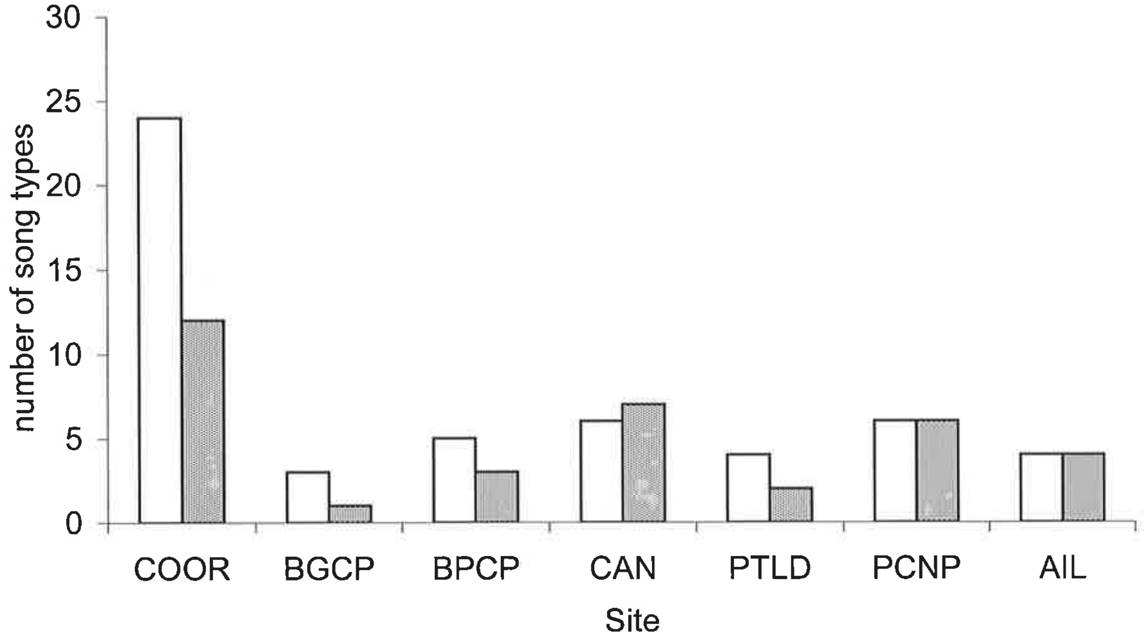


Figure 6.5 The number of song types recorded at each of six isolated sites, whose first component syllables were monotonous (open bars), or alternated between two frequencies (stippled bars). Abbreviations for sites in text.

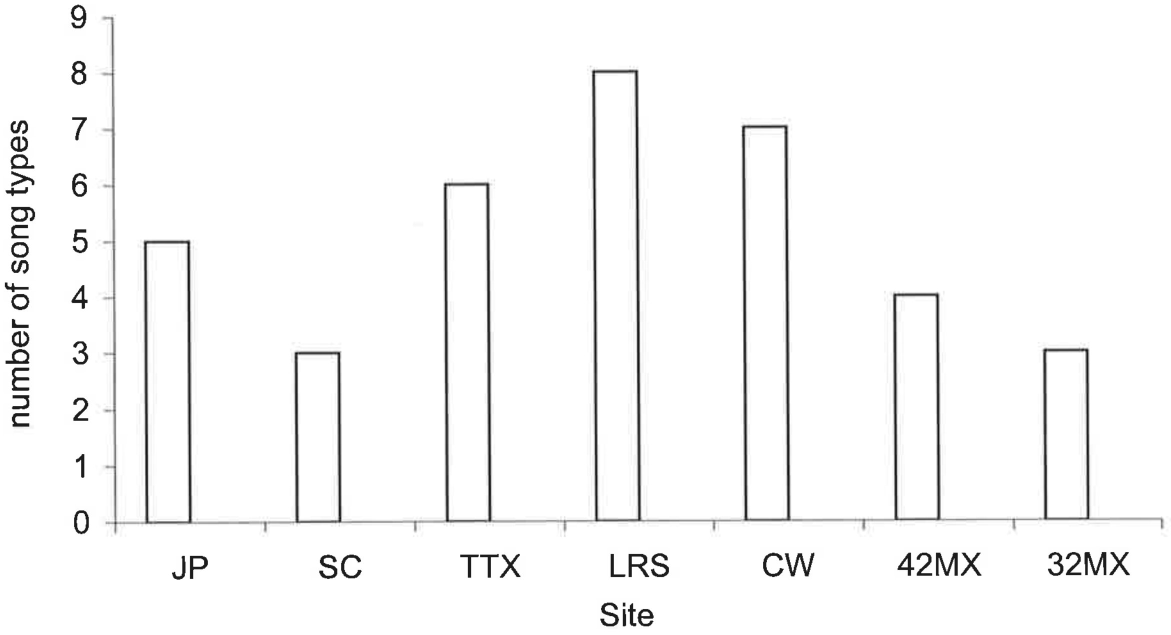


Figure 6.6 The number of song types recorded at each of seven sites within the Coorong National Park, in which the second component was present (open bars), or absent (stippled bars). Abbreviations for sites in text.

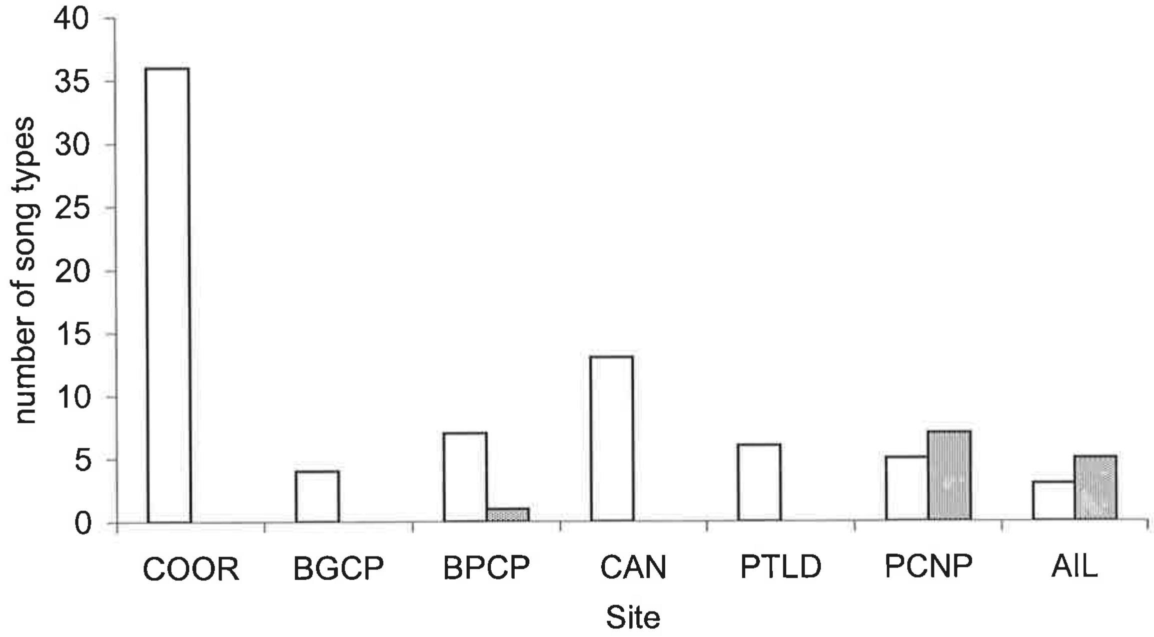


Figure 6.7 The number of song types recorded at each of seven isolated sites, in which the second component was present (open bars), or absent (stippled bars). Abbreviations for sites in text.

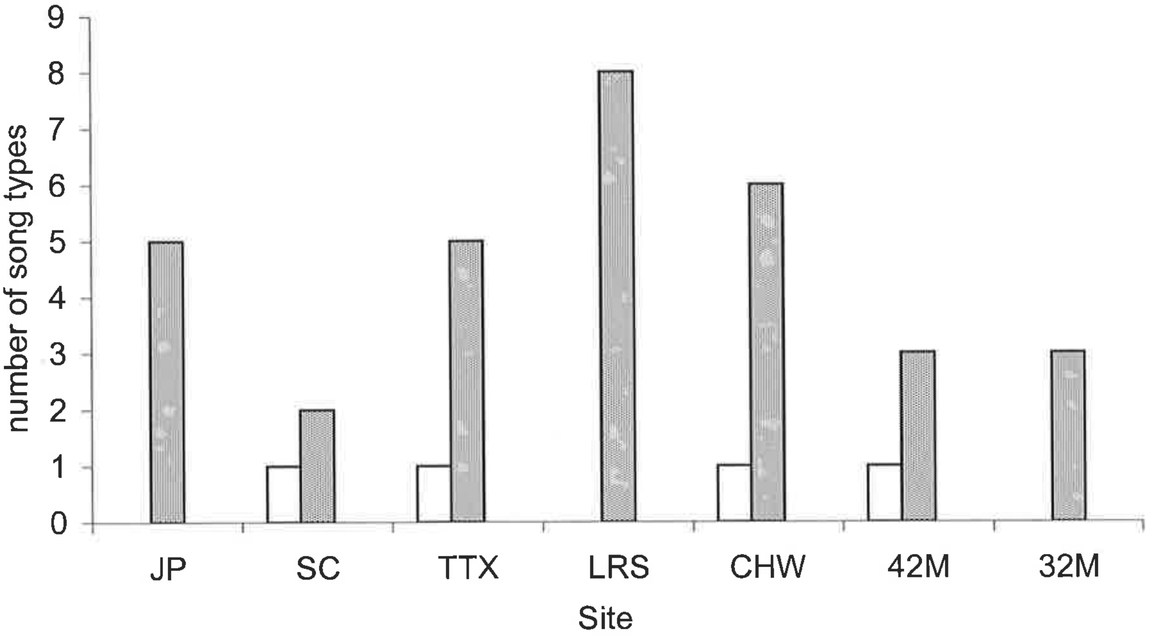


Figure 6.8 The number of song types recorded at each of seven sites within the Coorong National Park, whose third component contain two (open bars) or three syllables (stippled bars). Abbreviations for sites in text.

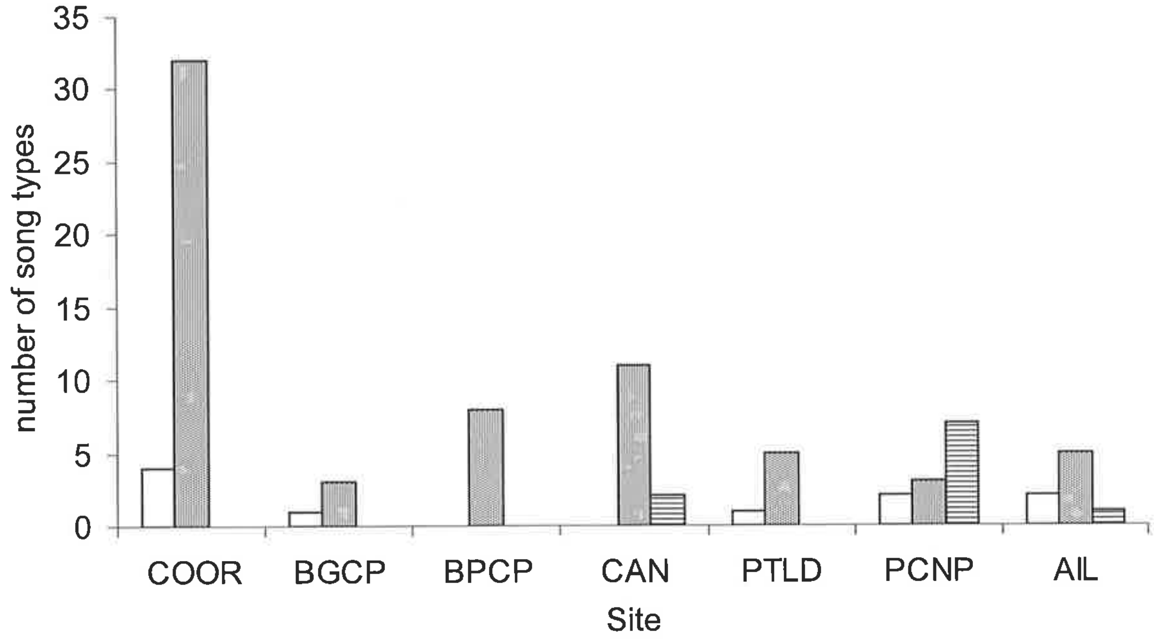


Figure 6.9 The number of song types recorded at each of seven isolated sites, whose third component contain two (open bars), three (stippled bars) or four (hashed bars) syllables. Abbreviations for sites in text

analyses confirm these apparent patterns of subspecific song divergence, with a significant difference detected between subspecies in the structure of the second component ($\chi^2 = 36.1$; $p < 0.0001$) and the third component ($\chi^2 = 21.3$; $p < 0.0001$), although the structure of the first component did not differ between the two subspecies ($\chi^2 = 1.02$; $p = 0.31$).

6.3.3 Discriminant function analyses

Based upon the seven parameters measured to describe each song, DFA revealed that a significant difference existed between the song recorded at the seven sites sampled within the continuous Coorong National Park population of bristlebirds (Wilk's $\lambda = 0.098$; $F_{36, 477} = 9.26$; $p < 0.0001$). Post-hoc analyses revealed that a significant difference between the songs of all pairs of sites, except Chinaman's Well and Salt Creek. Based upon these seven song parameters, 62.5% of songs were classified to the correct site.

DFA also revealed that a significant difference existed between the songs recorded at the seven isolated sites (Wilk's $\lambda = 0.002$; $F_{42, 1030} = 70.7$; $p < 0.0001$), with the songs recorded at all pairs of sites being significantly different from one another. This DFA classified 87.5% of songs to the correct isolated site. The proportion of songs classified to the correct isolated site was significantly greater than the proportion of songs classified to the correct site within the continuous Coorong population ($\chi^2 = 28.4$; $v = 1$; $p < 0.0001$).

The Squared Mahalanobis Distances (SMDs), a measure of the mean distance between the songs recorded at each site, in multi-dimensional space (Klecka 1980), were calculated between each pair of sites using DFA. SMDs thus provide a quantitative assessment of the degree of similarity between two sets of songs using multivariate analysis. Based upon these calculated SMD values, songs differed between isolated sites significantly more than between sites within the continuous Coorong population (Wilcoxyn Test: $Z = 2.69$; $p = 0.007$; Figure 6.10). A significant relationship was detected between the actual distance (in km) between sites, and the calculated SMDs between these sites for sites within the Coorong ($r^2 = 0.25$; $p = 0.02$; $n = 21$). However, no relationship was detected between geographic distance and SMD between isolated sites ($r^2 = 0.02$; $p = 0.59$; $n = 21$).

When the recorded songs were grouped by subspecies, DFA revealed a significant difference between the songs of the two subspecies (Wilk's $\lambda = 0.55$; $F_{6, 190} = 25.4$; $p < 0.0001$). The distribution of canonical scores for each of the two subspecies is presented in Figure 6.11,

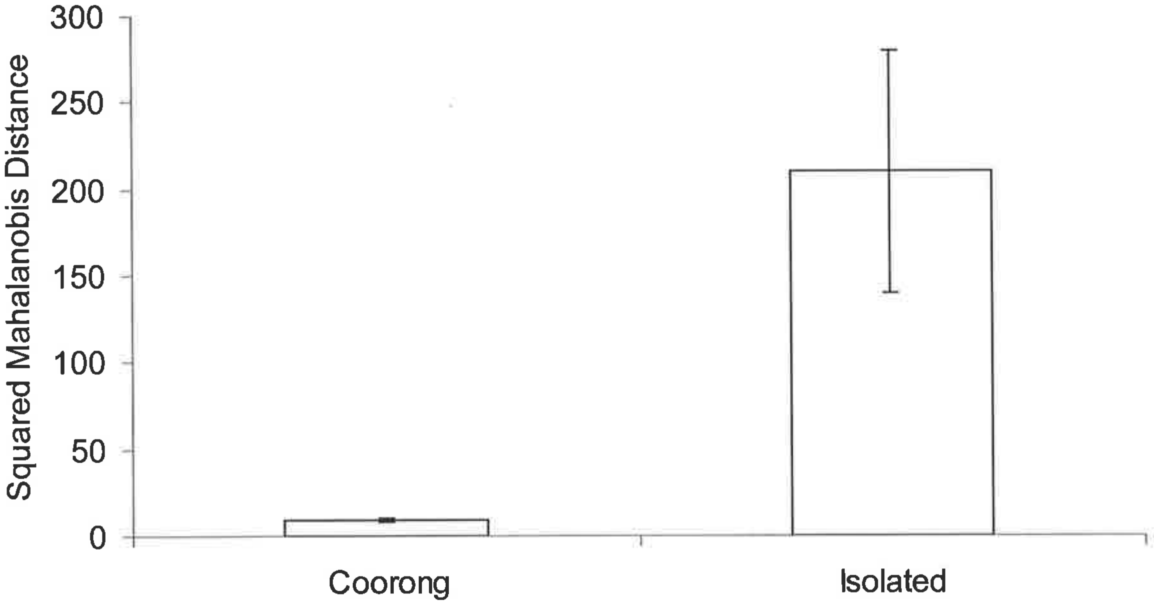


Figure 6.10 Mean (±SE) Squared Mahalanobis Distances (SMDs) calculated between the songs recorded at sites within the Coorong, and between isolated sites.

highlighting the distinctiveness of the songs of the two subspecies. The DFA performed classified 87.9% of songs to the correct subspecies. Furthermore, songs recorded at Portland were all classified correctly when initially grouped to *D. b. broadbenti*, and were all classified incorrectly by the DFA when initially grouped to *D. b. carychrous*.

6.4 Discussion

The results presented in this chapter suggest that song divergence has occurred between populations of rufous bristlebirds that have been isolated through habitat clearance, with multivariate tests demonstrating that songs of isolated populations differ from one another significantly more than songs from sites within continuous populations. However, at this stage one cannot exclude the effects of distance from these patterns of divergence. The two Coorong sites separated by the greatest distance (Jack's Point and 32-Mile Crossing) are separated by a distance of approximately 38 km. However, the minimum distance separating two isolated sites in this study was 21 km, between Beachport Conservation Park and Canunda National Park. Therefore, the lack of encountering identical song types between these isolated populations may simply be a reflection of the distances that separate them, rather than isolation *per se*. Futhermore, analyses of temporal and spectral song features suggested that the broad syllabic structure of the songs of *D. broadbenti* vary as much within the continuous Coorong population as between isolated populations.

If isolation has played a role in song divergence in *D. broadbenti*, such a result may be surprising, considering the relatively recent history of habitat clearance in this region. While the south-east of South Australia has been extensively cleared since European settlement, the coastal heath habitat suitable for rufous bristlebirds has only undergone significant clearance since the end of the Second World War (T. Croft pers. comm.). As such, bristlebird populations have only been anthropogenically isolated for as much as 56 years. Although (Thielcke 1969) observed significant song divergence between anthropogenically isolated populations of short-toed treecreeper *Certhia brachydactyla*, these populations had presumably been isolated for hundreds, if not thousands, of years. (Baker and Jenkins 1987) found that the songs of chaffinch on the Chatham Islands in New Zealand have only diverged as would be expected by their distance from mainland sites, suggesting that their time since isolation (approximately 90 years) was not long enough for significant song divergence due to isolation to occur. In addition, while the coastal heath habitat preferred by bristlebirds has

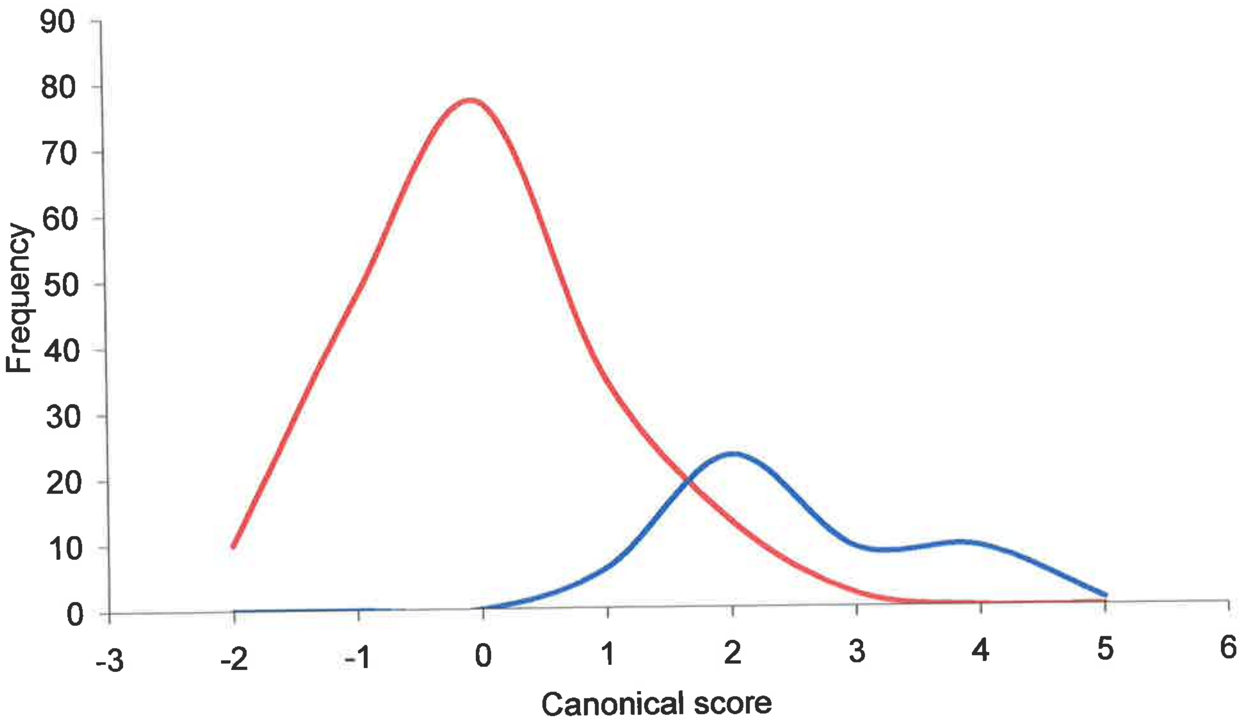


Figure 6.11 Distribution of canonical scores for the songs of *D. b. broadbenti* (red line) and *D. b. caryochrous* (blue line). The canonical scores for each song were produced by a discriminant function analysis grouping songs by subspecies, based upon seven song parameters (see text for further explanation).

become fragmented due to this clearance for agriculture, the habitat still remains relatively intact, compared to many other Australian vegetation types. For example, an estimated 66.5% of the original coastal heath of south-eastern South Australia remains intact, compared to 9.7% for *Eucalyptus camaldulensis* woodland, or 7.8% of *E. leucoxylon* woodland in the south-east of South Australia (Croft *et al.* 1999). Investigations into the impact of habitat fragmentation on cultural transmission and song divergence may wish to concentrate on avian species whose movements are limited by fragmentation (as is the case with *D. broadbenti*), but whose preferred habitat has become more seriously fragmented over a longer time period than that of *D. broadbenti*, such as species that inhabit *Eucalyptus* woodlands.

Why should we expect songs to diverge between anthropogenically isolated populations of *D. broadbenti*? In addition to song divergence as a result of restrictions to cultural transmission between isolated populations, the potential exists for abiotic and interspecific biotic factors to play a differential role in the structure of songs from different populations. Personal observations suggest that the habitat of *D. broadbenti* varies both structurally and floristically between many of the populations sampled in this study, especially with regard to the density and dominant species of vegetation present at different sites (Figure 6.12), although the differences are relatively subtle. Vegetation density has been shown to play an extremely important role in the evolution of avian song structure (Morton 1975, Marten and Marler 1977, Marten *et al.* 1977), and we would thus expect variation in this factor especially to result in song divergence between populations.

