Song Sharing and Repertoire Change as Indicators of Social Structure in the Noisy Scrub-bird

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Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary educational institution.

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Date: 2 March 2008

Abstract

The Endangered Noisy Scrub-bird is a small passerine that is seldom seen but often heard in its range on the south coast of Western Australia. The difficulties in observing this cryptic bird mean that little is known about its social system. The loud, conspicuous territorial song of the male provides a convenient, non-intrusive means by which to study this species.

The aim of this project was to investigate the patterns of song sharing and repertoire change in the Noisy Scrub-bird to provide indications of the social structure. It was found that groups of up to ten territorial males shared the same set of about five song types. Song groups were discrete, with members of a song group sharing most, if not all, of their song types. Males from different song groups had no song types in common.

Repertoire change was rapid and, with the exception of one individual, was found in every territorial male studied in the Mt Gardner population. It occurred simultaneously in all members of a song group, with males making the same changes to their shared songs. The source of repertoire change was mainly modification of existing song types with occasional divergence of a single song type into two distinct song types, as well as some innovation providing new song types. The average life of a song type was approximately 6 months. Although some song types persisted for the entire 16 month sampling period, they were continually modified and a year later could no longer be recognised as the same type.

Translocation of eight male scrub-birds to the Porongurup National Park provided an opportunity to combine individuals that initially did not share any songs. This allowed the process of song group formation to be studied. Within a one to two month period these males altered their songs so that they shared with their new neighbours. There was some evidence that the songs of dominant males were copied. Observation of the population established on Bald Island by translocation confirmed that there were no appreciable long-term effects on the songs of translocated Noisy Scrub-birds. Song group size, repertoire size and levels of song sharing were very similar to those found in the Mt Gardner population.

The striking feature of Noisy Scrub-bird song groupings was their discreteness and cohesiveness even in the presence of continual repertoire change. It is suggested that each song group consists of a dominant male whose songs are more attractive to females and/or effective in territory defence. This dominant male is surrounded by subordinate males that copy his effective songs. Repertoire change can be explained by the dominant male continually making changes to his songs, with the other males copying these changes to retain their mimicked effectiveness. Each song group may in fact represent a dispersed lek. The scenario suggested to explain Noisy Scrub-bird song groupings bears striking similarities to the hotshot hypothesis to explain lek formation whereby males cluster around a successful male.

This study demonstrates the potential of using song to investigate aspects of the social system of a species which is otherwise very difficult to observe. Management of an Endangered species such as the Noisy Scrub-bird will always benefit from increased knowledge about their social system. For example, this study showed that taking males from different song groups for translocation probably has little impact on their success at the new site because of their ability to rapidly alter

their songs to form new song groups. An additional benefit of regularly monitoring the songs of translocated males was that it allowed ongoing identification of individuals, even though their songs were continually changing.

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Chapter 1 – Introduction: Song Learning and its Consequences

1.1 The uses of song

Vocal communication has advantages, particularly in situations where vision is obscured, for example by dense vegetation (Falls, 1982). It allows large amounts of information to be broadcast quickly and efficiently in all directions, through or around barriers and over relatively large distances (Catchpole and Slater, 1995). Sound plays an important role in avian communication and can potentially transmit information such as species identity, individual identity, sex, reproductive status, natal area (if songs are learned prior to dispersal), aggressiveness, and the location of both singers and their territories (Brooks and Falls, 1975; Kroodsma and Byers, 1991). Vocalisations can be used to attract mates, during courtship, to defend a territory, for parent-offspring communication, to alert other birds of danger and, in group-living species, to maintain group cohesion (Cunningham *et al.*, 2004).

Male songbirds use song for two main reasons – to attract females and to repel other males (Krebs *et al.*, 1978; Kroodsma and Byers, 1991; Catchpole and Slater, 1995; Collins, 2004). For example, Krebs *et al.* (1978) demonstrated the role of song in territory defence in the Great Tit[1] by removing males and replacing them with song playback. Reoccupation of vacated territories by other birds was much slower when playback was present. Various other studies have shown that male birdsong attracts and stimulates females (see reviews by Catchpole and Slater, 1995; Collins, 2004).

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[1] Common names will be used in the text. Scientific names are given in Appendix 1.

In some bird species, vocalisations are innate, capable of developing in the absence of any contact with other members of the species. For example, the suboscine Eastern Phoebe can develop a normal song even when isolated from other members of the species or when deafened and unable to hear itself sing (Kroodsma, 2004). Other species need to hear conspecifics singing in order to learn their songs (Catchpole and Slater, 1995). Vocal learning has evolved separately in three orders of birds – hummingbirds, parrots and the oscine passerines (songbirds) (Kroodsma, 2004; Gammon and Baker, 2004; Beecher and Brenowitz, 2005). With the exception of the Three-wattled Bellbird, vocal learning has not been found in any suboscine studied so far (Kroodsma, 2004).

1.2 Song-learning strategies and their consequences

There are two song learning strategies amongst songbirds – closed-ended (or age-limited) learning and open-ended learning. Closed-ended learners can only acquire songs during a sensitive period in their first year of life, whereas open-ended learners are capable of learning new songs throughout their life (Nordby *et al*., 2002; Hultsch and Todt, 2004; Kroodsma, 2004; Beecher and Brenowitz, 2005). Species that are closed-ended learners include Song Sparrows (Nordby *et al.*, 2002), Zebra Finches (Clayton, 1987), Chaffinches (Lachlan and Slater, 2003) and Indigo Buntings (Payne and Payne, 1997). Open-ended learners include European Starlings (Chaiken *et al.*, 1994), Village Indigobirds (Payne and Payne, 1997), Canaries (Nottebohm and Nottebohm, 1978) and Great Tits (McGregor and Krebs, 1989).

Many hypotheses have been proposed to explain why birds learn their songs and the reasons may vary according to the species in question. For example, in species that usually learn songs from their father (e.g. Medium Ground Finch and Cactus Finch, Grant and Grant, 1996), song learning may facilitate kin recognition (McGregor and Krebs, 1982).

Beecher and Brenowitz (2005) have suggested that hypotheses to explain song learning fall into two categories – the repertoire hypothesis and the sharing hypothesis. The repertoire hypothesis proposes that song learning functions to provide the bird with a large repertoire. However, this is limited by the fact that about 80% of song birds have repertoires of fewer than five song types, with some only singing a single song type (Beecher and Brenowitz, 2005). Larger repertoires may be more attractive to females, although the evidence is mixed (Gil and Gahr, 2002; Kroodsma, 2004).

The sharing hypothesis suggests the purpose of song learning is to give the bird songs that it shares with particular conspecifics (e.g. neighbours, mates, kin, flock members) (Brown and Farabaugh, 1997; Beecher and Brenowitz, 2005). Song sharing is widespread among songbirds particularly with territorial neighbours, but also in lekking and communal breeders (Brown and Farabaugh, 1997; Payne and Payne, 1997). Song sharing can be advantageous. For example, first-year Indigo Buntings that share songs with their neighbours have a significantly higher mating and breeding success, possibly because it deceives other males into thinking that a young bird is an already-established territory holder (Payne, 1982). Beecher and

Brenowitz (2005) suggest that male-male competition may select for sharing and female choice may select for repertoire size.

Song sharing is a consequence of imitative learning, with neighbouring birds likely to have similar songs (Beecher and Brenowitz, 2005). The probability of neighbours sharing their songs is high if a young bird learns his songs and settles in his natal area, or conversely if he accurately learns his songs from his territorial neighbours in the area in which he settles after dispersal (Slater, 1985). Thus, song sharing is dependent on the accuracy of learning, the distance of dispersal and the timing of dispersal in relation to learning.

Therefore, a consequence of song sharing is that geographic variation in song is present in many species (Krebs and Kroodsma, 1980). The scale of the geographic variation may vary from very small, consisting of just a few birds, to large (Hausberger, 1997). Generally, large-scale geographic variation in song is considered to be a dialect (Kroodsma, 2004). Boundaries between dialects may be sharp with neighbouring dialects having no songs in common (as seen in single-song species, but also present in repertoire species such as the Corn Bunting, McGregor, 1980), or more gradual with an intermediate zone where birds may sing songs from both dialects (e.g. Saddleback, Jenkins, 1977). Smaller-scale geographic variation is sometimes referred to as microlects, microdialects or song neighbourhoods (Martens and Kessler, 2000) or song groups (Jenkins, 1977).

Dialects may be a result of several different processes (summarised in Sorjonen, 1987). Firstly, the racial specialisation model suggests dialects may reflect a population in which songs have been selected for good transmission in a certain habitat. Secondly, the historical model says they may be a result of a founding event in which only a small sample of songs are present and passed through the generations. Thirdly, social adaptation proposes dialects may be a consequence of male-male interaction and reflect social interaction between birds. The first two models imply relatively stable song characteristics over time, whereas the last model holds the potential for rapid changes in boundaries and song traditions as male relationships alter over time (Adret-Hausberger, 1986).

In many species, social interactions play a major role in song learning (see Snowdon and Hausberger 1997 for reviews on social influences). Geographic variation in song generally reflects social relations among birds rather than the genetic structure of the population (Kroodsma, 2004). Although there are some species which learn their songs from their father (e.g. Zebra Finch, Clayton, 1987; Medium Ground Finch and Cactus Finch, Grant and Grant, 1996; Stripe-backed Wren, Price, 1998), field studies have shown that most songbirds learn their songs after the time of natal dispersal to an area where an individual copies the songs of its neighbour, rather than singing the songs of its father (Payne and Payne, 1997).

Song can play a role in establishing social relationships. Song matching in Marsh Wrens may be a ritualised expression of dominance/subordinance, with the subordinate bird taking on the follower role in song matching interactions (Kroodsma, 1979). In the Brown-headed Cowbird, song is important in the establishment of dominance hierarchies (Dufty, 1986). The songs a male Village Indigobird sings appear to be more closely related to his past and current social circumstances than to his natal population, as they copy the songs of the most successful male (Payne, 1985).

Song is thought to be under strong sexual selection (Collins, 2004). Song traits that may be sexually selected include performance-related traits (eg time spent singing, song rate, length or amplitude etc), repertoire size, specific song content (song sharing, dialects, special syllables, song frequency), timing of singing, and countersinging patterns (Gil and Gahr, 2002). Singing comes with potential costs and constraints, for example energy and time budgets, physical and developmental constraints, social aggression, predation, age and experience, neural costs (developmental costs, maintenance costs, trade-offs in brain space, endocrine costs), and immunocompetence costs (Gil and Gahr, 2002).

Vocal traits may be indicators of male quality and in some cases may reflect survival capabilities, as well as overall male vigour or quality (Kroodsma and Byers, 1991). Song functions in communication, recognition and competition between territorial neighbours (Brown and Farabaugh, 1997). It can show from whom and where a bird learns its songs, and can reflect dominance and subordinance. Song sharing may be aggressive or affiliative, may be used in territorial disputes or to maintain group cohesion (Marler, 2004). The strong social context of song means that there is the potential to deduce information about the social system of a species by studying their songs.

1.3 Song in the Noisy Scrub-bird

The Noisy Scrub-bird is an Endangered songbird that is now found only in a small area on the south coast of Western Australia. Two studies have investigated the potential of using songs to identify individual Noisy Scrub-birds (Berryman, 2003; Portelli, 2004). Portelli (2004) found extensive song sharing amongst groups of territorial males, however this work was done in the non-breeding season when singing is reduced. Further investigation of individuality of voice was carried out by Berryman (2003). It was discovered that groups of up to seven territorial male Noisy Scrub-birds shared the same set of about six different song types and neighbouring song sharing groups had no song types in common. Within these song groups, repertoire change occurred as all members of the group made the same changes to their shared song types (Berryman, 2003).

The Noisy Scrub-bird appears to be unique in that repertoire change is extremely rapid (complete repertoire change within 6 months) and it takes place simultaneously amongst groups of song sharing birds. The presence of widespread song sharing and continual repertoire change in the Noisy Scrub-bird meant that ongoing identification of individuals by their songs was impractical. The logical follow-on to the studies reported by Berryman (2003) and Portelli (2004) was to further investigate song sharing, repertoire change and their possible significance, and this is addressed in this thesis. Sampling methods in the previous two studies were not appropriate to accurately quantify repertoire change and song sharing.

Berryman (2003) suggested that the pattern of song groupings and repertoire change observed in the Noisy Scrub-bird may be a result of the members of a song group copying the most dominant group member who continually modifies his songs. This thesis hypothesises that this is the case in the Noisy Scrub-bird and attempts to provide evidence to support the model proposed by Berryman (2003). A similar situation has been proposed for the Village Indigobird (Payne, 1985) and the Yellow-rumped Cacique (Trainer, 1989), although neither species exhibits quite such rapid repertoire change.

The Noisy Scrub-bird is a cryptic species that inhabits thick scrub. Its loud song provides the only practical means of monitoring the species, with the annual census consisting of counting and mapping the locations of singing males (Smith and Robinson, 1976; Smith and Forrester, 1981; Smith, 1985a,b). The primacy of singing in the monitoring of this species means that any information that song can provide in addition to simply indicating the presence of a bird is of great value.

This secretive species is rarely seen and very little is known about its social structure or mating system. Because singing plays a major role in the monitoring and management of this species, it would be useful to have a more complete understanding of what this singing signifies and how it relates to the social system. Some evidence suggests that male Noisy Scrub-birds are opportunistically polygynous (Danks *et al.*, 1996). As discussed earlier, patterns of song sharing may provide indicators of social system. It is hoped that this may be the case with the Noisy Scrub-bird. Any Endangered species will benefit from increased knowledge to make informed management decisions.

1.4 Aims and structure of the thesis

The aim of this study was to investigate further the patterns of song sharing and repertoire change in the Noisy Scrub-bird with the hope of providing some clues about the social system of this species. Ideally, it would provide evidence to support the scenario proposed by Berryman (2003) of a dominant bird providing the song model within each song group. This hypothesis suggests that the dominant bird (song leader) has songs that are more attractive to females. Neighbouring birds would therefore gain an advantage by copying the songs of this male in order to appear more attractive themselves. The song leader, in turn, would continually modify his songs to retain his individuality and his advantage. The other members of the group would then make the same changes to their shared songs to retain the advantage gained by copying the song leader's attractive songs, leading to an ongoing cycle of song change within the group.

The following chapters outline different aspects of Noisy Scrub-bird song that were investigated:-

Chapter 2 – *General Methods*

This chapter describes the study species and the study site more fully and gives details of the general recording and analysis methods.

Chapter 3 – *Territoriality and Radio-tracking*

The main aim of this aspect was to confirm that it was the same bird singing from the same location each day, a major assumption in this study. Also, comparisons were made between territories mapped through radio-tracking and those mapped by plotting the locations of singing birds. These were also compared to territories mapped by Dr Graeme Smith in the 1970s and in 1994. In addition, the mapped territories were compared to the territories recorded as present in that area in the annual census. From this, the accuracy of census techniques could be assessed.

Chapter 4 – *Song Sharing on Mt Gardner*

The aim of this part of the study was to investigate further the patterns of song sharing in the Mt Gardner population. The sampling methods used by Berryman (2003) did not take into account the effect of repertoire changes. Thus sampling needed to represent a snapshot in time in order to reflect the patterns of song sharing accurately without the confounding effects of repertoire change. Individual and group repertoire size, percentage song sharing and song group size were investigated amongst the birds on Mt Gardner, with four sampling sessions being carried out to monitor the stability of these features over time.

Chapter 5 – *Repertoire Change on Mt Gardner*

Fortnightly recording of ten focal males over a period of 16 months allowed the phenomenon of repertoire change to be explored. Changes in song types over time were tracked, and repertoire turnover and song persistence was measured. An attempt was made to quantify repertoire change in three individuals by intensively recording them over a 10 day period. Also, it was hoped that this would reveal if a particular individual was introducing the changes to the shared song types of these three birds. This could potentially provide evidence to support the hypothesis of Berryman (2003). In addition, song rate and song type matching were investigated to see if they indicated which of the three individuals was dominant.

<u>Chapter 6</u> – *The Effect of Translocation on the Songs of the Noisy Scrub-bird*

The information gained so far on song sharing and repertoire change generated many questions such as:

1) What effect does translocation have on song characteristics such as repertoire size?
2) Do scrub-birds have a preference for sharing songs?
3) Why do they share with some males and not with others?
4) How do they choose which bird to copy?
5) What would happen to their songs if several birds with no song types in common were put together?
6) How rapidly is a male replaced when he is removed from his territory?
7) Will the replacement male sing the songs of the original male?
8) Do song groups confer an advantage to their members?

The translocation of eight male Noisy Scrub-birds to Porongurup National Park provided an opportunity to address some of these questions. It allowed territorial male scrub-birds to be arranged into groups that no longer shared songs. This had the potential to reveal how song groups are formed and are maintained.

This chapter tested a key prediction regarding the singing behaviour of translocated Noisy Scrub-birds. The ability of scrub-birds to alter their songs rapidly, and the fact that song sharing seems to be a widespread phenomenon, means that birds are likely to have a preference for sharing songs with their neighbours and will alter their songs to do so. Therefore, the major prediction was that male scrub-birds who initially shared no songs at all would, over a short period of time, alter their songs so that they shared with others at the new site.

<u>Chapter 7</u> – *Song Sharing on Bald Island*

Bald Island is the site of a previously translocated population of Noisy Scrub-birds. An investigation of song sharing on Bald Island presented a chance to examine whether an established, translocated population developed and maintained normal song groupings 12 years after their initial release. The aim of this exercise was to examine features such as repertoire size (reflecting vocal diversity), song group size and degree of song sharing in the Bald Island population and to compare these features with those from the source population at Mt Gardner. Because Noisy Scrub-birds are capable of rapidly changing their songs (Chapter 5) and will alter their songs to form song groups at a new site (Chapter 6), it was predicted that scrub-birds on Bald Island would show similar patterns of song sharing and vocal diversity to the Mt Gardner population.

<u>Chapter 8</u> – *Overview of Findings and General Discussion*

This chapter provides an overall summary of the empirical results of this study, together with a discussion that develops a speculative model of how this may reflect social structure and the importance this could play in making management decisions. Direct evidence to support the social structure proposed by Berryman (2003) was difficult to obtain because of the secretive nature of the Noisy Scrub-bird. The predictions generated by this hypothesis are discussed in relation to the results of this study and are generally congruent with it. Ideally, information on the breeding success of individual males in relation to their song characteristics would be needed to identify if song was correlated with aspects of male fitness and provided a cue for female choice. This is unlikely to happen because it would require very intensive and invasive monitoring, something that is impractical and inadvisable in an Endangered species. Therefore, any information that can be gained through the non-invasive study of their songs is valuable in adding to our knowledge about this species.

Chapter 2 –
Study Subject and General Methods

2.1 Study subject

2.1.1 History

The Noisy Scrub-bird, is one of two extant members of the family Atrichornithidae. It is only found near Albany on the south coast of Western Australia (Figure 2.1). Its congener, the Rufous Scrub-bird, is found in the subtropical rainforest of eastern Australia. The nearest relatives of the Atrichornithidae appear to be the lyrebirds (Menuridae) (Bock and Clench, 1985; Sibley and Ahlquist, 1985).

The Noisy Scrub-bird was first collected in 1842 by John Gilbert in the Darling Range, and was subsequently found at three main locations in the southwest (Figure 2.2) – Mt William-Drakesbrook (near Waroona), Augusta-Margaret River, and the Albany area (Smith, 1977; Danks *et al.*, 1996; Danks, 1997). Abbott (1999) suggests that the range of the Noisy Scrub-bird may have been more extensive, with small, insular populations occurring from near Bindoon in the north, through the south-west, and to the east of Albany. From 1889 to 1961 there were no confirmed records of the Noisy Scrub-bird and the species was thought to be extinct (Robinson and Smith, 1976; Danks, 1994, 1997; Danks *et al.*, 1996). In 1961 a small population was rediscovered, confined to the Mt Gardner area of Two Peoples Bay (Webster, 1962a,b).

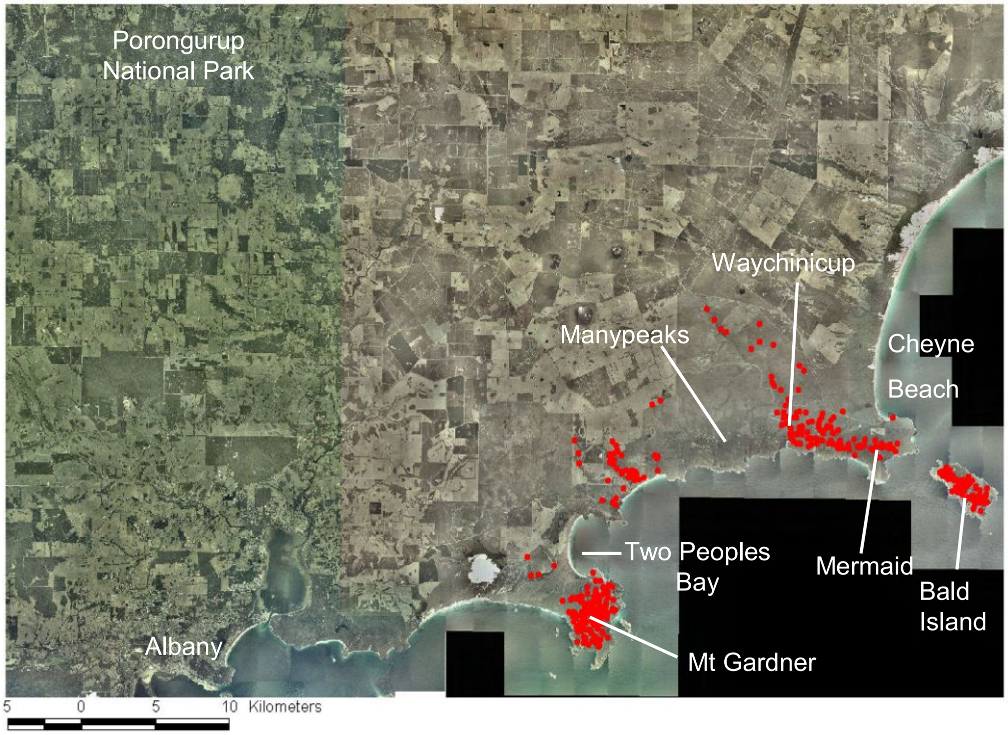

Figure 2.1: Current distribution (2005) of the Noisy Scrub-bird on the south coast of Western Australia (red dots) and the locations of some of the sites that are mentioned in the text.

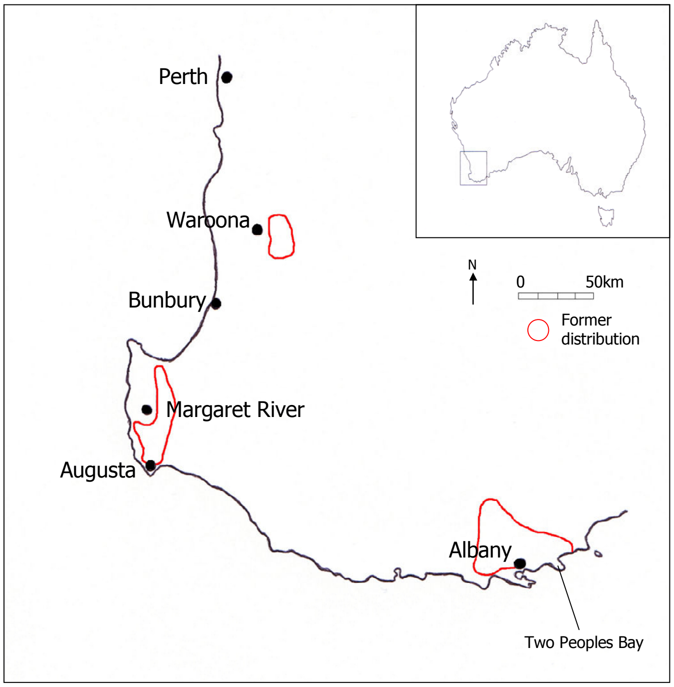

Figure 2.2: Historical distribution of the Noisy Scrub-bird (adapted from Danks *et al.*, 1996).

The major cause of decline of Noisy Scrub-bird populations since last century is thought to be habitat alteration as a result of changes in fire regime and land clearing (Smith, 1977; Danks, 1997; Abbott, 1999). In 1967 the Two Peoples Bay Nature Reserve was established (Figure 2.3), encompassing all the known scrub-bird habitat at the southern end of Two Peoples Bay, and around and between Lakes Gardner and Moates (Danks, 1997). A system of firebreaks and low fuel buffers helps protect the reserve from wildfire. Translocation is also a major conservation strategy, increasing the range of the species and providing the population with more resilience to wildfire (Danks, 1997; Comer and Danks, 2006). Translocations will be discussed in more detail in Chapter 6.