The principle pattern of variation found in this study occurred between the two recognised subspecies of *D. broadbenti*. Where little consistent syllabic variation was found between isolated populations of the same subspecies, a striking difference in a number of aspects of song structure were found between the two subspecies. Both song syllable structure (distribution of the number of syllables in the third song component, and presence or absence of the second component), and overall song structural features, such as spectral and temporal features, differed between the two subspecies. As such, the songs of *D. broadbenti* appear to have diverged along the barrier between the two subspecies, rather than along the more recent anthropogenic barriers that have resulted from habitat clearance. This pattern of song divergence is correlated with an equivalent morphological difference between the two subspecies. Early reports proposing the splitting of *D. broadbenti* into two subspecies suggested that the western subspecies was “much lighter in colour” than the eastern subspecies (Morgan 1919), an aspect of plumage variation supported by more recent appraisals (Schodde and Mason 1999). Furthermore, the patterns of song variation presented

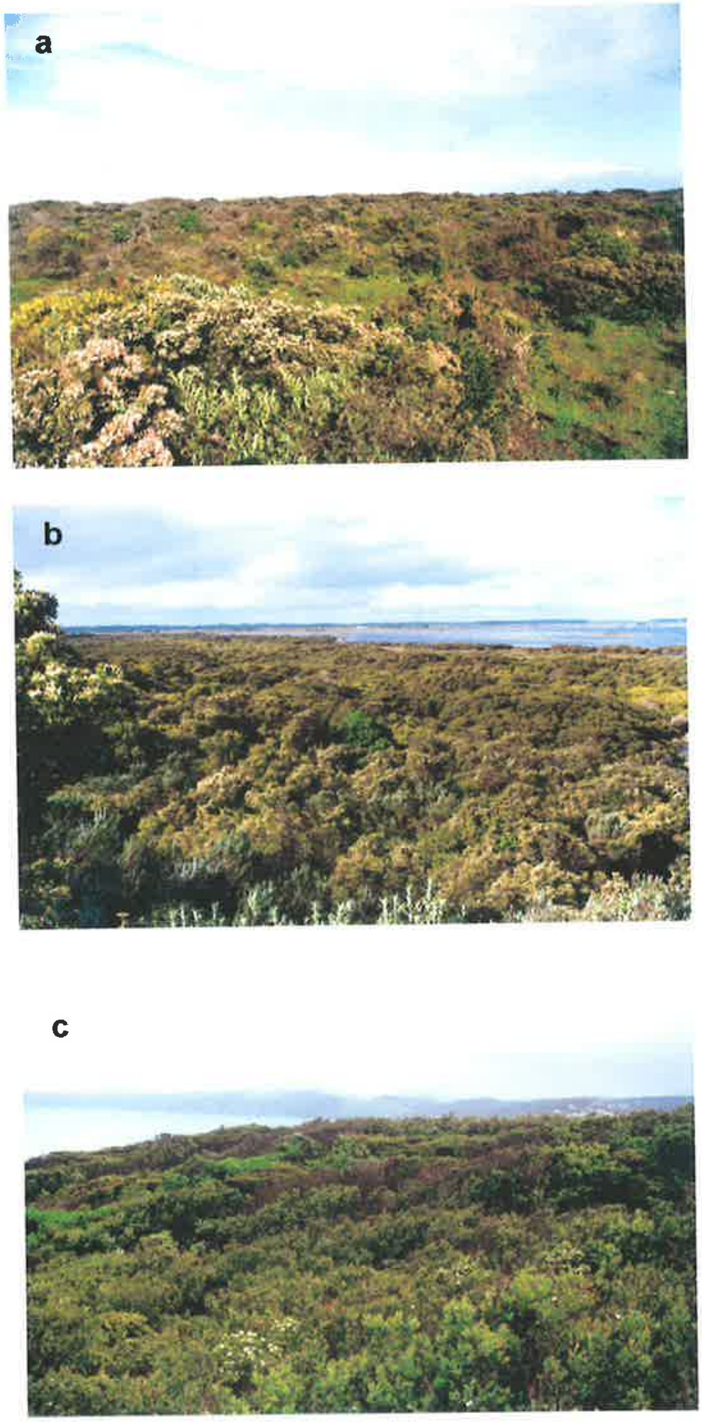


Figure 6.13 Examples of variation in the habitat preferred by *Dasyornis broadbenti*. Figure 6.13a is from the Coorong National Park, near the site Loop Road South; Figure 6.13b is from Beachport Conservation Park, and Figure 6.13c is from the Airey's Inlet site. While 6.13a and b are floristically similar, the vegetation at the Beachport site appears to be much denser than at the Coorong. The vegetation at Airey's Inlet is floristically different from both Beachport and the Coorong (being dominated by *Leptospermum myrcinoides* rather than *Leucopogon parviflorus*), and similar in vegetation density to Beachport rather than the Coorong.

here support the subspecies boundary proposed by (Schodde and Mason 1999), who suggested that the two subspecies meet "not at the states' border (as suggested by earlier authors, eg. Condon 1951, Blakers *et al.* 1984) but further eastwards, between east Portland Bay and Peterborough" (Schodde and Mason 1999, p139), coinciding with the Bassian Volcanic Barrier (Schodde *et al.* 1993). The fact that songs recorded at Portland, which lies between the two proposed boundaries, are best grouped with the songs of the western subspecies *D. b. broadbenti* suggests that, as suggested by Schodde and Mason (1999), the subspecies meet east of this point, but west of Port Campbell National Park. The subspecific analyses of song in this study, therefore, confirm the classification of Schodde and Mason (1999). More generally, such studies highlight the relevance and value of collecting behavioural information (including song) in order to understand taxonomic and phylogeographic patterns.

The results presented here provide us with many avenues for future research. As no broad structural differences were found between the songs of anthropogenically isolated populations of *D. broadbenti*, the data collected here can be used by future investigators as a baseline dataset, from which to measure future patterns of song divergence. Such long-term continued investigations may thus provide us with an accurate measure of the rate of song divergence between isolated populations, assuming that the populations remain isolated in the future. More immediate studies may also investigate genetic variation within and between the isolated populations identified in this study, as a method of correlating rates of cultural divergence with genetic divergence between these populations and subspecific taxa. Primarily, however, the suggestion that habitat clearance and fragmentation can influence cultural as well as genetic transmission should be investigated in other avian species that have become influenced by anthropogenic fragmentation, and that have been isolated from one another for longer periods of time.

Chapter 7 Individuality of Acoustic Signals in other Avian Species

7.1 Introduction

The underlying objective of this thesis was to demonstrate vocal individuality in a range of animal species, as a way of exhibiting the broad taxonomic potential of acoustic individual identification. In order to determine the extent of vocal individuality amongst animal species, a number of taxa were chosen for intraspecific vocal analysis, in addition to the two species for which the majority of data are presented. While the study of these taxa was not as intensive as it was for *Dasyornis broadbenti* or *Pseudophryne bibronii*, their study allows for more extensive conclusions to be made about both acoustic individuality in vocal species, and the potential for individual identification of vocal species by biologists.

As such, the songs of individuals of three additional species were analysed, to determine the extent of individuality in these species. These three taxa were chosen as study species for two primary reasons. First, current standard methods generally used to identify individuals are extremely difficult or impossible to use for these species, and second, all of the species are vocal, and recordings of their songs are easily obtained. Detailed descriptions of the three taxa, including further justification for their choice, are given below.

7.1.1 Willie Wagtail *Rhipidura leucophrys*

The willie wagtail *Rhipidura leucophrys* is a widespread and abundant species of flycatcher (Family Muscicapidae, Subfamily Rhipidurinae) that occurs throughout Australia, and in a variety of man-made habitats in New Guinea (Coates 1990, Simpson and Day 1996). As with many fantails, *R. leucophrys* is a gregarious and inquisitive species of bird, and therefore the species is not difficult to observe and monitor visually. However, *R. leucophrys* is also a species that has both good eyesight, and an acrobatic flying ability that allows it to change direction rapidly, both of which are adaptations to the general nature of its foraging behaviour (Webb-Pullman and Elgar 1998). These adaptations, however, also make the species difficult to capture using standard methods, such as mist-nets. In a study of the breeding biology of *R. leucophrys* (Goodey and Lill 1993), for example, the investigators were only able to capture and mark a maximum of one member of each breeding pair, and in some cases, neither bird was captured (A. Lill, pers. comm.). Despite the conspicuousness of *R. leucophrys*, alternative identification methods that do not require capture would thus benefit the study of this species, both from a practical perspective as well as an ethical one.

The singing behaviour of *R. leucophrys* also makes this species useful in the context of this thesis, as individuals possess repertoires of multiple song types (Walker 1979). It was therefore possible to test the potential for acoustic identification in a species with song repertoires in addition to *Dasyornis broadbenti*.

7.1.2 South-eastern Red-tailed Black Cockatoo *Calyptorhynchus banksii graptogyne*

The South-eastern Red-tailed Black Cockatoo *Calyptorhyncus banksii graptogyne* is one of five subspecies of *C. banksii* (Higgins 1999), and one of two nationally threatened subspecies (Garnett and Crowley 2000). The primary threats to *C. b. graptogyne* are thought to be continued clearance and degradation of both feeding and nesting habitat (Burnard and Hill 2001), and reduction in food resources as a result of inappropriate fire regimes in woodlands dominated by *Eucalyptus baxteri* and *E. arenacea*, the favoured food trees of the cockatoos (P. Koch pers. comm.).

Estimates of population size and other demographic data for *C. b. graptogyne* have, however, been hampered by a number of factors, not least of which is the difficulty involved in observing the birds within their feeding habitat (Burnard and Hill 2001). Parrots in general, and cockatoos in particular, have also proven difficult to individually identify in the field, through a combination of factors, including their relatively short legs precluding the use of colour tarsal bands. The use of tarsal bands has also proven risky for some cockatoos, as a number of species have been known the crush the metal bands with their beaks, resulting in injury to the animal (ABBBS 1997).

The use of patagial tags for the identification of cockatoos, while seen as a feasible alternative to tarsal bands, presents concerns with regard to the effects of such tags on the survivorship of marked individuals. While early work regarding the use of patagial tags on cockatoos suggested that they did not interfere with the behaviour or reproductive success of marked individuals (although there was some concern about increased predation; Rowley and Saunders 1980), subsequent research (Saunders 1988) found that patagial-tagged individuals suffered significantly higher mortality than individuals that were leg-banded. Saunders (1988) concluded that information gathered with the use of patagial tags should not be used in calculations of survival rates, and that "the use of patagial tags for rare, sensitive or endangered species is not recommended unless there is a compelling case for their use" (Saunders 1988, p568). As highlighted in Chapter 1, the very rarity of threatened animal taxa means that reduced survivorship due to identification techniques that involve trapping and handling will have a much greater impact on these taxa than for more common species, and must therefore be avoided. This is certainly the case for *C. b. graptogyne*, considering that the estimated population size of the taxa is less than 1000 individuals (Burnard and Hill 2001).

Developing alternative, non-invasive techniques for the identification of individual Red-tailed Black Cockatoos would thus benefit both the study and management of this endangered taxa. Individual vocal recognition and vocal individuality have been demonstrated in the Short-billed White-tailed Black Cockatoo *Calyptorhyncus funereus latirostris* (Saunders 1983). Considering the similarities in the social biology and behaviours of *C. funereus* and *C. banksii*, vocal individuality might also be expected in *C. banksii*, and may function in both mate and parent/chick recognition. As such, a preliminary study of vocal individuality in *C. banksii graptogyne* was undertaken, in order to determine whether the vocalisations of individual birds could be used by biologists and wildlife managers to identify individuals in the field, and thus aid in the management of this endangered taxa.

7.1.3 Sacred Kingfisher *Todiramphus sanctus*

The Sacred Kingfisher *Todiramphus sanctus* is widespread throughout much of eastern, western and northern Australia, and also occurs through much of the Indonesian archipelago and western Pacific (Higgins 1999). It inhabits a wide range of woodland and open habitats, including monsoon and temperate rainforests, although it generally avoids closed forest (Higgins 1999). Birds are migratory, breeding in the southern part of their range, with nesting occurring in burrows or tree-hollows (Higgins 1999).

While Sacred Kingfishers are generally conspicuous, acoustic identification may benefit the study of this species in a number of ways. Colour-bands are often difficult to observe in kingfishers, due to their relatively short legs. In addition, the conspicuousness of this species is largely a result of the consistency and volume of their vocalisations, particularly during the breeding season (Curl 1999). The primary reason, however, for targeting *T. sanctus* in this study is because it represents one of the first bird species for which the potential for acoustic identification of individuals was demonstrated (Saunders and Wooller 1988). A subsequent field study of *T. sanctus* (Curl 1999) drew similar conclusions to Saunders and Wooller (1988), both with regard to the potential for using the calls of *T. sanctus* for identification of individuals, and with regard to the call parameters that allow individual identification. The objectives for using *T. sanctus* in the present study were to:

1. Confirm the results of Saunders and Wooller (1988) and Curl (1999), especially with regard to Sacred Kingfishers recorded in a different region from these two studies.

2. Should the results of this present study support those of previous studies, to use the cross-correlation techniques developed here to translate call individuality in *T. sanctus* into a directly and immediately applicable system of acoustic identification of individuals for this species.

7.2 Individuality of Song in the Willie Wagtail, *Rhipidura leucophrys*

7.2.1 Methods

Recordings of focal Willie Wagtail individuals were made on the banks of the Torrens Lake, an artificial lake located immediately north of the central business district of Adelaide, South Australia (34°55'S, 138°35'E). The vegetation characteristics of the site are primarily planted lawn, which is managed through irrigation, fertilization and mowing. In addition, London plane trees *Platanus acerifolia* and red gums *Eucalyptus camaldulensis* have been planted, and are generally mature.

Recordings of Willie Wagtail songs were made using a Sony TCD-D8 DAT Walkman, with a Sennheiser ME-66 directional microphone. Recordings were generally done between 0500 and 0900, although a few recordings were obtained outside of these times. Individual birds were recorded when they were encountered and were singing, and recording ceased only when the bird stopped singing. Each recording is thus defined as a recording session. Recordings of focal Willie Wagtails were made occasionally between 29 September 1998 and 21 January 1999, and 24 October 2000 and 12 November 2000.

In addition to the recordings obtained from focal birds located around the Torrens Lake, recordings were also obtained from other individuals at locations along the lower Torrens in January 1999, west of the Torrens Lake. These recordings were made in order to determine the extent of local song dialects in *R. leucophrys*, as an estimate of the number of individuals that potentially share a song type (see Figure 7.1).

Methods used to analyse and compare the songs of Willie Wagtails are presented below under the appropriate sections.

7.2.2 Singing Behaviour

1998-1999

Recordings were obtained from 13 individuals in 1998-1999, with the locations of territories for each of these 13 birds presented in Figure 7.1. Eight birds recorded along the Torrens Lake had territories separated by a maximum distance of 1.7km (mean distance between territories: 725 ± 79m; "Torrens Lake" birds). Four birds held territories a minimum of 5.2 km downstream from the Torrens Lake ("Downstream" birds), and 970 (± 230) m from one another. The thirteenth bird recorded held a territory 1 km downstream from the Torrens Lake birds, and 3.5 km upstream from the downstream birds (Figure 7.1).

The songs of *R. leucophrys* were classified visually to song type. As with *D. broadbenti*, songs were considered to be the same song type if their entire structure was broadly the same. The song types of *R. leucophrys* were highly stereotypic, and varied much more between song types than between songs of the same song type, making visual classification simple (Figure 7.2).

In total, 11 different song types were recorded from 13 individuals in 1998. Repertoire size was determined for 11 of these 13 birds, as insufficient recordings were made of the songs of two birds (98-9 and 98-17) for repertoire size to be determined for these birds. The observed repertoire size for the remaining 11 birds ranged from two to five song types (mean = 2.5 ± 0.28; $n = 11$). For most birds, all observed song types were recorded within the first few song bouts (defined as a continuous bout of singing where a single song type is repeated), with no new song types recorded in subsequent

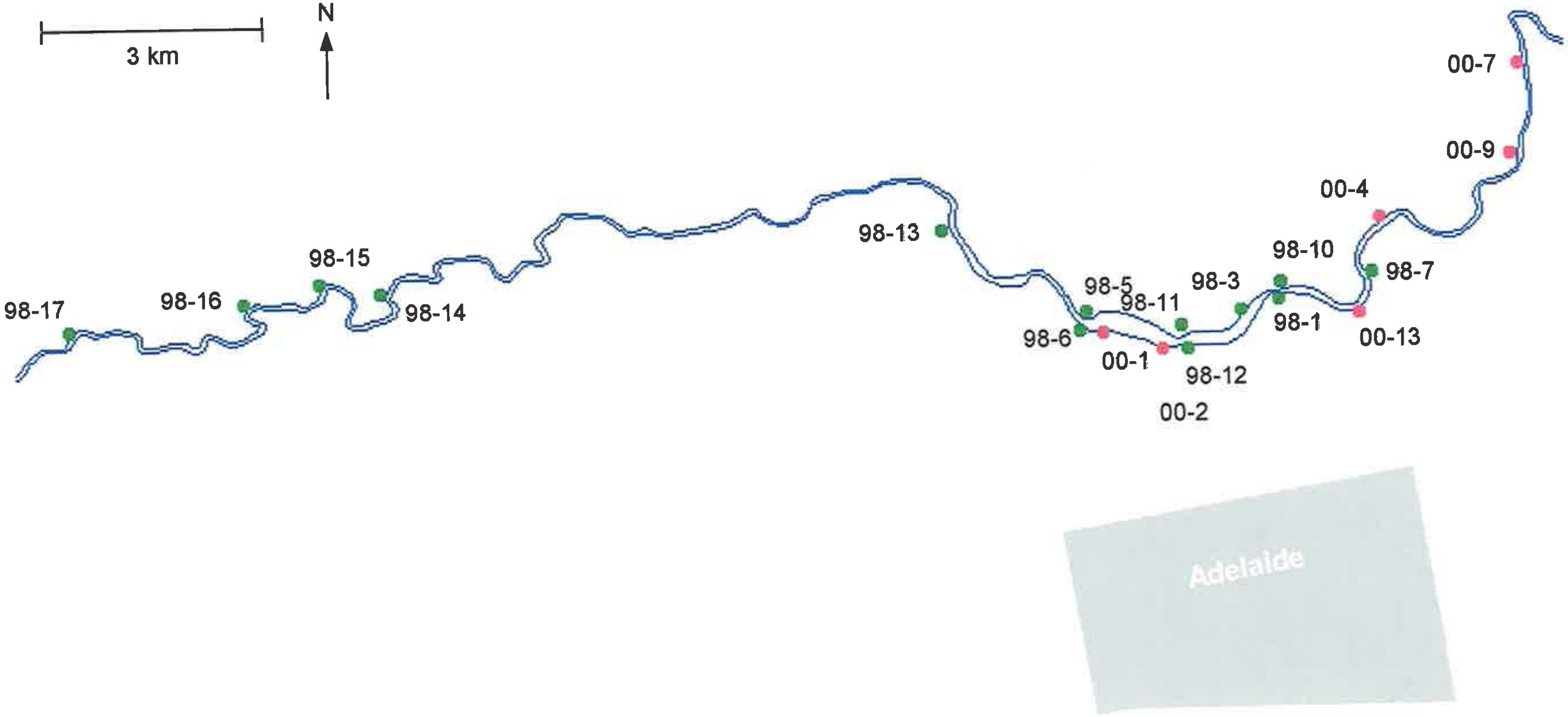


Figure 7.1 Map of the lower Torrens River, Adelaide, South Australia, indicating the territory locations of willie wagtails whose songs were recorded in 1998-1999 (green dots) and 2000 (red dots).

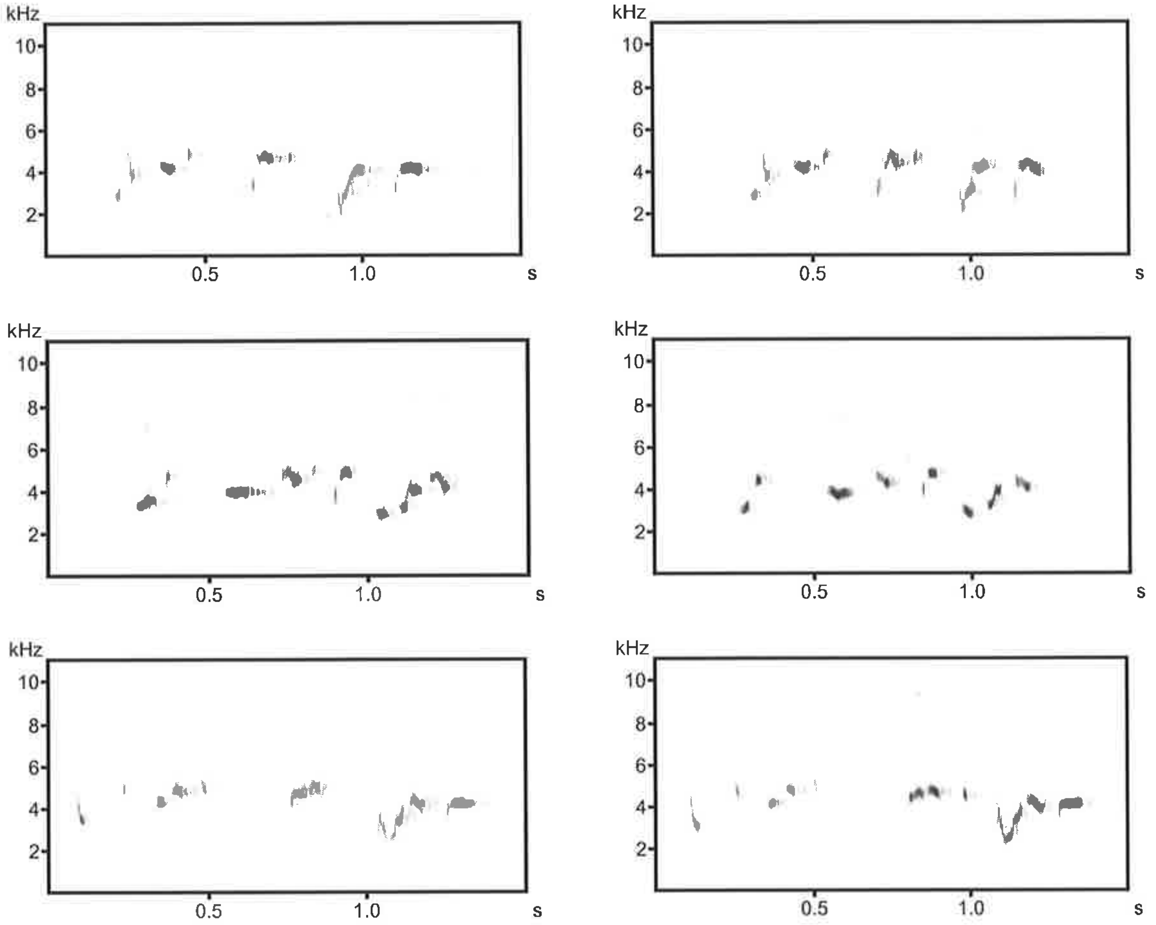
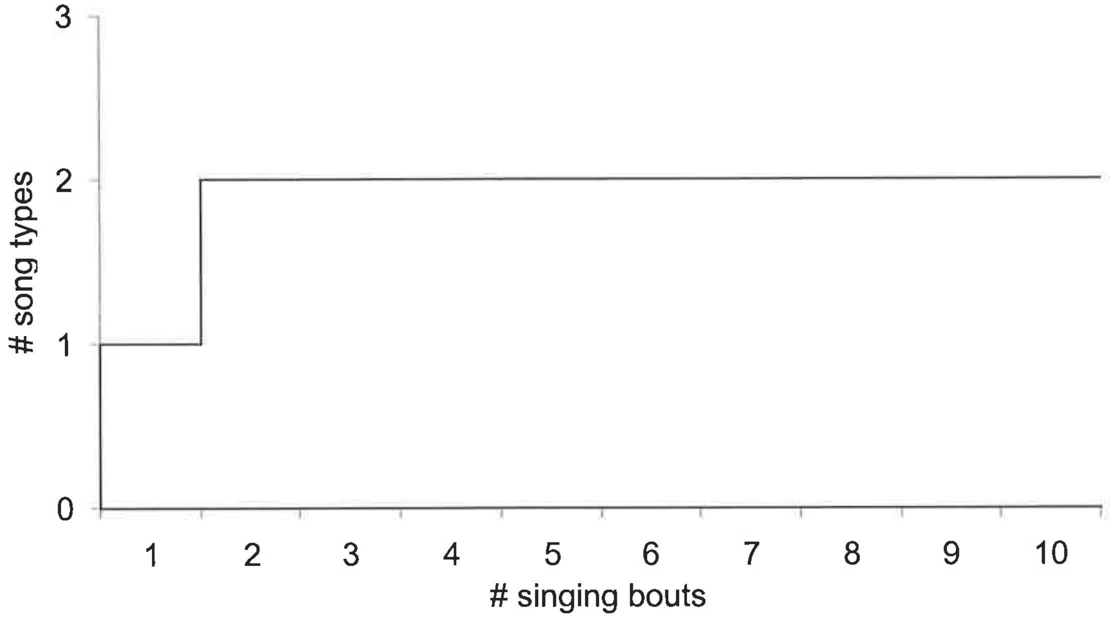
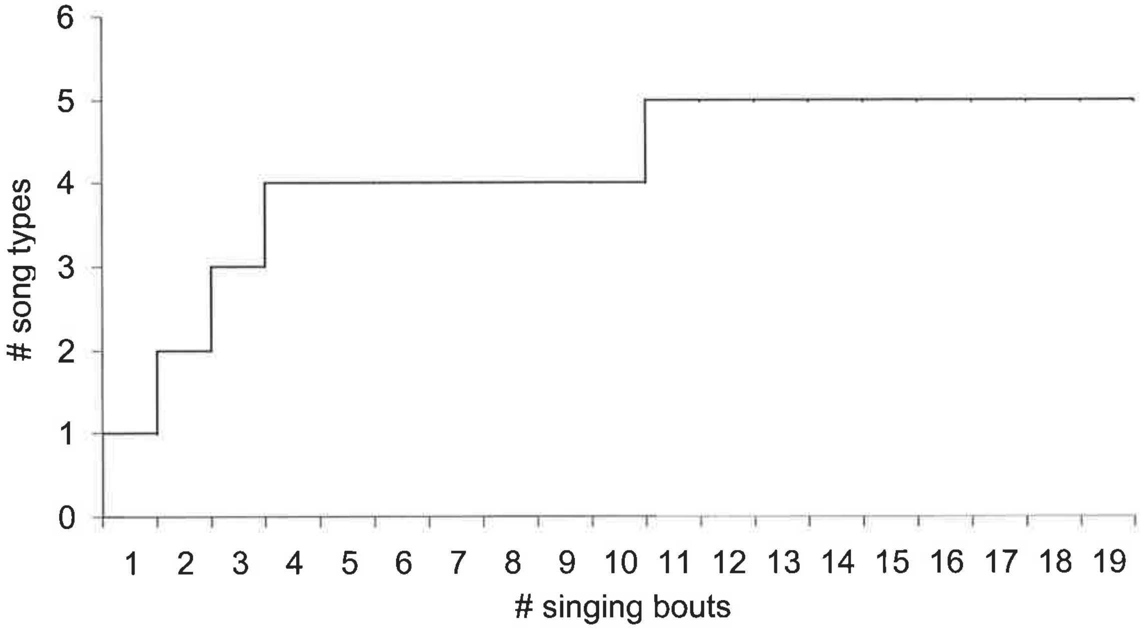


Figure 7.2 Sonograms of different song types of *Rhipidura leucophrys*, highlighting the variation within and between song types. The songs in each row are of the same song type, sung by two different individuals, while the song types of each row are different from other rows.



a. Willie Wagtail 98-1



b. Willie Wagtail 00-13

Figure 7.3 Examples of cumulative plots of the number of song types recorded as a function of the number of song bouts recorded for willie wagtails bouts (eg. Figure 7.3). I was thus generally confident that the observed repertoire sizes represent the actual repertoire sizes for these individuals. Furthermore, the complete song repertoire of most individuals was recorded during one recording session (defined as a continuous recording of the songs of a single individual), as individuals switched between song types frequently (Table 7.1).