The Noisy Scrub-bird is currently listed as Endangered after recently being upgraded from a Vulnerable status because of an estimated 60% reduction in the total population between 2000 and 2006 as a result of wildfires (Comer and Danks, 2006). Figure 2.4 shows the area of habitat that has been burnt in wildfires since 2000. The population size is now thought to number fewer than 1000 individuals (Comer and Danks, 2006).

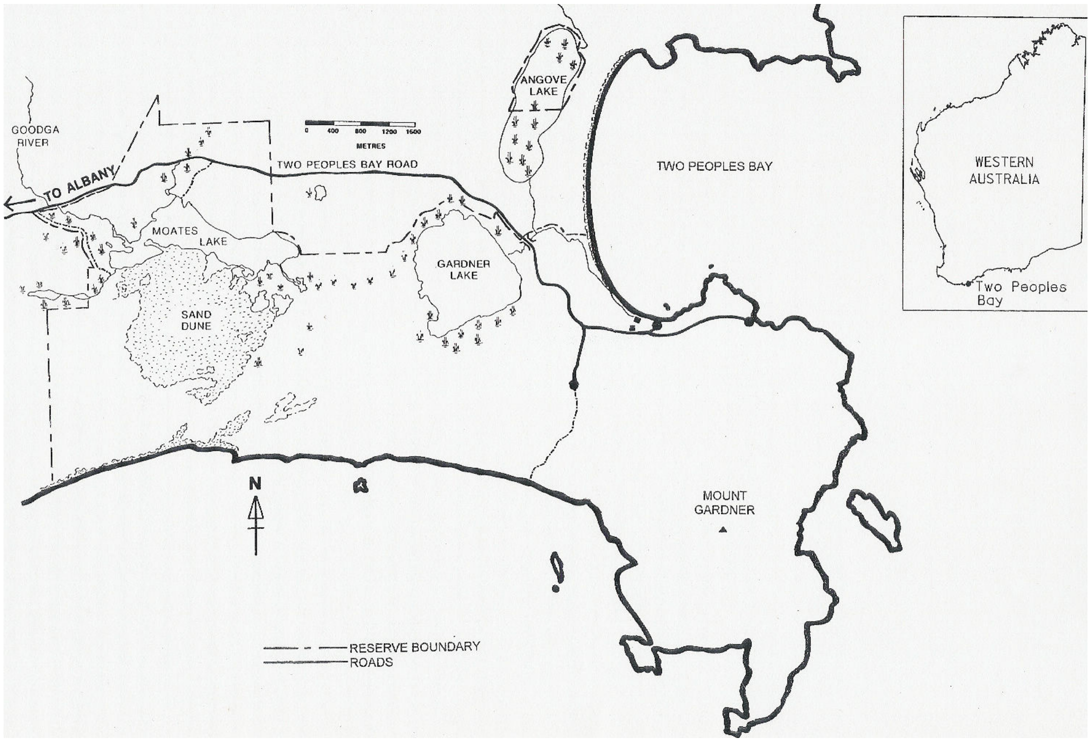

Figure 2.3: The location of Two Peoples Bay on the south coast of Western Australia (inset) and the extent of Two Peoples Bay Nature Reserve (adapted from Dept. Fisheries and Wildlife, 1980).

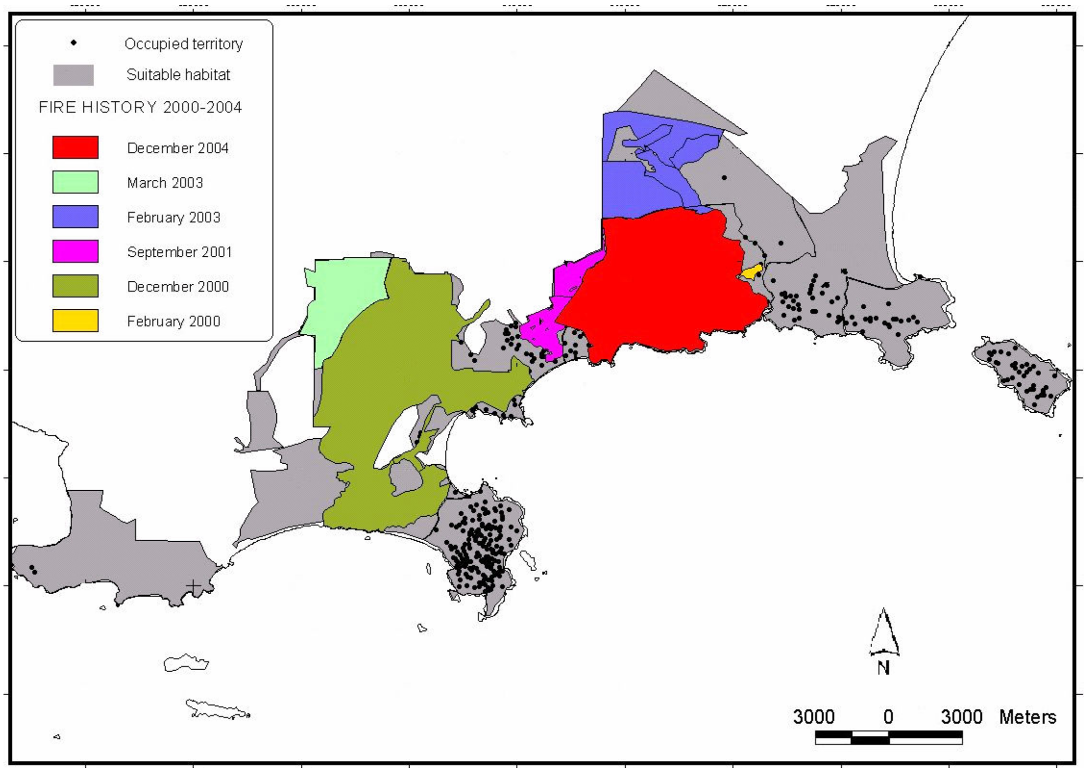

Figure 2.4: Fire history of Noisy Scrub-bird habitat between 2000 and 2005.

2.1.2 Habitat

Noisy Scrub-birds prefer dense thicket and low forest vegetation (Smith, 1985a,b, unpublished b; Danks, 1997). In the Mt Gardner area the common factors seem to be a dense understorey, abundant leaf litter and well developed litter invertebrate fauna (Danks, 1997). Most scrub-birds occupy vegetation that has not been burnt for 15 to >60 years, although vegetation burnt 3-4 years earlier can be used (Smith, 1977; Danks *et al.*, 1996). Noisy Scrub-birds forage mainly in leaf litter and debris on the ground, as well as among the leaves and stems of shrubs and sedges (Smith, 1976; Danks, 1991, 1997; Danks *et al.*, 1996). Ants, beetles and spiders make up 75% of the diet of adults in the breeding season (Danks and Calver, 1993).

2.1.3 Description

Noisy Scrub-birds (Figure 2.5) are small, semi-flightless, solidly built birds with strong pointed beaks, powerful legs, graduated tails and short rounded wings (Smith, 1985a; Danks *et al.*, 1996). They are brown above, and paler underneath with a buff coloured abdomen grading to bright rufous around the vent (Danks *et al.*, 1996). The species is sexually dimorphic. During the breeding season, females have a mean weight of 34.6g (n = 42, range = 31.5g - 39.2g) while males have a mean weight of 51.8g (n = 456, range = 47.0g – 57.0g) (Gilfillan *et al.*, in prep.). Males, but not females, bear distinctive throat markings and sing a loud, far-reaching, directional song within singing territories (Danks, 1997).

Figure 2.5: Male Noisy Scrub-bird (photo by Alan Danks)

Male Noisy Scrub-birds are territorial and defend their territory with loud song (Smith and Robinson, 1976; Smith and Forrester, 1981). They sing throughout the year, increasing their song output in April, reaching a peak around May/June. A high but variable level of singing is then maintained until October, after which it declines. The increase in singing coincides with the breeding season (Smith, 1976, 1985a; Smith and Robinson, 1976; Davies *et al.*, 1982). The population is censused by counting the number of males singing territorial song (described in Smith and Forrester, 1981; Smith, 1985b).

Their cryptic colour and ground-hugging behaviour in dense habitat make Noisy Scrub-birds difficult subjects to observe. They are inquisitive birds, quickly approaching to observe the cause of some disturbance before moving off, often unseen and unheard (Smith, 1985a). Males will react strongly to a human intruder and often come quite close, singing loudly and circling around through the vegetation (Smith and Robinson, 1976).

2.1.4 Vocalisations

Male Noisy Scrub-birds sing two types of song – short song and territorial song (Figure 2.6). Short song is more variable than territorial song but is similar in tonal quality. Smith and Robinson (1976) add that it is less than half the length of territorial song. However, it can approach and sometimes exceed the length of territorial song (Berryman, 2003). Thus, short song is something of a misnomer. Short song occurs throughout the year, but is much less frequently used than territorial song. Males use it on the rare occasions when they approach each other at the boundaries of their territories and may occasionally use it in response to a human intruder (Smith and Robinson, 1976). The major difference between short and territorial songs is that short song is simpler in structure and lacks a terminal flourish (see Figure 2.6).

The loud and distinctive territorial song of the Noisy Scrub-bird consists of a series of introductory notes, followed by 1-3 phrases, and a terminal flourish (Figure 2.7). It ranges in length from approximately 3 to 7 seconds (mean 4.79 seconds ± SE 0.105) and falls within the frequency range of 1 to 8 kHz. Each phrase contains a variable number of similar syllables (Berryman, 2003). Noisy Scrub-birds can be considered to sing with immediate variety (see Catchpole and Slater, 1995), as they rarely sing the same song type in succession (Berryman, 2003; Portelli, 2004).

Instead, they cycle through their repertoire in no strongly marked order (Berryman, 2003).

Smith and Robinson (1976) reported that males may have four or five patterns of territorial song, all of which may be given in the same bout of singing. They also reported that the song changes throughout the breeding season and from one year to the next, and that individuals of a group within hearing distance of each other have similar patterns of songs. However, no information on song group size, degree of song sharing or speed of repertoire change was provided. Portelli (2002, 2004) reported a slightly larger repertoire size, ranging between 4 and 7 song types (mean ± SE = 5.18 ± 0.33) and no evidence of repertoire or song type change over a 17 day period. It should be noted, however, that this latter study was done outside the breeding season when singing activity is reduced.

Berryman (2003) further investigated territorial song in the Noisy Scrub-bird. The aim was to attempt to identify individual males from their territorial songs. However, it became apparent that individual identification was impractical because of the high degree of song sharing and the rapidity of repertoire change. In the 25 males studied, repertoire size varied from three to eight song types per bird. Although the sampling methods were not designed to measure it, the study also confirmed the presence of repertoire change. This occurred over time as song types were modified, old song types were abandoned, and new song types were introduced. More than half of all song types in a repertoire could be replaced, or at least significantly modified, over a month, with complete repertoire renewal over six months.

It was also confirmed by Berryman (2003) that groups of neighbouring territorial males shared songs. Once again, sampling methods were not appropriate to investigate song groups because of the confounding effects of repertoire change. However, it was possible to determine that there was substantial song sharing amongst clusters of two to seven neighbouring birds, deemed to comprise a song group. In some cases, there was entire repertoire overlap between some members of the group. Song groups were discrete, with neighbouring song groups having no song types in common. Often there were no acoustic or other barriers between neighbouring song groups and the distance between two members of the same song group could be greater than between two individuals in adjacent song groups (Berryman, 2003).

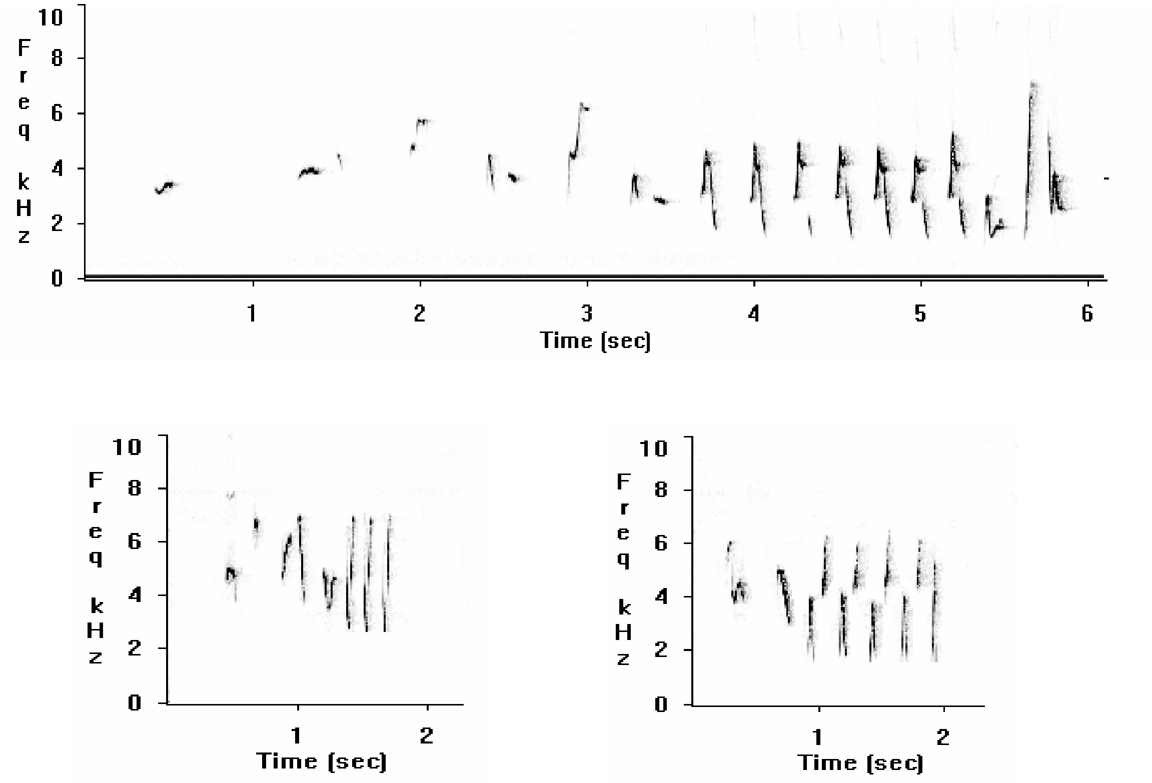

Figure 2.6: Frequency-time audiospectrograms of a territorial song (top) and two separate short songs (below) from a male Noisy Scrub-bird. Note the simpler structure of the short song compared to the territorial song and the absence of a terminal flourish.

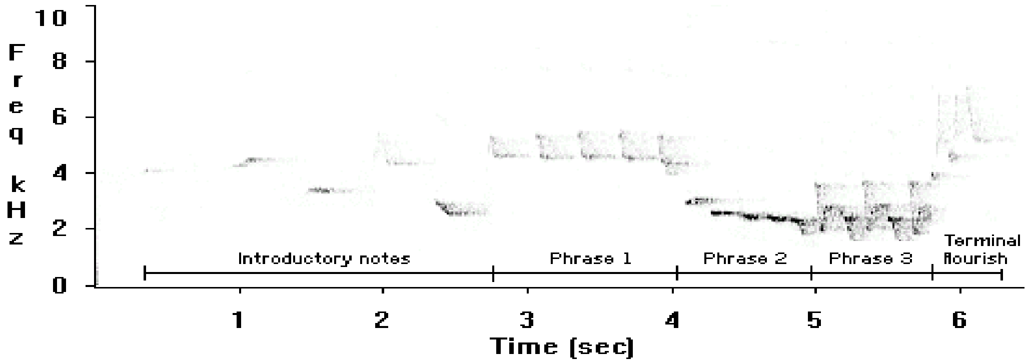

Figure 2.7: Territorial song of a male Noisy Scrub-bird, showing its constituent parts.

2.2 Study Area

The majority of this study took place at Two Peoples Bay Nature Reserve (4744ha), 36 km east of Albany on the south coast of Western Australia (Figure 2.1 and 2.3). More specifically, Noisy Scrub-birds in the Mt Gardner area of Two Peoples Bay were focussed upon. Mt Gardner (408m) forms part of a rocky headland, consisting of long unburnt vegetation, granite ridges, and a number of deep gullies. The vegetation ranges from heath and scrub/thicket, to low forest, with scrub-birds preferring the low forest and scrub/thicket habitats (Danks *et al.*, 1996).

Noisy Scrub-bird songs were also recorded on Bald Island (see Chapter 7), as well as at the more recent translocation site in the Porongurup National Park and the source population at Mermaid (Chapter 6).

2.3 Recording of territorial songs

The majority of recording was carried out between May and October in each year from 2004 to 2006. Smith and Robinson (1976) reported that territorial song output increases from May, peaking in June and July and then decreases. Thus, it seemed sensible to concentrate effort on this period of maximal singing. Results from the repertoire change recordings (Chapter 5) concur with Smith and Robinson’s observations of a mid-year increase in song output. The temporal pattern of recording varied as a result both of inclement weather and of the unpredictability of singing behaviour. Portelli (2002, 2004) found that time of day made no significant difference to the proportion of song types in a bird’s repertoire, and differences also were not apparent between days over a 17 day period.

Numbers used to identify scrub-bird territories were those of the Noisy Scrub-bird annual census conducted by the Department of Environment and Conservation (formerly the Department of Conservation and Land Management). For ease of reference, birds were named by preceding their territory number with letters representing the site at which they were recorded (MG = Mt Gardner, MM = Mermaid, BA = Bald Island).

It was assumed that all recordings made at the one territory were of the same territorial male. Chapter 3 contains a more detailed discussion of this assumption. There were undoubtedly separate singing individuals at each of the territorial locations where recordings were made because, on numerous occasions, songs came from all territories either simultaneously, or in such close succession that it was impossible for them to have been given by the same bird. At no time were songs ever heard from two parts of the same territory simultaneously. It is however possible that, during the span of the project, replacement of territorial males may have occurred without being detected. For example, in 2002 a male was caught late afternoon and held overnight. When he was returned to the capture site at first light the next morning another male was already singing in his territory. The repertoires of both males were so similar that, without knowing that replacement had taken place, it would have been assumed that it was the same bird (personal observation).

Scrub-birds were recorded using a Sony WM-D6C Walkman and either a Sony ECM-MS907 microphone, a Sennheiser microphone, or a Sony PBR-400 parabolic reflector combined with an AIWA CM1017 microphone, and were recorded onto SKC or Maxell tapes, position normal, with no noise reduction. Recording was carried out at distances that varied from 5 to 100m from the bird, but most often was within 20 to 50m. Every effort was made to avoid approaching too closely as this often resulted in the singing bird either going quiet, singing more frequently or switching to alarm calls and/or short song.

Previous work (Berryman, 2003) indicated that, on average, a recording of 14 consecutive territorial songs by any given individual was sufficient to sample all the songs in its repertoire. A recording of 10 consecutive songs sampled an average of 92% of the song types in an individual's repertoire. In most cases, therefore, a 10 song sampling method was used. This sample of 10 consecutive songs was considered adequate to sample the variety of song types and, while it may have missed very rare song types, still provided a representative sample of the song types used and their relative proportions, particularly if the bird was recorded on several mornings. Additionally, constraints on time and the need to record while weather conditions were suitable meant that a compromise had to be made between sampling the entire repertoire of each individual and sampling as many individuals as possible.

2.4 Analysis

Recordings were analysed using Syrinx (John Burt, www.syrinxpc.com) to produce audiospectrograms which were allocated on the basis of their visual similarity into song types for each individual bird. Division into song types based on visual comparison appeared to be the most efficient method due to the high degree of within song type variation present in each bird. This variation usually consisted of differences in the number of repeats of syllables within a phrase rather than structural changes to the song.

Other studies have also used visual comparison in preference to more objective methods. For example, Tracy and Baker (1999) found that independent observers agreed on 95% of the classification of House Finch syllables, and Nowicki and Nelson (1990) found visual classification produced similar results to a digital technique when analysing Black-capped Chickadee calls. Payne *et al.* (2000) reviewed the literature on classifying song similarity and found that visual classification was relatively accurate and compared well with computer-based techniques such as cross-correlations, neural networks, and multivariate analysis, especially for complex songs (such as those of the Noisy Scrub-bird). Also, the accuracy of computer-based classification methods can be reduced by poor quality recordings; and an element of subjectivity is introduced in the selection of settings to detect features of the songs (Jones *et al.*, 2001).

Describing song types in a song repertoire can be subjective and arbitrary, particularly if within song type variation is substantial. When this is the case, some songs may be difficult to classify to a given type either because they are intermediate between types or because they are not easily associated with any type (Podos *et al.*, 1992). Generally, scrub-bird songs could be easily assigned to a certain type, although some intermediates were found (refer to Figure 2.8 for an example). Any intermediates were assigned to the song type to which they were most similar.

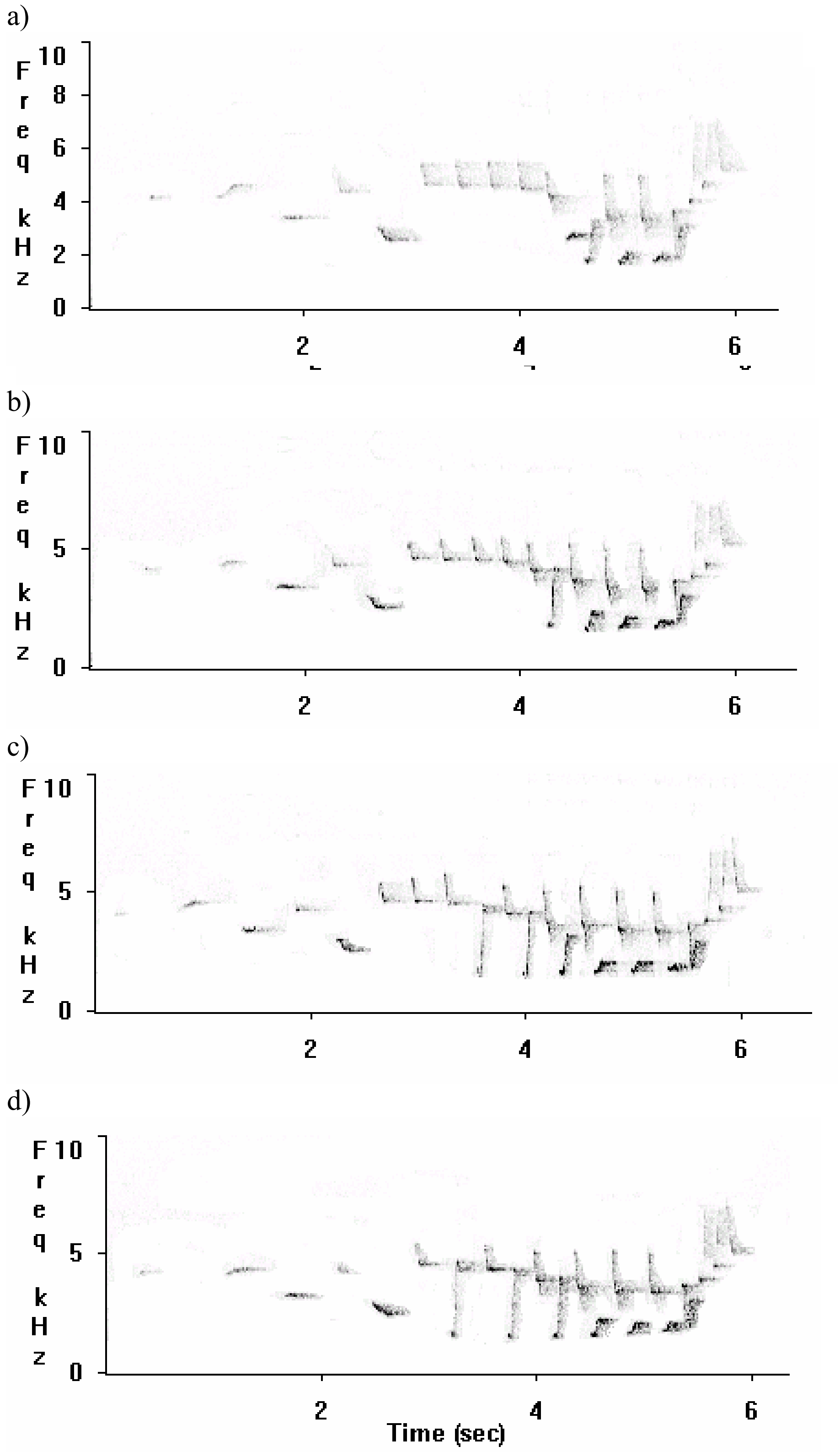

Figure 2.8: Song types and intermediates from MG4 – a) Song type E; b) Intermediate 1; c) Intermediate 2; d) Song type H.