Recordings obtained in 1998 suggested that local song dialects occur in willie wagtail populations. Territorial neighbours shared at least some proportion of the song types in their repertoires, with some neighbours sharing their entire repertoire (eg. 98-11, 98-3 and 98-12). Among the seven "Torrens Lake" individuals for which repertoire size estimates were made, between 80% and 100% of song types were shared between immediate territorial neighbours (mean = 92.0 ± 4.9%; $n = 5$ pairs of neighbours). The three "Downstream" birds for which repertoire size estimates were made shared between 50% and 80% of their song types with each other (mean = 62.0 ± 9.0%; $n = 3$ pairs of neighbours).

However, when the song types sung by the seven "Torrens Lake" birds were compared with those of "Downstream" birds (98-13, 98-14, 98-15, 98-16 and 98-17), no song was observed to be common between birds whose territories were on the Torrens Lake, and birds whose territories were further downstream.

2000

Recordings were obtained of the songs of six individuals in 2000. Recording locations for these six birds are also presented in Figure 7.1. Note that there is no relationship between the identification numbers of each bird between 1998 and 2000; for example, bird 98-1 is not necessarily the same individual as 00-1. All of the birds recorded in 2000 held territories around the Torrens Lake. The overall density of recorded individuals during the 2000 study period was lower than found in 1998, a reflection of the overall lower density of territory holders around the lake in 2000. As such the territories of the six birds recorded in 2000 were further apart than the territories of Torrens Lake birds recorded in 1998 (mean distance between territories: 1.6 ± 0.2 km; Figure 7.1).

For these six birds, 22 song types were recorded. Of these 22 song types, four were common with the 11 song types recorded in

Table 7.1 Repertoire sizes and song switching rates for individual *R. leucophrys* recorded in 1998-1999. The song switching rate is measured as the number of times a song is repeated before the individual switches to another song type. A value of 1 for song switching rate, for example, suggests that the bird sings each song type only once before switching to the next song type. The number of recording sessions required to record the complete song repertoire indicates whether the complete song repertoire of the individual can be recorded in one recording session.

ID	repertoire size	# recording sessions	mean song switching rate (±SE)[1]	range (song switching rate)	# songs/recording session	# recording sessions for complete repertoire
98-10	3	2	1.41 ± 0.19	1-4	12	2
98-11	2	1	1 ± 0	1	3	1
98-12	2	1	2.33 ± 1.33	1-5	7	1
98-13	2	1	1.17 ± 0.17	1-2	7	1
98-14	5	1	1.1 ± 0.1	1-2	11	1
98-15	2	1	1 ± 0	1	3	1
98-16	3	1	1.7 ± 0.5	1-6	14	1
98-1	2	2	1.46 ± 0.21	1-3	8	1
98-3	2	4	1.81 ± 0.29	1-5	7.25	1
98-5	2	2	1.89 ± 0.59	1-5	8.5	1
98-6	3	4	1.96 ± 0.23	1-5	6.5	2

Table 7.2 Repertoire sizes and song repetition rates for individual *R. leucophrys* recorded in 2000. See Table 7.1 legend for explanation of table.

ID	repertoire size	# recording sessions	mean song switching rate (±SE)[1]	range (song switching rate)	# songs/recording session	# recording sessions for complete repertoire
00-13	6	3	1.24 ± 0.16	1-3	7.33	1
00-1	4	6	1.52 ± 0.18	1-4	11.67	1
00-4	4	3	1.79 ± 0.28	1-6	6.67	1
00-7	4	3	2.33 ± 0.74	1-9	8.33	1

1998-1999. Over the two recording seasons, therefore, 29 different song types were recorded. Repertoire size was determined for four of these six birds in 2000, as there were insufficient song recordings to determine repertoire size for two birds (00-2 and 00-9). Observed repertoire size for the four birds ranged from four to six song types (mean = 4.5 ± 0.5; $n = 4$). As with recordings obtained in 1998, these observed repertoire sizes were generally good estimates of actual repertoire size for these individuals (e.g. Figure 7.3). In addition, as in 1998-1999, complete repertoires were recorded during the first recording session (Table 7.2).

For the four individuals for which repertoire size was determined, no song types were sung by more than one individual. However, one of the three song types used by 00-2 (for which repertoire size was not estimated) was also used by 00-13. Generally, however, song-type sharing was extremely low, relative to the levels of song sharing observed in 1998-1999. While it is possible that other individuals not recorded shared song types with the four birds for which repertoire size was estimated, it is likely that the distance between these four individuals precluded song-type sharing.

7.2.3 Analysis of Shared Song Types

Although song-type sharing was not consistently high or extensive for *R. leucophrys*, discrimination between individuals that were observed to share song types may benefit from the comparison of these shared song types between individuals. For each song type, therefore, a number of song features were measured, using Avisoft SAS-Lab Pro (Specht 1998), describing both temporal and spectral features of each song. The precise parameters measured to describe each song varied considerably, however, in relation to variations in structure between the different song types. On average, 11.0 ± 1.5 temporal and 5.0 ± 0.0 spectral features were measured for each song type. The data generated from these measurements was then used to perform discriminant function analyses (DFAs) on each song type, grouped by individual. Details of the methodology for DFA is described in Chapter 2.

Over the two recording periods, six song types were observed to be used by more than one individual. However, only three of these six song types were compared between individuals using DFA, as some individuals were only recorded singing the remaining shared song types once. These three song types were thus compared between the individuals recorded using them, to determine whether common song-types of *R. leucophrys* were individually-distinct.

Table 7.3 Summary of results of discriminant function analyses performed on shared songs of *Rhipidura leucophrys*, grouped by individual.

Song Type	# birds	# songs	Wilks λ	F	*p*	% correct
A	4	33	1.38×10^{-4}	33.4	<0.0001	100
B	6	60	4.96×10^{-3}	5.83	<0.0001	95
C	3	37	2.48×10^{-1}	8.32	<0.0001	100

The results of DFAs performed on the three song types analysed are summarised in Table 7.3. The results of these analyses show that the common song types used by Willie Wagtails are individually-distinct, with all shared songs being significantly different between individuals. Furthermore, DFA classified between 95% and 100% of songs to the correct individual (X = 98.3 ± 1.7%).

Although song types used by more than one individual exhibited vocal individuality, the length of the songs of Willie Wagtails, as well as the large number of syllables, preclude the use of these songs (in their entirety) in cross-correlation analyses (Khanna *et al.* 1997). The comparison of smaller groups of syllables among individuals has the potential to allow for the songs of Willie Wagtails to be compared using cross-correlation analysis. However, limiting the acoustic signals to be compared between individuals to syllables or groups of syllables may also reduce the accuracy of individual identification, as less information regarding song variation is being used to perform the analyses. Therefore, the identification potential of these smaller sections of *R. leucophrys* songs were initially subjected to DFA, in order to determine their identification potential as separate units.

7.2.4 Analysis of Common Syllable Groups

Classification and distribution of different syllable groups

For the three song types that were analysed in Section 7.2.3, each song was separated into 'syllable groups', defined by 'natural' periods of silence, which were markedly longer between syllable groups than between syllables within syllable groups. The reason that syllable groups were chosen as independent units for analysis rather than individual syllables was that the start and end of syllables were often indistinct, and thus defining separate syllables was also ambiguous in some cases. While the definition of syllable groups had a degree of subjectivity, the syllable groups analysed here were relatively easy to define based

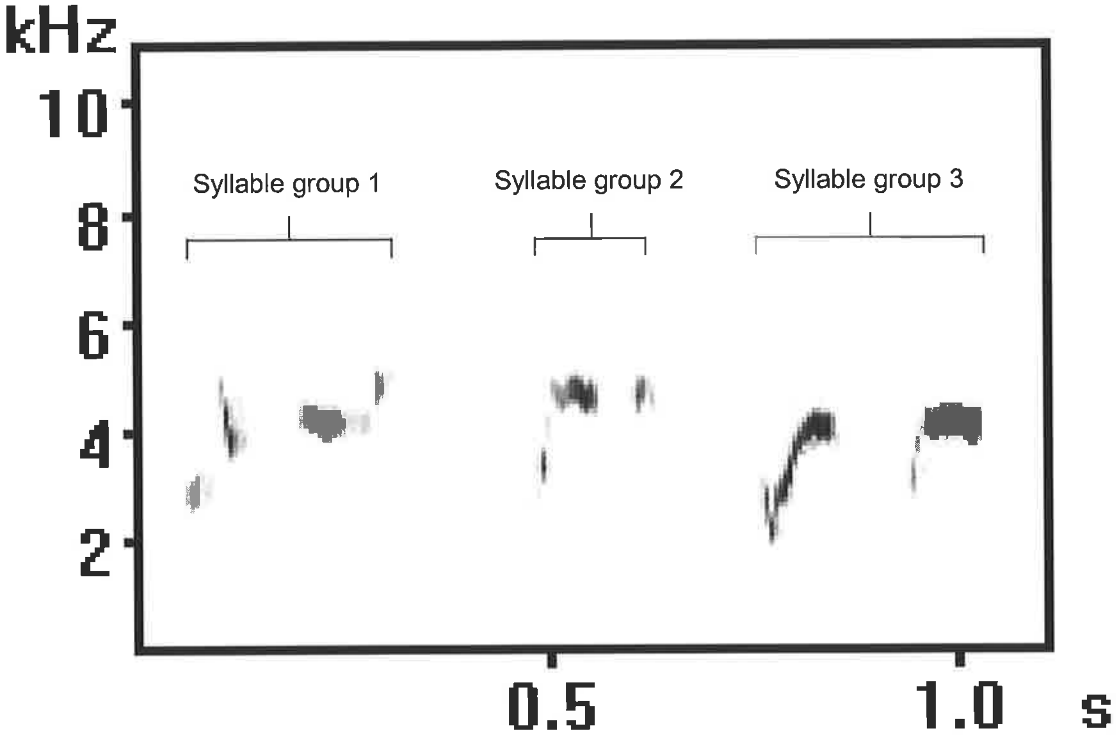


Figure 7.4 Example of the method used to split the song if *Rhipidura leucophrys* into its component syllable groups, using song type A as an example.

upon large periods of silence between syllable groups. An example of the syllable groups that comprise a song type is presented graphically in Figure 7.4.

Each of the three song types analysed was found to be comprised of three separate groups of syllables. Sonograms of each of the nine syllable groups analysed are presented in Figure 7.5. Each of these syllable groups was thus analysed initially using DFA (grouped by individual), and subsequently using cross-correlation analysis, depending on the success of DFA to discriminate between individuals on the basis of the parameters measured to describe each syllable group.

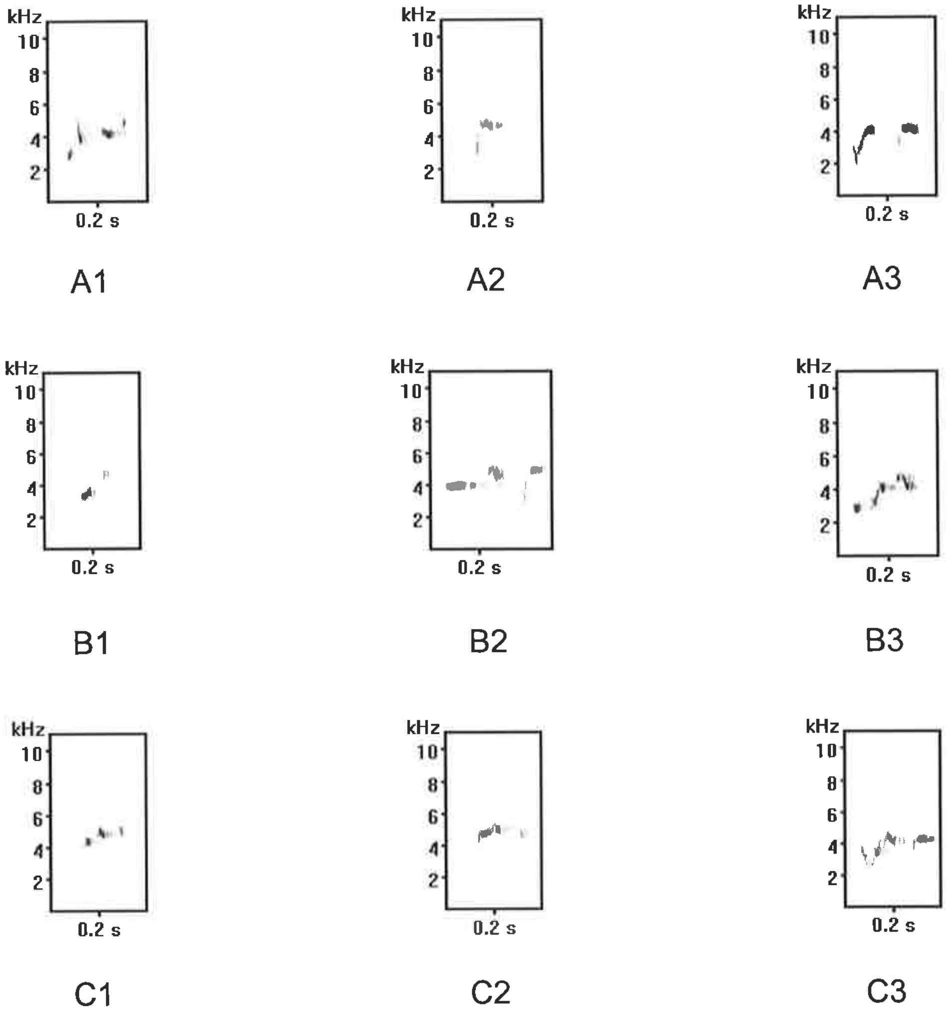
Discriminant Function Analyses

For each syllable group, eight parameters were measured (length, minimum frequency, time (from the start of the syllable group) at which minimum frequency occurred, maximum frequency, time at which maximum frequency occurred, frequency range, frequency at start of group, frequency at end of group), describing both temporal and spectral features of each group. The results of DFA performed on these nine syllable groups are summarised in Table 7.4. A significant difference was detected between individuals for all of the syllable groups examined, and between 50 and 93.8% of syllable groups were classified to the correct individual (mean = 82.0 ± 4.2%).

Cross-correlation Analyses

Each syllable group was subjected to a cross-correlation analysis, in order to determine the maximum proportion of r_x values that were correctly classified for each group, and at what r_x* this peak accuracy occurred. An example of the impact that correlation threshold had on identification accuracy is presented in Figure 7.6.

The results of cross-correlation analyses performed on each of the nine syllable groups are presented in Table 7.5. Identification accuracy ranged from 74.8% to 84.9% (mean = 80.7 ± 1.14%), at peak r_x* that ranged from 0.76 to 0.92 (mean = 0.83 ± 0.012). r_x values were significantly greater between syllable groups produced by the same individual than between syllable groups produced by different individuals, for all of the nine syllable groups analysed (Table 7.5).



A1 A2 A3

B1 B2 B3

C1 C2 C3

Figure 7.5 Sonograms of each of the nine syllable groups compared between individuals. Each syllable group has been named first by the song type from which it was derived (eg. song type A), and second by its position in the song (ie. 1, 2 or 3).

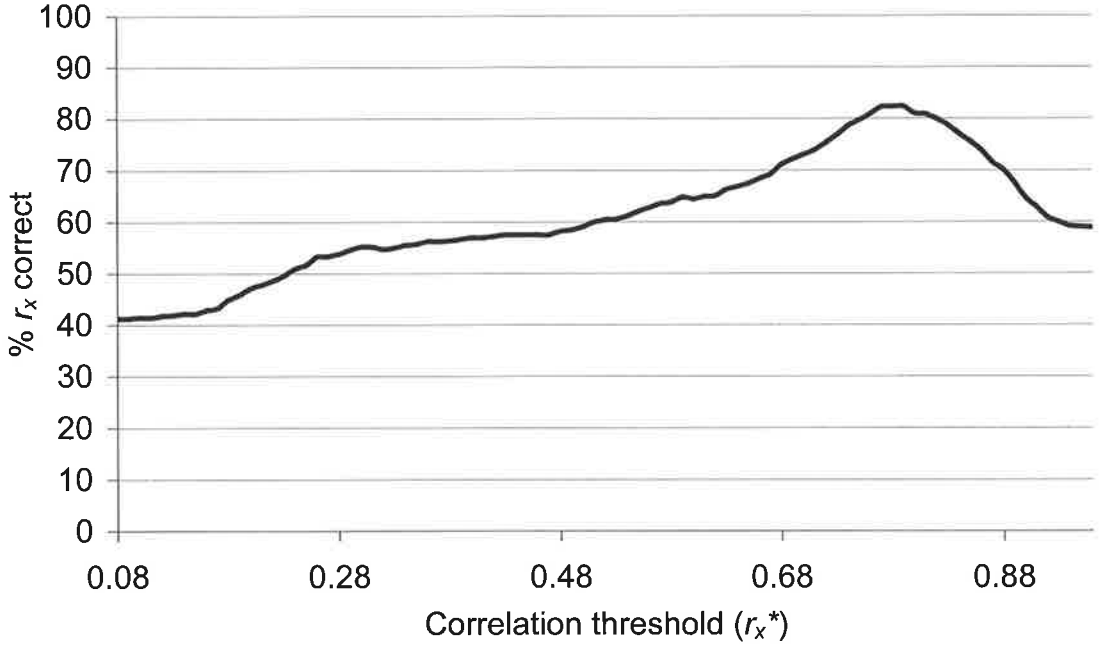


Figure 7.6 Example of the impact that correlation threshold (r_x*) has upon the identification accuracy of cross-correlation analyses for the syllable groups of *Rhipidura leucophrys*. Example taken from syllable group C2.

Table 7.4 Summary of results of discriminant function analyses performed on the syllable groups of shared songs used by *Rhipidura leucophrys*, grouped by individual.

Song type	# birds	# songs	Group #	Wilks λ	F	p	% correct
A	4	33	1	5.0×10^{-2}	6.88	<0.0001	84.4
			2	3.2×10^{-1}	3.04	<0.0001	50
			3	3.4×10^{-2}	8.35	<0.0001	93.8
B	6	60	1	2.9×10^{-2}	7.35	<0.0001	81.7
			2	1.6×10^{-2}	10.1	<0.0001	80.8
			3	1.3×10^{-2}	10.1	<0.0001	87.8
C	3	37	1	4.8×10^{-2}	17.2	<0.0001	83.8
			2	5.4×10^{-2}	16.05	<0.0001	86.5
			3	4.3×10^{-2}	18.3	<0.0001	89.2

Variation occurred in the r_x* at which peak identification accuracy occurred for each of the nine syllable groups analysed. As discussed in Chapter 5, practical acoustic identification using cross-correlation analysis would benefit if a single r_x* was used for all syllable groups, rather than r_x* values that are specific to each syllable group. For the syllable groups of *R. leucophrys*, this common peak r_x* was calculated as the mean of the peak r_x* values for each of the nine syllable groups, and equalled 0.83. At this r_x* , peak identification accuracy for the nine syllable groups analysed ranged from 70.6% to 84.8% ($X = 78.3 \pm 1.7\%$), and was not significantly different from identification accuracies achieved at the peak r_x* values of individual syllable groups (t-test = 1.24; df = 16; $p = 0.23$).

7.2.5 Discussion

The vocal behaviour of *Rhipidura leucophrys* presents both benefits and drawbacks to acoustic identification, relative to *Dasyornis broadbenti*. In contrast to *D. broadbenti*, individual Willie Wagtails appear to cycle through the different song types in their repertoire relatively rapidly, with the entire repertoire often being sung within a single session of singing. With respect to individual identification, such singing behaviours eliminate the need to be able to compare the different song types used by each individual. However, the use of shared song types between individuals appears to be far more restricted in *R. leucophrys* than for *D. broadbenti*. In 1998-1999, no common song types were found between individuals separated by distances as little as 5.2 km, while in 2000 only one song type was used by more than one individual, for six individuals whose territories were separated by an average distance of 1.58 km, and often as little as 350 m. In comparison to *R. leucophrys*, therefore, the use of common song types by *D. broadbenti* is relatively prevalent, with individuals separated by distances of up to 38 km found using common song types (although no common song types were found between isolated populations; Chapter 6). This suggests that, for *R.*

Table 7.5 Summary of results of cross-correlation analyses performed on the syllable groups of shared songs used by *Rhipidura leucophrys*.

Song type	# birds	# songs	Group #	peak threshold	% correct	p
A	4	33	1	0.85	78.6	<0.0001
			2	0.92	74.8	<0.0001
			3	0.87	81.1	<0.0001
B	6	60	1	0.84,0.85	83.6	<0.0001
			2	0.86	83.6	<0.0001
			3	0.84,0.85	84.9	<0.0001
C	3	37	1	0.79,0.81	79.6	<0.0001
			2	0.78,0.79	82.3	<0.0001
			3	0.76	78.1	<0.0001

leucophrys, the comparison of shared song types for the purposes of acoustic identification of individuals would be limited to extremely localised neighbourhoods of individuals.

However, the fact that song type sharing is extremely localised in this species can also benefit acoustic identification in *R. leucophrys*. Given that the complete repertoire for most individuals can be obtained during a single recording session, it may be possible to identify individuals simply through the identification of song types that are unique to each individual. Even in cases where song types are shared amongst a number of different birds, the number of individuals to be compared in this fashion is likely to be relatively small. Comparisons of components of these shared song types between individuals for *R. leucophrys*, using both DFA and cross-correlation analysis, suggest that at least six individuals can be identified by comparing shared song components, with identification accuracies of up to 93.8%, using cross-correlation analysis.

Acoustic identification of individual *R. leucophrys* would thus occur through the execution of the following procedure. An initial recording from an individual would be recorded, with the expectation that all of the song types in that individual's repertoire would be recorded in that single recording session. Subsequent recordings of individuals could then be compared with this initial recording in two ways. First, the song types identified in each recording could be compared; if no overlap in the song types recorded was observed, the two recordings could thus be safely assigned to two different individuals. If, however, common song types were found between the two recordings, then a second phase of analysis would occur, in which syllable groups were compared using cross-correlation analysis. As shown above, comparisons between common syllable groups were accurately classified as having been produced by the same or different individuals, using cross-correlation analysis. The critical factors behind the success of acoustic identification in such a system are the relatively small size of each bird's song repertoire, and the relative ease in which complete repertoires can be recorded for each bird. As demonstrated with *D. broadbenti*, larger repertoires that are difficult to obtain mean that the principle tool for acoustic identification in such systems may be limited to the comparison of shared song types.

7.3 Vocal Individuality in the South-eastern Red-tailed Black Cockatoo, *Calyptorhynchus banksii graptogyne*

7.3.1 Methods

7.3.1.1 Field site and recording methods

The calls of *Calyptorhynchus banksii graptogyne* were recorded in the Casterton region of south-west Victoria (37°35'S, 141°23'E) during November 1999. This location and timing of these recordings corresponded with a study on nest predation of the South-eastern Red-tailed Black Cockatoo (Jarmyn 2000), and as such the location of a number of nest trees was already known. Nest trees were dead red gums *Eucalyptus camaldulensis* and were located in isolation in cleared paddocks. Within each nesting pair, males and females were identified by the sexually dimorphic plumage of the species.

Calls were recorded each evening between 1500 and 1800 hours. Call were recorded with some consistency at this time, as a result of the behaviour of breeding individuals. When breeding, males regularly return to nests in the mid to late afternoon to feed their mate, and call consistently to their mates at this time. Recordings could thus be obtained by monitoring a known nest tree in the mid to late afternoon for the return of the resident male, at which time call recordings were obtained. As a result of this opportunistic recording method, the majority of recordings obtained were of male individuals, although recordings were also made of female food-begging calls. Subsequent analyses and determinations of vocal individuality were only conducted on the calls of males for the purposes of this study. Individuals were identified by locating the nest trees of nesting pairs, with the assumption that subsequent calls at the same nest tree were made by the same individuals.

7.3.1.2 Analysis of call features

Calls were described quantitatively by measuring 13 discrete call variables, eight of which described spectral features of each call (Figure 7.7). Eight of these 13 features described components of the peak harmonic, defined as the harmonic with the greatest amplitude. The remaining five parameters described overall features of each call, or features related to the fundamental harmonic. Initial observations suggested that two different call types were recorded, which differed with regards to their overall structure (eg. Figure 7.8). Calls were thus qualitatively classified as ‘perch calls’ or ‘flight calls’, these terms being used after the behaviours that were often associated with each call type. The terms used to describe these call types, however, bear no relation to the function of the different call types, or how each call was classified; calls were classified visually based on structure, independent of associated behaviours. However, in order to confirm the visual classification of calls to each call type, the parameters measured to describe each call were initially used to perform a DFA, grouped by call type. Following this analysis, calls that were classified differently by the DFA and the visual classification were excluded from subsequent analyses.

Based upon the 13 measured call parameters, a DFA was performed for the calls of each call type, grouped by individual. Detailed methods and justification for the use of DFA are presented in Chapter 2.

7.3.1.3 Cross-correlation analysis

Following the exclusion of calls that were difficult to assign to call type, cross-correlation analyses were performed on the remaining calls. The general methods and justification for cross correlation analysis are given in Chapter 2. The calls for each call type were analysed separately using this method.

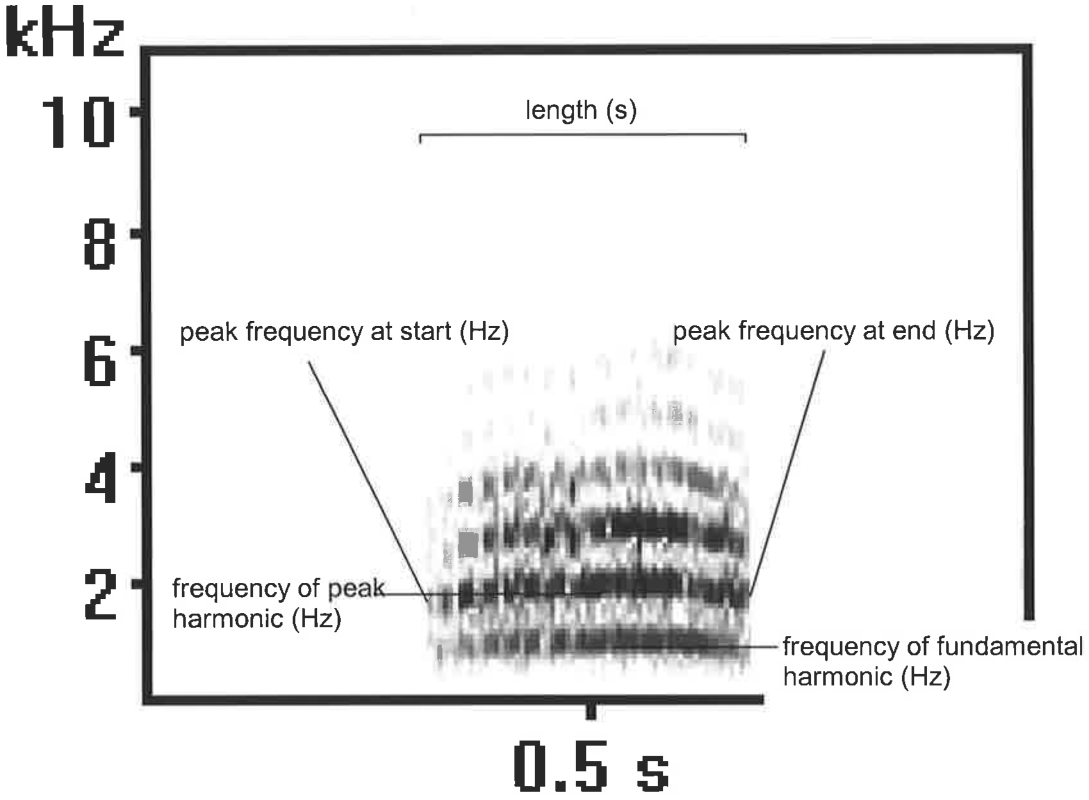


Figure 7.7 Example of a Red-tailed Black Cockatoo call, highlighting five of the seven parameters measured to describe the features of each call.

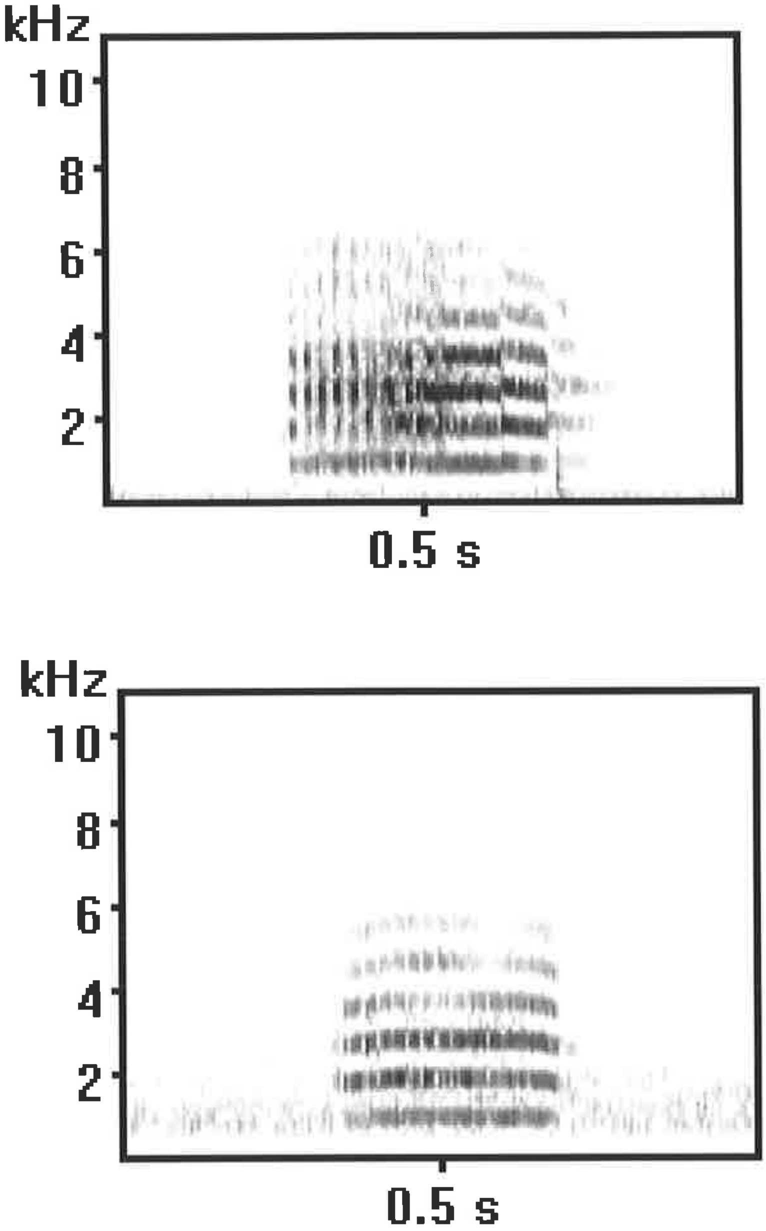


Figure 7.8 Example sonograms of calls defined as 'perch' calls (top) and 'flight' calls (bottom).

7.3.2 Results

7.3.2.1 Singing behaviour

In total, 69 calls from five individual males were recorded. Three of these five individuals were recorded on more than one occasion. Initial visual inspection resulted in 44 of these calls being classified as 'perch' calls, with the remaining 25 calls being classified as 'flight' calls. However, the subsequent DFA grouping calls to call type revealed that 10 of these calls (five perch calls, five flight calls) were misclassified, and were thus excluded from all subsequent analyses of call individuality. Despite the exclusion of these 10 calls, visual classification of the different call types of Red-tailed Black Cockatoos accurately represented quantitative classification of these calls, with 84.1% of calls being classified as the same call type by both methods (DFA: Wilk's $\lambda = 0.51$; $F_{7,61} = 8.27$; $p < 0.0001$). A histogram of the canonical scores for the single discriminant function constructed (Figure 7.9) reveals the relatively low structural overlap between the calls of these two call types. The call parameters that best discriminated between the two call types were peak frequency, peak harmonic, and frequency of peak harmonic at the start of each call (Table 7.6).

As a result of this DFA, subsequent analyses were based upon 39 perch calls from five individuals, and 20 flight calls from four individuals.

7.3.2.2 Analysis of features between individuals

'Perch' calls

Due to high correlations between call parameters (r>0.8), two parameters were excluded from the DFA of perch calls grouped by individual (mean frequency difference between peak harmonic and fundamental harmonic, and frequency range of peak harmonic). The subsequent DFA revealed a high level of individuality of perch calls for the five recorded individuals. 94.9% of calls were classified to the correct male, with 100% of calls being correctly classified for three of the five males (DFA: Wilk's $\lambda = 1.1 \times 10^{-2}$; $F_{40,96} = 5.54$; $p < 0.0001$). Figure 7.10 shows scatterplots of combinations of the first three canonical functions, which highlights the relative intra-individual call stability, relative to the inter-individual call

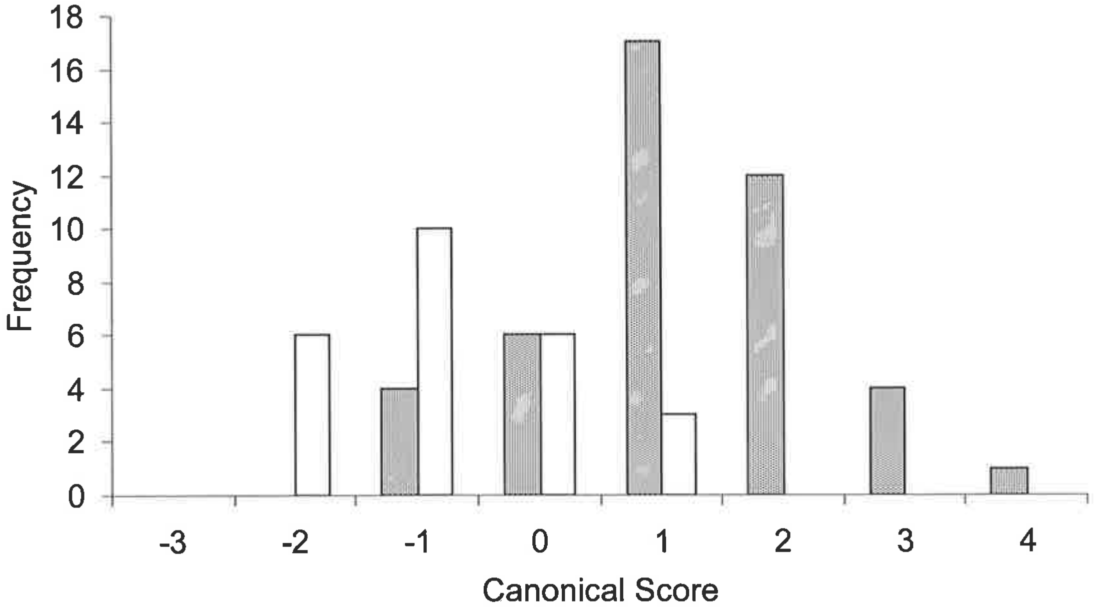


Figure 7.9 Canonical scores for the single canonical function constructed for the calls of *C. b. graptogyne*, grouped by call type. Open bars are canonical scores calculated for 'flight' calls; stippled bars are canonical scores calculated for 'perch' calls.

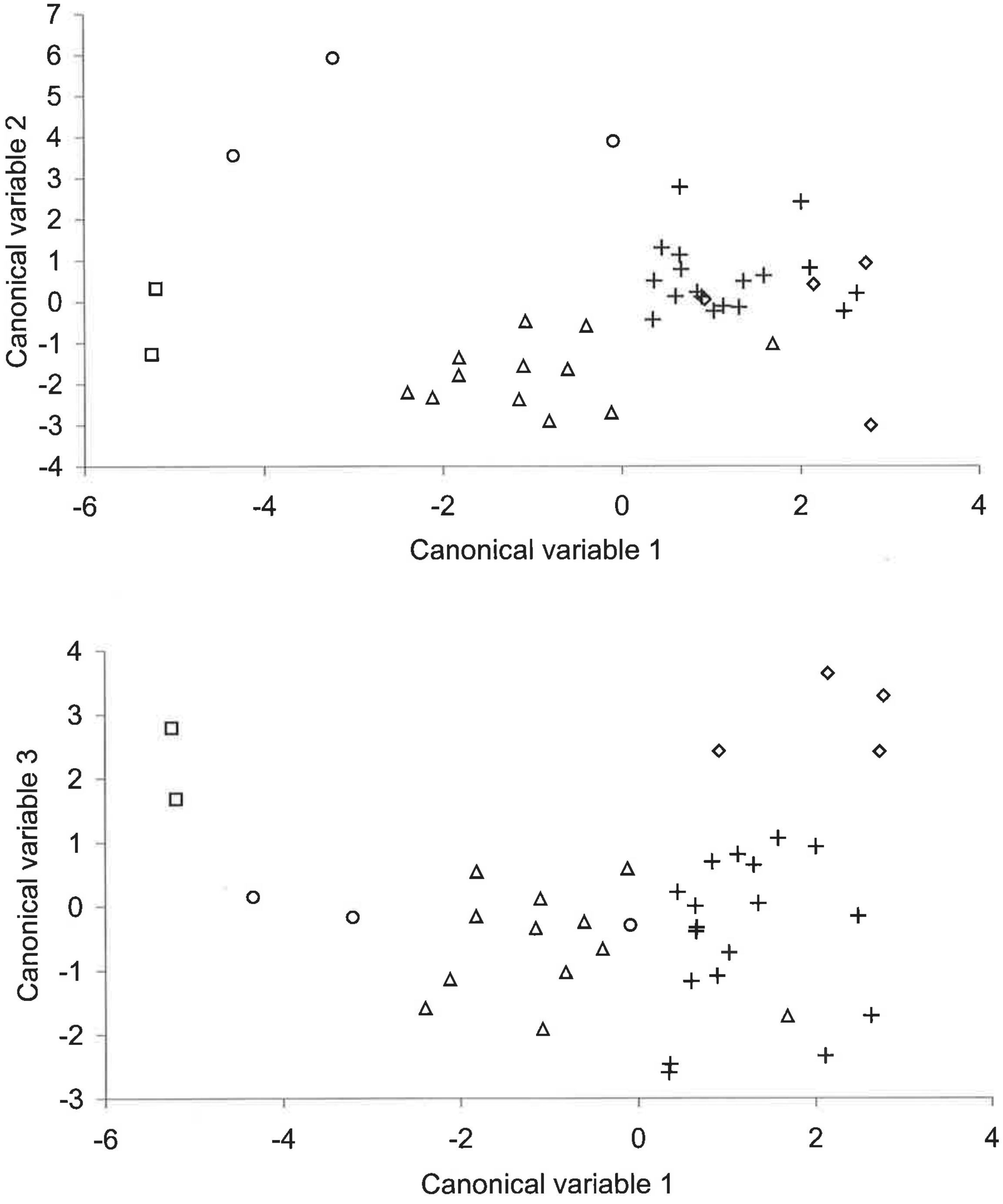


Figure 7.10 Distribution of the 'perch' calls of *Calyptorhyncus banksii graptogyne* in acoustic space, defined by the plots of canonical scores for the first three canonical variables constructed by discriminant function analysis. Each point on the plot represents one call, while each different shape represents one individual.

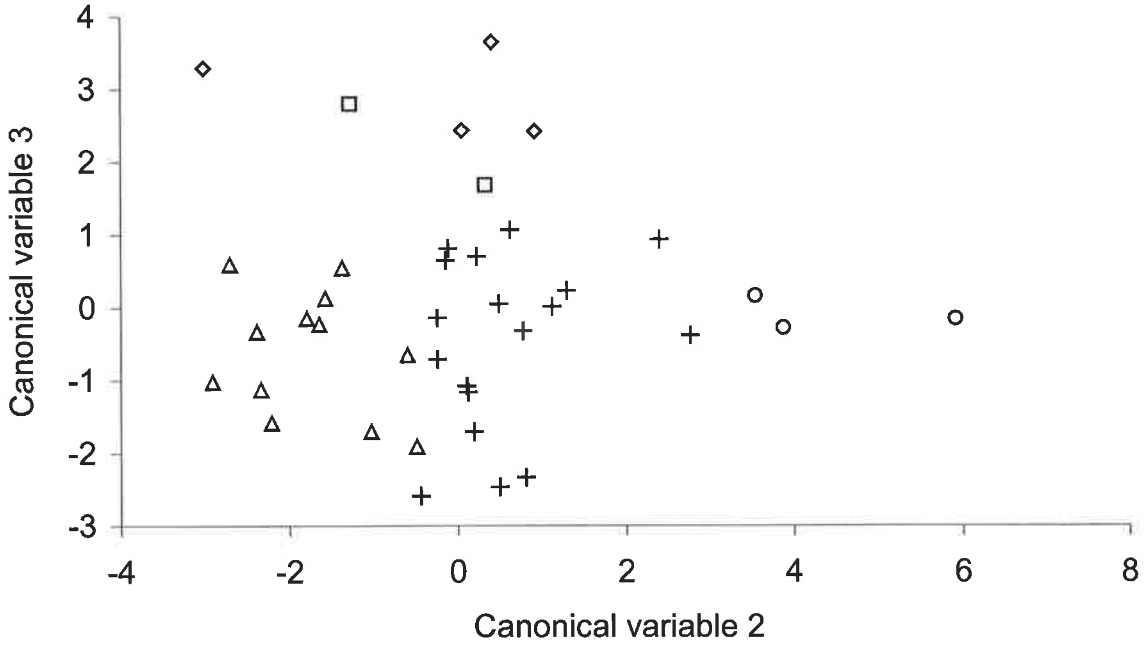


Figure 7.10 (continued).

Table 7.6 Standardised coefficients for the canonical variables constructed from the discriminant function analysis performed on the calls of *Calyptorhyncus banksii graptogyne*, grouped by call type.

Call Parameter	Coefficient for Canonical Variable
Call Length (s)	1.006
# Harmonics	-0.76
Time of maximum frequency (s)	0.35
Mean Frequency of Fundamental Harmonic (Hz)	0.23
Frequency at start of peak harmonic (Hz)	1.42
Mean Frequency of peak harmonic (Hz)	-2.97
# of peak harmonic	1.72

variation. The three canonical functions used to construct these scatterplots explained 90.8% of the variation in the analysis.

Table 7.7 highlights the importance of each call parameter to the DFA, providing an indication of which parameters were important in discriminating between individuals. From this table, the most important identifying parameters appear to be peak frequency and maximum frequency, which exhibited high standardized coefficients for three of the four discriminant functions used to construct the analysis.

'Flight' calls

Due to high correlations between a number of flight call parameters, one parameter was excluded from the subsequent DFA (frequency range of peak harmonic). While the number of calls and individuals used to perform the DFA on flight calls was less than for analyses on perch calls, a similarly high level of individuality was observed for this call type, with 100% of calls being classified to the correct individual (DFA: Wilk's $\lambda = 6.98 \times 10^{-3}$; $F_{18,31} = 8.4$; $p < 0.0001$). A scatterplot of the first two canonical functions of this analysis again highlight the relatively high variance between individuals with regard to the structure of this call type, in comparison to the intra-individual variance (Figure 7.11). These two canonical functions used to construct this scatterplot explained 98.3% of the variation in the DFA.

Table 7.8 highlights the significance of each call parameter to the DFA. As with the analysis of 'perch' calls, the most important parameters for individual discrimination using 'flight' calls were maximum frequency of the peak harmonic, as well as the peak harmonic number.

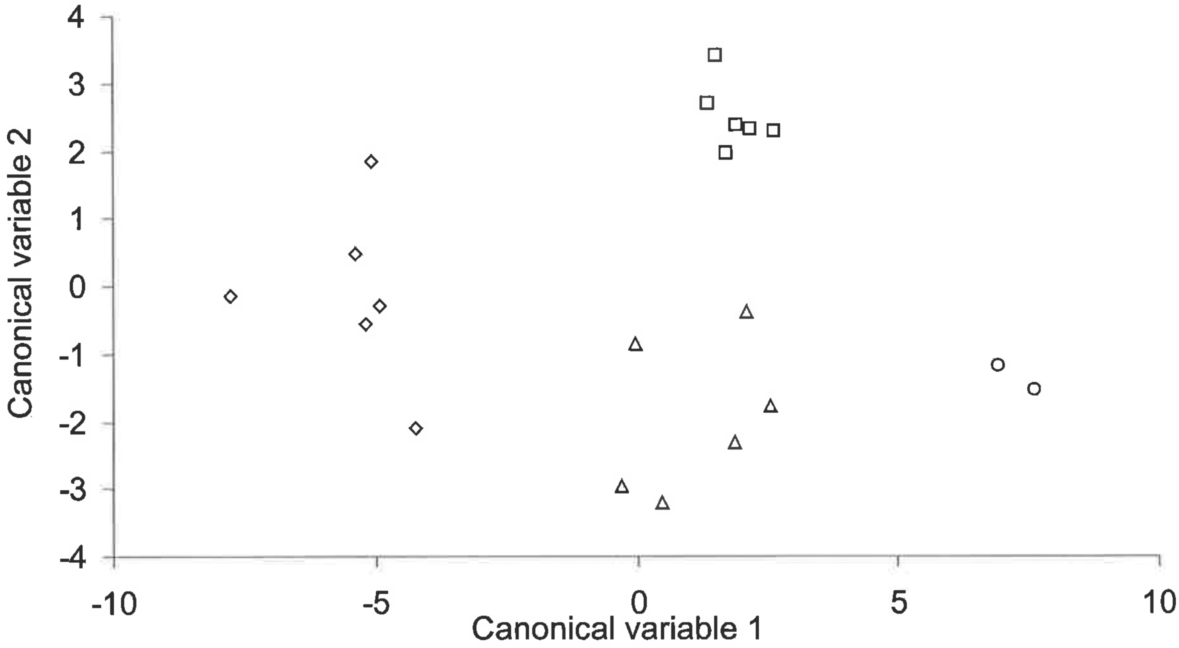


Figure 7.11 Distribution of the 'flight' calls of *Calyptorhyncus banksii graptogyne* in acoustic space, defined by the plots of canonical scores for the first two canonical variables constructed by discriminant function analysis. Each point on the plot represents one call, while each different shape represents one individual.

Table 7.7 Standardised coefficients for the three canonical variables (CVs) constructed by the discriminant function analysis performed on 'perch' calls of *Calyptorhyncus banksii graptogyne*. For each call parameter, a high coefficient (independent of whether it is positive or negative) indicates the discriminating ability of the parameter. Eigenvalues are indicators of the proportion of variation that can be attributed to each canonical variable.

Call parameters	CV 1	CV 2	CV 3
# harmonics	0.004	-1.071	0.266
length	-0.948	0.557	-0.058
time of maximum frequency	-0.757	0.809	0.453
time of minimum frequency	-0.362	0.440	0.618
frequency at start of peak harmonic	3.330	-1.327	2.612
peak harmonic number	-2.270	0.407	-5.288
maximum frequency of peak harmonic	-1.208	-0.066	2.252
mean frequency of peak harmonic	-0.483	-2.470	2.129
minimum frequency of peak harmonic	-1.020	4.700	-3.965
frequency at end of peak harmonic	1.909	-0.891	2.627
Eigenvalue	3.783	3.030	1.570
Cumulative Proportion of variation	0.410	0.738	0.908

Table 7.8 Standardised coefficients for the two canonical variables (CVs) constructed by the discriminant function analysis performed on 'flight' calls of *Calyptorhyncus banksii graptogyne*. For each call parameter, a high coefficient (independent of whether it is positive or negative) indicates the discriminating ability of the parameter. Eigenvalues are indicators of the proportion of variation that can be attributed to each canonical variable.

Call parameter	CV 1	CV 2
# harmonics	2.390	0.220
length	-0.662	0.370
mean frequency of fundamental harmonic	-0.868	-0.254
frequency at start of peak harmonic	1.908	-2.055
maximum frequency of peak harmonic	-9.629	4.015
peak harmonic number	7.389	-2.337
Eigenvalue	19.437	3.954
Cumulative Proportion of variation	0.816	0.983

7.3.2.3 Cross-correlation analysis

'Perch' calls

The maximum proportion of correct r_x values achieved for the 'perch' calls of *C. b. graptogyne* was 71.6%, which occurred at an r_x* of 0.71 (Figure 7.12). r_x values between the calls of the same individual were significantly higher than r_x values between the calls of different individuals (t-test = 9.2; df = 818; $p < 0.0001$).

'Flight' calls

The maximum proportion of correct r_x values achieved for the 'flight' calls of *C. b. graptogyne* was 77.4%, which occurred at r_x* values of 0.78 and 0.79 (Figure 7.13). As with 'perch' calls, r_x values calculated between the calls of the same individual were significantly greater than r_x values between the calls of different individuals (t-test = 2.6; df = 274; $p =$ 0.008).

7.3.3 Discussion

Although based upon a relatively small sample size with regard to the number of individuals recorded, the results presented here suggest that acoustic identification of individuals is a potentially useful tool in the identification of individual Red-tailed Black Cockatoos. This suggestion is supported by examples from the literature from another *Calyptorhyncus* species, *C. funereus*, in which (Saunders 1983) demonstrated that the calls of this species functioned both in mate recognition and parent-offspring recognition. Personal observations suggest that a similar system of recognition may occur in *C. b. graptogyne*, with vocalisations by individual males eliciting behavioural responses by their mate, although apparent recognition errors can occasionally occur (B. Jarmyn pers. comm.). Such a system of acoustic recognition awaits testing in this species.