Chapter 3 –
Territoriality and Radio-tracking

3.1 Introduction

Many bird species are territorial and defend their territories with song (Catchpole and Slater, 1995; Collins, 2004) and the Noisy Scrub-bird is no exception (Smith 1976, 1985a). The Noisy Scrub-bird is rarely seen and difficult to capture. Therefore the only practical means of monitoring it is by its loud territorial song (Smith and Forrester, 1981; Smith, 1985a,b; Danks, 1994, 1997).

One of the major assumptions of this project is that a scrub-bird territory is equivalent to one individual male (i.e. it is the same bird singing in the same spot each day). The secretive nature of the Noisy Scrub-bird, combined with the thick scrub that it inhabits, means that it is very difficult to observe it at close range without it being aware of an observer's presence (Smith, unpublished a). The only practical means of following the movements of scrub-birds is by either radio-tracking or by using the territorial song of the male, although the latter method does not guarantee the identity of the individual. Females (which are not known to sing) and non-territorial males (which are capable of singing but are rarely heard), are even more difficult to observe (Robinson and Smith, 1976; Smith and Robinson, 1976; Danks, 1997). Territorial males on the other hand regularly sing loud territorial song, providing a convenient means by which to follow their movements and map their territories.

The aim of this study was to investigate the validity of the assumption that it is the same bird singing from the same location each day and also to determine home range and territory boundaries and size. Home range is defined as "that area traversed by an individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943). For the purposes of this study, territory will be defined as the area which a male Noisy Scrub-bird defends with territorial song.

The identity of singing birds was confirmed through radio-tracking, which also provided information on home range. Territories were determined by mapping the locations of singing males. Territory mapping based on the locations of singing males was previously done by Dr Graeme Smith in the early 1970s (Smith, 1985a) and again in 1994 (unpublished data). Therefore, a further aim was to compare current territory boundaries and sizes to those studied previously. Also, the territories mapped in this way were compared to the territories recorded as present in the area in the annual census. This allowed assessment of the accuracy of the census techniques currently employed.

3.2 Methods

3.2.1 Mapping of singing locations

The locations of singing male Noisy Scrub-birds were mapped to determine their territories using the methods described by Smith (1994) to map Western Bristlebird and Western Whipbird territories. This method was also used to map scrub-bird territories at the same time as the bristlebird and whipbird surveys were carried out in the 1970s (Smith, 1985a) and in 1994 (unpublished data). Smith's method of survey involved locating singing birds during morning and afternoon walks along the tracks, with all locations visited a minimum of 10 times. Locations of singing birds were mapped on aerial photographs and these data, combined with information about birds singing at the same time, were used to delineate home range boundaries. Smith's work in the early 1970s (Smith, 1985a) included information on the 80% core area and 100% territory sizes based on this mapping, although it is unclear how Smith decided to draw these territorial boundaries. Since the time of Smith's surveys, advances in GPS technology, GIS mapping programs and territory analysis programs have allowed a more sophisticated approach to analysing territory mapping data.

In more detail, my own survey effort involved morning and afternoon walks (in the three hours after sunrise and the three hours before sunset) around the 4WD tracks in the Tick Flat study area on the Mt Gardner headland (Figure 3.1). All areas within the Tick Flat study area were within hearing distance of the tracks. An average of at least 15 minutes per walk was spent listening in all areas to allow time for any scrub-birds to sing. A GPS and compass were used to take two bearings to allow triangulation of the location of the singing bird. Surveys were carried out at similar times of year to Smith's 1994 surveys (Table 3.1) so that results would be comparable although the first survey in 2005 was a month earlier than Smith's. Because singing activity in both July and August is usually high, this should not have impacted the results greatly.

The data for Smith's October 1994 sampling session were missing, and from the remaining data it appears that he must have collected more than just morning and afternoon locations for some of the territories. If Smith sampled morning and afternoon of each day of his August and September sessions then a maximum of 36 locations per territory would be expected. Table 3.2 shows the actual number of locations collected for each territory.

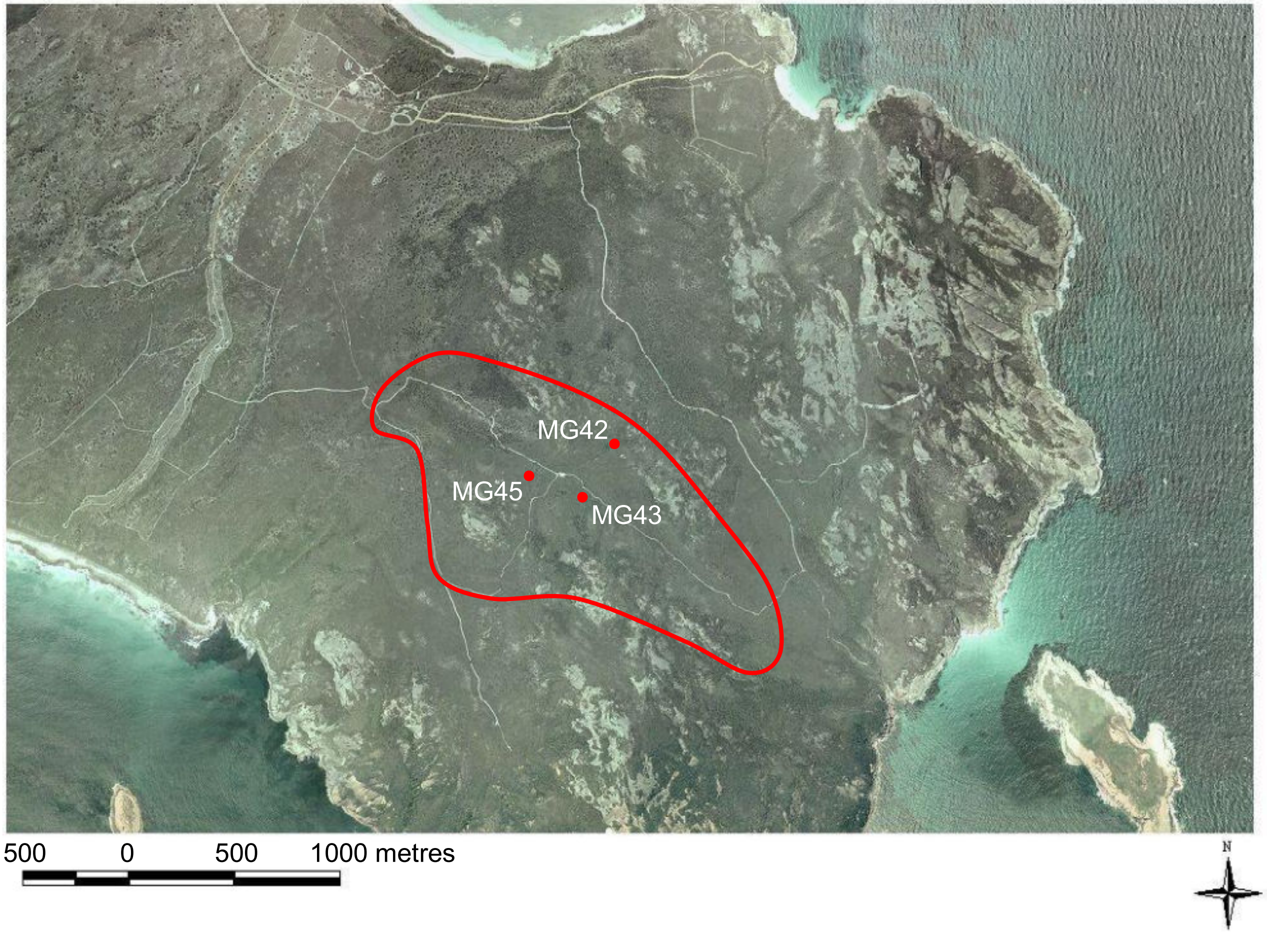

Figure 3.1: The Tick Flat study area (bounded by red) on the Mt Gardner headland of Two Peoples Bay Nature Reserve and the locations of the three territories from which male scrub-birds were captured for radio-tracking.

Table 3.1: 2005 and 1994 survey dates.

2005	1994
23-29 July	22-27 August
12-16 September	5-16 September
3-14 October	10-15 October

Table 3.2: Number of locations of a singing scrub-bird in each territory collected in 1994 and 2005.

Territory number	1994	2005
38	20	31
42	32	34
43	45	37
45	54	35
46	32	27
48	37	not occupied
55	26	30
56	30	28
59	6	not occupied
69	not surveyed	32
82	19	30
297	21	not occupied
304	not surveyed	30
352	11	21

3.2.2 Radio-tracking

Three territorial male Noisy Scrub-birds were captured and fitted with radio-transmitters in 2005. Attempts were made to capture more males but these attempts were not successful. Scrub-birds were captured using a modified mist-net and playback to lure them into the net. Playback territorial songs were either from the individual itself or from a neighbour within hearing distance to avoid introducing any new song types. Mist-net lines had been cleared in all territories occupied in the Tick Flat area in 2005, with the exception of MG352. Capture of males from these territories was opportunistic – wind speed and direction and cloud cover played a big role in which territories were targeted for capture as both wind and sun made the net more visible, decreasing the likelihood of a successful capture.

The harness used for transmitter attachment consisted of a rubber band glued to the transmitter with a loop either side to fit over the bird's wings, sitting on its back like a backpack. It was easily and quickly fitted, allowing the bird to be processed in the field and released within 5-10 minutes of capture, minimising disturbance to the bird. The transmitter and harness weighed less than 2g (~4% of a male's weight). The advantage of a rubber band harness was that the stretchiness allowed the bird to slip out of the harness if any part of the transmitter or harness became entangled on vegetation (as happened with both MG42 and MG43). Otherwise, the harness should have dropped off within a month or two when the rubber band perished and broke, eliminating the need to recapture a bird to remove the harness.

The first bird, MG45 (see Figure 3.1 for location), was captured on 1 July; however, a faulty transmitter battery meant that no usable data were collected. On 12 July MG42 was captured. He was tracked until 24 July when the transmitter antennae became entangled in vegetation and pulled the transmitter off. MG43 was tracked from 19 July to 14 August. It is interesting to note that MG43 had been captured eight years earlier as the territorial male in the same territory. The most parsimonious assumption is that he has occupied the same territory for the entire length of time.

During radio-tracking sessions, locations of the transmitters were recorded at least 30 minutes apart. Initially MG42 was tracked intensively. Once MG43 was captured, time was split between tracking the two birds, although at first MG43 was focused upon to ensure adequate data was collected from him. Overall, 112 and 204 locations were collected from MG42 and MG43 respectively. A total of 112 fixes were obtained from MG42 over 12 days of tracking, ranging from 1-19 fixes per day. MG43 yielded 204 fixes over 24 days, ranging from 2-21 fixes per day. As with the mapping of singing scrub-birds, two bearings were taken to allow the individual's location to be triangulated. Any vocalisations were noted in conjunction with each location taken. When vocalisations were heard, the identity of the singer was confirmed by checking that the transmitter signal was coming from the same location.

Capture and handling of the birds may have had an impact on their behaviour at least initially, however they did resume normal singing behaviour within a few hours and presumably their movements also returned to normal. It is unlikely that the radio-tracking itself had much impact on the birds' movement because every effort was made to avoid approaching the bird too closely.

3.2.3 Analysis of location data

The two bearings taken for each observation of either the singing or the radio-tracked birds were used to triangulate the location of the bird with the Arcview 3.2 GIS program (www.esri.com/software/arcview). The locations of singing birds were obviously clustered and easily identifiable as separate territories (Figure 3.2).

The *x* and *y* coordinates produced by Arcview for every location for each territory were then used to determine territory size with Ranges 6 (Kenward *et al.*, 2003) using the Minimum Convex Polygon (MCP) method. MCP consists of drawing a polygon around the location points in which no internal angle exceeds 180° (Burgman and Fox, 2003).

As defined previously, and for the purposes of this study, home range is the total area normally used by a scrub-bird; and territory is the area in which it sings territorial song. Location data from radio-tracking were used to determine home range and singing locations were used to map territories.

A problem with the definition of home range is that it is the area that an individual ‘normally’ uses, thus some of the movements may be outside of the normal area. A commonly used method to correct for this is to remove the outlying 5% of points (White and Garrott, 1990). Although this is an arbitrary figure, it provides an objective, repeatable means of measuring home range. Therefore, total home range in this study has been calculated to include 95% of the individual’s locations. The Ranges software was used to calculate the home range size by excluding the outlying 5% of locations away from the harmonic mean (centre of activity).

The MCP method has several advantages and disadvantages as summarised by White and Garrott (1990). Its major benefits are its simplicity, ease of calculation and flexibility of shape. Its drawbacks are that it is insensitive to irregularly shaped home ranges and that as the number of locations increases, the home range size increases indefinitely. Once again, the removal of the outlying 5% of points can help to correct for this (White and Garrott, 1990).

One important assumption of the MCP method is that locations should be statistically independent. White and Garrott (1990) suggest that, as a general rule, locations can be considered independent if sufficient time has elapsed for the individual to move from one end of its home range to the other. The minimum 30 minute intervals between Noisy Scrub-bird radio-tracking locations are probably just sufficient because the tracked birds were capable of moving roughly that distance within 30 minutes. Locations of singing males for territory mapping were definitely independent, as they were taken once each morning and evening.

Although some of the assumptions of the MCP are problematic, it provided a convenient and robust method of determining home range and territory size for the Noisy Scrub-birds studied. In addition to calculating the 95% home range size, the 80% core area was also estimated. To determine territory size, all of the singing locations were used and an 80% core area calculated. There were two reasons why the 100% instead of 95% territory size was calculated. Firstly, the definition of territory for these purposes was the area in which a scrub-bird sang territorial song. Thus all points should be included. Secondly, it allowed for comparison with Smith's 100% and 80% territory sizes (Smith, 1985a).

Photocopies of aerial photographs showing Smith's 1994 singing locations were available. These points were entered into Arcview and used to calculate territory sizes. Accuracy of these points was not exact because the photocopies of the aerial photographs were unclear and it was difficult to place the points exactly.

3.3 Results

3.3.1 Mapping of singing locations

The locations of singing Noisy Scrub-birds in the Tick Flat study area were obviously clustered and easily identifiable as separate, non-overlapping territories (Figure 3.2). Territory size ranged from 0.62ha to 2.50ha (Table 3.3). Mean territory size was 1.54ha and the 80% core area was 0.89ha. Territory sizes calculated from Smith's 1994 singing locations were smaller, averaging 0.73ha and ranging from 0.06ha to 1.85ha (Table 3.4).

Three territories present in 1994 were no longer occupied in 2005. In 1994 the area where MG69 and MG304 were present was not surveyed. Figure 3.3 shows the territory boundaries in 1994 and 2005. Overall, the locations of the majority of the territories that were present in both 1994 and 2005 have not changed substantially.

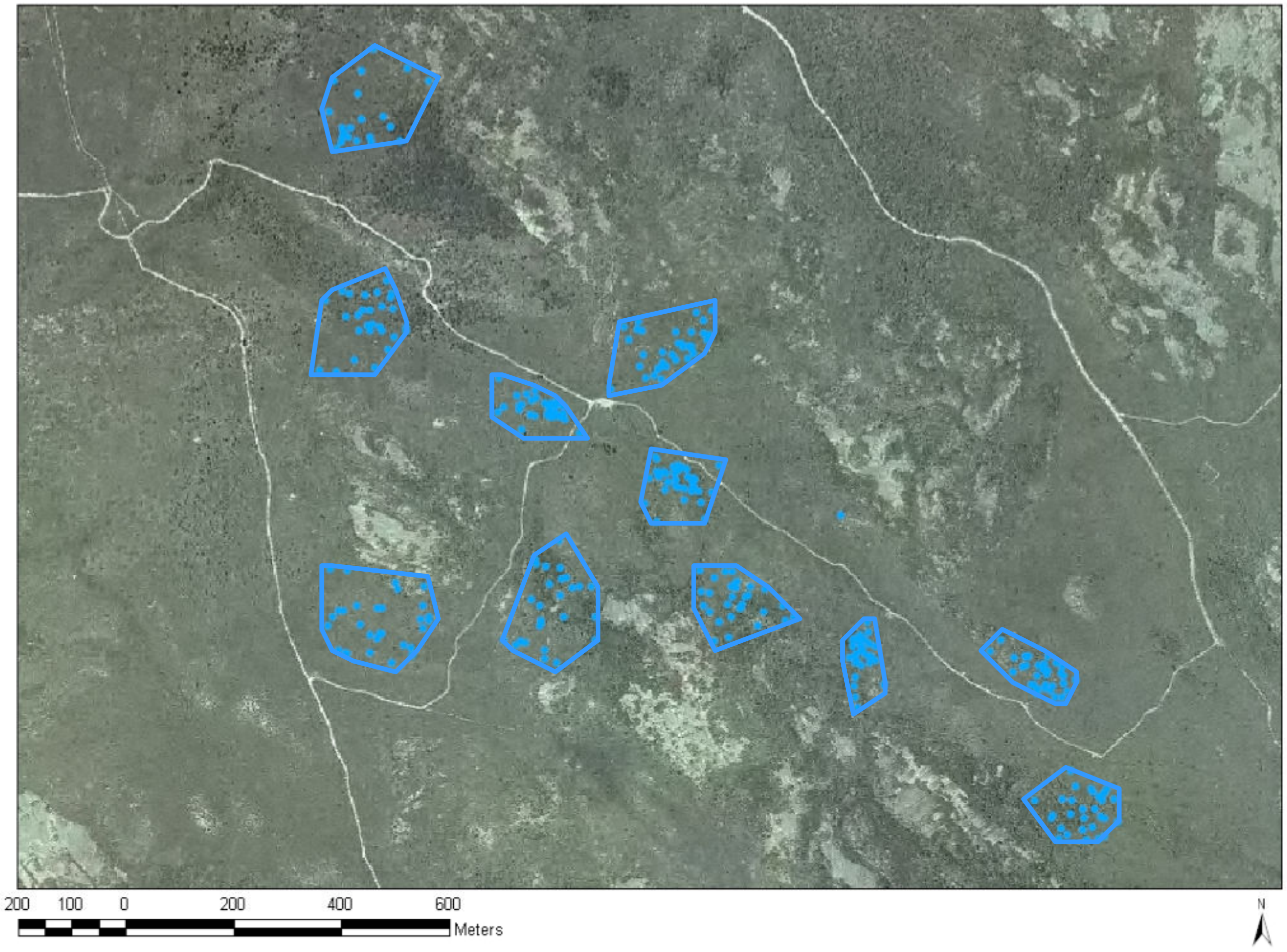

Figure 3.2: Locations of singing males in the Tick Flat study area in 2005. Groups of locations identified as territories are bounded by lines.

Table 3.3: 100% territory size and 80% core area of the territories present in the Tick Flat study area in 2005.

Territory number	Territory size (ha)	Core area (ha)	Number of locations
38	0.62	0.23	31
42	1.63	0.98	34
43	1.26	0.54	37
45	0.92	0.42	35
46	2.38	1.70	27
55	1.38	0.94	30
56	1.93	1.02	28
69	0.79	0.46	32
82	2.50	1.72	30
304	1.28	0.80	30
352	2.24	0.93	21

Table 3.4: Territory sizes in hectares in the Tick Flat study area in 1994 and 2005.

Territory number	1994	2005
38	0.89	0.62
42	1.85	1.63
43	0.98	1.26
45	0.56	0.92
46	0.64	2.38
48	0.56	not occupied
55	0.80	1.38
56	0.32	1.93
59	0.06*	not occupied
69	not surveyed	0.79
82	1.19	2.50
297	0.77	not occupied
304	not surveyed	1.28
352	0.13*	2.24

* territory sizes that may have been affected by small sample sizes (<15 locations).

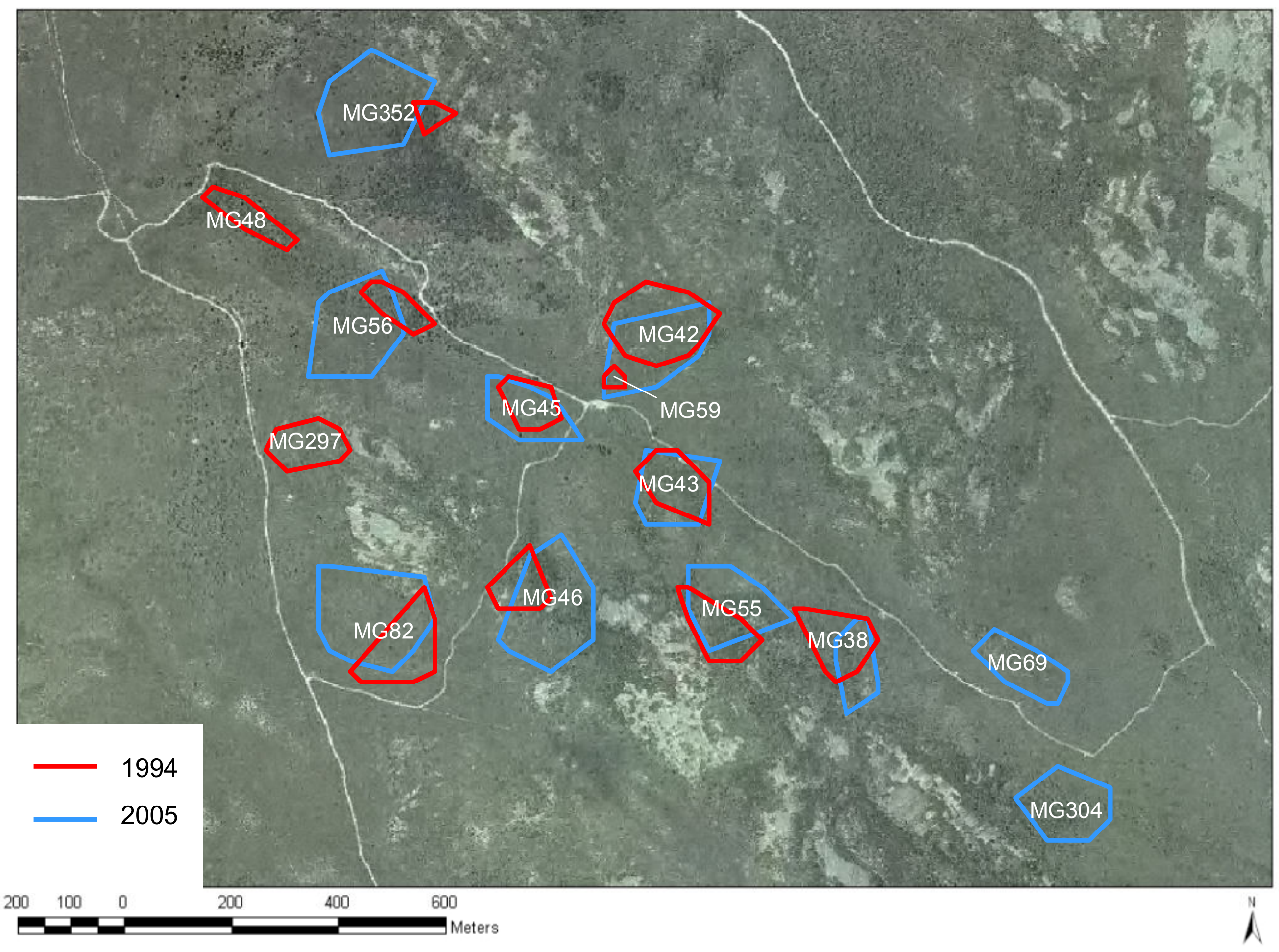

Figure 3.3: Boundaries of the territories present in the Tick Flat Study area in 1994 and 2005.

3.3.2 Radio-tracking

The radio-tracking locations for MG42 were much more dispersed than for MG43 (Figure 3.4) as is reflected by the larger home range size, even though the number of locations was approximately half (Table 3.5). Home range sizes calculated using the radio-tracking locations from MG42 and MG43 were much larger than territory size (Table 3.5). When a polygon was drawn around all locations from which the birds sang territorial song during radio-tracking, it was observed that the territory was concentrated in the centre of the home range with a peripheral area in which the bird did not sing (Figure 3.5).

To illustrate the effect that sample size has on territory size, the territory mapping based on singing locations was combined with the radio-tracking locations where territorial song was heard. This gave a sample size of 83 and 86 locations respectively for MG42 and MG43 and increased territory size from 1.63ha to 4.95ha for MG42 and from 1.26ha to 2.33ha for MG43 (Table 3.5).

Table 3.5: Home range and territory sizes (hectares) of MG42 and MG42.