Previous descriptions of the calls of *C. banksii* recognise four distinct call types for this species: a contact call, an advertising call, a food-begging call and an alarm call (Higgins 1999). The two types of call analysed in this present study are both considered by previous authors as contact calls, although no previous study has identified different classes of contact

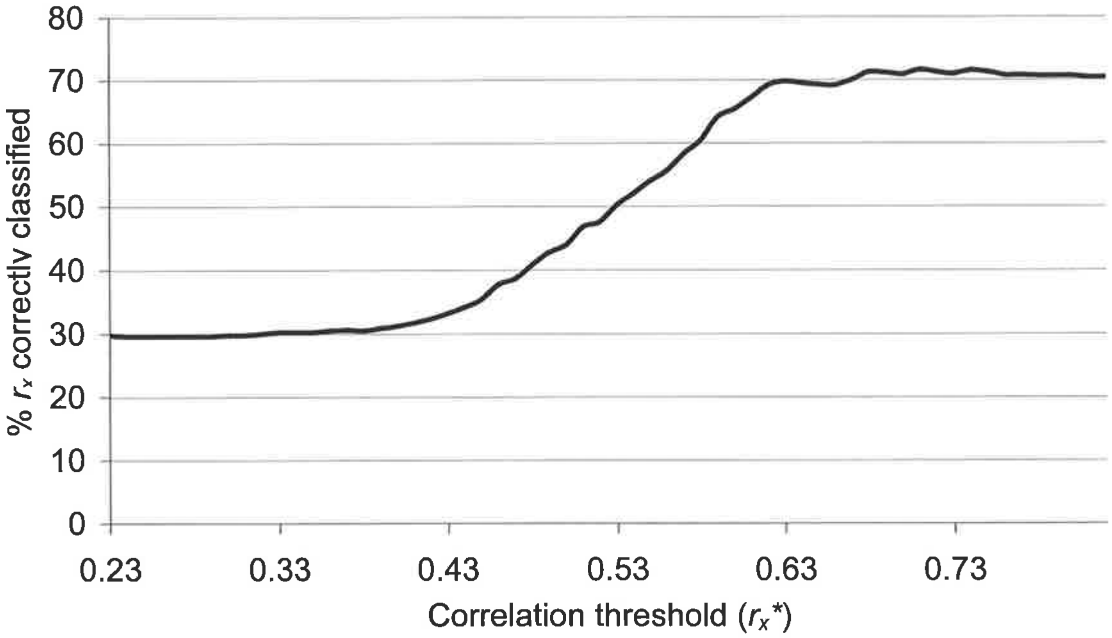


Figure 7.12 The impact of correlation threshold (r_x*) on the percentage of 'perch' call r_x of *Calyptorhyncus banksii graptogyne* that have been correctly classified as having been produced intra- or inter-individually.

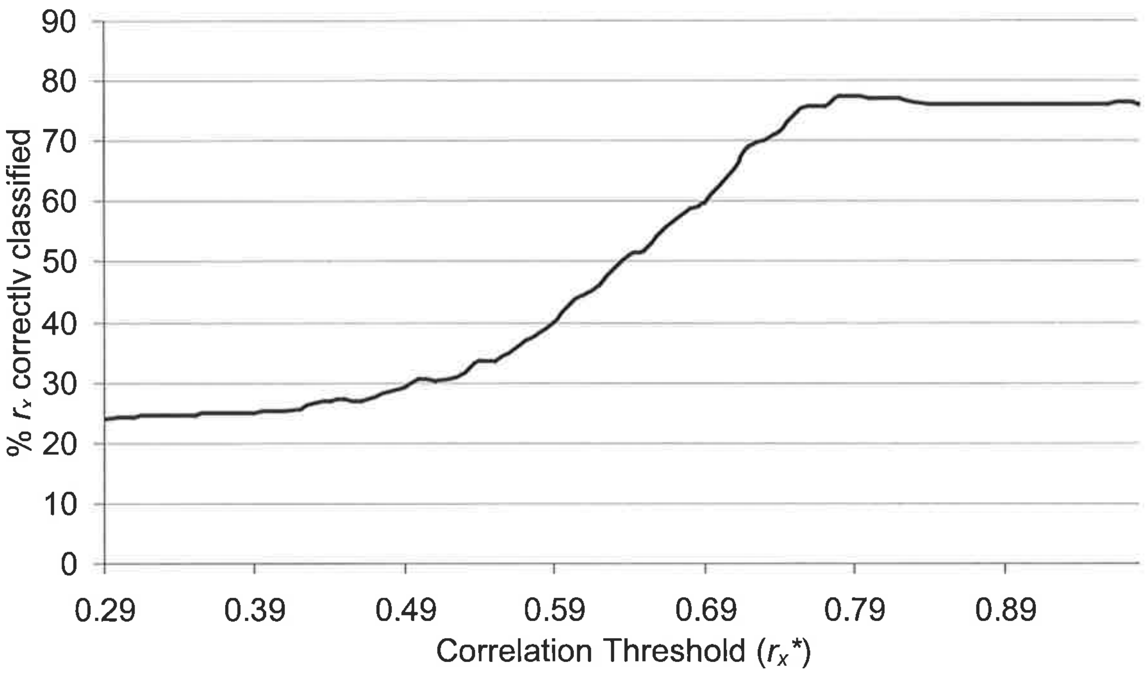


Figure 7.13 The impact of correlation threshold (r_x*) on the percentage of 'flight' call r_x of *Calyptorhyncus banksii graptogyne* that have been classified as having been produced intra- or inter-individually.

call. Whether the two classes of contact call identified in this study are functionally distinct (as well as structurally) remains to be seen.

Contact calls are given by both sexes, and individual identification based upon the analysis of such calls may thus allow entire populations to be surveyed and monitored. Furthermore, early reports suggest that contact calls may vary intersexually (Tavistock 1929), although this suggestion would need to be confirmed using a more analytical and quantitative approach. Acoustic identification of individuals should thus allow for a better understanding and management of this endangered taxa, as more accurate information can be obtained using non-invasive methods of individual identification, than is currently available for this subspecies of cockatoo.

7.4 Individuality of Calls in the Sacred Kingfisher, *Todiramphus sanctus*

7.41 Methods

7.4.1.1 Field site and recording methods

Recordings of Sacred Kingfisher calls were obtained from two sites in the Southern Mount Lofty Ranges, South Australia. The first site was located at Cromer Conservation Park, approximately 40 km north-east of Adelaide (34°46'S, 138°58'E). The site consists of open woodland (Specht 1972), with the overstorey dominated by pink gum *Eucalyptus fasciculosa* and long-leaved box *E. goniocalyx*. The second site was located at Scott Conservation Park 80 km south of Adelaide (34°24'S, 138°44'E), consisting of open woodland (Specht 1972) dominated by pink gum *E. fasciculosa* and blue gum *E. leucoxylon*. Individuals were located and subsequently re-identified by locating nest trees of breeding pairs, with the members of the pairs being identified through the sexually-dimorphic plumage of the species. Recordings were obtained from these two sites between 20 November 2000 and 20 December 2000.

7.4.1.2 Analysis of features

The most common calls used by *T. sanctus* is the 'Loud Staccato Call' (Higgins 1999), which has also been called the 'kek' or 'tek' call in the literature (Saunders and Wooller 1988). Each call was described by measuring eight features of each call syllable, and seven features of the overall call structure (Figure 7.14). Using these call parameters, quantitative comparisons between the calls of different individuals were conducted, using both univariate analyses of each parameter, and DFA to compare the multivariate structure of the calls. Separate analyses were conducted on the overall call structure, and on the structure of each syllable in the calls. These second analyses were done in order to determine whether the individual syllables of the calls of *T. sanctus*, which are all grossly similar in structure (see Figure 7.14), are individually-distinct, and may thus be used in isolation for individual identification.

7.4.2 Results

7.4.2.1 Singing behaviour

In total, 40 staccato calls were recorded from three different individuals, all of which were male birds. All three of these birds were recorded on more than one occasion. While a number of other individuals were observed and monitored, staccato call recordings were not obtained for these individuals, although other call types were recorded (eg. Shriek calls and Ascending Roll calls (Higgins 1999). Example sonograms of all recorded call types, including staccato calls, are presented in Figure 7.15.

7.4.2.2 Analysis of features between individuals

7.4.2.2.1 Overall call structure

All seven parameters measured to describe the overall call structure of the staccato calls of *T. sanctus* differed significantly between individuals (Table 7.9). Calculations of coefficients of variation reveal that two measures of frequency, minimum and maximum call frequency, had the lowest CV_R values, a measure of the parameter's individuality (Table 7.9). The temporal parameter with the lowest CV_R value was the number of syllables, with a ratio of 0.848. Total call length had the highest CV_R value (0.956). From these ratio calculations, the spectral features of the calls of *T. sanctus* appear to have greater potential for individual discrimination than temporal features, although the number of syllables in a call is also likely to be important.

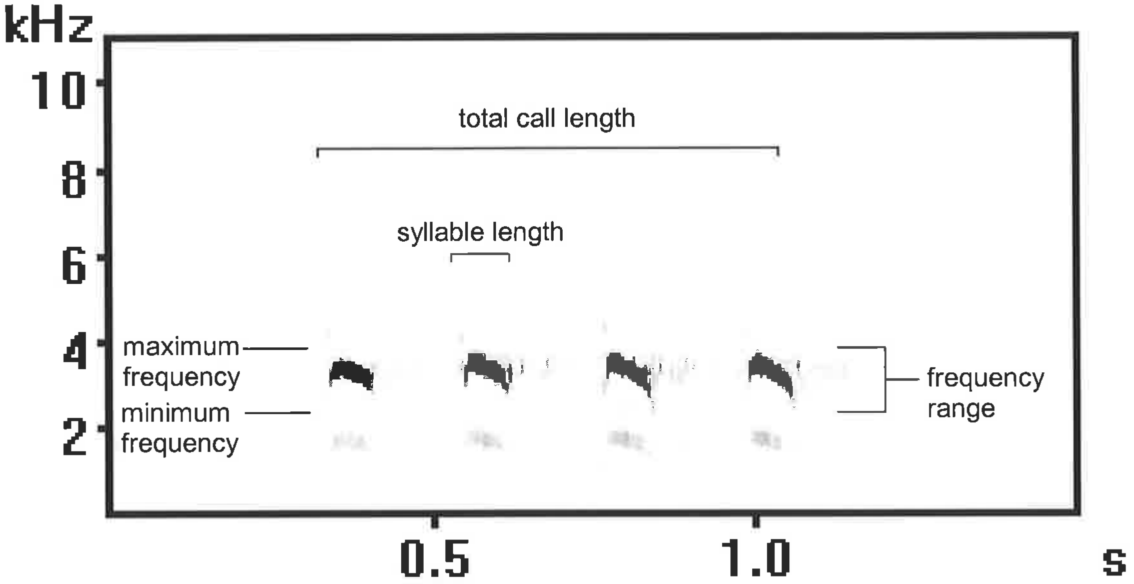
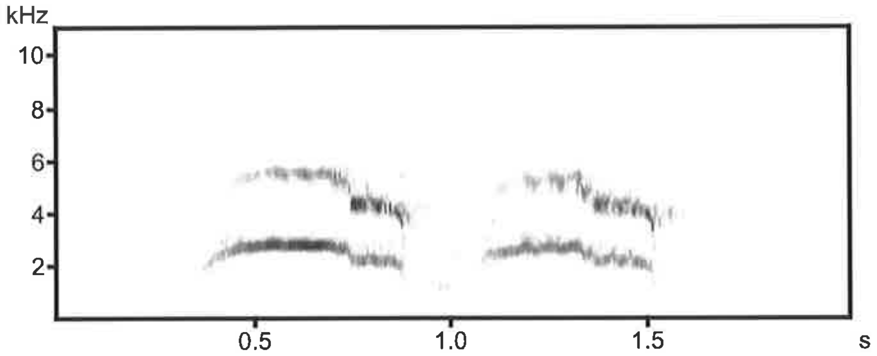
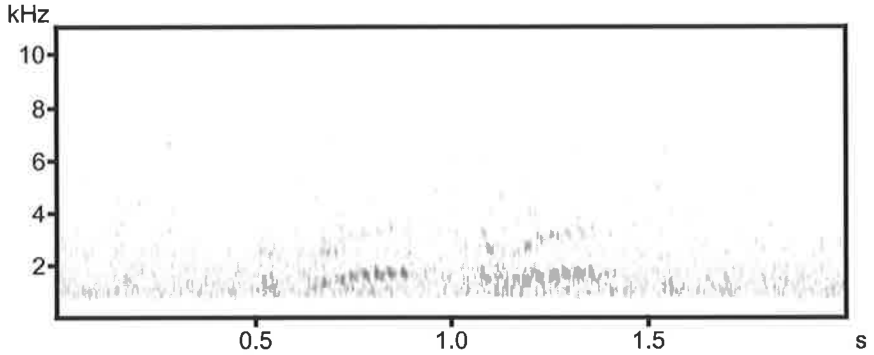


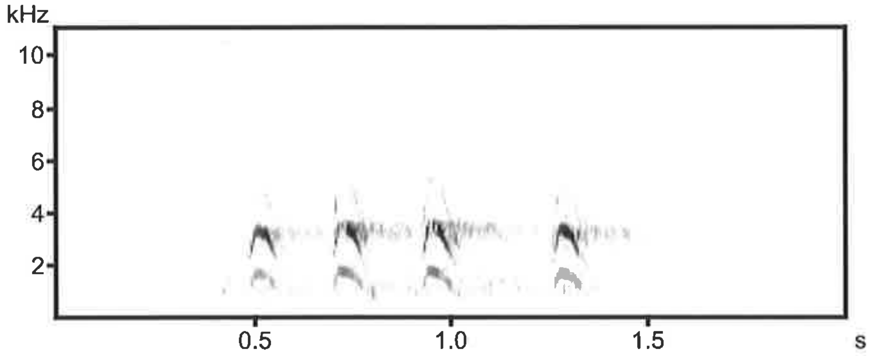
Figure 7.14 Graphical description of the Loud Staccato Call of *Todiramphus sanctus*, including descriptions of call features measured for analyses.



a. Shriek (recorded Scott Conservation Park 4/12/00)



b. Ascending Roll (recorded Cromer Conservation Park 20/11/00)



c. Loud Staccato (recorded Cromer Conservation Park 11/12/00)

Figure 7.15 Sonograms of the different types of calls recorded for *Todiramphus sanctus*. Call descriptions after Higgins (1999).

Table 7.9 Coefficients of variation and results of univariate statistical tests between individuals for each of the parameters measured to describe the staccato calls of *Todiramphus sanctus*, ranked in ascending order of intra-inter CV ratio.

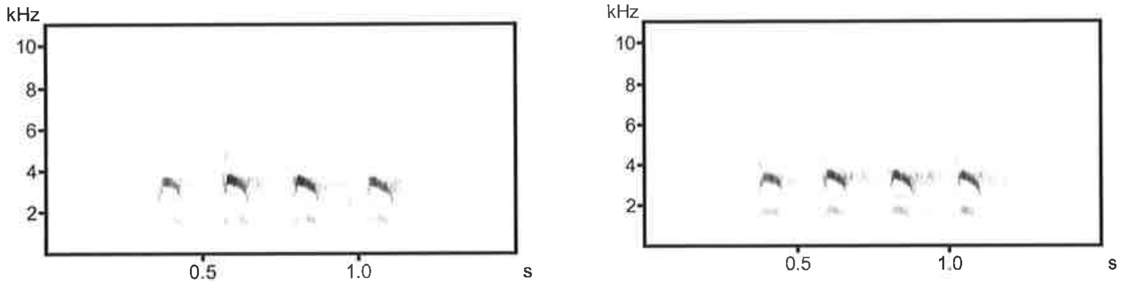
Parameter	Intra-Ind. CV	Inter-Ind. CV	Intra-Inter CV Ratio	p
maximum frequency	1.52	3.81	0.40	<0.0001
minimum frequency	3.92	8.25	0.48	<0.0001
# syllables	9.99	11.77	0.85	0.0006
range	13.49	15.27	0.88	<0.0001
mean syllable length	12.39	13.00	0.95	0.0007
mean intersyllable length	8.01	8.39	0.95	0.001
length	13.83	14.46	0.96	0.0019

Examples of staccato calls for the three individuals recorded are presented in Figure 7.16, highlighting variation in call structure within and between individuals. One parameter was removed from the DFA performed on the staccato calls of *T. sanctus* (frequency range), due to its high correlation (r>0.8) with other parameters. For the three individuals for which staccato calls were recorded, DFA revealed that the overall structure of the calls was individually-distinct, with 97.5% of calls being classified to the correct individual (Wilk's λ = 3.82 x 10-2; $F_{10,66} = 27.2$; $p < 0.0001$). Figure 7.17 shows the distribution of the canonical scores for the two canonical functions constructed in the analysis; these two functions explained 100% of the variation in the analysis.

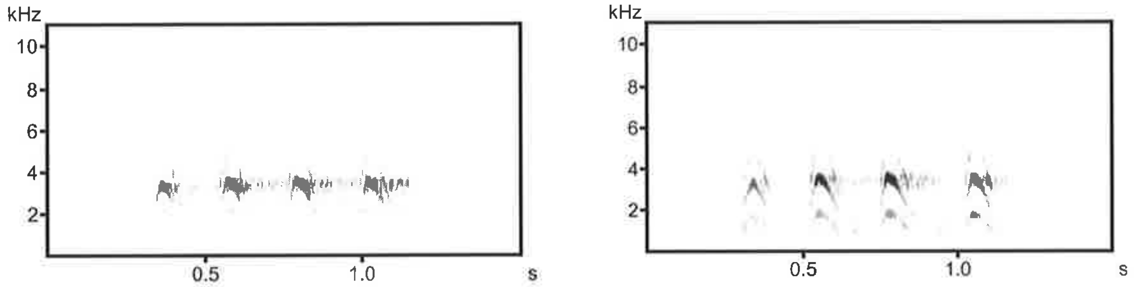
The most significant call parameters used to construct the analysis were the number of syllables in each call, and the maximum call frequency (for the first discriminant function), and the total call length (for the second discriminant function; Table 7.10). This result supports the previous suggestion following analyses of coefficients of variation, that maximum call frequency is an important discriminating feature, although total call length was also found to be important in this case. As with the results of previous work on call individuality in *T. sanctus* (Saunders and Wooller 1988), both call length and syllable number appear to be strong indicators of individual identity, although this present study also found that maximum call frequency may also be important. However, the importance of call length in discriminating between individuals when using DFA contradicts the results of calculations of CV_R, in which call length had the highest ratio (and was thus likely to be of least importance in individual identification).

7.4.2.2.2 Comparisons of individual syllables

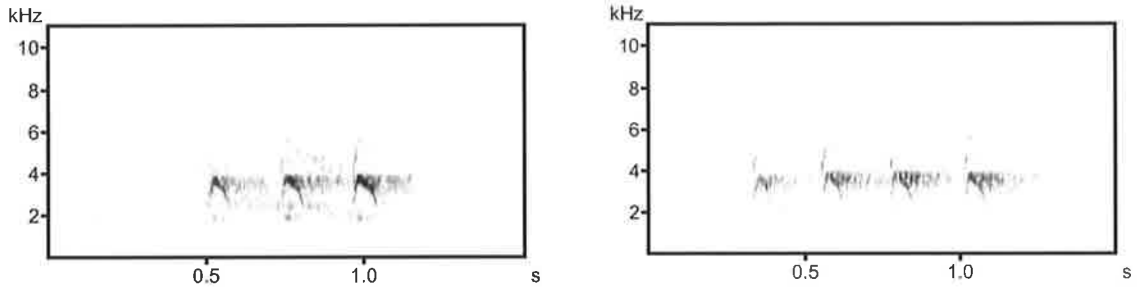
Previous studies have highlighted the significance of the number of syllables, as well as call length, in identification of individual *T. sanctus*. However, while the results of the DFA on



a. Bird C1 - recorded Cromer CP 20/11/00 b. Bird C1 - recorded Cromer CP 11/12/00



c. Bird C2 - recorded Cromer CP 27/11/00 d. Bird C2 - recorded Cromer CP 11/12/00



e. Bird S2 - recorded Scott CP 4/12/00 f. Bird S2 - recorded Scott CP 4/12/00

Figure 7.16 Example sonograms of staccato calls produced by the three individuals of *Todiramphus sanctus* recorded in this study.

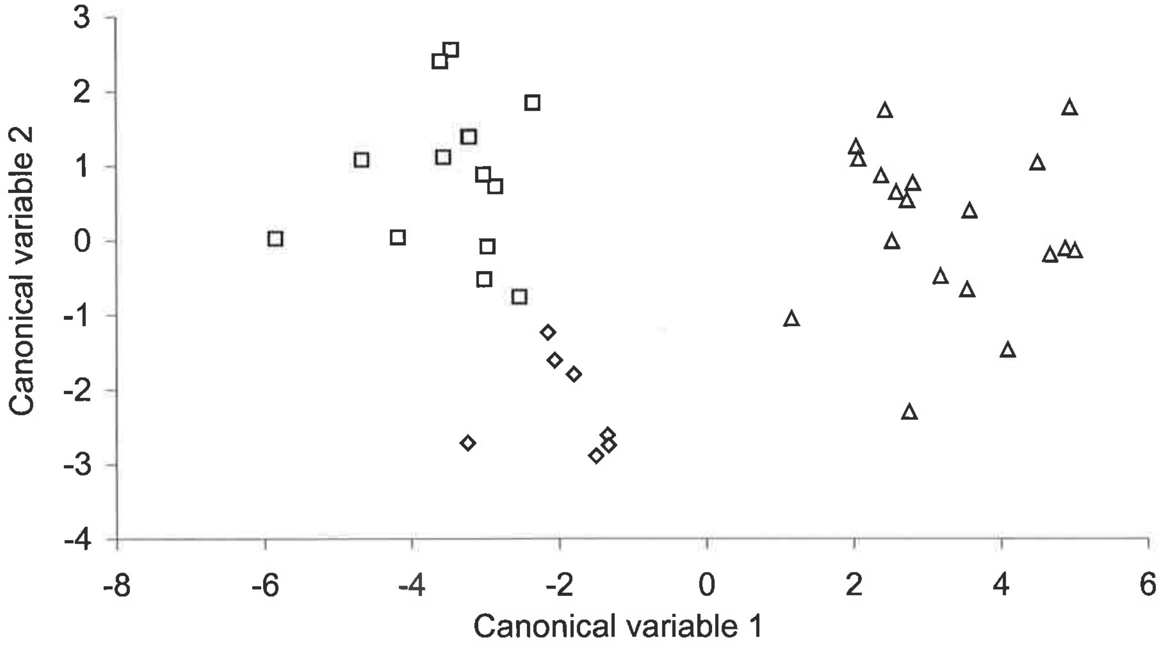


Figure 7.17 Distribution of staccato calls of *Todiramphus sanctus* in two-dimensional acoustic space, defined by the plot of canonical scores of the first two canonical variables constructed by the discriminant function analysis. Each point on the plot represents a single call, while each different shape represents a different individual (open squares: C2; open diamonds: C1; open triangles: S2).

Table 7.10 Standardised coefficients for the two canonical variables (CVs) constructed by the discriminant function analysis performed on the staccato calls of *Todiramphus sanctus*. For each call parameter, a high coefficient (independent of whether it is positive or negative) indicates the discriminating ability of the parameter. Eigenvalues are indicators of the proportion of variation that can be attributed to each canonical variable.

Call Parameter	CV 1	CV 2
maximum frequency	1.311	-0.107
# syllables	-1.667	0.617
frequency range	-0.530	0.738
mean intersyllable length	-0.257	0.849
call length	0.977	-1.189
Eigenvalue	10.681	1.239
Cumulative Proportion of variation	0.896	1.000

whole calls here suggested that the number of syllables was important, some overlap was exhibited in the number of syllables between individuals, and that the number of syllables that an individual used varied for some birds; this measure of individuality would, therefore, only be useful in identifying a small number of individuals. In addition, as suggested elsewhere in this thesis, cross-correlation analyses are likely to be more accurate when shorter acoustic signals, or those composed of fewer syllables, are compared between individuals. In order to be able to make comparisons between calls with different numbers of syllables, the structure of each syllable was compared between individual birds.

Of the eight parameters used to describe each call syllable, seven differed significantly between individuals (Table 7.11). Calculations of coefficients of variation revealed that the spectral features of syllables generally varied very little, both within and between individuals, in comparison to temporal features of the syllables. In addition, spectral features tended to exhibit lower CV_R values, with the exception being syllable length. Maximum syllable frequency thus appeared to have the greatest potential for discriminating between individuals, with the time at which minimum and maximum frequency occurred having the lowest discriminating ability (Table 7.11).

A DFA performed on all call syllables, using the eight parameters measured to describe each syllable, showed that the syllables that comprise each call are individually-distinct, when treated as independent cases in the analysis (Wilk's $\lambda = 0.124$; $F_{12,248} = 38.0$; $p < 0.0001$), with *post-hoc* tests classifying 89.4% of call syllables to the correct individual. However, quantitative observations suggested that, across all individuals, the first syllable of a call differed from subsequent call syllables, a factor that may increase intra-individual variation in syllable structure (Figure 7.18; Table 7.12). A second DFA was therefore performed with the first syllable of each call excluded. This second analysis classified 96.9%

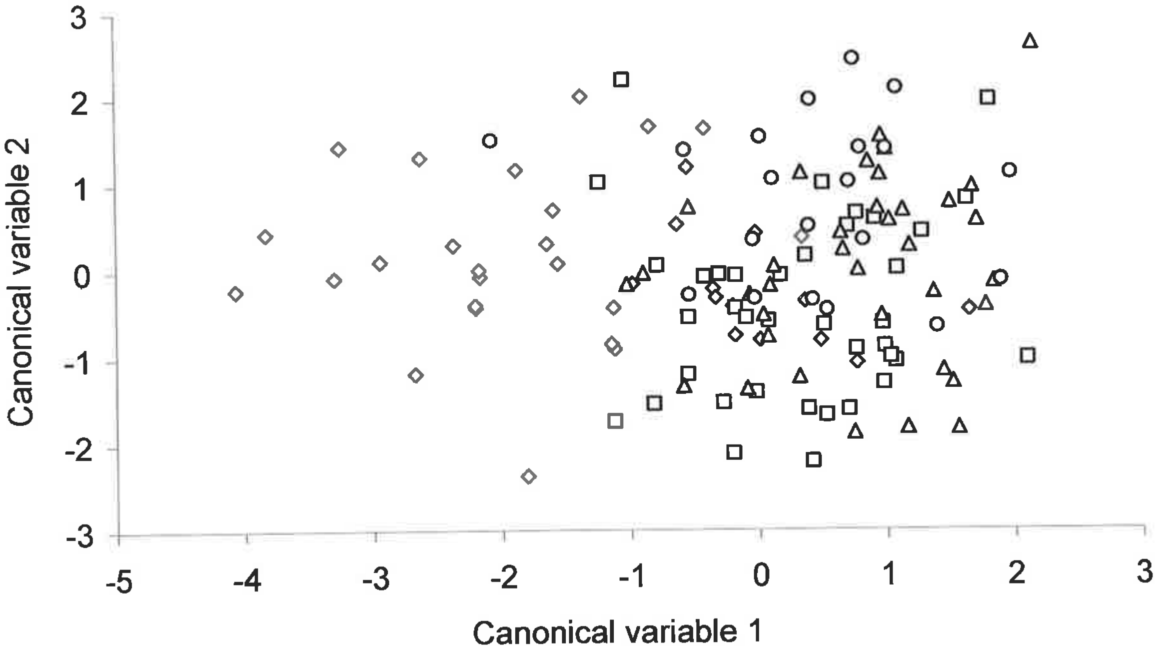


Figure 7.18 Scatterplot of the first two canonical variables constructed by a discriminant function analysis, grouped by syllable number, for the staccato calls of *Todiramphus sanctus*. This plot highlights the suggestion that the first syllable in each call (red diamonds) differs in structure from the remaining syllables (second syllable: open squares; third syllable: open triangles; fourth syllable: open circles), a suggestion supported by the results of the discriminant function analysis (see Table 7.11).

Table 7.11 Coefficients of variation and results of univariate statistical tests between individuals for each of the parameters measured to describe each syllable of the staccato calls of *Todiramphus sanctus*, ranked in ascending order of CV_R.

Parameter	Intra-Ind. CV	Inter-Ind. CV	CV_R	p
maximum frequency	2.88	4.14	0.69	<0.0001
length	12.68	15.11	0.84	<0.0001
minimum frequency	6.03	6.52	0.93	<0.0001
frequency at end of syll.	6.46	6.61	0.98	<0.0001
frequency at start of syll.	7.32	6.32	1.16	<0.0001
frequency range	23.74	14.81	1.60	<0.0001
time of min. freq.	55.73	25.96	2.15	0.114
time of max. freq.	46.42	10.11	4.59	<0.0001

Table 7.12 Squared Mahalanobis Distances (SMDs) and p-values (in parentheses) between syllable numbers, highlighting the difference between the first and subsequent syllables of the staccato call of *Todiramphus sanctus*. The SMDs are an indicator of the distance between two types of syllables in multidimensional acoustic space, while p values are the results of discriminant function analyses between each pair of syllable types. As can be seen, p values less than 1 x 10^{-4} were observed between the first syllable and all other syllable types, while the mininum p value between any other pair of syllable types was 0.002.

	Syllable number B			
Syllable number A	1	2	3	4
1	-	2.9 (<0.0001)	4.3 (<0.0001)	3.7 (<0.0001)
2		-	0.47 (0.15)	1.6 (0.002)
3			-	0.82 (0.09)
4				-

of syllables to the correct individual, with the syllables included in this analysis differing significantly between individuals (Wilk's $\lambda = 0.075$; $F_{10, 174} = 46.3$; $p < 0.0001$). The proportion of syllables classified correctly was significantly greater when the first syllable of each call was removed from the analysis ($\chi^2 = 4.34$; $p = 0.03$).

7.4.2.3 Cross-correlation analysis

A single cross-correlation analysis was performed on the staccato calls of *T. sanctus* individuals, with each staccato syllable treated as a separate case, as in Section 7.4.2.2.2. As in Section 7.4.2.2.2, the first syllable of each call was excluded from this analysis.

The effect of the r_x* on the proportion of r_x values that were correctly classified is presented graphically in Figure 7.19. The peak percentage of r_x values classified to the correct individual for the three individuals recorded was 78.9%, at an r_x* value of 0.71. r_x values calculated for comparisons between syllables produced by the same individual were significantly higher than r_x values calculated between syllables of different individuals (t-test = 52.1; df = 4849; $p < 0.0001$).

However, while this analysis compared each syllable separately, it was unnecessary to compare the syllables within each call, as investigators would already know with absolute certainty that these call syllables were produced by the same individual. Therefore, the average r_x values for all of the syllables within each call were calculated between each pair of calls, to determine whether identification accuracy was improved by only comparing the syllables of different calls. The peak percentage of r_x values classified correctly for this analysis was therefore 83.8%, a significant improvement in accuracy from the use of individual syllables ($\chi^2 = 13.36$; $p = 0.003$). The r_x* at which this peak identification accuracy occurred using these average correlation values was slightly lower than when individual syllables were compared, at 0.68 (Figure 7.20). As with individual syllables, the average r_x values calculated between the calls of the same individual were significantly higher than the average r_x values between the calls of different individuals (t-test = 24.5; df = 778; $p < 0.0001$).

7.4.3 Discussion

Although the results presented here are representative of only three individuals, the general conclusions derived from these data are consistent with those of previous studies (Saunders and Wooller 1988, Curl 1999). The staccato calls of *Todiramphus sanctus* thus appear to be individually-distinct, both at the scale of the whole call, and the individual syllable. This present study has also strengthened the argument for vocal individuality in *T. sanctus*, by providing evidence of vocal individuality in birds who breed in a region geographically distinct from the study sites of both (Saunders and Wooller 1988) and (Curl 1999).

Furthermore, this present study has demonstrated that cross-correlation analysis can be used with a high degree of accuracy to discriminate between individuals on the basis of the average structure of the staccato syllables within calls. Demonstrating that individual kingfishers are able to be identified acoustically using this technique thus allows for the subsequent identification of previously unknown individuals.

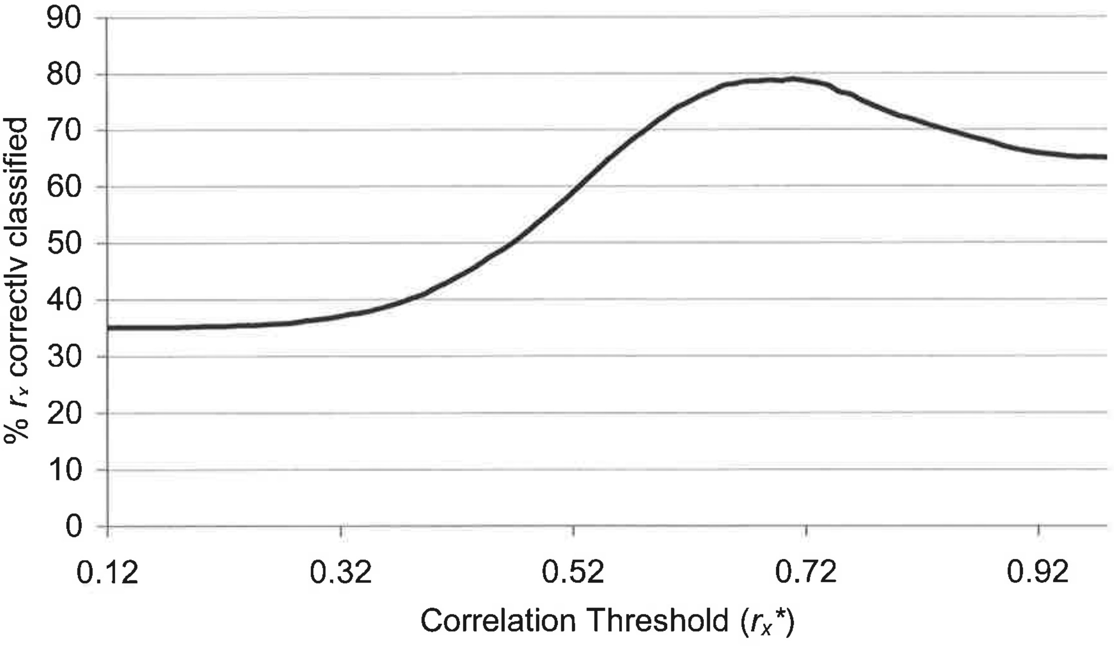


Figure 7.19 Plot highlighting the impact of correlation threshold (r_x*) on the percentage of r_x values correctly classified as having been produced by the same individual or two different individuals, for the staccato call syllables of *Todiramphus sanctus*.

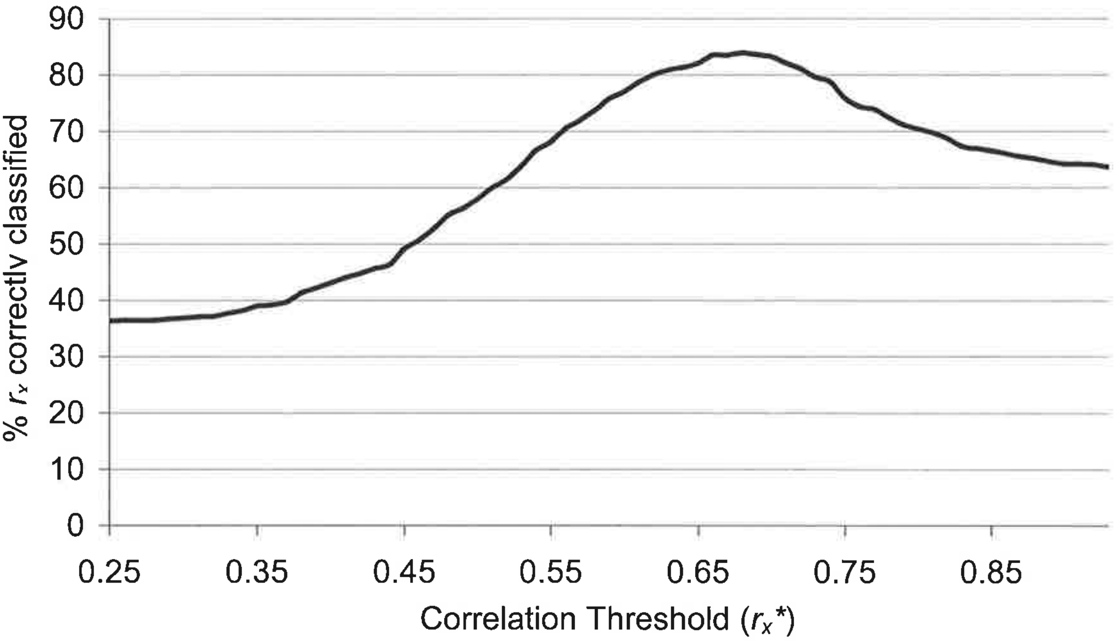


Figure 7.20 Plot highlighting the impact of correlation threshold (r_x*) on the percentage of r_x values correctly classified as having been produced by the same individual or two different individuals, for the staccato calls of *Todiramphus sanctus*, when the r_x values for all of the syllables of the two calls are averaged.

7.5 General discussion

The results of this chapter further the suggestion that vocal individuality is widespread among both passerine and non-passerine avian species. All three taxa for which data are presented in this chapter exhibited high degrees of vocal individuality, and the potential for acoustic identification of individuals was also strong for each of these taxa. In addition, results presented here highlight the importance of conducting pilot studies on target species, both to investigate the vocal behaviour of the taxa, and to discern the cross-correlation settings (eg. r_x*) that are likely to maximise the accuracy of individual identification. However, the limited scope of these data, especially with regard to the number of individuals recorded, suggest that, should one wish to develop such techniques for these species, more extensive pilot studies be undertaken.

A more thorough discussion of the implications of vocal individuality to acoustic identification of individuals is presented in Chapter 9.

Chapter 8 Environmental Degradation of the Songs of *Dasyornis broadbenti*: Acoustic Compromise in a Ground-Dwelling Passerine

8.1 Introduction

In previous chapters, intraspecific variation in acoustic signals has been quantified for a number of animal species, and the potential for using this variation to identify and monitor individuals has been discussed. However, these results may have been influenced by the conditions at which songs were recorded under, with regard to atmospheric conditions, wind speed and direction, calling position of the recorded individual, and the distance between the investigator and the calling animal, as well as actual variation between the songs of different individuals. This chapter aims to determine the effects of environmental attenuation and degradation on the acoustic signals of *Dasyornis broadbenti*, with the ultimate aim of determining how such effects influence our perception of intraspecific variation, and our ability to accurately discriminate between conspecific individuals based on the structure of their songs.

The environment through which acoustic signals are transmitted can significantly influence the structure of these signals, when they reach the intended receiver. With regard the physical environment, the primary factors that influence sound degradation are spherical attenuation of sound, absorption of sound by the atmosphere, absorption and reflection of sound by the ground (termed the 'ground effect'), and scattering of sound energy by objects such as vegetation. In addition, perturbations in the environment can also result in excess attenuation, such that attenuation may be greater at times of increased atmospheric turbulence.

Animals are able to minimise these physical restrictions on sound communication either through adaptions to the structure of their acoustic signals, or alterations to their singing behaviour. For example, ground effects tend to have the greatest impact on the structure of acoustic signals with a frequency of approximately 1 kHz or less (Morton 1975, Marten and Marler 1977, Marten *et al.* 1977), although sound attenuation also increases at higher frequencies as a result of ground effects (Morton 1975). In addition, scattering and atmospheric absorption have their greatest impact on higher frequencies (Morton 1975), with excess sound attenuation increasing with sound frequency above approximately 2 kHz (Marten *et al.* 1977). Thus the acoustic signals of animals would best serve long-distance communication if their frequencies are as low as possible, but above 1 kHz, especially for species who sing from close to ground level (Marten *et al.* 1977). While the structure of many avian acoustic signals comform to these general principles, a great deal of variation still occurs, as a result of phylogenetic, morphological or other evolutionary constraints (van Buskirk 1997, Palacios and Tubaro 2000, Podos 2001).

Behaviourally, animals alter their singing behaviour either temporally or spatially to maximise sound transmission. For example, Wiley and Richards (1978) suggested that a possible reason for the universal dawn chorus in birds is that atmospheric turbulence is at a minimum at this time, and birds take advantage of this period of atmospheric stability to maximise song transmission. Birds are also well known to alter their singing position spatially, by singing from high perches, thus minimising both ground effects, and in many cases, reducing sound attenuation as a result of scattering by vegetation (Marten and Marler 1977).

For a terrestrial passerine, the acoustic benefits that come from singing from higher perches may be compromised by other factors. Primarily, singing from higher perches, and from above vegetation, may result in birds becoming more conspicuous to predators, although singing from perches may also benefit predator avoidance in some species, by allowing increased anti-predator vigilance (Krams 2001). Energetic compromises may also exist, especially in cases where other activities such as foraging generally occur at ground level. Therefore, the acoustic advantages of singing from higher, more open song perches must be weighed against the costs involved with singing from these perches.

The Rufous Bristlebird is a medium-sized (60g) insectivorous passerine, that forages almost exclusively on the ground. While *D. broadbenti* does occasionally sing from the tops of shrubs (pers. obs.) and perches above ground level, its predominantly terrestrial nature suggests that the majority of social behaviours - including singing - occur while the birds are at or near ground level. Because of this terrestrial preference, long-distance communication may be compromised in *D. broadbenti*, should signalling from the ground significantly influence acoustic transmission in this species. This study thus aims to determine whether transmission of the songs of *D. broadbenti* are influenced by transmission at ground level, rather than transmission at some level above ground level. Such information should thus provide an assessment of how environmental degradation of Rufous Bristlebird songs influences our perception of vocal individuality and the ability to identify individuals acoustically.

8.2 Methods

8.2.1 Study Sites

Experiments were carried out at Tea-Tree Crossing (TTX) in the Coorong National Park, near the township of Salt Creek (36°07'S, 139°38'E). This location comprised of coastal heath vegetation dominated by *Leucopogon parviflorus*, *Acacia longifolia* and *Olearia axillaris*. More details of this vegetation community are given in Chapter 4. This habitat type is typical of the habitat preferred by *Dasyornis broadbenti* in the Coorong National Park. All experiments were performed on a single day (28 April 2001), between 0800 and 1400 hours. The weather was calm, with very light breezes and less than 20% cloud cover.

8.2.2 Synthesis of songs and playback procedure

Male bristlebird songs were synthesized from recordings obtained as part of other studies, using the graphic synthesizer of Avisoft SAS-Lab (Specht 1998). For the playback experiments, four male song types were randomly chosen (Figure 8.1), all of which were originally recorded in the Coorong National Park. Four replicates of each of these four song types were used in the experiment, thus comprising a total of sixteen songs.

The synthesized bristlebird songs were played from a laptop computer, which was connected through an amplifier to a loudspeaker. As no data existed for the sound pressure level of natural rufous bristlebird songs, the sound level for playback of synthetic songs was set by estimating natural sound pressure levels by ear. The songs were then re-recorded using a Sony DC-8 DAT recorder and Sennheiser ME-66 directional microphone at a set recording level. In addition to recording the songs, a B&K 200 sound pressure level meter was also used to measure peak sound pressure level (SPL; in dB) for each song. Recordings and SPL readings were taken at four distances from the loudspeaker: 10m, 20m, 50m and 100m. Each playback procedure was carried out twice; once with the loudspeaker placed at ground level (0m height), and once at 2m above ground level (2m height) This height of 2m was chosen, as ground effects on sound transmission have been demonstrated to be negligible at source heights greater than approximately 1m (Morton 1975).

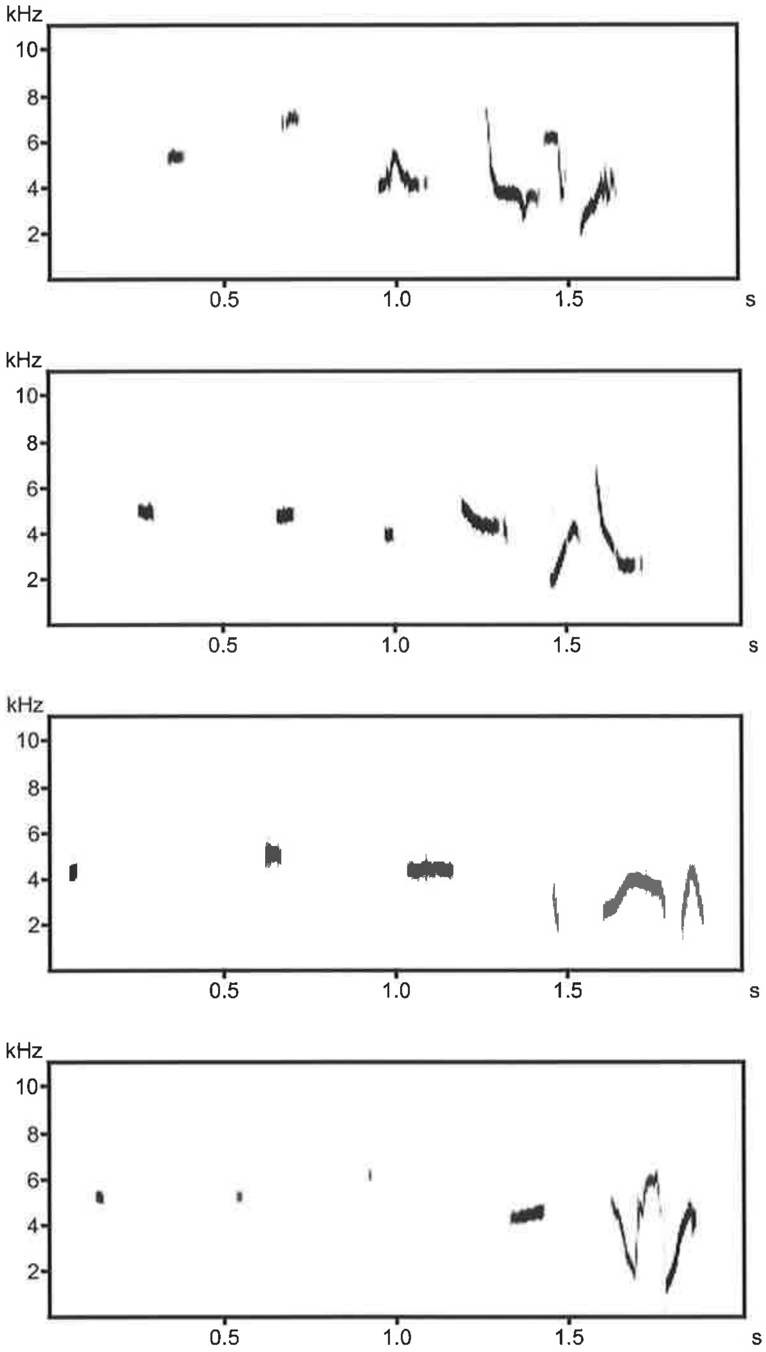


Figure 8.1 Example sonograms of the four male song types of *Dasyornis broadbenti*, synthesized for degradation experiments.

8.2.3 Analysis of recordings

Measurements of sound pressure level were analysed by comparing rates of song attenuation with distance between the two source heights tested, and between the results obtained from both source heights and a theoretical calculation of optimal attenuation (see Section 8.3.1).

In addition to analyses of sound pressure level, the third component of each degraded song was cross-correlated against its undegraded equivalent, and by cross-correlating degraded songs against each other, in order to assess the overall degradation of song structure with distance and source height. Cross-correlations were conducted in order to make comparisons with the cross-correlation results obtained in Chapter 5, as a way of determining how environmental degradation of songs influences acoustic identification using the cross-correlation technique. In addition, various temporal and spectral components have previously been shown to be influenced by environmental degradation (Morton 1975, Marten and Marler 1977, Marten, et al. 1977), but cross-correlation allows us to determine the impact of degradation on the entire signal (Hauser 1997).

The third component of the male song was thus analysed exclusively using cross-correlation analysis. As with cross-correlation analyses conducted in other chapters, all cross-correlations were conducted using the Avisoft Correlator software package (Specht 2000).

8.3 Results

8.3.1 Sound Pressure Level

Theoretical models propose that, as a result of spherical spread of sound energy radiating from a source, sound energy will decrease by 6 dB for every doubling of distance between the source and the receiver (Wiley and Richards 1978). For songs recorded at a distance of 10m with the source at ground level, the mean sound pressure level was 67.3 (± 0.68) dB, and following this law of spherical spread, the mean expected sound pressure level at a distance of 100m between the source and receiver was 47.4 (±0.68) dB. For songs recorded at 10m with the source at a height of 2m, the mean sound pressure level was 78.1 (±0.75) dB, and the expected sound pressure level at a distance of 100m was 58.2 (±0.75) dB.

For both source heights, sound attenuation was significantly greater than expected by spherical spreading alone. At a source height of 0m, the mean observed sound pressure level at a distance of 100m from the source was 7.2 (±1.2) dB less than expected by spreading (observed SPL at 100m: 40.2 ± 1.1 dB; expected SPL at 100m: 47.4 ± 0.7 dB), and was significantly less than expected (t-test = 5.4; df = 30; $p < 0.0001$). At a source height of 2m, mean observed sound pressure level at a distance of 100 m was 10.1 (±0.99) dB less than expected by spreading alone (observed SPL at 100m: 48.1 ± 1.5 dB; expected SPL at 100m: 58.2 ± 0.8 dB). Again, the observed SPL at 100m at a source height of 2m was significantly less than expected by spreading alone (t-test = 6.1; df = 30; $p < 0.0001$). There was, however, no difference in excess attenuation between the two source heights (t-test = -1.9; df = 30; $p = 0.068$). Therefore, the environment through which rufous bristlebird songs were transmitted appeared to significantly impact upon the attenuation of the songs, irrespective of the height of the song source.

The relationships between source-to-receiver distance and sound pressure level for each of the two source heights tested is shown graphically in Figure 8.2. Sound pressure level exhibited a significant negative relationship with distance at both source heights (Height 0m: $r^2 = 0.84$; $F_{1,62} = 319.1$; $p < 0.0001$; Height 2m: $r^2 = 0.73$; $F_{1,62} = 169.0$; $p < 0.0001$). At a source height of 0m, the relationship between distance and sound pressure level can be expressed as:

$$\text{SPL} = 91.5 - 26.5 \times \log_{10}(\text{Distance})$$

At a source height of 2m, the relationship between distance and sound pressure level can be expressed as:

$$\text{SPL} = 105.3 - 27.9 \times \log_{10}(\text{Distance})$$

where distance is expressed in metres and SPL is expressed in dB. As decibels are a log measure of sound pressure level, only the distance axis was log-transformed. While there was no difference between the slopes of the two regressions (ANCOVA: $F_{1,124} = 1.16$; $p = 0.28$), there was a significant difference between the intercepts (ANCOVA: $F_{1,127} = 49.2$; $p < 0.0001$).