	MG42			MG43		
	Total size	Core area	No. obs.	Total size	Core area	No. obs.
Home range	7.76	6.71	112	3.52	1.87	204
Territory	1.63	0.98	34	1.26	0.54	37
All t-song	4.95	1.95	83	2.33	0.76	86

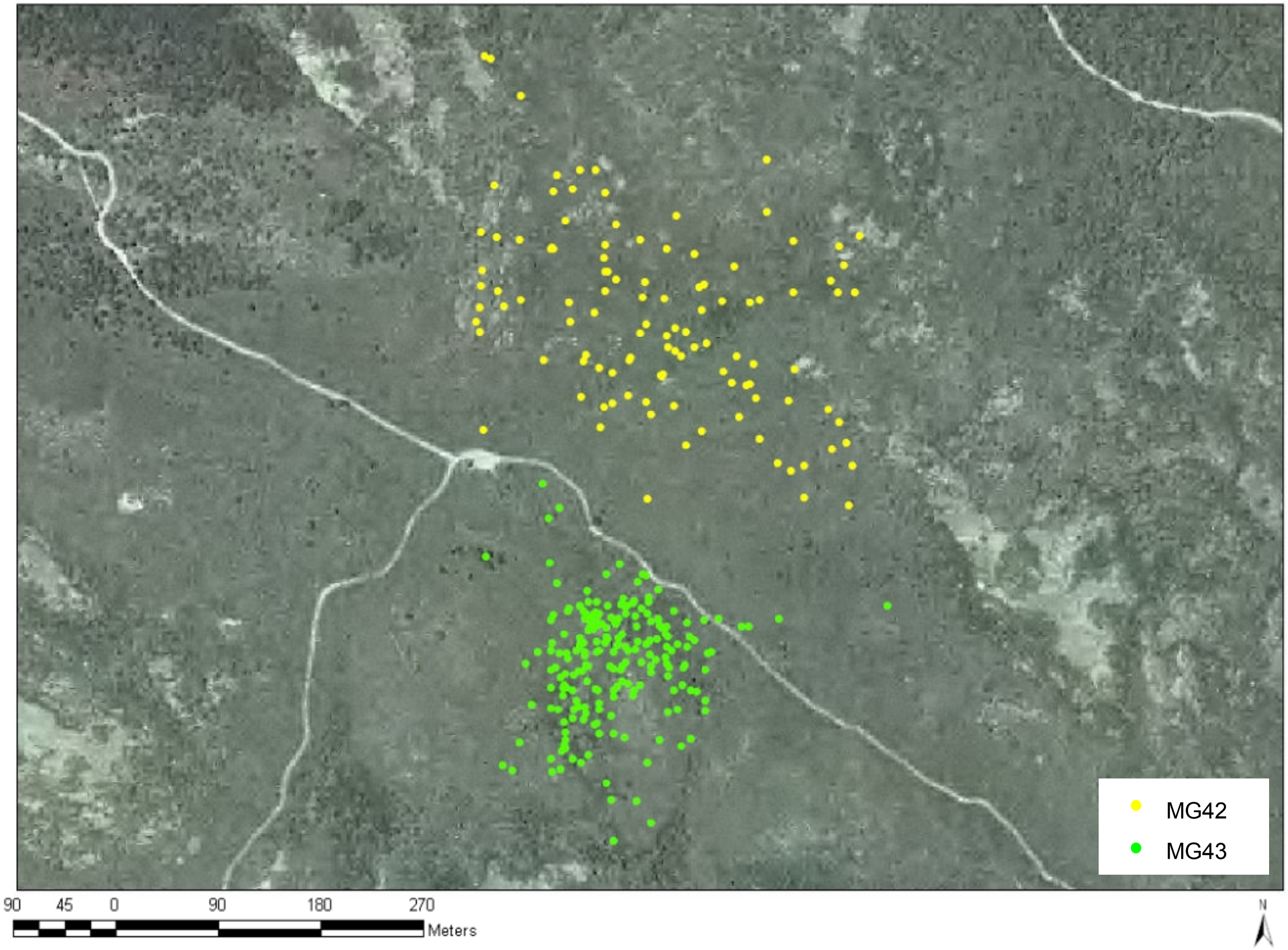

Figure 3.4: Locations of MG42 and MG43 during radio-tracking.

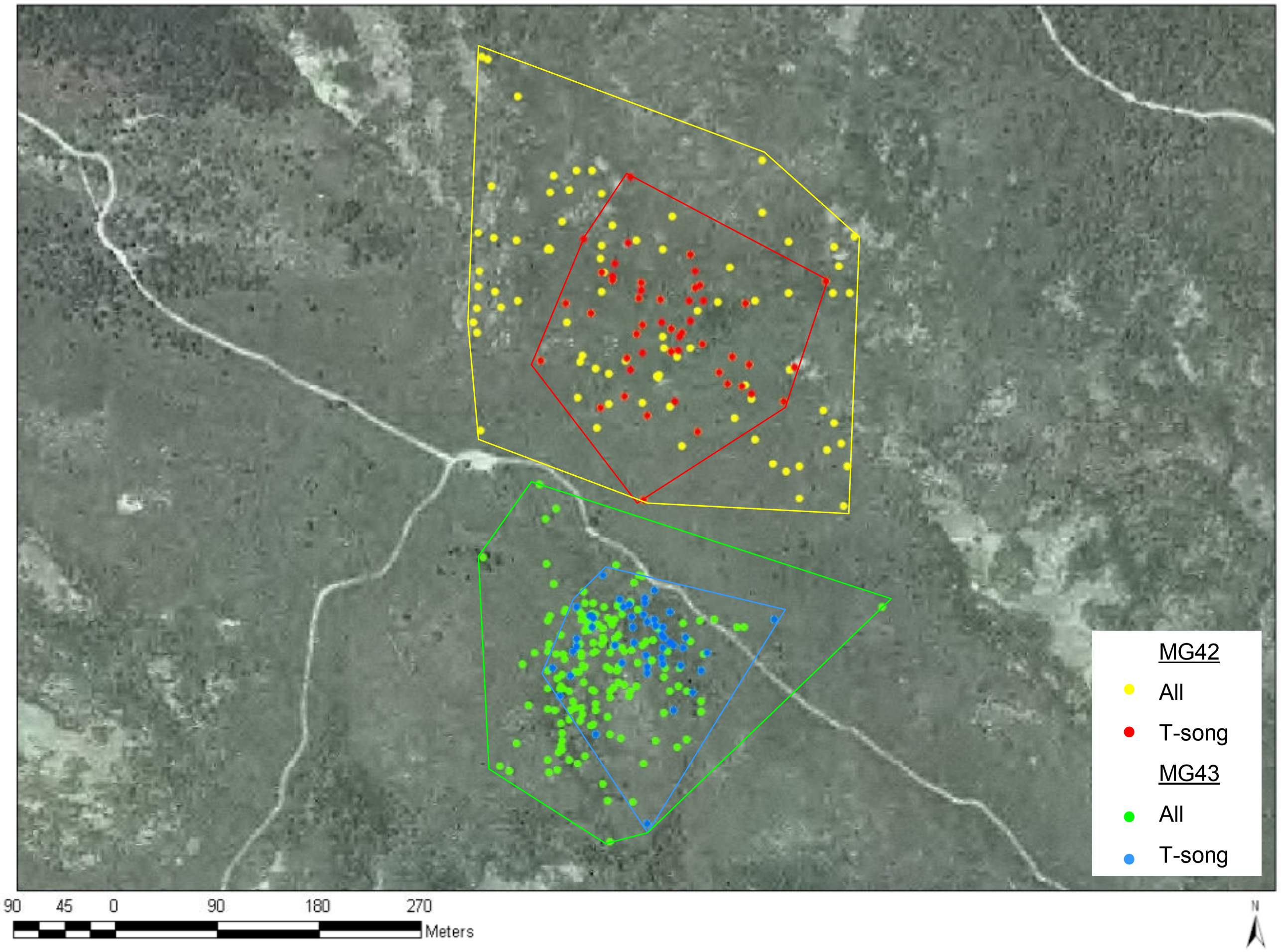

Figure 3.5: All radio-tracking locations representing the home ranges of MG42 and MG43 (bounded by yellow and green) and the territory area (bounded by red and blue) in which territorial song was heard.

There were four occasions during radio-tracking in which other scrub-birds were observed within the home range of the bird being tracked. At no time was any bird (other than the bird being tracked) heard to sing territorial song within the home range. Within the home range of MG42 there were two occasions on which another scrub-bird was detected. The first time, the other bird was startled by myself and gave eight alarm calls. MG42, who had already passed through that area and was about 30m away, rapidly returned to the spot and proceeded to sing short song frequently for about 8 minutes. There was no response from the other bird. On the second occasion, a single alarm call was heard within the home range of MG42. There was no response from MG42; he was distant and may not have heard the call.

In the case of MG43, another bird was heard giving alarm calls within his territory. MG43 responded by immediately switching to short song and approaching. A week later another bird was heard singing short song within his territory, but MG43 did not respond. At the time he was in a hollow some distance away and may not have heard the other bird clearly.

3.3.3 Comparisons to the annual census

The 2005 census recorded a total of 23 territories occupied in the Tick Flat study area compared to the 11 detected through mapping the locations of singing males (Figure 3.6). In some cases it is likely that a single individual was recorded as belonging to more than one territory and this has been indicated in Figure 3.6 based on personal observations made between 2002 and 2006.

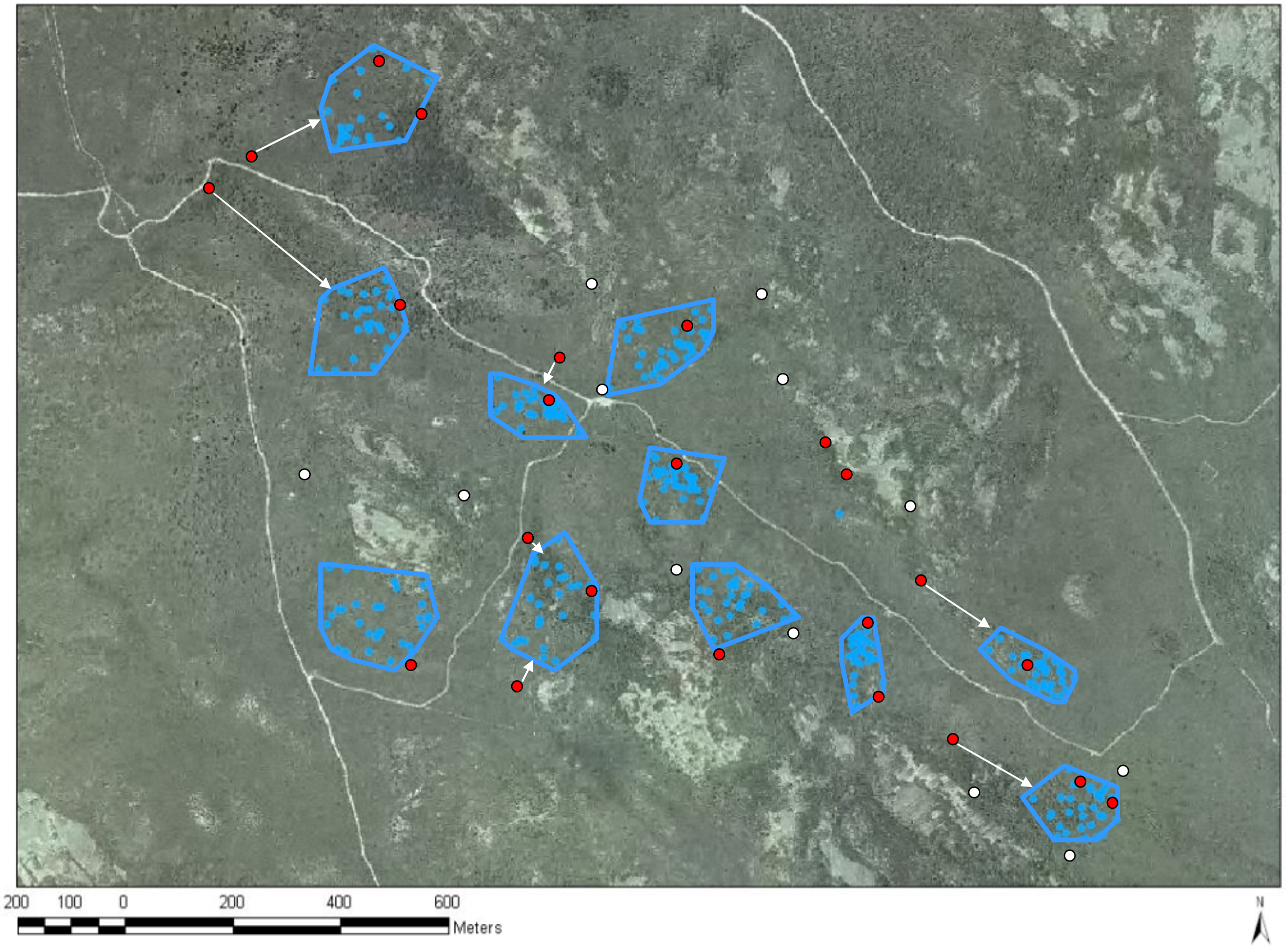

Figure 3.6: 2005 locations of singing males showing territory boundaries. Red dots show the territories recorded as occupied in the annual census. White arrows indicate which individual they potentially could be.

3.4 Discussion

The aims of this chapter were to investigate the home range and territory of male Noisy Scrub-birds, to compare to past results and current census techniques. Most importantly, the major aim was to provide evidence through radio-tracking to support the assumption that it is the same bird singing in the same spot each day.

Only two males were successfully radio-tracked – MG42 and MG43. The transmitters remained on these birds for 13 and 27 days respectively. During this time, no other Noisy Scrub-birds sang territorial song within the home range of the tracked birds, although on several occasions the presence of other scrub-birds was observed. In the case of MG43 this included another bird singing short song within his territory. It was not a neighbouring territorial male as all were singing within their territories at that time. Short song appears to be used in territorial disputes (Smith and Robinson, 1976; Davies *et al.*, 1982) and is often observed in capture attempts where males will respond to playback by approaching the speakers and switching to short song (pers. obs.). It is possible that this was a subordinate bird challenging the territory holder.

While this does show that territory takeover attempts may occur, it also shows that for this period at least, only the territory holders sang territorial song within their home range. Therefore, the assumption that it is the same bird singing in the same location each day appears to be supported. It is possible that territory turnover does occur occasionally however, and this will probably go undetected (see Chapter 6 detailing the presence of subordinate males singing the same set of song types when they take over a territory). The fact that MG43 had been captured as the territorial male in the same territory eight years previously provides additional evidence that a male may occupy a territory for an extended period of time. It is not known how long Noisy Scrub-birds live because they are so rarely recaptured. MG43 was the oldest individual recorded in the wild; he was at least 10 years old.

Noisy Scrub-bird territories within the Tick Flat study area were non-overlapping and ranged in size from 0.62 to 2.50ha (mean 1.54ha). The core area in which 80% of the observations were recorded ranged from 0.23 to 1.72ha (mean 0.89ha). This was much smaller than the territory sizes reported by Smith (1985a) of 6ha (range 4-9ha) and a core area of 1.25ha (range 0.75-2.25ha). However, it was unclear what methods he used to determine territorial boundaries so it was difficult to make direct comparisons. It should be noted that detailed observations from 1971-1976 were combined to draw these boundaries which would mean that many location points were used. This would provide a greater spread of points than the sample of approximately 30 locations for each of the territories studied in 2005. Also, it is likely that an area surrounding the points was included in the territory estimations, whereas the method used in this study draws a polygon around the outermost points, resulting in a smaller territory size.

To illustrate the effect that sample size has on territory size, the territory mapping based on singing locations was combined with the radio-tracking locations where territorial song was heard. This gave a sample size of 83 and 86 locations respectively for MG42 and MG43 and increased territory size from 1.63ha to 4.95ha for MG42 and from 1.26ha to 2.33ha for MG43. The 80% core area using all territorial song locations for MG42 was 1.95ha and 0.76ha for MG43. This compares more closely with Smith's (1985a) territory size range of 4-9ha and core area of 0.75-2.25ha.

Graeme Smith's location data from 1994 were available (unpublished) and were used to calculate territory size with the Mean Convex Polygon (MCP) method used for the 2005 locations. In contrast to Smith's territory sizes from the 1970s, this yielded much smaller territories, smaller in fact than those in 2005. The mean territory size in 1994 was 0.73ha compared to 1.54ha in 2005. The MCP method is sensitive to sample size, with smaller samples providing smaller territory sizes (White and Garrott, 1990). Smith's 1994 sample sizes varied from 6 to 54 (mean 27.7) observations, whereas the 2005 sample size ranged from 21 to 37 locations (mean 30.5). While Smith's sample sizes varied more widely and accounted for some of the particularly small territory sizes, overall territory size was generally smaller in 1994 regardless of the number of locations. The Tick Flat area is long unburnt and it may be possible that, as the vegetation ages, it becomes less suitable for scrub-birds, forcing them to increase the area over which they forage and which they defend vocally.

Territory mapping of the Tick Flat study area revealed that in comparison to the annual census there were only 11 territories as opposed to the 23 detected by the 2005 census. The census method involves visiting each area three times and locating singing males (Smith and Forrester, 1981). Maps are used which have all previously recorded territories marked on them, and a singing male is usually recorded as belonging to the territory dot to which he is closest. If he is not within approximately 100m of any of the territory dots then a new territory is created.

By censusing an area three times, it creates the potential for a single scrub-bird to be recorded as up to three different singing males, depending on where he is singing in his territory at the time. Analysis of results of census data from 1973-76 showed that one visit may underestimate the real number of territories by up to 52%, two visits by up to 18% and three to five walks will miss no more than 3% (Smith and Forrester, 1981; Davies *et al*., 1982). However, at this time there were no more than 74 territories on the Mt Gardner headland (Davies *et al.*, 1982), whereas by 2005 the census recorded 126 territories in the area. The maps that are used to census show all previous territories (numbering ~375) on the headland and therefore where once there may have been only a few dots in the area near where a bird is singing, now there are many. Therefore, the problem is that many of the territories either encompass, or are close to, more than one territory dot and consequently may be recorded as several territories over multiple visits

In 2006 a single sweep census was done to compare the number of singing males to that of the census done in the conventional method of three visits to all areas. There were 92 singing males in the single sweep compared to 132 using the traditional census method (Tiller *et al*., 2006). The true number probably lies somewhere between. A single sweep would underestimate the number of singing males as it would miss birds that were not singing at the time the area was censused. Census methods need to be consistent to allow comparison between years but as the number of territory dots in the area increases, the potential for an overestimation of the actual number of territories also increases.

The assumption that each Noisy Scrub-bird territory represents an individual male appears to have some support, although it should still be treated with some caution. Noisy Scrub-bird territories are discrete and their non-overlapping nature means that confusing the identity of birds within a familiar area is unlikely, although it may occur in areas where individuals' movements and territory boundaries are not known. The following chapter discusses song sharing amongst territorial males.

Chapter 4 –
Song Sharing on Mt Gardner

4.1 Introduction

As discussed in Chapter 1, geographic variation in bird song is common (see Krebs and Kroodsma, 1980; Mundinger, 1982) and may occur in isolated populations (e.g. Golden Bowerbird, Westcott and Kroon, 2002; Superb Lyrebird, Powys, 1995), or in contiguous populations (e.g. Saddleback, Jenkins, 1977; Village Indigobird, Payne, 1985). In a contiguous population, song change may occur gradually across the range of the population (e.g. Greenish Warbler, Irwin, 2000); variation may occur relatively rapidly with intermediate songs occurring along a contact zone between the variants (e.g. Saddleback, Jenkins, 1977); or it may be abrupt, with sharp boundaries between groups with different songs (e.g. Corn Bunting, McGregor, 1980).

In a preliminary study (Berryman, 2003) the Noisy Scrub-bird appeared to conform to the final option of abrupt song change with sharp boundaries between song groups. Groups of up to seven individuals in neighbouring territories all shared the same set of song types. In contrast, birds from neighbouring song groups shared no song types with each other.

More work was needed to confirm these findings because the sampling methods did not take into account the process of repertoire change. Also, the sample size was relatively small (25 individuals) and was mainly confined to those territories that were close to the 4WD tracks and easily accessible. It was thought desirable that as many individuals in the Mt Gardner area as possible be recorded to give an accurate picture of song group size, distribution and stability, as well as repertoire size and degree of song sharing. This chapter describes song sharing in the Mt Gardner population of Noisy Scrub-birds with the aim of further investigating the previously described patterns of song sharing and song groupings.

4.2 Methods

Two major considerations needed to be taken into account when planning the methods used to determine the spatial patterns of song sharing on Mt Gardner. Firstly, the fact that repertoire change occurs in this species meant that the sampling protocol had to be designed to minimise the effect of this temporal change in song structure on the apparent variation between birds. Secondly, as many birds as possible in a given area, and an adequate proportion of each bird's repertoire, needed to be sampled to represent accurately the degree of song sharing.

Thus, there needed to be a compromise between minimising the total period spent collecting recordings and maximising the number of birds recorded within that timeframe. In addition, the fact that this work was carried out mainly during winter meant that suitable periods of fine weather were limited, further reducing the time available for recordings.

Based on previously developed sampling methods (Berryman, 2003), it was decided that at least 10 songs per bird would provide an adequate sample of that individual's repertoire (on average about 92% of the song types in a scrub-bird's repertoire were sampled within 10 songs). All scrub-bird territories within a given area were visited with at least 30 minutes (often 1-2 hours) spent within hearing distance to allow the bird time to sing. To minimise the effect of temporal change in song types, all birds were recorded within two weeks of each other. Neighbouring birds were usually recorded within two to three days of one another.

Ideally, all scrub-bird territories in the Mt Gardner area would have been visited, preferably with at least one repeat of the process in order to pick up any extra birds that were not singing at the time. Figure 4.1 shows the areas that were surveyed and the dates on which these sessions took place. In total, songs from 71 of the 131 occupied territories in 2004 were recorded. Although this appears to represent a relatively low proportion, there were some territories in which singing was infrequent. Many of these territories were missed as the bird was not singing at the time the recordings were carried out, particularly during the September session. Also, the southern part of the headland was only surveyed once, further increasing the number of territories that were missed. Furthermore, census methods may in fact over-estimate the number of singing males in any given year (for a more detailed discussion of this see Chapter 3). An extra sampling session was carried out in July 2005, covering the same area as the July 2004 session. This allowed comparisons to be made between years.

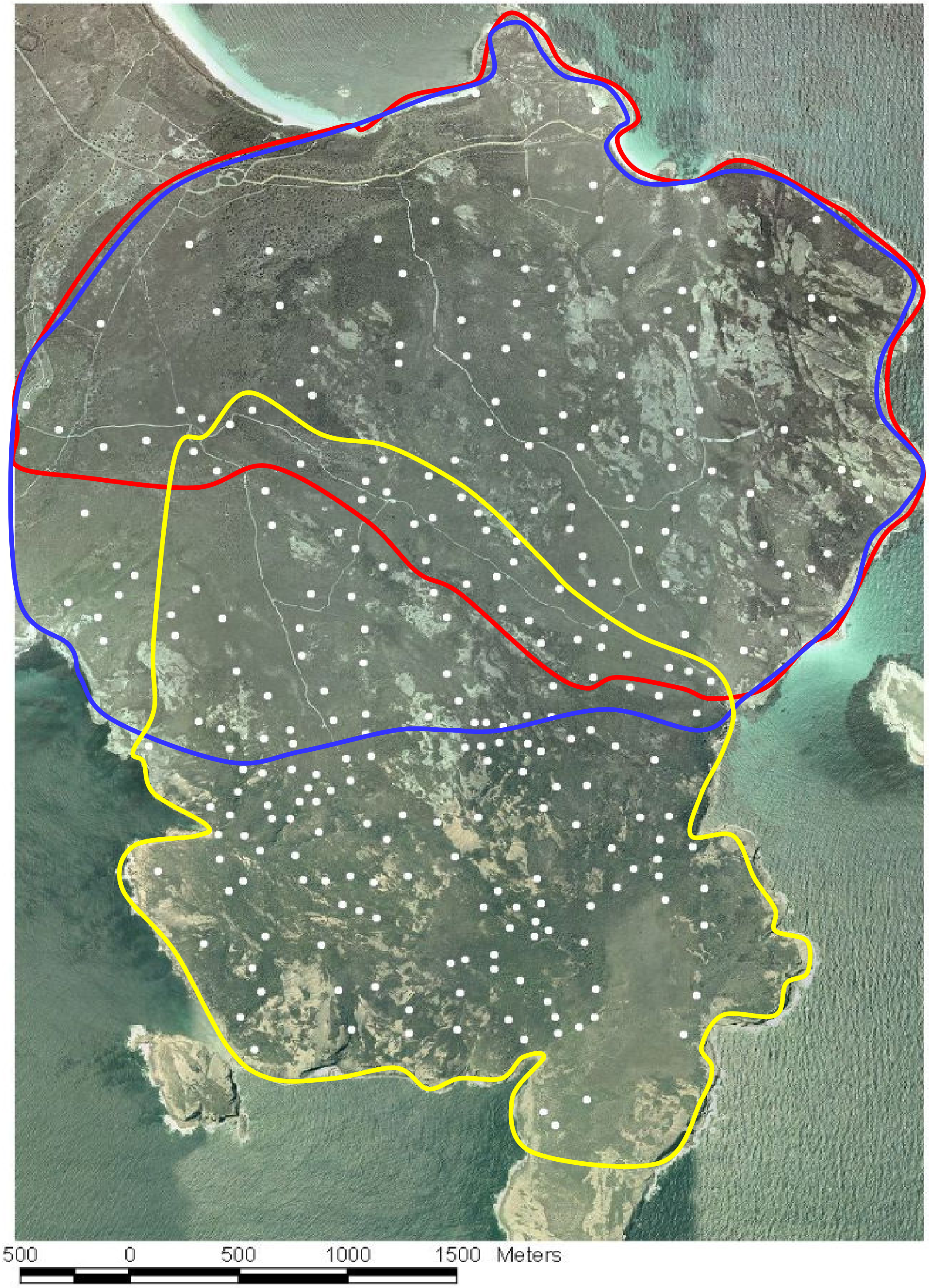

Figure 4.1: Map of Mt Gardner showing all Noisy Scrub-bird territories (white dots) and the areas in which recordings took place. The area surveyed between May 18 and June 2 2004 is bounded with red; a blue boundary shows the survey area for July 10-15 2004; and yellow is September 14-17 2004.