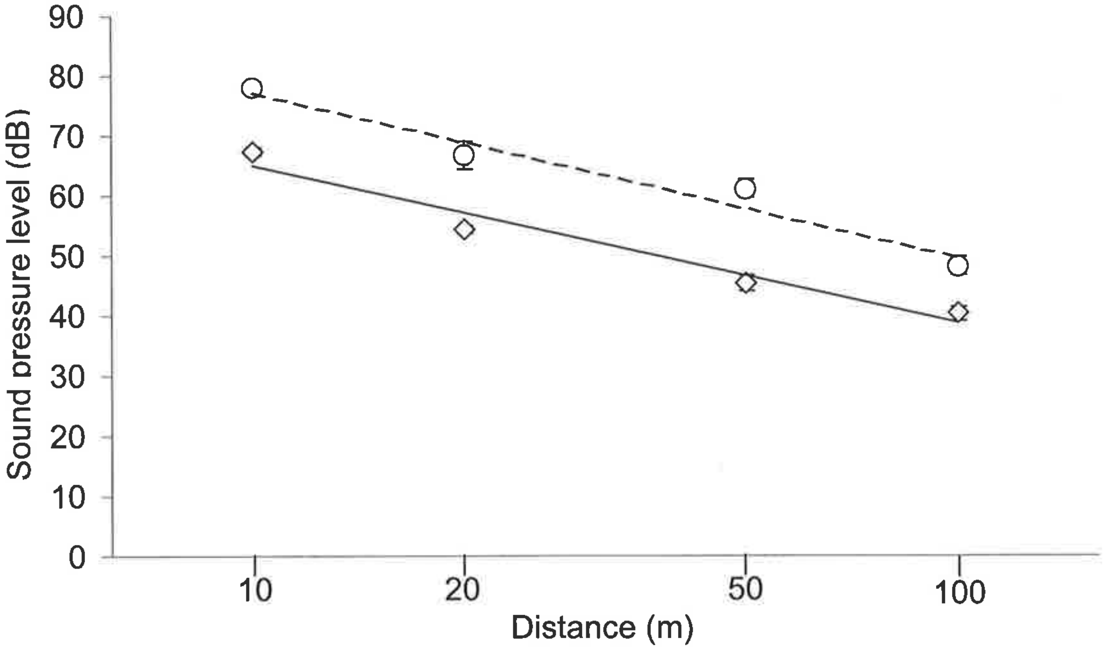


Figure 8.2 Relationship between source-to-reciever distance and sound pressure level for the male songs of *D. broadbenti,* for source heights of 0m (open diamonds, solid line) and 2m (open squares, hashed line). Error bars ± standard error. Sound pressure level exhibited a significant relationship with distance for both source heights (Height 0m: $r^2 = 0.84$; $F_{1,62} = 319.1$; $p<0.0001$; height 2m: $r^2 = 0.73$; $F_{1,62} = 169.0$; $p<0.0001$).

8.3.2 Cross-correlation Analyses

In addition to the effects of source height and distance on the attenuation of *D. broadbenti* songs, the percieved song structure was also influenced by these factors. Figure 8.3 provides graphical examples of how distance between source and receiver influenced the structure of the songs in this study.

When cross-correlation analyses were conducted comparing undegraded synthetic songs with their degraded equivalents, r_x decreased with increasing distance between the source and receiver, for both source heights (Height 0m: $r^2 = 0.58$; $F_{1,62} = 84.0$; $p < 0.0001$; Height 2m: $r^2 = 0.45$; $F_{1,62} = 51.1$; $p < 0.0001$; Figure 8.4). For songs recorded with the source at ground level, the relationship between distance and song similarity (expressed as r_x) can be expressed as:

$$r_x = 0.55 - 0.004 \text{ x (Distance)}$$

while the relationship between song similarity and distance with the source at a height of 2m can be expressed as:

$$r_x = 0.65 - 0.003 \text{ x (Distance)}$$

where distance is expressed in metres and song similarity is expressed as the r_x value calculated between each undegraded song and its degraded equivalent. The slopes of the two relationships were significantly different (ANCOVA: $F_{1,124} = 6.05$; $p = 0.015$), as were the intercepts (ANCOVA: $F_{1,127} = 10.2$; $p = 0.002$).

In addition to comparing degraded songs with their undegraded synthetic equivalents, degraded songs were also compared with each other using cross correlation analysis. These analyses were performed, because the song recordings to be used to identify individuals using cross-correlation analysis will have degraded to some degree, as there will always be some degradation between the singing individual and the recorder. Although comparisons with undegraded songs are interesting, for the purposes of testing the accuracy of cross-correlation for individual identification, the comparison of different classes of degraded song is more relevant.

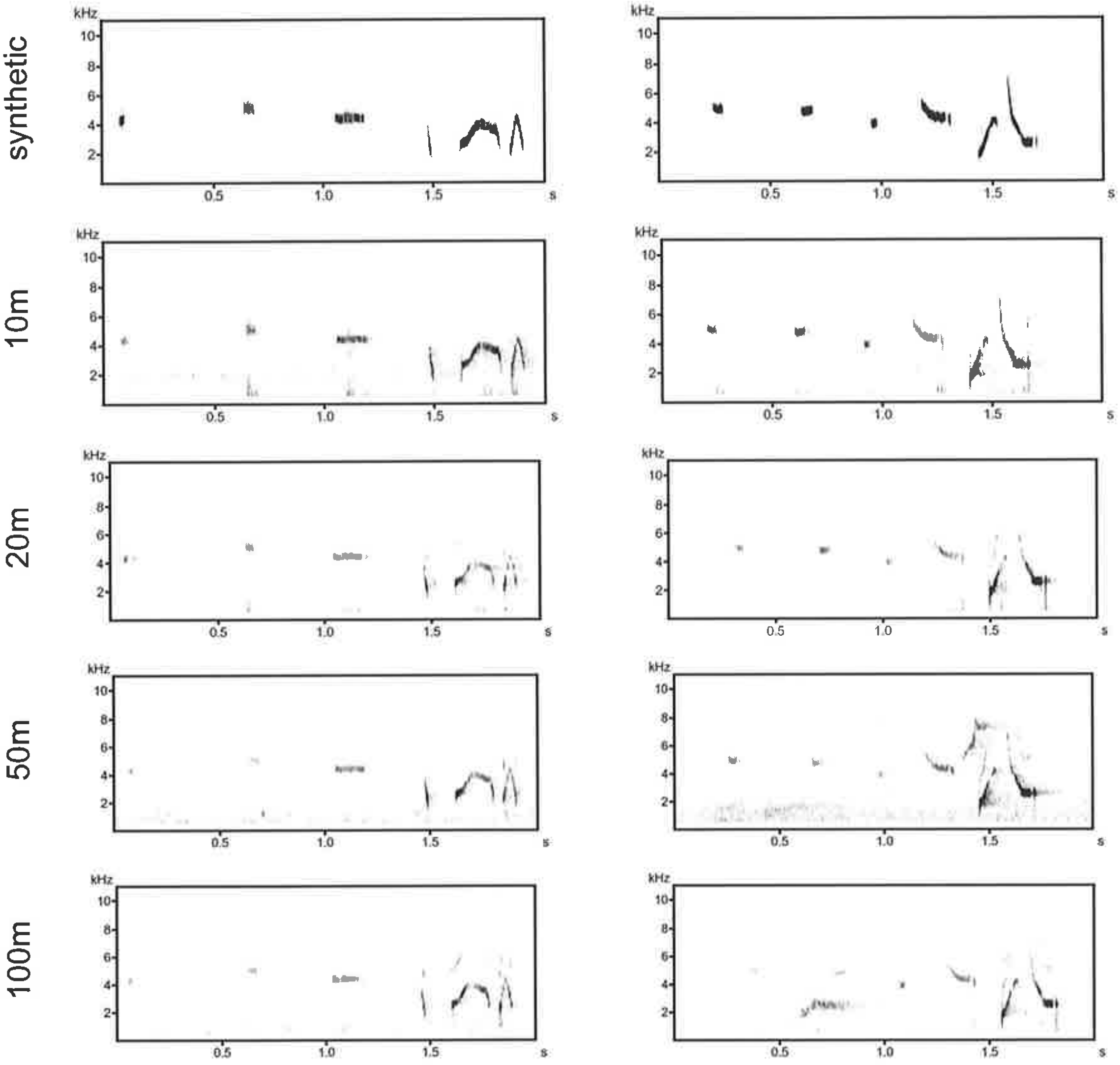


Figure 8.3 Example sonograms of two of the four synthesized male songs of *D. broadbenti*, both undegraded and when re-recorded at 10m, 20m, 50m and 100m between the source and receiver, at a source height of 0m. In these examples, amplitude was standardised for the purposes of graphical presentation.

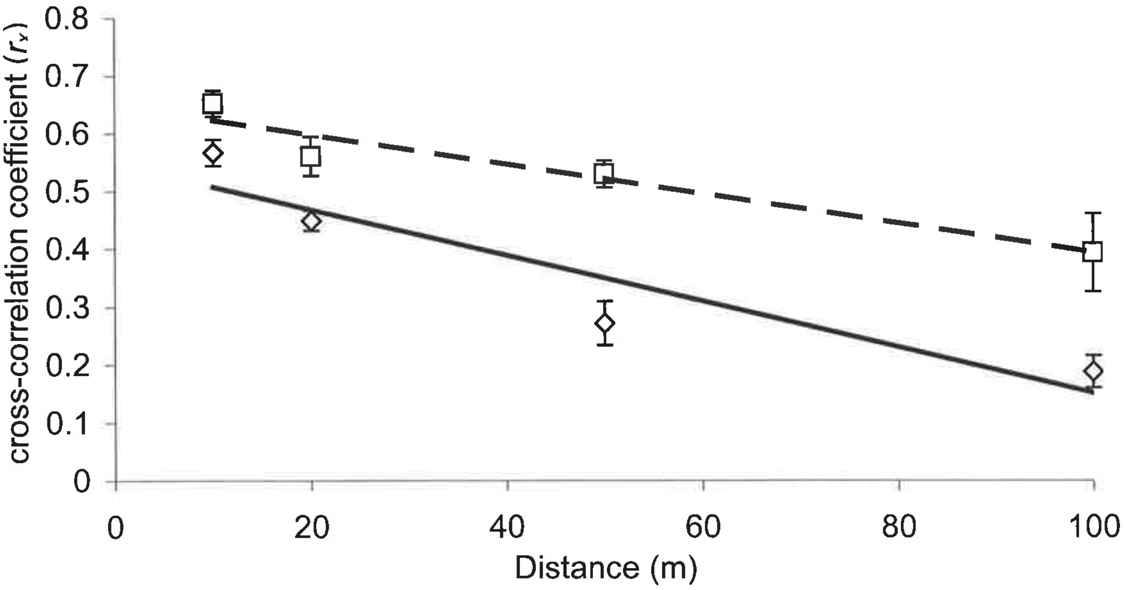


Figure 8.4 Relationship between source-to-reciever distance and cross-correlation coefficient (r_x) between undegraded synthetic male songs of *D. broadbenti* and re-recorded songs, at source heights of 0m (open diamonds, solid line) and 2m (open squares, hashed line). Note that neither line intercepts the y-axis at 1.0, as such a theoretical comparison is not equivalent to comparing two synthetic songs, but is equivalent to comparing a synthetic song with a degraded song recorded from a distance of 0m.

Each degraded song was therefore compared with other degraded versions of the same song, which varied with respect to the distance and height from which they were recorded. Results of cross-correlation analyses between pairs of degraded songs are summarised in Figure 8.5. For songs whose source height was the same, r_x values peak where the distance between the source and receiver is the same for both of the songs being compared. For example, where the distance between the source and receiver for one song is 10m, r_x values between this song and others declines with increasing distance between the source and receiver for the other song. Similarly, where the distance between source and receiver is 20m for one song, r_x values increase with distance between source and receiver of the second song up to 20m, and then decline with further increase in this distance. When the source height for both songs is the same (either 0m or 2m), mean correlation coefficients are greater than 0.64 ± 0.05, irrespective of the respective distances from which the two songs were recorded, up to a distance of 100m.

A slightly different pattern emerges, however, when the source height of the two songs being compared is different. In cases where one of the songs to be compared was recorded from a distance of 50m or 100m, the distance from which the second song was recorded appears to make little difference to the mean values of r_x. Where one song was recorded from a distance of 100m, the distance from which the second song was recorded did not significantly influence the r_x values produced between the two songs (1-Way ANOVA: $F_{3,24} = 0.19$; $p = 0.9$). Mean r_x values decline with the distance between the recorder and singer in cases where one of the songs was recorded from 10m or 20m distance. Overall, however, mean r_x values did not fall below 0.564 ± 0.03 for any pair of songs recorded at different distances, and from different heights.

One general pattern that emerges, irrespective of the relative heights of the two songs being compared, is that the decline in r_x values level out as the distance approaches 100m, with no difference in mean r_x being detected between a distance of 50m and 100m, for songs recorded at the same height (t-test = 1.2; df = 62; $p = 0.24$), or songs recorded at different heights (t-test = 0.18; df = 54; $p = 0.86$).

8.4 Discussion

The results of sound degradation experiments conducted on synthetic songs of *D. broadbenti* suggest that the transmission of these songs is influenced by whether the source is at ground

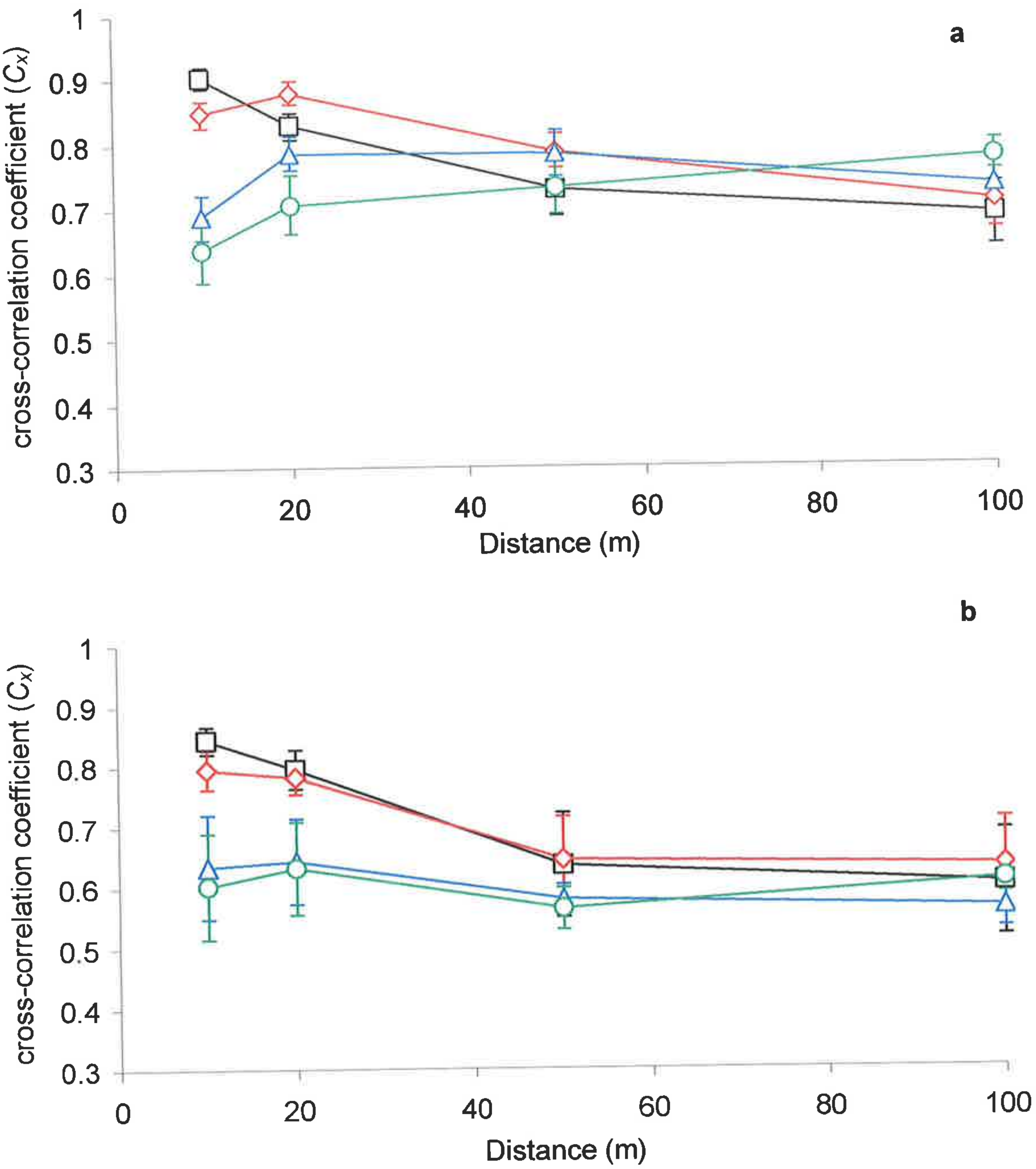


Figure 8.5 Relationships between source-to-receiver distance and cross-correlation coefficient between pairs of degraded songs, for songs recorded at the same height (a) and different heights (b). For both graphs, the four lines indicate that one of the songs was recorded from a distance of 10m (□), 20m (◇), 50m (△) and 100m (○). The distance along the x-axis represents the distance between the source and receiver of the second song recorded.

level, or 2m above ground level. Both song attenuation, and degradation of the song structure, were significantly greater when the source speaker was placed at ground level, than when placed at a height of 2m.

Considering that rufous bristlebirds appear to spend a large proportion of their time at ground level, the acoustic communication system of this species may be severely restricted by their ground-dwelling nature. However, very little information currently exists on whether bristlebirds sing consistently from higher positions. Personal observations suggest that individuals do indeed sing from perches above the ground, although the proportion of songs sung from perches at different heights is difficult to identify, as most songs are sung with the birds well hidden. Although the cryptic nature of the species makes estimates of singing position difficult, future studies may attempt to determine this information.

Alternatively, the role and function of acoustic signals in the social system of bristlebirds suggests that, in some contexts, long-distance transmission of songs is not required. Observations of bristlebird behaviour suggest that both males and females use acoustic signals primarily to defend territories during the breeding season, with song also potentially playing roles in mate attraction and pair-bond maintenance. Estimates of the size of Rufous Bristlebird territories during the breeding season average 2.3 ha (Seymour and Paton 2000). To perform both functions of territory defence and pair-bond maintenance, the songs of Rufous Bristlebirds would only require effective communication distances in the scale of tens, rather than hundreds, of metres, although mate attraction may require longer communication distances. While acoustic communication in rufous bristlebirds may be restricted by the ground-dwelling nature of the birds, their ecology may result in such long-distance communication not generally being required (Richards and Wiley 1980).

Singing from ground level significantly influences the transmission of acoustic signals in *D. broadbenti*, and long-distance communication may therefore be compromised in this ground-dwelling species. Both ground effects (Roberts *et al.* 1981) and the scattering effects of vegetation (Marten and Marler 1977, Marten, et al. 1977) are likely to play a role in this observed pattern, as the structure of the habitat means that bristlebirds are able to sing from above vegetation, even at heights as low as 2m from the ground. Behavioural factors, as outlined above, are likely to be the primary determinants of whether individual bristlebirds choose to do so.

Implications for the acoustic identification of individuals

With regard to the use of cross-correlation for acoustic identification, how do these results impact upon identification accuracy? Both source height and source-to-receiver distance appear to influence the results of cross-correlation analyses, although the impact upon song structure did not appear to be as great as the impact on sound pressure level. The greatest impact on the results of cross-correlation analyses between pairs of degraded songs resulted in mean r_x values of 0.56 ± 0.03, between songs recorded at different heights. However, in many cases the impact of distance was not so dramatic; mean r_x values between songs whose source heights were the same did not drop below 0.64 ± 0.05. Given that these minimum values were produced between songs recorded at distances of 100m, the impact of environmental degradation on individual identification when using cross-correlation analysis are unlikely to be of great significance, especially compared to the impact of song variation between individuals. In addition, r_x values did not decline significantly after a distance of 50m; the most dramatic decline in r_x thus occurs when the distance between the recorder and speaker are closer than 50m. However, it is also these closer distances that give us the greatest r_x values when comparing equivalent songs. The optimal r_x* for the identification of individual male bristlebirds was identified in Chapter 5 as 0.6, a value that was only crossed in the most extreme cases of song degradation.

Despite the suggestion that the effects of environmental degradation are of lesser importance in determining the results of cross-correlation analyses, the quality of songs used in such analyses should still be carefully considered. If one were to use cross-correlation analyses in a system of acoustic identification, the songs being compared should be of comparable, and preferably good quality, in order to ensure that the results obtained accurately reflect song variation, rather than variation in recording conditions. In additon, the experiments for which results are presented here were conducted on a single day under constant environmental conditions; variation in environmental conditions between days is also likely to influence the results of cross-correlation analyses. Investigators should therefore also be wary of these effects influencing identification accuracy. As described in Chapter 2, acoustic signals compared throughout this thesis were only included if they met some minimum qualitative recording quality, with poor recording being excluded from cross-correlation analyses. Such was the case especially for the comparison of *D. broadbenti* songs, where recording quality varied as a result of the shy nature of the species (which resulted in relatively large distances between singing birds and the recorder), and the variable weather conditions of the site.

One possible way of ensuring, or at least maximising, recording quality is to choose recording times where sound transmission is likely to be at its greatest. One possible explanation for bird dawn choruses, for example, is that atmospheric disturbance is at its lowest at this time, and thus birds can maximise the transmission of their acoustic signals (Wiley and Richards 1978). Investigators may thus benefit from recording at such times, as recording quality is likely to improved, as well as the rate of song collection (due to increased song production by the birds). Such practical considerations to song recording and collection are thus likely to improve the confidence one has in acoustic identification of individuals when using cross-correlation techniques.

Chapter 9 General Discussion

As stated in Chapter 1, a biological investigator's ability to identify and discriminate between individuals of the same species can have an important influence on both the questions that one can answer, and the quality of information that can be gathered. The results presented in this thesis suggest that such individual identification can be achieved for a range of animal species in a non-invasive manner, through the analysis of intraspecific variation in the acoustic signals of such species. As a way of demonstrating this suggestion, I will now summarise the results for each of the taxa for which results are presented.

Pseudophryne bibronii, the only non-avian taxa dealt with in this thesis, provided a unique example to test for vocal individuality. As with the calls of many anuran amphibians, the calls of *P. bibronii* are simple and pulsatile, a signal that is well suited to cross-correlation analysis, as suggested by previous authors (Baptista and Gaunt 1997). However, analyses presented in this thesis demonstrate that the calls of individuals vary greatly, especially between nights. Acoustic identification of individuals in this species, therefore, would be limited to surveys conducted on single nights, with little possibility for acoustic identification to be used to monitor individuals over time. Such a limited useful timeframe is unlikely to improve on existing methods of estimating population demographics for this species. However, this study represents the first to attempt to demonstrate vocal individuality in an anuran species. Such individuality may be present in other species, especially in cases where vocal recognition of individuals has been demonstrated (Davis 1987, Owen and Perrill 1998).

The results presented for the Rufous Bristlebird *Dasyornis broadbenti* highlight the need to conduct appropriate pilot studies before attempting to identify individuals acoustically. Initial observations of the singing behaviour in this species suggested that the songs of this species vary enormously, and that this variation may be attributed to vocal individuality. However, detailed observations of singing behaviour, as presented in this thesis, have shown that each individual possesses a large repertoire of different song types, with male repertoires being significantly larger than female repertoires. Futhermore, many of the song types encountered were found in the repertoires of more than one individual; that is, individuals often shared song types. Although song type sharing was most common between neighbouring territory holders, common song types were found to be used by individuals whose territories were separated by distances of up to 38km. The presence of these common song types was therefore used as the basis for further studies of vocal individuality and acoustic identification of individuals in this species. When song types that were common to more than one individual were compared between individuals, common song types exhibited a high degree of individuality, which translated into high levels of identification accuracy when using cross-correlation analysis. Although acoustic identification of individuals in *D. broadbenti* is limited to the comparison of shared song types, the prevalence of many song types, along with the strong individuality of these song types, suggests that acoustic identification has strong potential in this species.

The results presented for *D. broadbenti* also highlight the challenges set by species with extensive song repertoires, with regard to acoustic identification of individuals. Although common syllable types appeared to be a way of overcoming the problems associated with song repertoires, the syllable types perceived as qualitatively common were distinct to the song type from which they were drawn. As such, attempts to compare different individuals across the different song types encountered were not successful. Such comparisons, however, are still to be done for other avian species with extensive song repertoires.

Vocal individuality was demonstrated for the remaining three avian species for which results are presented. For the Willie Wagtail *Rhipidura leucophrys*, acoustic identification was achieved through a two-step analysis, made possible by the fact the individuals cycle through the song types in their relatively small repertoires during single sessions of singing. Many of the song types sung by individual Willie Wagtails were found to be unique to those individuals, and as such individual identification was achieved through the visual identification of those song types. In cases where song types were shared between individuals, vocal individuality was also demonstrated. The South-eastern Red-tailed Black Cockatoo *Calyptorhyncus banksii graptogyne* and the Sacred Kingfisher *Todiramphus sanctus* are both species in which all individuals use a small number of distinct call types that are presumably functionally, as well as structurally distinct, in much the same way as the different call types of *P. bibronii*. Quantitative analyses of the contact calls of *C. b. graptogyne* and staccato calls of *T. sanctus* suggest that vocal individuality is also present in these taxa; the results presented for *T. sanctus* support previous studies of vocal individuality for this species (Saunders and Wooller 1988, Curl 1999).