Recordings were processed using Syrinx sound analysis software and all resultant spectrograms were compared visually to each other to identify any shared song types (for justification of this method see Chapter 2). This comparison yielded groups of song-sharing scrub-birds (termed a song group) which were then mapped.

For each individual, the number of different song types in its repertoire was determined, as well as the percentage of these song types that were shared with at least one other bird. For each song group, the group repertoire size was determined by counting the total number of different song types sung by the members of that group.

STATISTICA software package (Statsoft, 1999) was used to look for differences in individual repertoire size, song group size, group repertoire size and % song sharing between each of the four sampling sessions. Individual repertoire size (number of song types per bird) was examined using a repeated measures ANOVA with the covariate of number of songs recorded. The covariate was used because the greater the number of songs recorded, the greater the possible size of repertoire that could be detected. Unfortunately, time constraints and the unpredictability of singing behaviour meant that widely varying numbers of songs were recorded for different individuals.

A repeated measures analysis was chosen to compare individual repertoire size because, in many cases, recordings were made at the same territory over time. Consequently, if the assumption is made that it is the same individual singing from a particular territory (discussed in Chapter 3), then the data cannot be considered to be independent. While there is no guarantee that this holds true for all territories over the span of these sampling sessions, it seems reasonable to assume that the data are in fact dependent and thus require a repeated measures analysis.

Initially, a comparison was made between May 2004, July 2004 and July 2005. September 2004 was excluded from this analysis because a different area of the headland had been focused on and it greatly reduced the number of territories that had repeated measures to analyse. As it was, fewer than half the birds had data for all three sessions. So that the September session could be included, and also to reduce the effect of an incomplete data set on the previous test, a subsequent pair-wise repeated measures comparison between each of the sampling sessions was carried out. The modified Bonferroni correction (Quinn and Keough 2002) was used to adjust the p-value to give an experiment-wide error rate of 0.05, given the multiple tests. Analysis of the May 2004 and September 2004 pair could not be carried out because the sample size was too small for repeated measures with a covariate.

The size of song groups (number of birds per group) was tested for all sampling sessions simultaneously, using ANOVA. The data were first log-transformed to correct for correlations between means and variances. The group repertoire size (number of different song types per song group) was analysed using the same method as song group size.

The percentage of song types shared by at least one other bird was analysed using the same method as individual repertoire size with the exception that no covariate was included. The method used to determine song sharing was based on the proportion of song types in an individual's repertoire that were shared by at least one other individual. The number of songs recorded per bird had very little, if any, impact on this because even if only one song was recorded, the collective sample of songs from the rest of the group should have included several examples of each song type shared by that group.

4.3 Results

In total, territorial songs were recorded at 71 scrub-bird territories in 2004 (30 in May, 47 in July and 28 in September). On average, 14.3 songs were recorded from each individual. Comparison of spectrograms of all song types given by all individuals revealed that song sharing occurred amongst groups of up to 9 neighbouring scrub-birds, termed a song group. Tables 4.1 - 4.4 show the song types sung by each individual and how song sharing birds can be split into discrete groups. Figures 4.2, 4.3 and 4.4 map the song groupings in May, July and September 2004 respectively. A combined map of these song groupings is shown in Figure 4.5. Figure 4.6 shows the song groupings in July 2005 and Figure 4.7 provides a comparison between the July 2004 and July 2005 song group boundaries. During all of these sampling sessions, neighbouring song groups had no song types in common.

Song group size varied from one individual to a maximum of nine individuals. In May 2004 the mean song group size was 3.3 birds per group, in July 2004 it was 3.9 birds per group, in September 2004 each song group had an average of 2.3 members and in July 2005 the average was 3.1 birds per group (Table 4.5). Group repertoire size (the total number of different song types present in the repertoires of members of a song group) varied from 5.4 to 7.6 song types per group (Table 4.5). The ANOVA testing song group size in all Mt Gardner sampling sessions showed no differences ($F_{(3,38)} = 0.84$, $p = 0.480$). Likewise, group repertoire size in all sampling sessions also showed no significant differences ($F_{(3,38)} = 1.061$, $p = 0.377$).

In the intervals between the three 2004 sampling sessions, some individuals were observed to have changed song group (Figure 4.5). Between May and July 2004 two individuals, MG352 and MG375, switched song groups. In May, MG352 belonged to a group of two but by July had changed his songs to share with the larger neighbouring song group of eight other individuals. However, the other bird in his original group (MG351) was not recorded in July so it is not known whether just MG352 or the entire group amalgamated with the larger song group.

In May 2004, MG375 shared his repertoire with the Firebreak Valley song group (see Figure 4.2). By July 2004 he no longer shared with the Firebreak Valley group; instead he shared with MG53 and MG57 (Figure 4.3). Between July 2004 and September 2004 the Wave Sign group, which initially had seven members, split into two separate groups (see Figures 4.3 and 4.4). However, not all individuals were recorded again in September; thus it was not clear what the actual boundaries of the new song groups were.

The comparison of boundaries between July 2004 and July 2005 (Figure 4.7) also revealed some change in song group boundaries. Most notable was the splitting of the Firebreak Valley song group into two smaller groups. Other changes to boundaries were the result of birds not being recorded in both sessions, with the exception of MG46 who switched to the neighbouring song group some time in the 12 month interval.

Song sharing was measured by the percentage of song types in a bird's repertoire that were shared by at least one other bird. The degree of song sharing amongst members of a song group varied from 81.3% to 95.7% (Table 4.5). In May 2004, seven out of the nine song groups present had complete song sharing between all members of the song group. The initial repeated measures ANOVA revealed that there were no significant differences in song sharing between the May 2004, July 2004 and July 2005 sessions ($F_{(2,30)} = 2.52$, $p = 0.097$). A pair-wise repeated measures comparison (Table 4.6) confirmed this and also showed that the September 2004 session did not differ significantly either.

Individual mean repertoire size varied from 4.6 to 5.5 song types per individual. The maximum individual repertoire size was 9 song types in May, 8 in July and 7 in September. The apparent minimum individual repertoire size was as low as one song type. However this was a result of only one song being recorded from some individuals. The initial comparison of individual repertoire size of all sampling sessions excluding September 2004 revealed no significant differences over time ($F_{(2,28)} = 1.51$, $p = 0.239$). The covariate of the number of songs recorded was non-significant ($p > 0.08$ across all three times). The pair-wise comparison of each sampling session (Table 4.7) also revealed that there were no significant differences in individual repertoire size between any of the sessions. After the modified Bonferroni correction, covariates for these were also non-significant.

Table 4.1: The song types present in each individual’s repertoire in the May 2004 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A “1” in a column indicates the presence of that song type in an individual’s repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

	Song types																																																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX
24	1	1	1																																														
32	1	1	1																																														
19				1	1	1	1	1																																									
20				1	1	1	1	1																																									
21					1	1																																											
34									1	1	1	1																																					
36									1	1	1	1																																					
335													1	1	1	1	1	1	1	1	1																												
73													1		1	1	1	1	1		1																												
72													1	1	1	1	1	1	1		1																												
274																						1	1	1	1	1	1	1																					
45																						1		1	1	1	1	1																					
43																						1		1	1	1	1	1																					
42																						1		1	1	1	1	1																					
352																													1	1	1																		
351																													1	1	1																		
53																																1	1	1	1															
5																																				1	1	1	1	1	1									
6																																				1	1	1	1	1	1									
8																																				1	1	1	1	1	1									
9																																				1		1	1	1	1									
14																																				1	1	1	1	1	1									
2																																				1	1	1	1	1	1									
4																																				1	1	1	1	1	1									
13																																				1	1	1	1	1	1									
375																																				1	1	1	1	1										
304																																										1	1	1	1	1	1	1	1	
69																																										1		1		1	1	1		1
235																																										1		1		1	1	1	1	
66																																										1		1	1	1	1	1	1	

Table 4.2: The song types present in each individual's repertoire in the July 2004 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

Song types

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
24	1	1	1	1	1																		
20						1	1	1	1	1													
21						1	1	1	1	1	1												
34												1	1	1	1	1							
36												1	1	1	1	1							
335																	1		1	1	1	1	1
72																	1	1	1	1			1
73																	1	1	1	1	1		1
325																							
274																							
42																							
43																							
45																							
46																							
56																							
174																							
352																							
53																							
375																							
57																							
256																							
6																							
5																							
7																							
9																							
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13																							
234																							
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61																							
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114																							
81																							
82																							
85																							
86																							
293																							
298																							
87																							

	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV
24																									
20																									
21																									
34																									
36																									
335																									
72																									
73																									
325	1	1		1	1						1														
274	1	1	1	1	1																				
42	1	1	1	1	1	1																			
43	1	1	1	1		1	1																		
45	1	1	1		1	1		1																	
46	1			1		1																			
56	1				1	1	1		1	1															
174						1	1		1	1															
352						1	1		1	1															
53												1	1	1											
375													1	1	1										
57												1	1	1	1	1	1								
256														1											
6																		1	1	1	1	1	1		
5																			1	1	1	1	1		
7																		1	1	1	1	1	1	1	1
9																		1	1	1		1	1	1	1
14																				1		1			1
2																			1	1	1	1	1		
4																			1	1	1	1			
13																			1	1	1	1	1		
234																									
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86																									
293																									
298																									
87																									

	AW	AX	AY	AZ	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR
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335																						
72																						
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14																						
2																						
4																						
13																						
234	1	1	1	1		1	1															
66	1	1	1	1			1	1														
62	1	1	1	1	1																	
61	1	1	1	1																		
69	1	1	1	1			1	1														
304	1	1	1	1		1	1	1														
38									1													
244										1	1	1	1	1	1							
88																1	1	1	1	1	1	
91																1	1	1	1	1	1	1
114																			1			
81																						
82																						
85																						
86																						
293																						
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87																						

	BS	BT	BU	BV	BW	BX	BY	BZ	CA	CB	CC	CD
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73												
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114												
81	1	1	1	1	1	1						
82	1	1	1		1							
85		1			1		1	1	1	1	1	
86					1		1	1	1	1	1	
293					1			1				1
298	1	1	1	1	1							
87		1			1		1	1	1	1	1	

Table 4.3: The song types present in each individual's repertoire in the September 2004 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

Song types

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
69		1	1	1			1	1																		
304	1	1	1	1			1																			
234	1	1	1	1	1	1	1																			
88									1	1	1	1	1													
91											1	1	1													
114									1	1	1		1	1												
324									1		1	1		1												
81															1	1	1	1								
298															1	1	1	1	1							
145																				1	1	1	1	1	1	
318																				1	1	1	1	1		1
354																										
125																										
337																										
111																										
271																										
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132																										
303																										
98																										
269																										
293																										
87																										

	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ
69																										
304																										
234																										
88																										
91																										
114																										
324																										
81																										
298																										
145																										
318																										
354	1	1	1																							
125		1	1																							
337	1	1	1																							
111				1	1	1	1	1	1																	
271					1		1		1																	
120				1	1		1	1	1	1																
314						1	1		1																	
102											1	1	1	1	1											
301											1	1	1		1	1										
280												1														
230																	1	1	1	1	1	1				
132																							1	1	1	1
303																										
98																										
269																										
293																										
87																										

	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU
69																					
304																					
234																					
88																					
91																					
114																					
324																					
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298																					
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120																					
314																					
102																					
301																					
280																					
230																					
132																					
303	1	1	1	1	1	1															
98				1																	
269							1	1	1	1	1	1	1								
293														1	1	1	1	1	1	1	
87															1	1		1		1	1

Table 4.4: The song types present in each individual's repertoire in the July 2005 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

Song types

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
304	1	1	1	1	1	1	1	1																		
69	1	1		1		1	1		1																	
61		1	1		1	1	1																			
62		1	1	1	1	1	1																			
363		1		1	1	1																				
34										1	1	1	1	1												
36										1	1	1	1	1												
38															1	1	1	1								
72																			1	1	1	1	1			
73																			1	1	1	1	1	1		
335																			1	1	1	1		1	1	
29																				1	1		1	1		1
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	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ
304																										
69																										
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363																										
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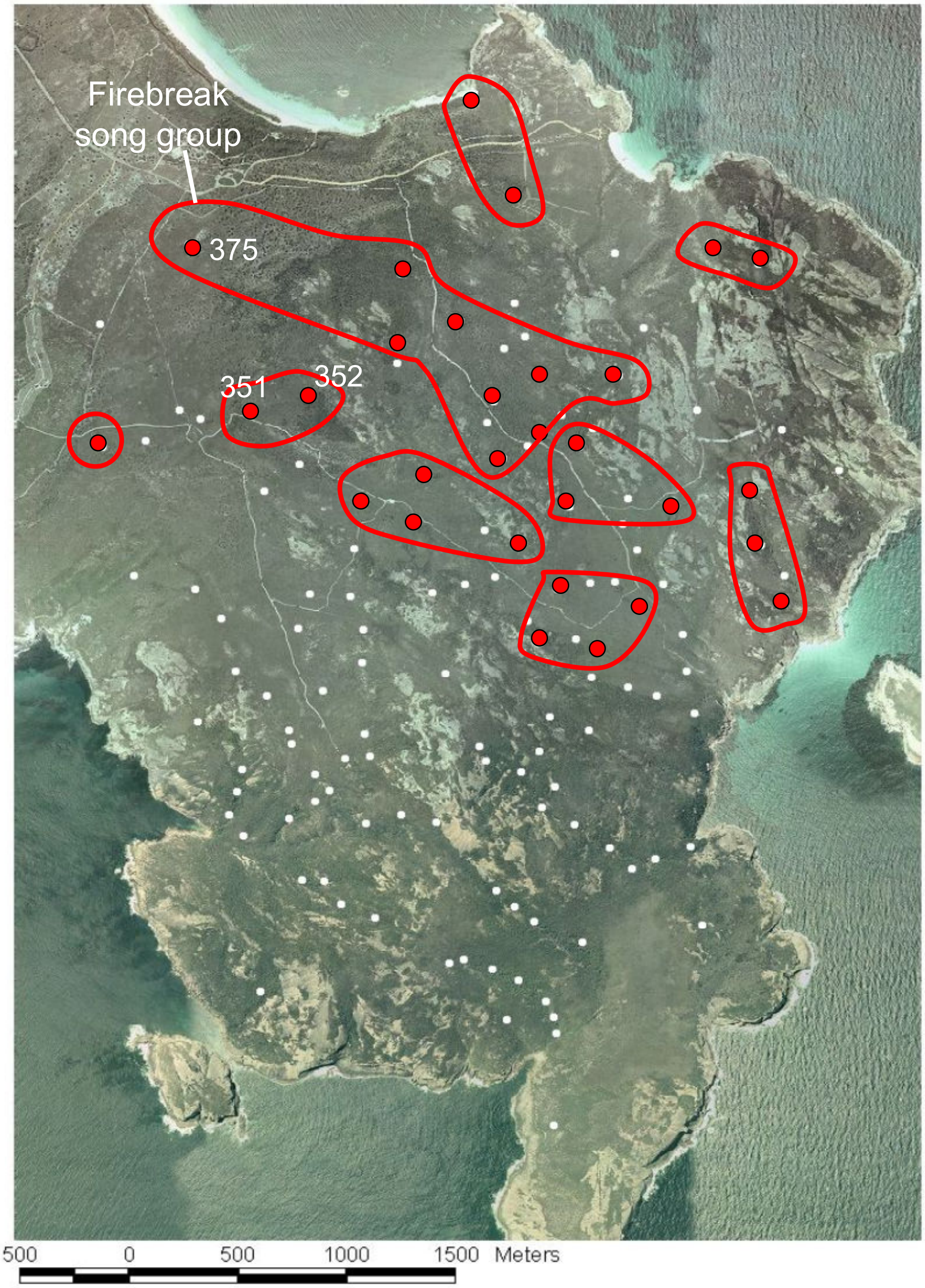


Figure 4.2: May 2004 song groupings. Territories at which songs were recorded are represented by red dots and groups of birds that shared songs are bounded by a red line. White dots show territories noted as occupied in the 2004 census that were not recorded in this sampling session. Song groups and territories mentioned in the text are labeled.

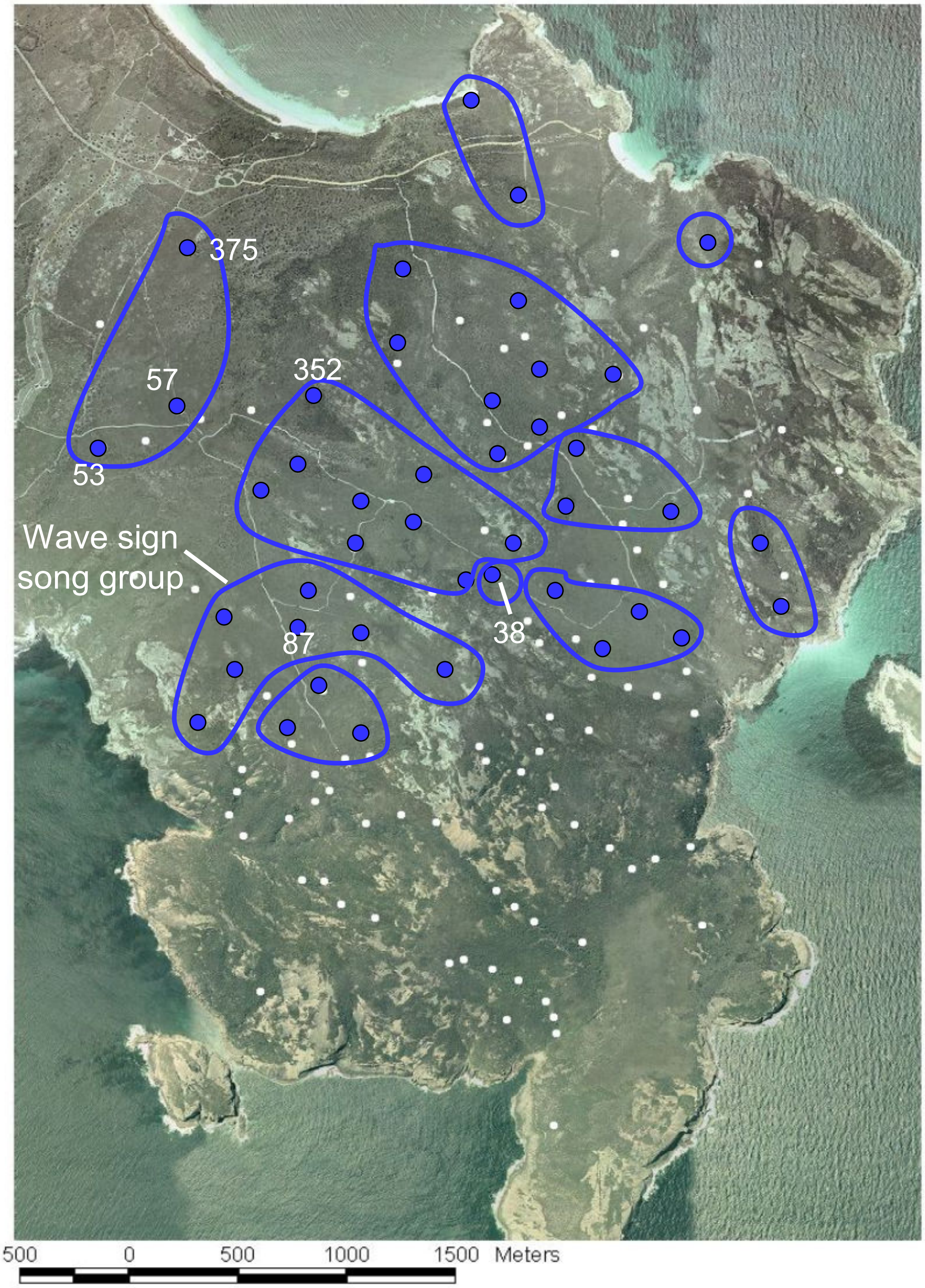


Figure 4.3: July 2004 song groupings. Territories at which songs were recorded are represented by blue dots and groups of birds that shared songs are bounded by a blue line. White dots show territories noted as occupied in the 2004 census that were not recorded in this sampling session. Song groups and territories mentioned in the text are labeled.

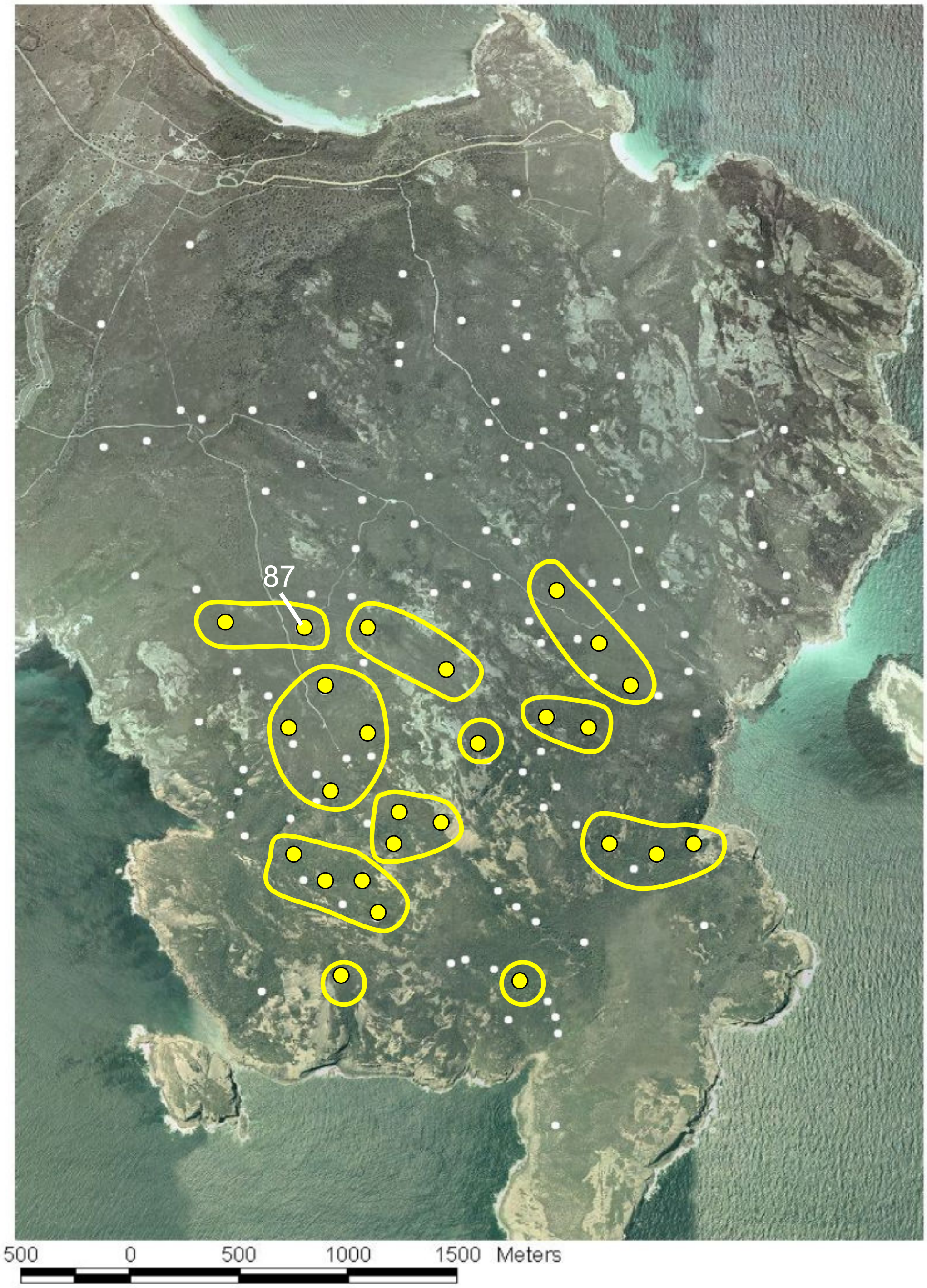


Figure 4.4: September 2004 song groupings. Territories at which songs were recorded are represented by yellow dots and groups of birds that shared songs are bounded by a yellow line. White dots show territories noted as occupied in the 2004 census that were not recorded in this sampling session. The territory mentioned in the text is labeled.