The apparently extensive nature of vocal individuality in birds thus raises the question of whether there is a universal function for vocal individuality, such as in individual recognition. Although individual recognition is likely to be a widespread phenomenon amongst avian species (as partially demonstrated by the widespread nature of vocal individuality), the context in which recognition is useful is likely to vary interspecifically, and will depend upon the social biology of the species, as well as the importance of acoustic communication in this social biology. In addition, although vocal individuality is a necessary precursor for acoustic recognition of individuals, its presence does not necessarily demonstrate unequivocally individual recognition, as individually-distinct acoustic signals may simply reflect intraspecific variation in the morphology and physiology of individuals (Matessi *et al.* 2000), or social influences (Mitani and Brandt 1994). A functional role for vocal individuality in individual recognition requires the execution of playback experiments that both test whether individual recognition occurs in the taxa under scrutiny, and, if so, in what social contexts it occurs. Such a demonstration has now been shown in an enormous diversity of avian species, although most of these studies lack the quantitative analyses of acoustic individuality presented in this thesis. Irrespective of the potential social functions of vocal individuality, the taxa presented in this chapter add to a growing list of vocal animals for which the potential for acoustic identification of individuals has now been recognised.

Comparison of Discriminant Function Analysis and Cross-Correlation Analysis for Assessing Vocal Individuality

The most widely used technique to date for assessing vocal individuality has been discriminant function analysis (DFA), a technique that has been used in this thesis to test the potential of using acoustic signals to identify individuals. However, discriminant function analysis has important limitations with regard to its potential as an identification tool. Cross-correlation analysis, however, has been shown in this thesis to be a directly applicable tool for individual identification. The principle advantage that cross-correlation analysis has over DFA is that it allows for both the re-identification of known individuals, and for the immediate identification of new individuals. Given that discriminant function analysis has been used extensively in the literature to promote acoustic identification of individuals in a range of animal species, how do the results of the two techniques used in this thesis compare?

Across all of the species for which data are presented in this thesis, the *post hoc* method of signal classification using discriminant function analysis consistently produced higher rates of correct identification compared to cross-correlation analysis. Such a general result is not altogether unexpected, as the method of classification used by DFA classifies each signal to a known individual with prior knowledge of which individual the signal belongs to. As a result, the analysis attempts to find the 'best fit' for each signal based on the parametric signal data used to perform the analysis, which will produce the highest proportion of correctly classified signals. Cross-correlation analysis, on the other hand, assesses the similarity between two signals with no prior knowledge of the identity of the individuals that the signals belong to. The disparity between the two analytical techniques may be one of the more important reasons for the observed differences in identification accuracy between the techniques.

Such a disparity has important consequences with regard to previous assessments of acoustic identification potential. As suggested previously, most prior studies of vocal individuality and the potential for individual identification based upon acoustic signals have used discriminant function analysis to demonstrate this potential (Eakle, et al. 1989, Galeotti and Pavan 1991, McGregor and Byle 1992, Hamao 1993, McGregor, et al. 1994, Peake, et al. 1998). However, given that DFA has extremely limited potential for identification of animal individuals in a practical setting, and that DFA produces consistently different results to alternative, more applicable techniques (such as cross-correlation), a re-assessment of the potential for acoustic identification in these study species is perhaps warranted.

However, species for which high classification accuracies were produced using DFA also exhibited relatively high identification accuracies using cross-correlation analysis. Therefore, while the margin of error may be higher when using cross-correlation analysis than is expected from the results of DFA, demonstrating vocal individuality with DFA may be a strong indicator that acoustic identification of individuals is possible using other techniques that are more applicable to identification in field situations.

Protocol for the development and implementation of acoustic identification of individual animals

The results presented in this thesis indicate that vocal individuality is widespread amongst vocal avian species, and that successful identification of individuals based upon acoustic signals appears possible in a broad range of taxa. Presented here, therefore, is a protocol for the development and implementation of systems of vocal identification of individuals, which will allow investigators of particular animal taxa to explore and potentially implement the option of using acoustic signals to census and monitor individuals in their study populations.

1. **Pilot Study**: As discussed elsewhere in this thesis, a pilot study is a critical first step in the development of a system of acoustic identification for a new target species. Such a pilot study would need to be conducted on a small number of individuals

whose identity was well known through other methods (such as radio-tracking or colour banding). The pilot study has two important roles. First, if the vocal behaviour of the target species is not well known, a pilot study would allow investigators to gain some understanding of the singing behaviour of the target species, especially with regard to vocal repertoires and how individuals in a population use common song or syllable types. Such knowledge is critical for understanding the types of signals that are to be compared between individuals for identification purposes. For example, the type of acoustic identification system that can be developed for a species with very few signal classes that are universal (such as for *T. sanctus* and *C. banksii*) will be different from one that can be developed for species where individuals possess a large number of signal types, which may differ in structure from the signals possessed by other conspecific individuals (such as for *D. broadbenti* and *R. leucophrys*). Second, when using cross-correlation analysis for individual identification, a pilot study must be undertaken in order to identify the correlation thresholds (r_x*) that yield the maximum identification accuracy for the target species. As the results in this thesis suggest, optimal identification accuracy is achieved at r_x* values that vary both between species, and even between the different types of vocalisation used within a species. Although the pilot study would require the capture and marking of a small number of individuals, the subsequent development of a system of acoustic identification would eliminate the need to capture and mark individuals in more extensive surveys and population studies. In addition, it may be possible to investigate singing behaviour in captive populations, should the opportunity arise.

2. **Song Collection**: Once the vocal behaviour and r_x* values were identified for the study taxa, recordings of vocalisations could then be extensively collected from the study area. Each pair of vocalisations recorded could then be directly compared using cross-correlation analysis, and, with knowledge of the optimal r_x* value, an immediate assessment could be made on whether each pair of vocalisations was produced by the same individual, or two different individuals. New recordings would thus be compared with a library of recordings from previously identified individuals to immediately determine whether a new vocalisation was produced by one of the known individuals, or a new, previously unknown individual, who would then be added to the library of known individuals. With knowledge of the time and place of each recording, subsequent recordings could then be used to obtain information on survival and movement of individuals, and population turnover.

Benefits and Limitations of an Acoustic Identification Technique

The use of a system of individual identification based upon animal vocalisations has some obvious benefits to the study of animals, not least of which because such a system eliminates the need to capture and mark individuals for identification. This benefit is not to be taken lightly; growing evidence from a variety of marking techniques and study taxa suggests that such identification techniques can have an impact on the ecology and behaviour of target animals that is far from trivial (Morton 1984, Burley 1986, Marks and Marks 1987, Saunders 1988). Investigators studying animal populations thus have one of two options if they wish to conduct population studies with high precision: they can either conduct specific investigations to accurately assess the impact that capture and the particular marking technique they are using has on the ecology of the target animals, and take these effects into account in subsequent studies, or they can rely on alternative, non-invasive identification techniques to collect population data. Acoustic identification of individuals is an example of one technique that can be successfully used as a non-invasive alternative.

Aside from these important benefits, the use of acoustic identification is associated with other specific advantages not present in other non-invasive techniques. Primarily, acoustic identification only requires an investigator to 'hear' (or obtain recordings of) individuals in a study population; a population can thus be monitored without actually visually observing the individuals that comprise the population. Such an advantage has obvious advantages in the study of cryptic species, or those species that are otherwise difficult to observe visually due to, for example, their habitat. Amongst the threatened avian fauna of Australia are a number of species that are known for their cryptic nature, as well as being famous for their vocalisations. These include all three species of bristlebird (*Dasyornis brachypterus*, *D. longirostris* and *D. broadbenti*), the two lyrebird species (*Menura alberti* and *M. novaehollandiae*), the scrub-birds (*Atrichornis rufescens* and *A. clamosus*), chowchilla (*Orthonyx spaldingii*), logrunner (*Orthonyx temminckii*) and the two whipbird species (*Psophodes olivaceus* and *P. nigrogularis*). The study and management of these threatened and cryptic species could thus benefit through the use of acoustic identification techniques.

Acoustic identification of individuals, however, does have limitations, which make it applicable to some species more than others. The principle limitation is that it requires that target individuals sing or call, and would thus especially suit the study of more vociferous species. If vocal production is skewed towards a particular subset of the population (for example, if only males or territory holders sing), then surveys based upon acoustic identification would be biased towards these vocal individuals, and fail to accurately take into account the proportion of the population that is less vocal or silent. However, the reliance of acoustic identification on vocal production may not disadvantage the technique as much as might be expected, as many surveys of avian populations and communities already rely on vocalisations to estimate both species richness and population densities of individual species, especially when such surveys are conducted in dense or visually obstructive vegetation (Blakers, et al. 1984, Baker 1998). In many cases, therefore, acoustic identification may not be limited by this reliance on vocal production any more than other survey methods.

An important limitation of acoustic identification, especially when based upon procedures such as cross-correlation analysis, is the level of identification error involved in the method, as well as the limited size of populations whose individuals can potentially be identified. While high levels of identification accuracy were obtained for most of the species for which results were presented in this thesis, identification of individuals based on their acoustic signals was very rarely perfect, and compared relatively small numbers of individuals. Current standard techniques of individual identification (such as tarsal banding), while limited by the requirement of capture, generally allow for the unambiguous identification of large numbers of individuals of the same species with perfect identification accuracy.

The conclusions drawn from this thesis are, in some respects restricted by their sample sizes, with regard to the number of individuals for which acoustic signals were compared. For many threatened or endangered taxa, however, population sizes are small, such that the sample sizes used in this thesis are in fact a realistic approximation of actual population size or density. It is for these species - those which are threatened with extinction - that systems of acoustic individuality would perhaps best suit, as the loss of even a few individuals through the effects of capture and marking would have a far greater impact on overall population size than for more populous species. Futhermore, these small sample sizes may not necessarily be restrictive if acoustic identification is used for specific tasks. For example, acoustic identification may be used to sub-sample populations and obtain measures of population density, as a way of testing the accuracy of standard but less accurate methods used to measure density. The population density of many cryptic species of bird is estimated from the number of singing birds per unit area, but knowing irrefutably that each singing bird is a different individual is difficult, and can introduce biases in the estimates produced (Baker 1998). The accuracy of this method can thus be tested using acoustic identification on a subsample of a population, and the potential exists for the more extensive survey results to be corrected against the more accurate results obtained from the subsample.

The benefits and limitations of acoustic identification must therefore be examined by each individual investigator, and compared with the costs and benefits of alternative identification techniques. Eliminating the requirement of capture, and allowing identification of cryptic taxa, must be weighed against the potentially increased margin of identification error. Whether one decides to use acoustic identification of individuals to monitor animal populations will strongly depend upon the taxa under scrutiny, as well as the objectives of the study and the relative importance that each investigator places on the costs and benefits of this identification system.

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Appendix A. Descriptions of Parameters Measured to Describe the Calls of *Pseudophryne bibronii*

Note: abbreviations in parentheses following each description indicate the units of the parameter.

1. Advertisement calls

As described in the text, the advertisement calls of *P. bibronii* consist of two distinct call components, differentiated primarily by differences in pulse rate. The parameters measured to describe each advertisement call are thus based on these two components.

Lengths of first and second component (**LGTH1** and **LGTH2**): The length of time of the first and second components (s)

Pulse numbers of first and second component (**P#1** and **P#2**): The number of pulses in the first and second component

Pulse rates of first and second component (**PRATE1** and **PRATE2**): The pulse rate of the first and second component, calculated as the pulse number divided by the length (Hz)

Peak frequencies of first and second component (**PEAK1** and **PEAK2**): The frequency of maximum amplitude for the first and second component, as taken from a log power spectrum (Hz)

Mean 25% quartile frequencies of first and second component (**M(25)1** and **M(25)2**): The mean of the 25% quartile of the instantaneous spectrum. The 25% quartile is calculated for each point in time across the signal, and the mean of these values is calculated (Hz)

Mean frequencies of first and second component (**MEAN1** and **MEAN2**): Equal to the mean of the 50% quartile of the instantaneous spectra. Calculated in the same way as the 25% quartile (Hz)

Mean 75% quartile frequencies of first and second component (**M(75)1** and **M(75)2**): The mean of the 75% quartile of the instantaneous spectrum. Calculated in the same way as the 25% quartile (Hz)

Frequency spreads of first and second component (**SPREAD1** and **SPREAD2**): The difference between the mean 75% quartile and the mean 25% quartile. This parameter provides a measure of the signal's 'pureness' (Hz)

Length between first and second component (**ICL**): The length of time between the first and second call components (s)

Total length (**LGTH**): The total length of the call, calculated as the sum of LGTH1, LGTH2, and ICL (s)

Total pulse number (**P#**): The total number of pulses in the call, calculated as the sum of P#1 and P#2

Total pulse rate (**PRATE**): The overall pulse rate of the call, calculated as P# divided by LGTH (Hz)

Peak frequency (**PEAKF**): The frequency of maximum amplitude for the entire call, as taken from a log power spectrum (Hz)

2. Territorial Calls

As the territorial calls of *P. bibronii* consist of a single continuous component, the parameters measured to describe these calls are similar to those used to describe features of the entire advertisement call.

Total length (**LGTH**): The total length of the call (s)

Total pulse number (**P#**): The number of pulses in the call

Pulse rate (**PRATE**): The pulse rate of the call, calculated as P# divided by LGTH (Hz)

Peak call frequency (**PEAKF**): The frequency of maximum amplitude for the entire call, as taken from a log power spectrum (Hz)

Mean 25% quartile frequency (**M25**): The mean of the 25% quartile of the instantaneous spectrum. Calculated as with advertisement calls

Mean Frequency (**MEANF**): Equal to the mean of the 50% quartile of the instantaneous spectrum. Calculated as with advertisement calls

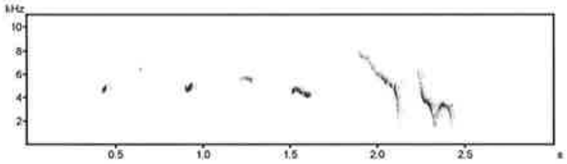
Mean 75% quartile frequency (**M75**): The mean of the 75% quartile of the instantaneous spectrum. Calculated as with advertisement calls

Frequency spread (**SPREAD**): The difference between M75 and M25. A measure of the pureness of the call

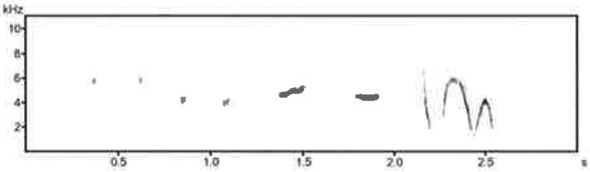
Appendix B. Sonograms of Rufous Bristlebird Song Types

1. Male Song Types

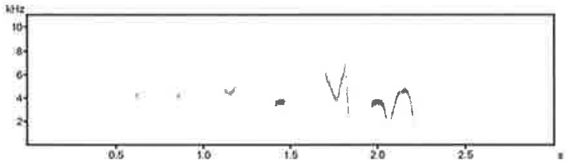
Song Type B



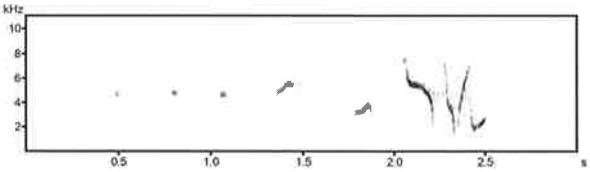
Song Type E



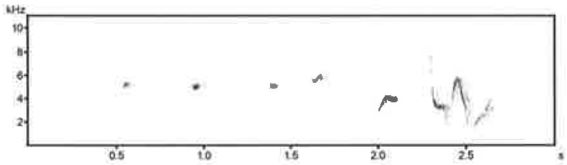
Song Type G



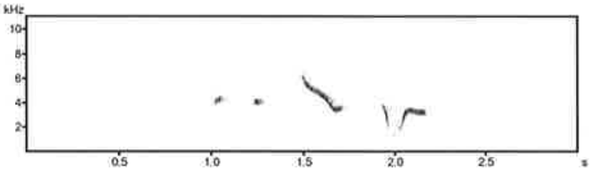
Song Type N



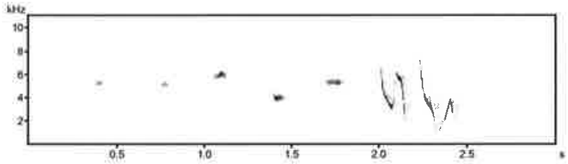
Song Type H



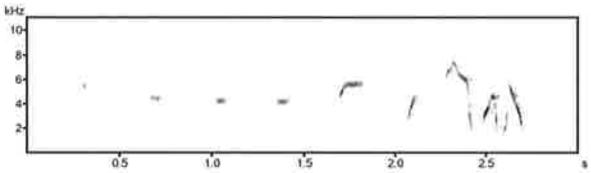
Song Type O



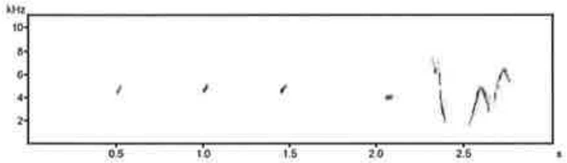
Song Type K



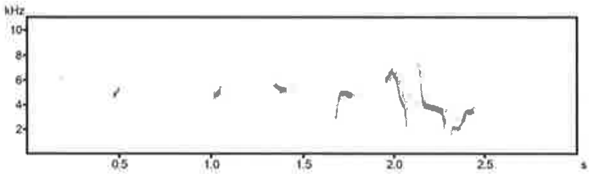
Song Type Q



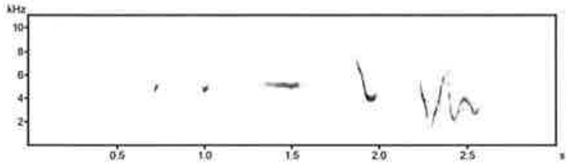
Song Type R



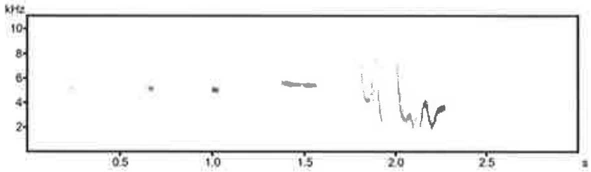
Song Type T



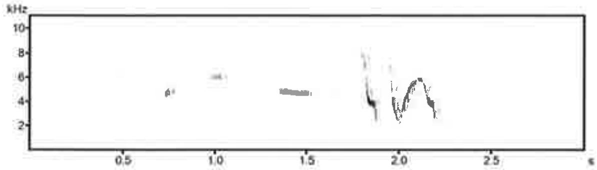
Song Type S



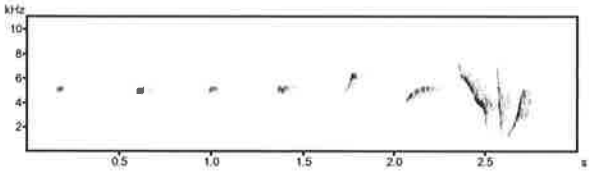
Song Type V



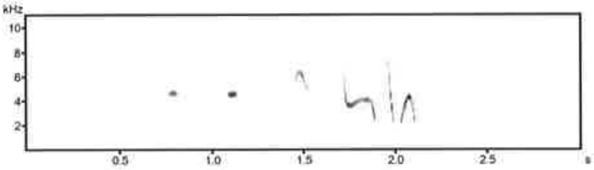
Song Type X



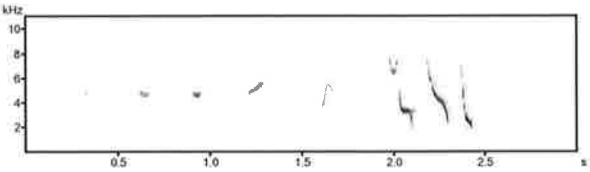
Song Type W



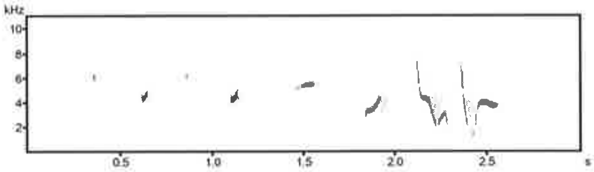
Song Type Y



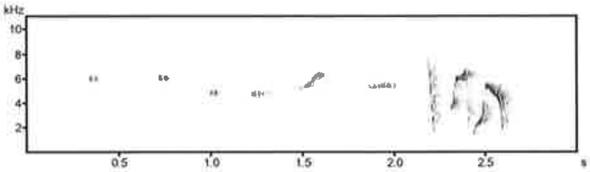
Song Type Z



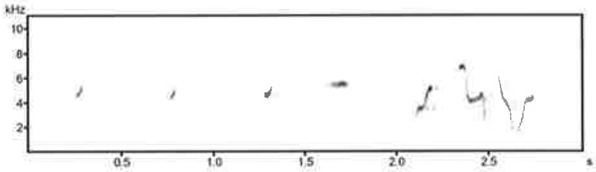
Song Type AB



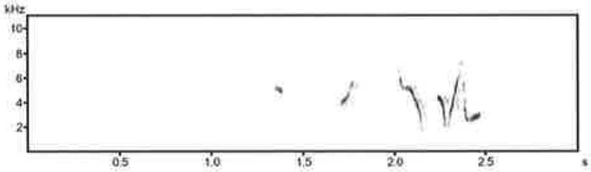
Song Type AE



Song Type AF

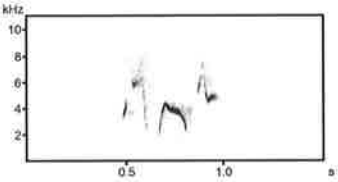


Song Type AK

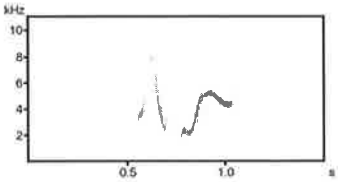


2. Female Song Types

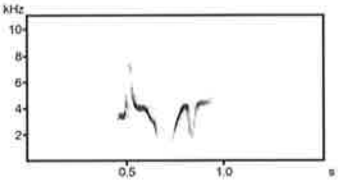
Song Type E



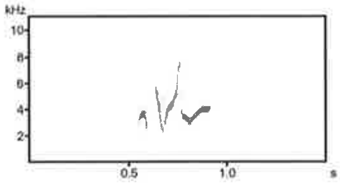
Song Type F



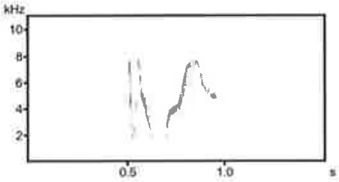
Song Type G



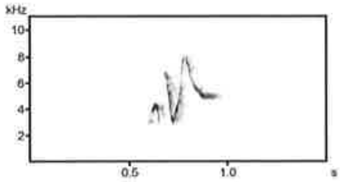
Song Type H



Song Type I



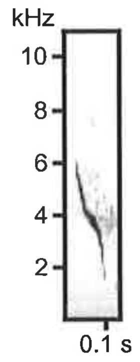
Song Type J



Appendix C. Syllable types of male Rufous Bristlebird

Note: Only those syllable types analysed in Chapter 5 are shown.

1



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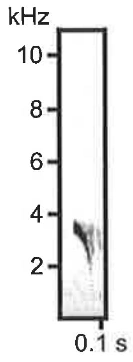

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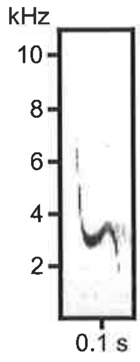

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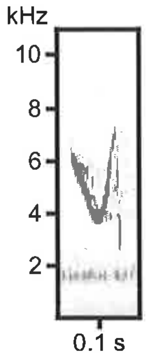

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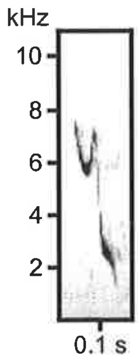

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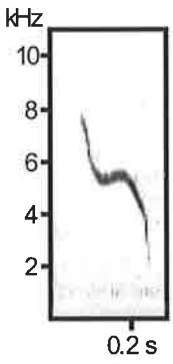

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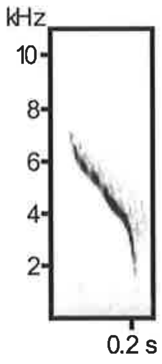

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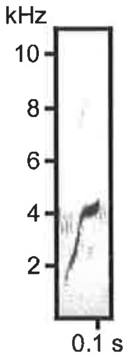

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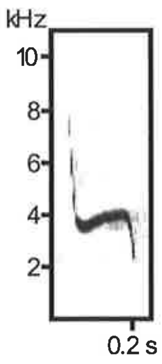

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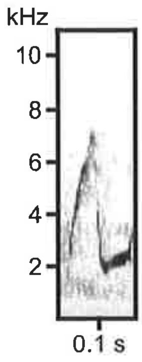
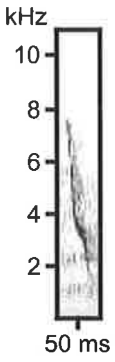


8



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