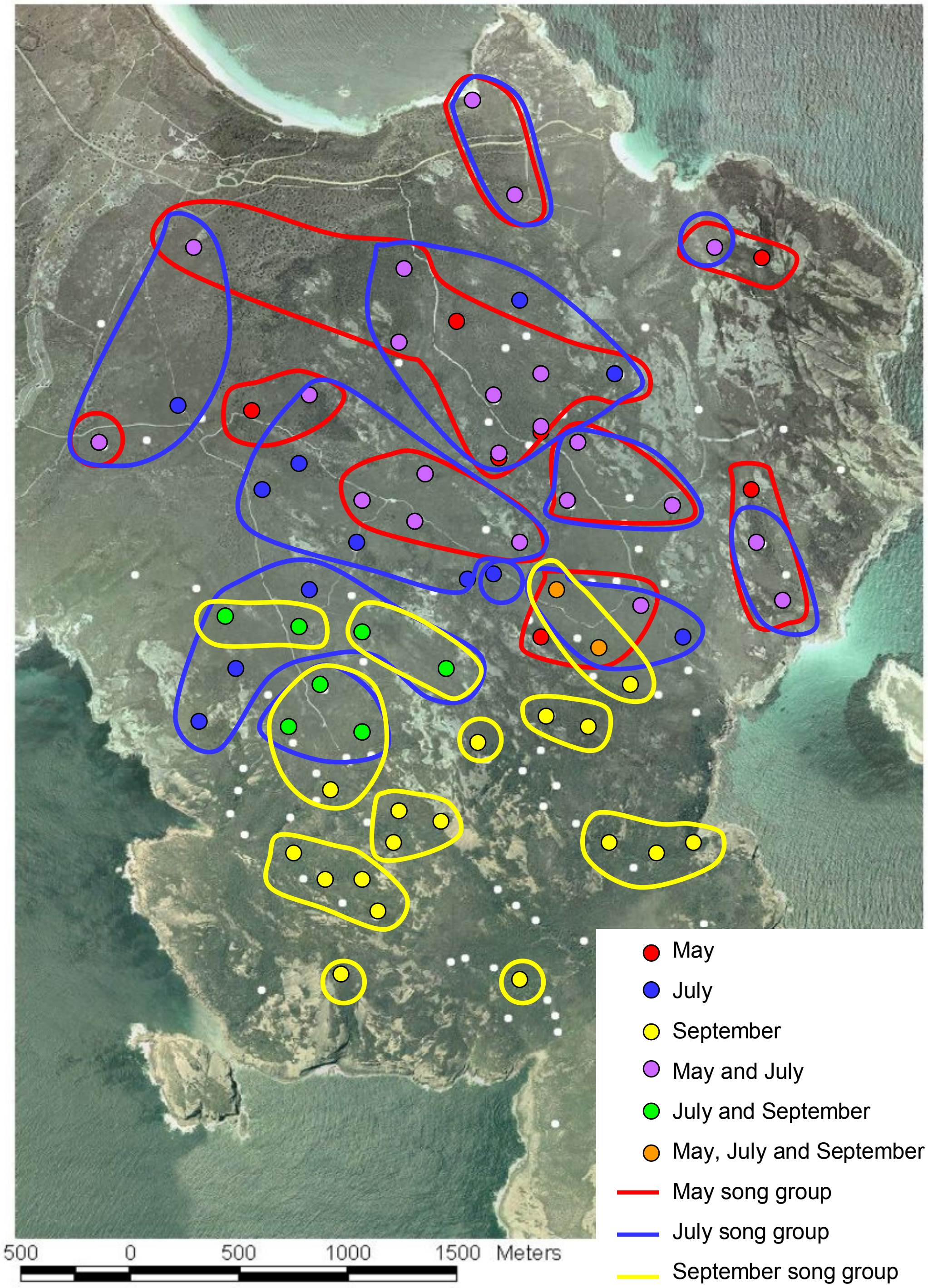


Figure 4.5: Combined 2004 song groupings. Territories at which songs were recorded are represented by coloured dots corresponding to when they were recorded and groups of birds that shared songs are bounded different coloured lines for each sampling session. White dots show territories noted as occupied in the 2004 census from which songs were not recorded.

Figure 4.6: July 2005 song groupings. Territories at which songs were recorded are represented by red dots and groups of birds that shared songs are bounded by a red line. White dots show territories noted as occupied in the 2005 census that were not recorded in this sampling session.

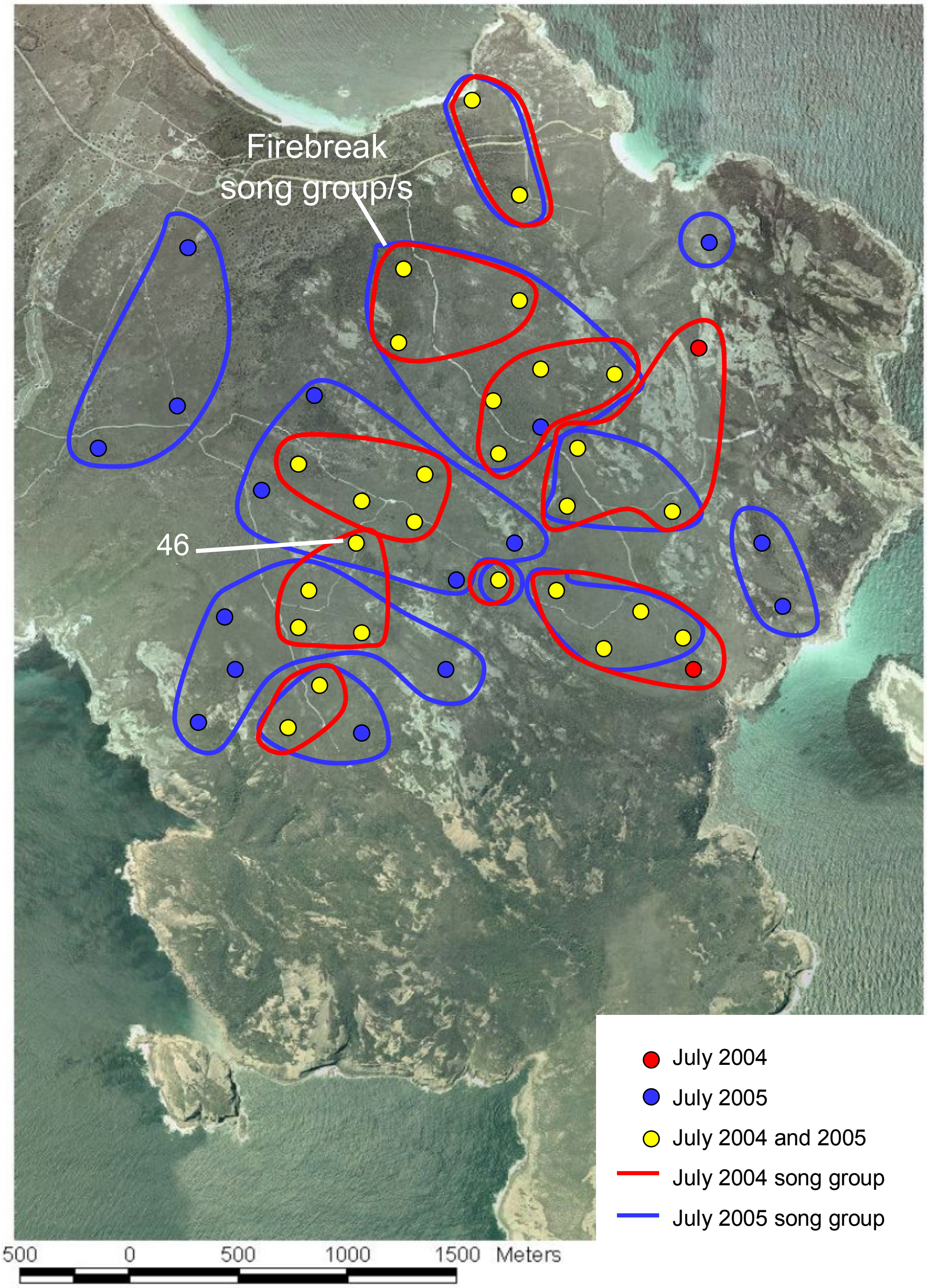


Figure 4.7: Comparison of the July 2004 and July 2005 song groupings. Territories at which songs were recorded are represented by coloured dots corresponding to when they were recorded and groups of birds that shared songs are bounded different coloured lines for each sampling session.

Table 4.5: Summary of song group size, repertoire size and the degree of song sharing in the Mt Gardner area in May, July and September 2004 and July 2005.

	May-04	Jul-04	Sep-04	Jul-05
No. birds recorded	30	47	28	28
Mean no. songs recorded/bird	19.1	14.2	9.2	10.6
Std error	1.53	0.99	0.71	0.77
Min no. songs recorded	2	1	1	3
Max no. songs recorded	36	34	19	19
Mean individual repertoire size (song types/bird)	5.5	5.0	4.6	5.4
Std error	0.30	0.23	0.31	0.24
Min individual repertoire size	2	1	1	3
Max individual repertoire size	9	8	7	8
No. song groups	9	12	12	9
Mean song group size	3.3	3.9	2.3	3.1
Std error	0.78	0.83	0.31	0.42
Min song group size	1	1	1	1
Max song group size	9	9	4	5
Mean group repertoire size (song types/group)	5.4	6.8	6.2	7.6
Std error	0.73	0.82	0.46	0.8
Min group repertoire size	3	1	3	4
Max group repertoire size	9	12	8	11
Mean % songs shared with at least 1 other bird	95.7	89.6	81.3	86.0
Std error	3.37	3.68	5.84	4.42
Min % shared	0	0	0	0
Max % shared	100	100	100	100

Table 4.6: Results of pair-wise repeated measures comparisons of song sharing between all Mt Gardner sampling sessions.

	May 04	Jul 04	Sep 04	July 05
May 04		$F_{(1,24)}=0.020$ $p=0.889$	$F_{(1,1)}=0.339$ $p=0.664$	$F_{(1,15)}=2.661$ $p=0.124$
Jul 04			$F_{(1,9)}=1.017$ $p=0.339$	$F_{(1,26)}=1.615$ $p=0.215$
Sep 04				$F_{(1,5)}=0.987$ $p=0.366$
Jul 05				

Table 4.7: Results of paired comparisons of individual repertoire size for each sampling session

	May 04	Jul 04	Sep 04	July 05
May 04		$F_{(1,23)}=0.966$ $p=0.336$	*	$F_{(1,14)}=3.183$ $p=0.096$
Jul 04			$F_{(1,8)}=0.813$ $p=0.394$	$F_{(1,25)}=0.792$ $p=0.382$
Sep 04				$F_{(1,4)}=2.945$ $p=0.162$
Jul 05				

*sample size too small

4.4 Discussion

The most notable feature of Noisy Scrub-bird song groupings was their discreteness and the high level of song sharing amongst the members of a song group, confirming the observations of Berryman (2003). No differences were found in individual repertoire size, song group size, group repertoire size or song sharing between any of the sampling sessions, indicating that these features are relatively stable over time. During the four sampling periods, no individual was found to possess songs from more than one song group. Generally, the degree of song sharing within a group was high, with the greatest extent of song sharing present in May 2004 (mean = 95.7%). In fact, out of the nine song groups detected in May 2004, seven had complete song sharing amongst all members of the group. Other species in which song sharing is complete between members of a song group include the Village Indigobird (Payne 1985) and the Yellow-rumped Cacique (Trainer, 1989).

The level of song sharing was calculated as the percentage of the song types in a bird's repertoire that were shared by at least one other individual in the song group. Even though complete repertoires for each bird were probably not recorded, this should provide an accurate measure of song sharing because the total number of songs recorded for the entire group should be more than sufficient to sample all the song types sung by that particular group (with the exception of very rare song types). However, if only a small number of birds from each song group was sampled and if the number of songs recorded from each individual was low, there is the possibility that the level of song sharing may appear lower than it actually was. Although no significant differences in song sharing were found, this may account for the lower figure of 81.3% sharing in September 2004.

There were several instances of changes to song group boundaries occurring that were not a result of sampling methods. The first was MG352 changing song group between May 2004 and July 2004. In May 2004, MG352 and MG351 comprised a song group but unfortunately MG351 was not singing at the time of the July 2004 recordings so it was not clear whether both birds made the switch to the larger neighbouring group or whether just MG352 made the change. It is not entirely unexpected for birds on the boundaries to change their repertoire to match a neighbouring group. The fact that scrub-birds are continually in the process of changing the song types in their repertoire over time (see Chapter 5) means that individuals would have the potential to alter their repertoire to match the songs of another group.

In May 2004, MG375 shared his repertoire with the Firebreak Valley song group. At the time of recording he had only recently started singing in this territory and his nearest neighbour from the song group was nearly 1km away. It is likely that he had moved from the Firebreak Valley area to set up a new territory. By July 2004 he no longer shared with the Firebreak Valley group; instead he shared with MG53 and MG57. These territories are slightly closer (~800m) and often more audible, depending on the wind direction. Presumably individuals find it easier to share songs accurately with birds they can clearly hear.

Another case of change in song group boundaries occurred between July 2004 and September 2004 in the Wave Sign group. In July 2004 there were seven individuals recorded in this song group, whereas in September 2004 only four of those birds were singing at the time of sampling. Interestingly, what had previously been one song group had split into two. Prior to the September sampling session, MG87 had been removed from his territory and kept in captivity for a period of 15 days. During this time another scrub-bird regularly visited the aviaries and sang, to the extent that MG87 went quiet. It is possible that during this time MG87's songs were influenced by the other bird and that subsequently these song changes were introduced back into the Wave Sign group when MG87 was released two weeks prior to the September sampling session.

Logically, it would be expected that the greatest changes in song group boundaries would be seen in the 12 month interval between the July 2004 and July

2005 sampling sessions than between any of the 2004 sessions. The major change to boundaries between 2004 and 2005 was the Firebreak song group splitting into two smaller groups. This is similar to what was observed in the Wave Sign group between July 2004 and September 2004. It does not appear that changes to song group boundaries are any more pronounced with greater time intervals (i.e. 12 months compared to 2 months).

The size of song groups varied from one individual to a maximum of nine individuals. The mean song group size in May 2004 was 3.3 birds per group, in July 2004 it was 3.9 birds per group and in September 2004 each song group had an average of 2.3 members. Although not statistically significant, the smaller song group size in September 2004 was most likely caused by a higher proportion of birds not singing during the sampling session and thus being missed from the analysis. If all the territories occupied in 2004 had been sampled, these figures may well have been higher. However it was impractical to spend the amount of time in every territory that would be required to ensure that every bird was recorded.

Likewise, sampling methods would generally have underestimated repertoire size (average 92% of song types in a bird’s repertoire given within 10 songs (Berryman, 2003)). Therefore the actual repertoire sizes were probably slightly higher. Considering the high level of song sharing within a song group, group repertoire size may be a better reflection of an individual’s actual repertoire size.

Overall, the majority of individuals belonged to a song sharing group of two or more individuals, or at least had neighbours who were not recorded that were likely to share songs with them. There was one exception to the rule (MG38) that did not appear to share songs with any other individual. In addition, he was unusual in that he had a relatively small repertoire size of three very similar song types.

In comparison to the song groupings present in 2002 (Berryman, 2003), the level of song sharing differed quite markedly (52% as opposed to an average of 81.3 - 95.7% in 2004). This was because the methods used in 2002 did not take into account the effects of repertoire change. As a result, there were many cases in which one bird was recorded, and its neighbour not recorded until some time later, by which stage song types had changed to the extent that they could not be accurately identified as the same song type. Also, repertoires were cumulative and therefore appeared larger than they actually were at any one point in time. Hence, birds that were recorded regularly appeared to have much larger repertoires and birds that were only recorded on one or two occasions appeared to have comparatively small repertoires. Thus, the level of song sharing when comparing two such birds would be relatively low.

The spatial patterns of song sharing seen in the Noisy Scrub-bird could not occur purely by chance. Song sharing occurred amongst discrete groups of up to nine neighbouring males. Within a song group, song sharing was often complete, or close to it, whereas neighbouring song groups had no song types in common. Comparisons to other species and a discussion of song groupings in relation to repertoire change and the possible reasons for these observed patterns have been deferred until Chapter 8. Repertoire change amongst the song groups present in the Mt Gardner area is examined in the following chapter.

Chapter 5 –
Repertoire change on Mt Gardner

5.1 Introduction

The songs of some bird species, such as Song Sparrows (Nordby *et al.*, 2002), and Nightingales (Kipper *et al.*, 2004), are constant over time and do not alter, whereas those of other species, such as Village Indigobirds (Payne, 1985), Thrush Nightingales (Sorjonen, 1987), Yellow-rumped Caciques (Trainer, 1989) and Great Tits (McGregor and Krebs, 1989) change over time.

Possible sources of repertoire change include improvisation, copying errors, the introduction of new songs by immigrants, or drift in song structure as minor changes accumulate (Lemon, 1975; Payne *et al.*, 1981; Podos *et al.*, 2004). Repertoire change has previously been reported in the Noisy Scrub-bird (Smith and Robinson, 1976) although no information was presented on either the rate or the source of repertoire change. Berryman (2003) reported that territorial songs changed rapidly over time. All members of a song group made the same changes to their shared song types, with songs noticeably different within as little as a month (Berryman, 2003). The source of this change was most likely attributable to modification of existing song types and the introduction of new song types. However, more work was needed to confirm this because the sampling methods used by Berryman (2003) were not designed to investigate repertoire change.

This study primarily set out to investigate the source of repertoire change in the Noisy Scrub-bird. The aim was to sample the songs of 10 individuals at frequent intervals over a period of 12 months or more in order to track the process of repertoire change, measure repertoire turnover and song type persistence. More specifically, it was hoped to identify any individuals that were introducing changes to the shared song types of a song group.

5.2 Methods

5.2.1 Repertoire change

Ten territories in the Mt Gardner area of Two Peoples Bay Nature Reserve were selected for recording to monitor changes in the bird's repertoire of song types. Selection of territories was non-random. They were chosen for ease of access and as a representation of four different song groups (Figure 5.1). Every 7-14 days these territories were visited and any singing recorded. Usually a sample of 10 or more songs was recorded from each singing bird (as described in Chapter 2). If a bird was not singing then at least 30-60 minutes would be spent waiting for it to sing.

Recording of all the focal birds on any given day was usually not feasible because of time constraints and only occurred once. Hence, sampling of two or three birds from each song group was invaluable as it meant that on most occasions at least one bird from each song group was recorded. As such, sampling was aimed at monitoring repertoire change in song groups rather than individuals. Thus, it is probably more correct to say that four song groups were selected to monitor any changes to their songs. If the assumption is made that all birds within a song group make the same changes to their shared song types over time (as shown in Berryman 2003), then the group can be treated as a whole, looking at group rather than individual repertoire change.

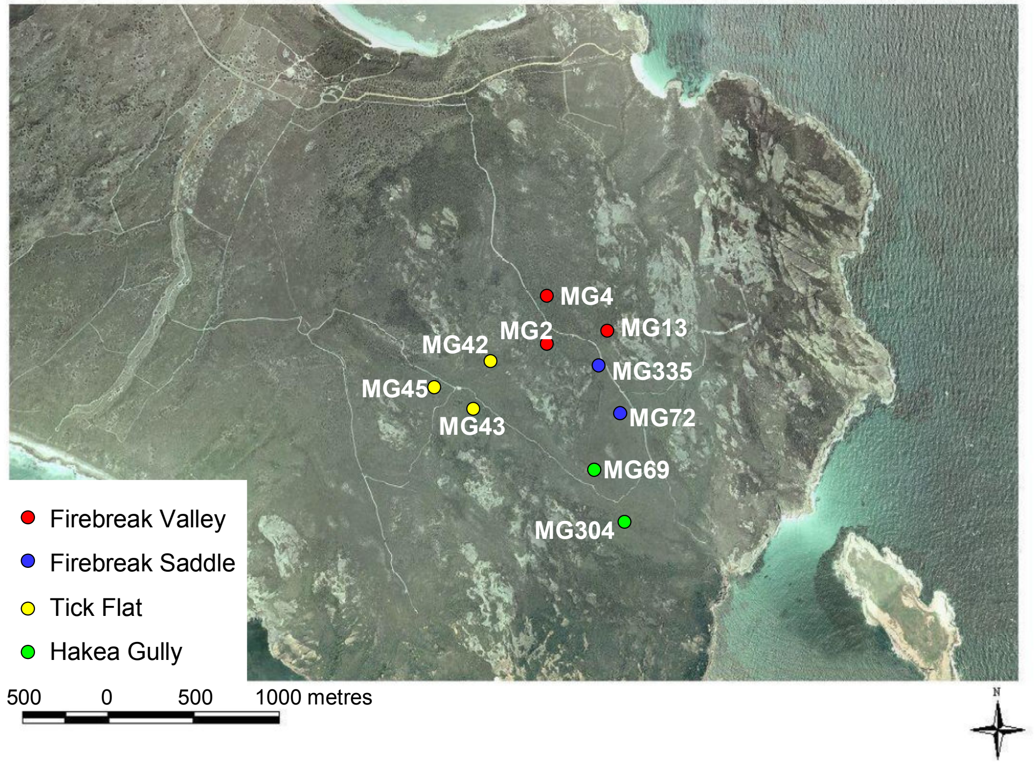


Figure 5.1: Locations of the 10 focal territories in the Two Peoples Bay Nature Reserve. Territories that are the same colour belong to the same song-sharing group.

Recordings were made at varying times throughout the day. During the summer, non-breeding months it was more important to focus on the early morning and late afternoon peaks in singing. Smith and Forrester (1981) reported that maximum song output was in the two to three hours after sunrise. Singing can, however, occur at any time of the day, even if only for a brief burst. The time of day when each bird was recorded varied. However, Portelli (2004) reported that the song types delivered, and their relative proportions in a repertoire, remained consistent throughout the day, although the quantity of song did vary.

Recordings were carried out over a 16 month period from 15 April 2004 to 9 July 2005. This encompassed more than the entire seasonal cycle of song activity and provided a 4 month period of overlap in which repertoire turnover after 12 months could be determined.

Sampling of the songs present in each group's repertoire was carried out at intervals of not more than 14 days. Based on previous work on repertoire change (Berryman 2003) it was decided that this was a suitable period over which to pick up changes and probably the maximum interval after which songs were easily recognisable as the same type, even if they had been altered during this time (an example of this can be seen in Figure 5.5). A longer interval between recordings may have prevented recognition of songs as the same type and led to the conclusion that repertoire change was occurring through innovation rather than modification.

Each recording was analysed using the methods described in Chapter 2, with the resulting spectrograms sorted into the song types present for each song group during each sampling session. These were then sorted to show the presence of each of these song types in the repertoire over time and the changes that occurred to these song types.

5.2.2 Intensive recordings

In an attempt to quantify the rate of repertoire change and potentially identify which individual was introducing the changes, three territories (MG42, MG43 and MG45 – see Figure 5.1 for locations) were selected for intensive recording over a nine day period from 1 to 9 May 2005. Six half-hour recording sessions were carried out each day simultaneously at all three territories except when the weather was unsuitable for recording. The times of these sessions were 0630-0700, 0830-0900, 1030-1100, 1230-1300, 1430-1500 and 1700-1730h WST.

These recordings were converted to wave files using Syrinx (John Burt, www.syrinxpc.com) and sorted into song types. It was planned to use Sound Analysis Pro (Tchernichovski and Mitra, 2004) to measure the changes in acoustic features of each song type sung by each individual over the nine day sampling period. However, on closer examination the majority of the songs were not of adequate quality to support rigorous analysis. To enable accurate measurements of acoustic features the recording needs to have a high signal-to-noise ratio with very little background noise. An example of high and low quality recordings is shown in Figure 5.2. Unfortunately, weather conditions during the sampling period were often unfavourable and the number of good quality recordings was too small to warrant further analysis using this approach.

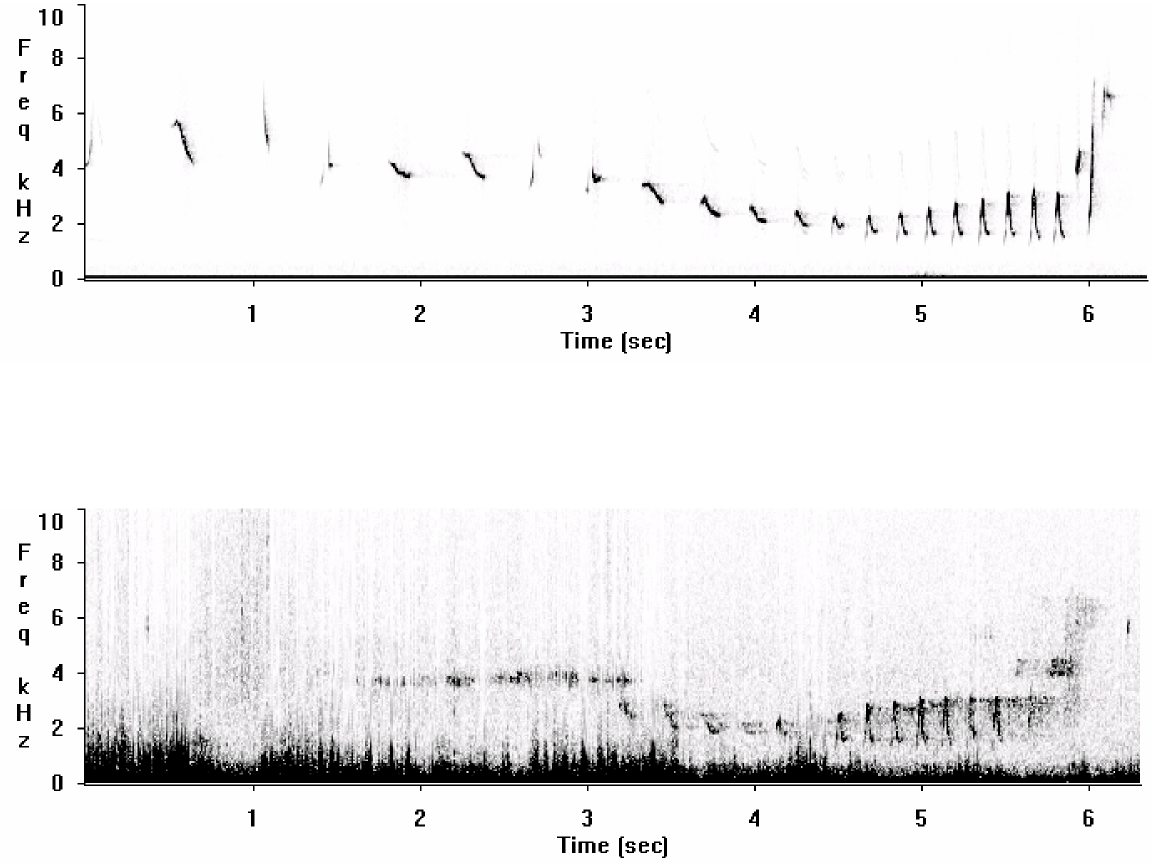


Figure 5.2: An example of the quality of recording required for detailed analysis (top) and a poor-quality recording of the same song type that is unsuitable for further analysis (bottom).

5.2.3 Variation in repertoire size over time

The sampling of the 10 focal individuals over the 16 month period also allowed seasonal changes in repertoire size to be monitored. Group rather than individual repertoire size was studied because the sampling methods were designed to detect changes in the repertoires of each of the four song groups as a whole. The 16 month sampling period was divided into half-monthly intervals. For each sampling interval, the number of song types detected in each song group was noted. In the few rare cases in which no individuals from a song group were recorded during a given sampling interval, repertoire size was inferred from the preceding and subsequent intervals. For each sampling interval, the mean repertoire size of the four groups was calculated to provide a measure of the change in repertoire size over time.

5.2.4 Song rate

The intensive recordings of MG42, MG43 and MG45 in May 2005 provided an opportunity to assess song rate in these three individuals. Song rate is a measure of the number of songs per minute. Only the portion of each set of recordings during which all three birds were recorded simultaneously was used to calculate song rate so that results were directly comparable.

5.2.5 Song matching

The simultaneous recordings of these three individuals also allowed song matching to be examined. When digitised with Syrinx, the time that each recording was started was used to set the timer to name each file automatically with the exact time that song was sung. Each file (containing a single song) was examined to determine what song type it contained. A list of these file names and their types was then arranged into chronological order to reveal any cases where a song type sung by one individual was matched with a song of the same type sung by a different individual.

The song matching data from the three territories were analysed using ANOVA with territory number as the independent variable and the number of times that an individual was matched by each of the other two individuals as the dependent variable. A Least Squares Difference test was then carried out to determine if song matching varied between each of the possible combinations of individuals. Song rate was used as a covariate because the more often a bird sang, the greater the opportunities for other individuals to match it.

5.3 Results

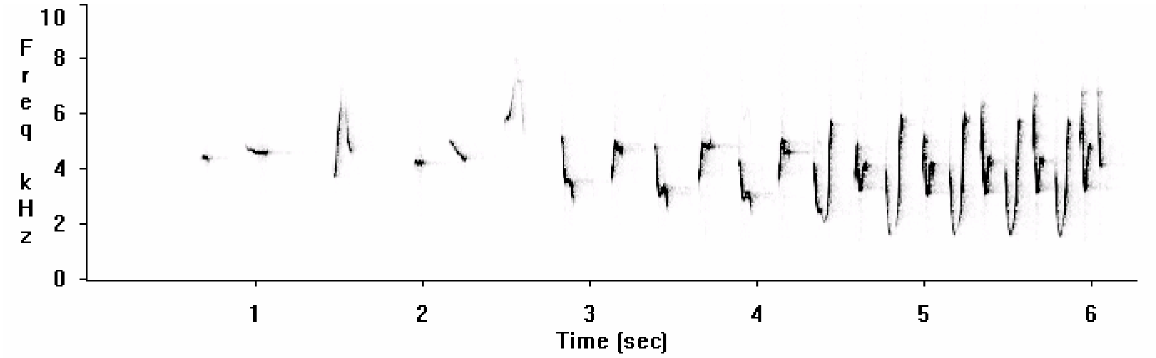
5.3.1 Repertoire change

Repertoire change occurred through modification of existing song types (Figure 5.3), divergence of song types into two separate types (Figure 5.4) and the introduction of new song types. Tables 5.1 – 5.4 show how repertoire composition altered over time in each of the song groups. Figure 5.5 gives an example of how three members of a song group make the same changes to a shared song type.

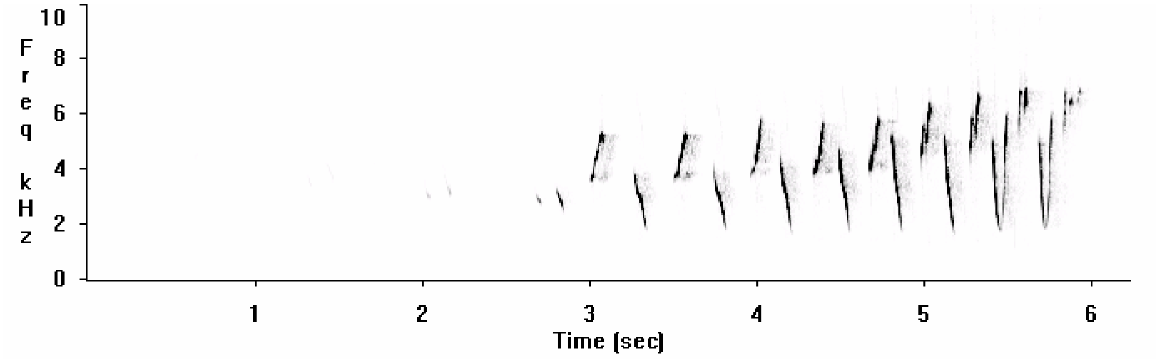
The average life of a song type for each song group ranged between 5.1 ± 1.1 (mean ± SE) and 7.2 ± 2.1 months (Table 5.5). Eight out of a total of 62 different song types (12.9%) detected in the four song groups persisted for the entire 16 month sampling period. It is important to note that even though some song types were deemed to persist for this length of time, they were continually being modified (refer to Figure 5.3 for an example of this). In nearly all cases, song types showed some modification during the intervals between each sampling period (Figure 5.6).

If individuals had been sampled only at 12 month intervals then repertoire turnover would be said to be complete because song types would no longer be recognisable as the same type. However, with the regular sampling regime, the progression of song types was apparent and on average 44% of the song types were still present in the repertoire of a song group after a period of 12 months, albeit in a modified form.

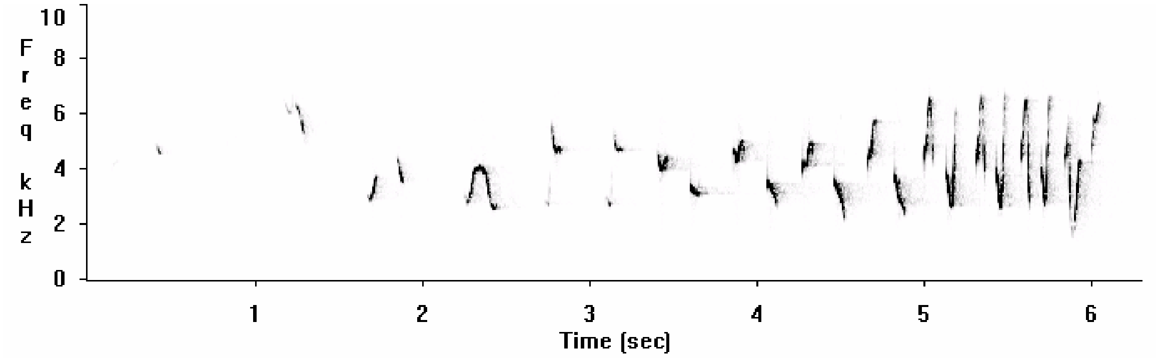
14 June 2004



27 November 2004



19 February 2005



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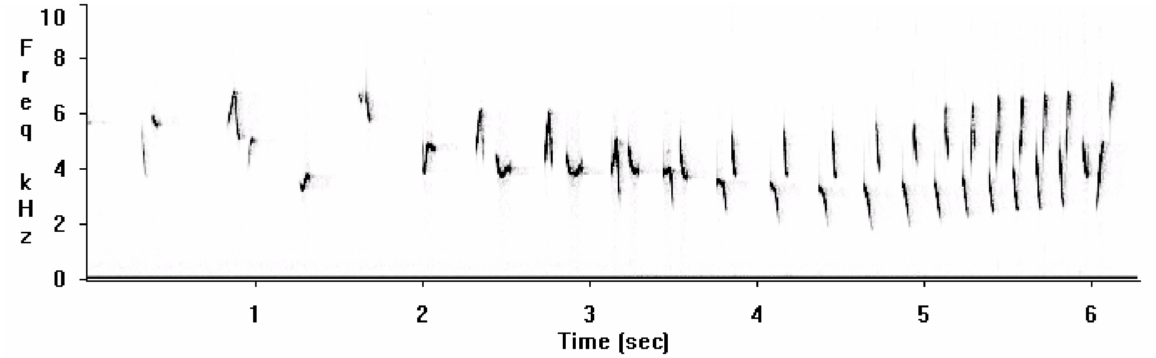

Figure 5.3: Modification of a song type given by the Tick Flat song group over a 12 month period.

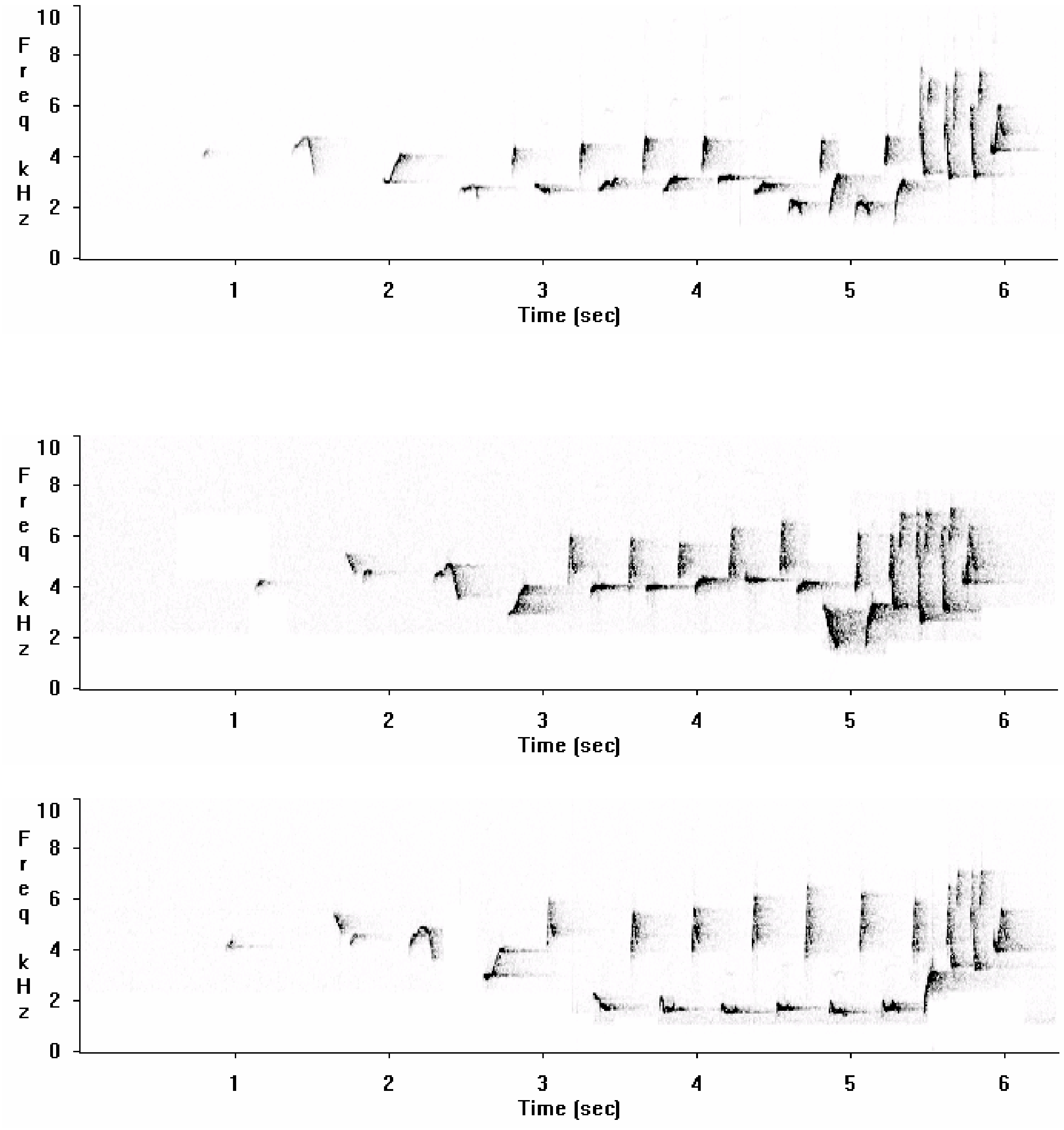

Figure 5.4: Example of divergence of a single song type (top) into 2 separate song types. This divergence occurred in an 11 day period.

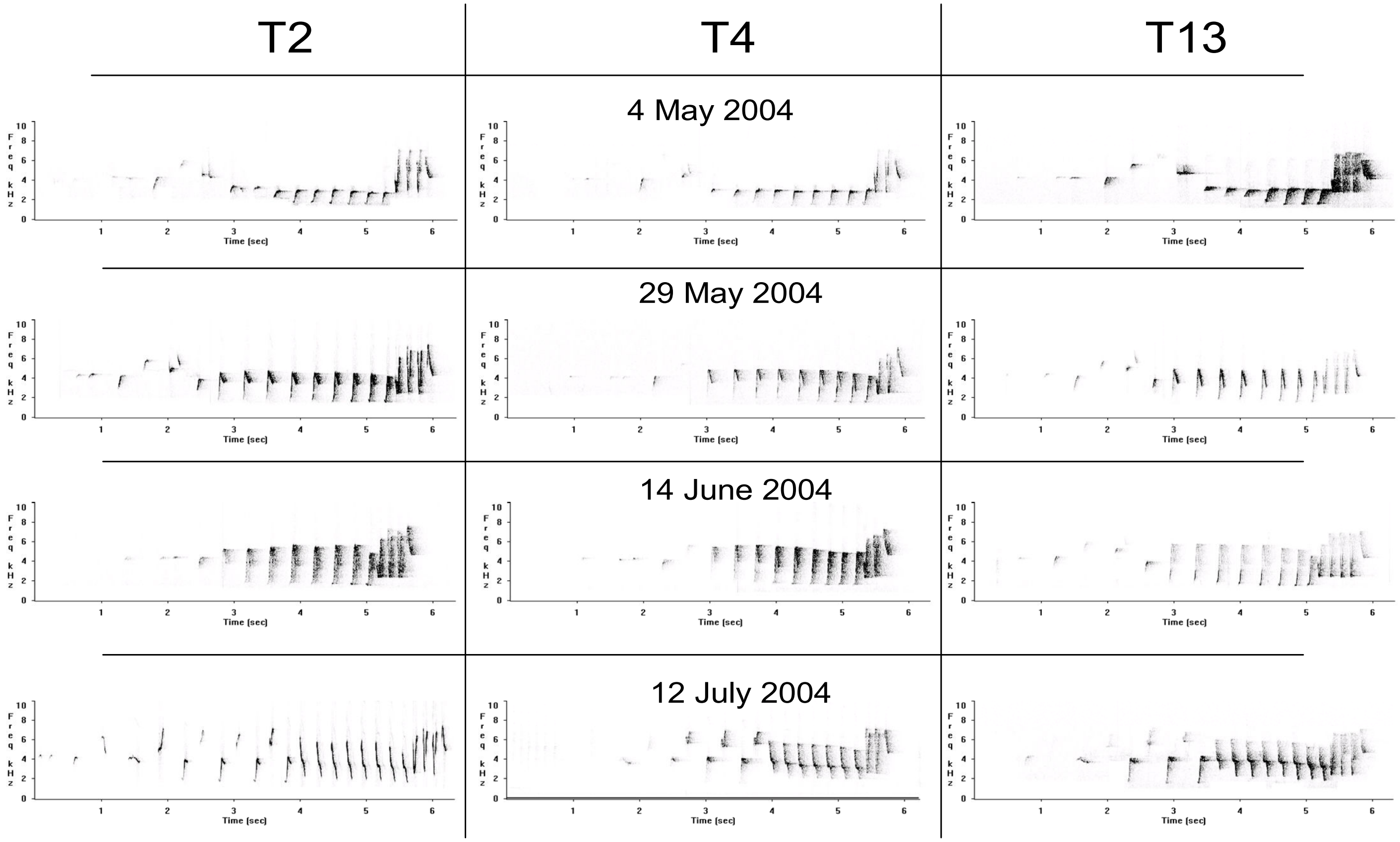

Figure 5.5: An example of how three members of a song group make the same changes to a shared song type.

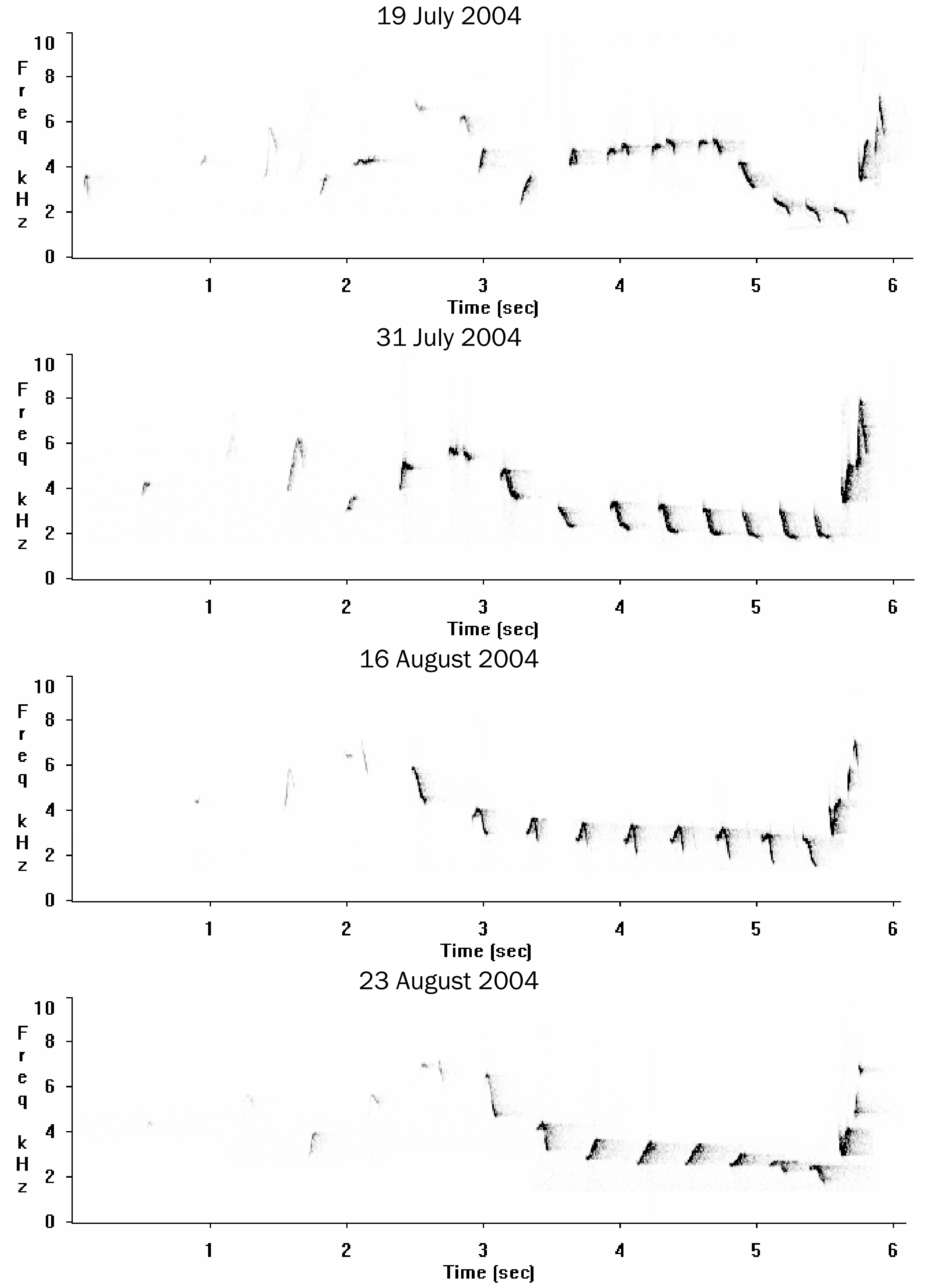

Figure 5.6: Example of the degree of modification seen in a single song type over a period of 5 weeks.

Table 5.1: Persistence of song types in the Firebreak Valley song group. Each row represents a different song type. Grey shading indicates the presence of that song type in the song group's repertoire during that sampling interval.

	16-30 Mar 2004	1-15 Apr 2004	16-30 Apr 2004	1-15 May 2004	16-31 May 2004	1-15 Jun 2004	16-30 Jun 2004	1-15 Jul 2004	16-31 Jul 2004	1-15 Aug 2004	16-31 Aug 2004	1-15 Sep 2004	16-30 Sep 2004	1-15 Oct 2004	16-31 Oct 2004	1-15 Nov 2004	16-30 Nov 2004	1-15 Dec 2004	16-31 Dec 2004	1-15-Jan 2005	16-31 Jan 2005	1-14 Feb 2005	15-28 Feb 2005	1-15 Mar 2005	16-31 Mar 2005	1-15 Apr 2005	16-30 Apr 2005	1-15 May 2005	16-31 May 2005	1-15 Jun 2005	16-30 Jun 2005	1-15 Jul 2005
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B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
C	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
D	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																				
E	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
F	▨	▨																														
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Table 5.2: Persistence of song types in the Tick Flat song group. Each row represents a different song type. Grey shading indicates the presence of that song type in the song group's repertoire during that sampling interval.

	16-30 Mar 2004	1-15 Apr 2004	16-30 Apr 2004	1-15 May 2004	16-31 May 2004	1-15 Jun 2004	16-30 Jun 2004	1-15 Jul 2004	16-31 Jul 2004	1-15 Aug 2004	16-31 Aug 2004	1-15 Sep 2004	16-30 Sep 2004	1-15 Oct 2004	16-31 Oct 2004	1-15 Nov 2004	16-30 Nov 2004	1-15 Dec 2004	16-31 Dec 2004	1-15-Jan 2005	16-31 Jan 2005	1-14 Feb 2005	15-28 Feb 2005	1-15 Mar 2005	16-31 Mar 2005	1-15 Apr 2005	16-30 Apr 2005	1-15 May 2005	16-31 May 2005	1-15 Jun 2005	16-30 Jun 2005	1-15 Jul 2005
K		▨	▨																													
L		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																					
M		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨															
N		▨	▨	▨	▨	▨	▨	▨																								
O		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
P			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																		
Q			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨														
R					▨	▨	▨	▨	▨																							
S								▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
T												▨																				
U																▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

Table 5.3: Persistence of song types in the Hakea Gully song group. Each row represents a different song type. Grey shading indicates the presence of that song type in the song group's repertoire during that sampling interval.

	16-30 Mar 2004	1-15 Apr 2004	16-30 Apr 2004	1-15 May 2004	16-31 May 2004	1-15 Jun 2004	16-30 Jun 2004	1-15 Jul 2004	16-31 Jul 2004	1-15 Aug 2004	16-31 Aug 2004	1-15 Sep 2004	16-30 Sep 2004	1-15 Oct 2004	16-31 Oct 2004	1-15 Nov 2004	16-30 Nov 2004	1-15 Dec 2004	16-31 Dec 2004	1-15-Jan 2005	16-31 Jan 2005	1-14 Feb 2005	15-28 Feb 2005	1-15 Mar 2005	16-31 Mar 2005	1-15 Apr 2005	16-30 Apr 2005	1-15 May 2005	16-31 May 2005	1-15 Jun 2005	16-30 Jun 2005	1-15 Jul 2005
V		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
W		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																				
X		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Y		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
Z		▨	▨	▨																												
AA		▨	▨	▨	▨	▨	▨																									
AB		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AC		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨							
AD		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																				
AE		▨	▨	▨	▨	▨	▨	▨	▨	▨																						
AF																		▨	▨	▨												
AG																		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AH																				▨												
AI																						▨	▨									
AJ																						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AK																								▨	▨	▨	▨	▨	▨	▨	▨	▨
AL																									▨							
AM																												▨	▨	▨	▨	▨
AN																													▨	▨	▨	▨
AO																																▨

Table 5.4: Persistence of song types in the Firebreak Saddle song group. Each row represents a different song type. Grey shading indicates the presence of that song type in the song group's repertoire during that sampling interval.

	16-30 Mar 2004	1-15 Apr 2004	16-30 Apr 2004	1-15 May 2004	16-31 May 2004	1-15 Jun 2004	16-30 Jun 2004	1-15 Jul 2004	16-31 Jul 2004	1-15 Aug 2004	16-31 Aug 2004	1-15 Sep 2004	16-30 Sep 2004	1-15 Oct 2004	16-31 Oct 2004	1-15 Nov 2004	16-30 Nov 2004	1-15 Dec 2004	16-31 Dec 2004	1-15-Jan 2005	16-31 Jan 2005	1-14 Feb 2005	15-28 Feb 2005	1-15 Mar 2005	16-31 Mar 2005	1-15 Apr 2005	16-30 Apr 2005	1-15 May 2005	16-31 May 2005	1-15 Jun 2005	16-30 Jun 2005	1-15 Jul 2005
AP	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AQ	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AR	▨	▨	▨	▨	▨	▨	▨	▨	▨																							
AS	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨															
AT	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																					
AU			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
AV			▨	▨	▨	▨	▨	▨	▨	▨	▨																					
AW			▨	▨	▨	▨	▨																									
AX								▨																								
AY								▨																								
AZ										▨	▨	▨	▨	▨	▨																	
BA												▨	▨	▨	▨	▨	▨	▨	▨	▨												
BB														▨	▨	▨	▨															
BC															▨																	
BD																	▨	▨	▨	▨	▨											
BE																							▨	▨	▨	▨	▨	▨	▨	▨		
BF																									▨	▨	▨	▨	▨	▨		
BG																									▨	▨	▨	▨	▨	▨	▨	▨
BH																									▨	▨	▨	▨	▨	▨	▨	▨
BI																									▨	▨	▨	▨	▨	▨	▨	▨
BJ																											▨	▨				

Table 5.5: Mean persistence in months of song types in each of the four song groups.

Song group	Mean life of song types (months) ± SE
Firebreak Valley	7.2 ± 2.1 (n=10)
Tick Flat	6.5 ± 1.4 (n=11)
Hakea Gully	5.4 ± 1.1 (n=20)
Firebreak Saddle	5.1 ± 1.1 (n=21)

5.3.2 Variation in repertoire size over time

The repertoire size of song groups was larger during the winter breeding months than the summer months (Figure 5.7). Mean group repertoire size peaked at 8.3 ± 1.1 and 8.3 ± 0.6 song types per group in June and July 2004 respectively and dropped to a low of 3.5 ± 0.3 song types in January 2005.

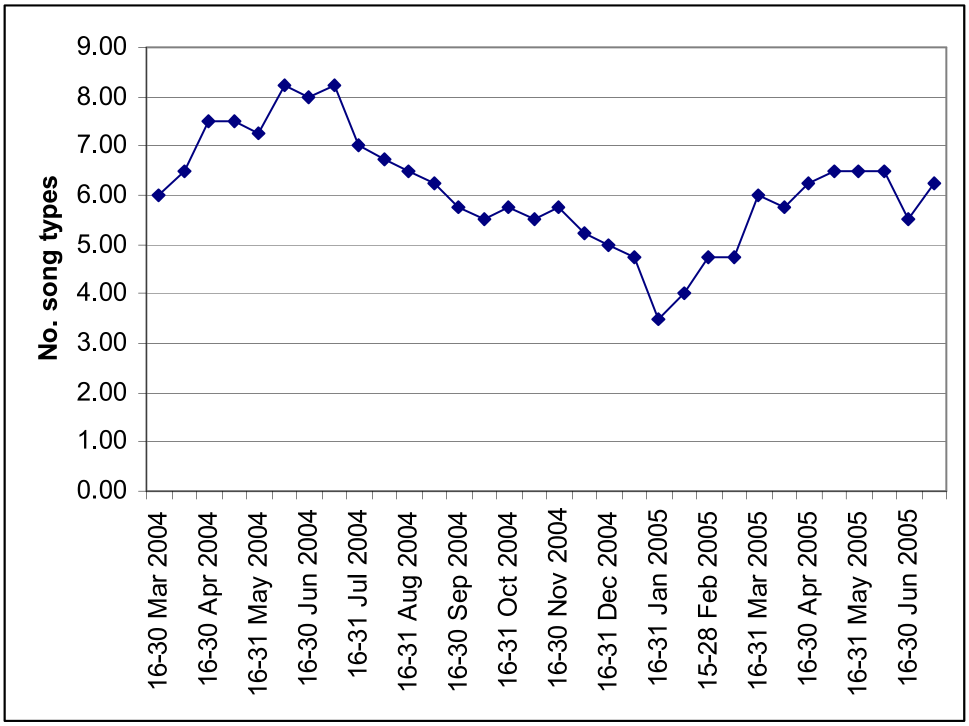


Figure 5.7: Song group repertoire size (averaged from the 4 song groups studied) over a 16 month period. Standard errors of means were from ±4% to ±25% of means. Breeding season extends from April to October.

5.3.3 Song rate

Song rates in the three individuals studied ranged from 0.53 ± 0.11 to 0.80 ± 0.12 songs/ minute (Table 5.6). All three of these individuals had been captured for radio-tracking within a few months of this sampling (see Chapter 3). As a routine part of their capture, they were all weighed and their total head length, wing length, tail length and tarsus diameter were measured (Table 5.6). Out of interest, these measurements were compared to song rate. The only measurement that appeared to show any congruence with song rate was weight.

Table 5.6: Song rate and morphometric measurements of the individuals in the three territories selected for intensive recordings.

	Song rate ± SE (songs/minute)	Weight (g)	Head-bill (mm)	Wing (mm)	Tail (mm)	Tarsus diam. (mm)
MG42	0.62 ± 0.12	50.0	45.3	77	130	3.4
MG43	0.53 ± 0.11	48.0	44.5	81	101	3.7
MG45	0.80 ± 0.12	51.5	42.9	81	71	3.6

5.3.4 Song matching

Song type matching was observed regularly between MG42, MG43 and MG45 during the intensive recordings in May 2005. However, it did occur less often than expected by chance (Table 5.7). By chance alone, it would be expected that 20% of songs were matched (each individual had 5 song types in his repertoire). MG45 was matched by the other two individuals the most frequently and MG43 was matched the least (Table 5.8).

Table 5.7: Observed incidence of song matching (% songs matched by the other two study individuals).

	% songs matched
MG42	13.5
MG43	18.5
MG45	16.0

Table 5.8: Incidence of song type matching between the three study individuals.

		matched by…		
		MG42	MG43	MG45
1st song	MG42		57	57
	MG43	55		50
	MG45	65	63	

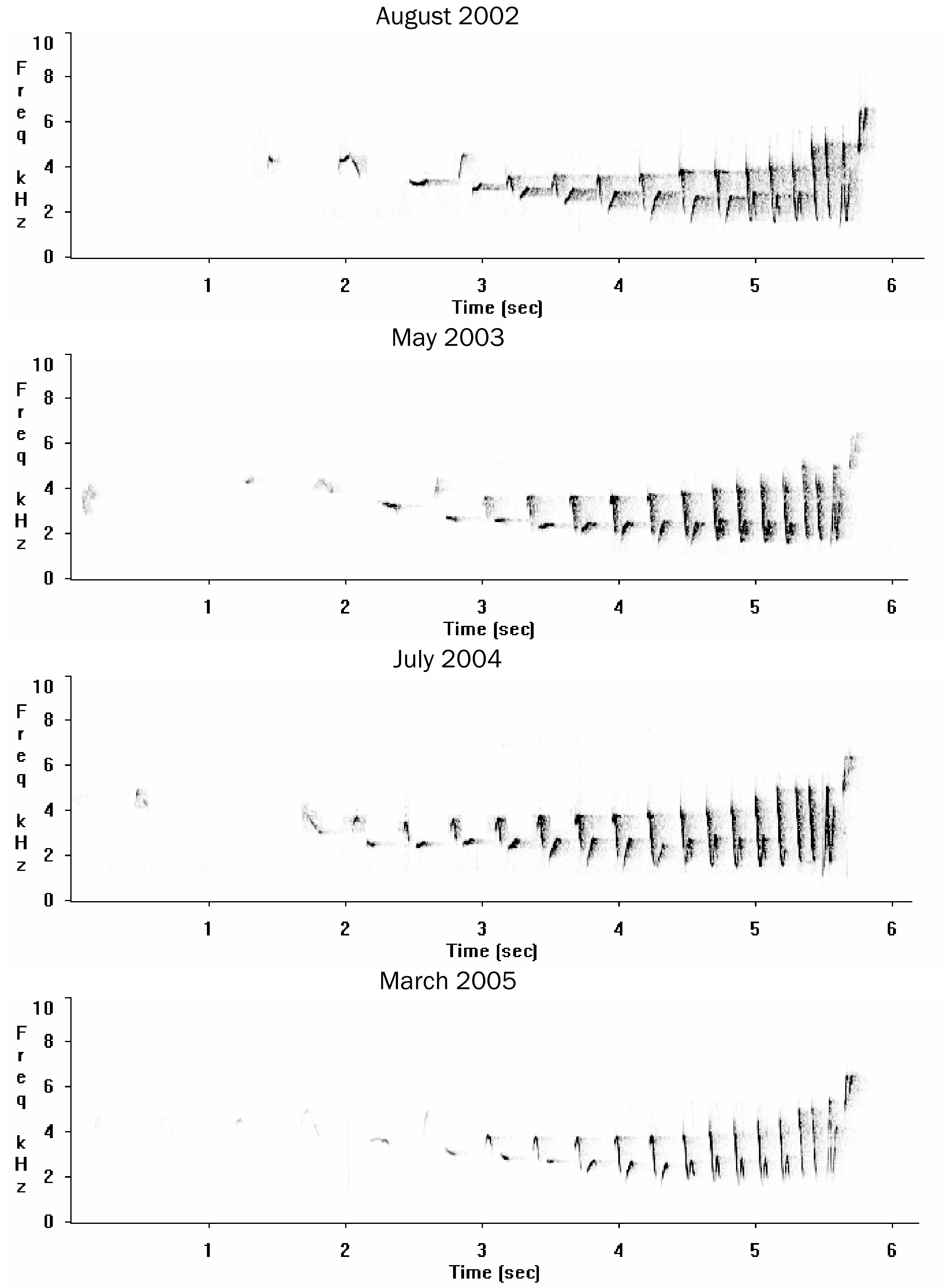
Song matching varied significantly between territories ($F_{(2,2)} = 54.13$, $p = 0.018$) and the Least Squares Difference test revealed that all groups were different from each other (Table 5.9). The covariate of song rate was not significant ($F_{(1,2)} = 11.802$, $p = 0.075$).

Table 5.9: Results of a Least Squares Difference test of the incidence of song matching.

	MG42	MG43	MG45
MG42		0.048	0.021
MG43	0.048		0.008
MG45	0.021	0.008	

5.3.5 An exception to the rule…

One interesting exception to the rule of constant repertoire change was observed in MG38. He was not one of the study birds, but incidental recordings of him over four consecutive breeding seasons from 2002 to 2005 revealed that the same song type remained in his repertoire unchanged over this period (Figure 5.8).


August 2002

May 2003

July 2004

March 2005

Figure 5.8: One of the song types sung by MG38 that remained unchanged for four consecutive years from 2002 to 2005

5.4 Discussion

The aim of this study was to further investigate repertoire change in the Mt Gardner population of Noisy Scrub-birds. Repertoire change was rapid and, with the exception of one individual, it was found in every individual studied in the Mt Gardner population. The source of repertoire change was mainly modification of existing song types with occasional divergence of a single song type into two distinct song types and some innovation providing new song types.

The average life of a song type was approximately six months. Although some song types persisted for the entire 16 month sampling period they were continually being modified and a year later could no longer be recognised as the same type. In some cases change was very rapid and this may account for some of the apparently new song types that appeared in the repertoires of the song groups. Although sampling was relatively frequent, if a song could not easily be recognised as the same type as the previous session then it was called a new song type. While rapid modification undoubtedly explains some of the new song types, there were definitely cases where novel song types bearing no similarity to existing song types did appear.

Without sampling to detect the progression of song type change over time, repertoire change would be said to be complete from one year to the next. The rate of repertoire change in several other species also appears to be rapid. For example, 78% of Yellow-rumped Cacique songs are distinct from those present in the same colony the previous year (Trainer, 1989). As with Noisy Scrub-birds, much of this variation appears to be a result of gradual modification of song types over time and all member of the colony make the same changes to their shared song types. Village Indigobirds also undergo repertoire change, with all or most of their 20 or so song types unrecognisable after 4-5 years (Payne, 1985). Other reported rates of repertoire change include 12% of Starling song types being unrecognisable after 3 years (Adret-Hausberger 1986), and the repertoire of Great Tits altering by 32-46% per year (McGregor and Krebs, 1989).

Another aim of this study was to attempt to identify any individual that was introducing changes to the shared songs of the other members of the song group. Unfortunately the sampling designed to test this was unsuccessful because of bad weather and it could not be repeated because of time constraints. However, this aspect would be well worth investigating in the future. Although it is very labour-intensive, it could yield very interesting results as to how coordinated repertoire change occurs in a song group.

One by-product of the work on repertoire change was a measure of repertoire size over time, as well as information on song rate and song matching. Repertoire size showed a definite seasonal trend with a peak during the winter breeding months, more than twice that of the of the summer repertoire size. This is in accord with the earlier work of Berryman (2003) and presumably is a consequence of the increased competition during the breeding season.

Song rate varied between MG42, MG43 and MG45, and the limited data suggested there may be some congruence with body weight. The heavier the bird, the more frequently it sang. However, the three individuals did not provide an adequate sample from which to draw any definite conclusions about a relationship between weight and song rate. Further investigation would be interesting, although measuring song rate is time-consuming and capturing scrub-birds just to measure them is impractical.

Song type matching occurred less often than expected by chance, suggesting that it may in fact be actively avoided. Potentially, song matching could vary seasonally as seen in the Song Sparrow. In this species, song type matching is more common early in the breeding season (Beecher *et al.*, 2000). The work on the Noisy Scrub-bird was also carried out early in the breeding season, so the incidence of song matching may decline even further at other times of the year.

Song matching in the Noisy Scrub-bird may provide a mechanism by which an individual could check the accuracy of its song against the bird it is matching. If this were the case it would be expected that the song leader would be matched much more frequently than the others, at least if they conform with the dominance scenario proposed by Berryman (2003) and discussed further in Chapter 8.

It was hoped that the incidence of song matching between MG42, MG43 and MG45 would indicate that a certain individual was consistently taking on a leader role in song matching. Such a situation occurs in Marsh Wrens, with the dominant male matched by the subordinate (Kroodsma, 1979). While MG45 was matched more often than MG42 and MG43, he also matched them on many occasions. Without more evidence of the dominance relationships between the three birds it is difficult to draw conclusions about whether the leader role in song matching reflects dominance.

In addition, the experimental design was problematic in that it did not sample the entire song group. However, this was unavoidable because there were no song groups that were both small enough (limited by three sets of recording equipment) and easily accessible enough to permit simultaneous intensive sampling. Therefore, a compromise was made and three individuals central within a song group of five birds were selected. The assumption was made that if there was a dominant bird it would most likely be towards the centre of the group. Also, these three birds were more consistent singers than the two not sampled, something that may indicate male quality and dominance (e.g. Gottlander, 1987; Nystrom, 1997; Welling *et al.*, 1997)

Observations from playback during capture attempts suggest that song type matching may be more common in an aggressive context (pers. obs.). Matched counter-singing during an escalation of aggression has also been reported in Black-capped Chickadees (Shackleton and Ratcliffe, 1994; Otter *et al.*, 2002). Song type matching in other species has been proposed to function as a graded signal of aggression (Krebs *et al.*, 1981) and this has been demonstrated in Song Sparrows (Burt *et al.*, 2001). Therefore, song type matching may play a much more important role on the rare occasions when there is a close interaction between two males, as opposed to the singing that normally occurs between males in established territories.

The major finding of this study of temporal changes in Noisy Scrub-bird songs was a confirmation of rapid, cohesive repertoire change in song groups. This repertoire change was a result of modification and divergence of existing song types, together with a small amount of innovation. It occurred simultaneously in all members of a song group. Because of experimental limitations, it was not possible to identify which bird or birds were responsible for introducing any changes to the shared song types. The significance of song matching in conjunction with the phenomenon of discrete song groupings will be discussed in Chapter 8. The following chapter examines the effects that translocation has on the songs of Noisy Scrub-birds.

Chapter 6 – The Effect of Translocation on the Songs of the Noisy Scrub-bird

6.1 Introduction

The previous three chapters dealt with territoriality, song sharing, and repertoire change within the Mt Gardner population. Mt Gardner is the original population, from which most other populations have been derived through translocation. Indeed, a large part of the success of Noisy Scrub-bird conservation can be attributed to the translocation program (Danks, 1994, 1997). Fire management and habitat protection have also played an important role (Danks, 1994, 1997) and captive breeding was attempted between 1975 and 1981 but only successfully raised one chick (Smith *et al.*, 1983; Danks, 1994, 1997).

Translocation in this case refers to moving individuals from one site, to another that was part of their former range, with the aim of establishing a viable population. Translocations are a commonly used tool in the management and conservation of species (Fischer and Lindenmayer, 2000). Habitat quality at the release site, location of the release site relative to the species historical range, and the number of individuals released are all important predictors of translocation success (Wolf *et al.*, 1998). Release of a large number of individuals (n>100) is more likely to result in success (Fischer and Lindenmayer, 2000). However, both New Zealand Robins and Saddlebacks have been successfully translocated using small numbers of founders (Taylor *et al.*, 2005).

Since 1983, translocation using a small number of founders has played a major role in the management of the Noisy Scrub-bird and has resulted in an increase in the population index from 143 singing males in 1983 to 765 singing males in 2001 (Comer and Danks, 2006). The establishment of new sub-populations through translocation provides the species with more resilience to wildfire, a key threatening process for this species. Between 2001 and 2006 the habitat of approximately 60% of the total population was lost in wildfires (Comer and Danks, 2006). Additionally, translocation increases the species range and total population size beyond that which would have occurred naturally (Danks *et al.*, 1996; Comer and Danks, 2006). Translocation has been a very successful strategy – within the first 10 years the proportion of the total population originating from translocations had risen to 42.8% (Danks, 1994). By 2001 the translocated Manypeaks population alone accounted for 55% of the total scrub-bird population (Comer and Danks, 2006).

Over the 20 years between 1983 and 2003, a total of 206 scrub-birds (136 males and 70 females) have been translocated to eight locations (Danks, 1994; Danks *et al.*, 1996; Comer and Danks, 2006). In the first translocation, between 1983 and 1985, scrub-birds were taken to Mt Manypeaks, 15km north east of Mt Gardner. Further translocations have taken place to Nuyts Wilderness, Quarrum Nature Reserve, Mt Taylor, Mermaid, Bald Island, Stony Hill and the Darling Range (see Table 6.1). Translocations have succeeded at Mt Manypeaks, Mermaid and Bald Island. The Mt Taylor translocation was initially successful but failed after a wildfire. The Nuyts, Quarrum and Stony Hill translocations were all unsuccessful, presumably because the habitat was unsuitable at the release site (Danks, 1994; Danks *et al.*, 1996; Comer and Danks, 2006). In the Darling Range birds have persisted for over 5 years at some sites but it is still too early to tell if this translocation has been successful (Comer and Danks, 2006; Gilfillan *et al.*, in prep.). Further information on the Bald Island translocation is provided in Chapter 7.

Table 6.1: Summary of translocations 1983-2003. The translocation was considered a success when the number of singing males exceeded the number of males released (adapted from Gilfillan *et al.*, in prep.).

Year	Release area	Males:Females	Success
1983-1985	Mt Manypeaks	18:13	1988
1986-1987	Nuyts	16:15	-
1989-1990	Quarrum	15:11	-
1990-1992	Mt Taylor	6:6	1993
1992-1994	Mermaid	8:2	2001*
1992-1994	Bald Island	8:3	1997
1994	Stony Hill	5:0	-
1997-2003	Darling Range	60:20	?

* may have exceeded release number earlier but wasn't censused annually

The major role that translocation plays in the conservation of the Noisy Scrub-bird means that any information that has the potential to increase understanding of the processes involved is very important. The translocation of Noisy Scrub-birds to Porongurup National Park offered a unique opportunity to study the effect that translocation had on the songs of the individuals involved. More specifically, it allowed an in-depth look at the changes an individual made to the songs in his repertoire when removed from his original song group and subsequently released into an area where other males sang non-shared song types. Noisy Scrub-bird translocations have been occurring since 1983, however the effect that translocation has on the territorial songs of the translocated male scrub-birds has not been studied until now.

The information gained so far on song sharing and repertoire change generates many questions such as:

1) What effect does translocation have on song characteristics such as repertoire size?
2) Do scrub-birds have a preference for sharing songs?
3) Why do they share with some males and not with others?
4) How do they choose which bird to copy?
5) What would happen to their songs if several birds with no song types in common are put together?
6) How rapidly is a male replaced when he is removed from his territory?
7) Will the replacement male sing the songs of the original male?
8) Do song groups confer an advantage to their members?

The translocation of male scrub-birds to Porongurup National Park had the potential to address some of these questions. It allowed territorial male scrub-birds to be arranged into groups that no longer shared songs.

This chapter tests a key prediction regarding the singing behaviour of translocated Noisy Scrub-birds. The ability of scrub-birds to rapidly alter their songs and the fact that song sharing seems to be a widespread phenomenon means that birds are likely to have a preference for sharing songs with their neighbours and will alter their songs to do so. Therefore, the key prediction was that male scrub-birds who initially shared no songs at all, would over a short period of time alter their songs so that they shared with others at the new site. To test this prediction, information was needed about the song groupings at the capture site and the song types present in the repertoires of males targeted for capture. This provided a baseline against which any singing at the new site could be compared.

6.2 Methods

Translocations took place in June-August 2006. Only male scrub-birds were translocated because this was the first year of the translocation. In early translocations roughly equal numbers of males and females were released. However, in the case of translocations that failed, these birds were lost to the population and a more conservative approach was needed. A new strategy was developed whereby smaller groups consisting solely of male scrub-birds were released. Males are more easily captured and to some extent more expendable. If they are still singing the following year then the site is obviously capable of supporting scrub-birds and females too are released (Danks, 1994, 1997; Danks *et al.*, 1996).

Noisy Scrub-birds for translocation were captured from the Mermaid Point area near Cheyne Beach, 70km east of Albany (see Figure 6.1). The territorial songs of males within this area were recorded between 11 May and 19 June 2006. Song groupings were determined as detailed in Chapter 4. Recorded songs also provided a baseline sample of that individual's initial pre-capture repertoire and supplied material to use for playback during capture.

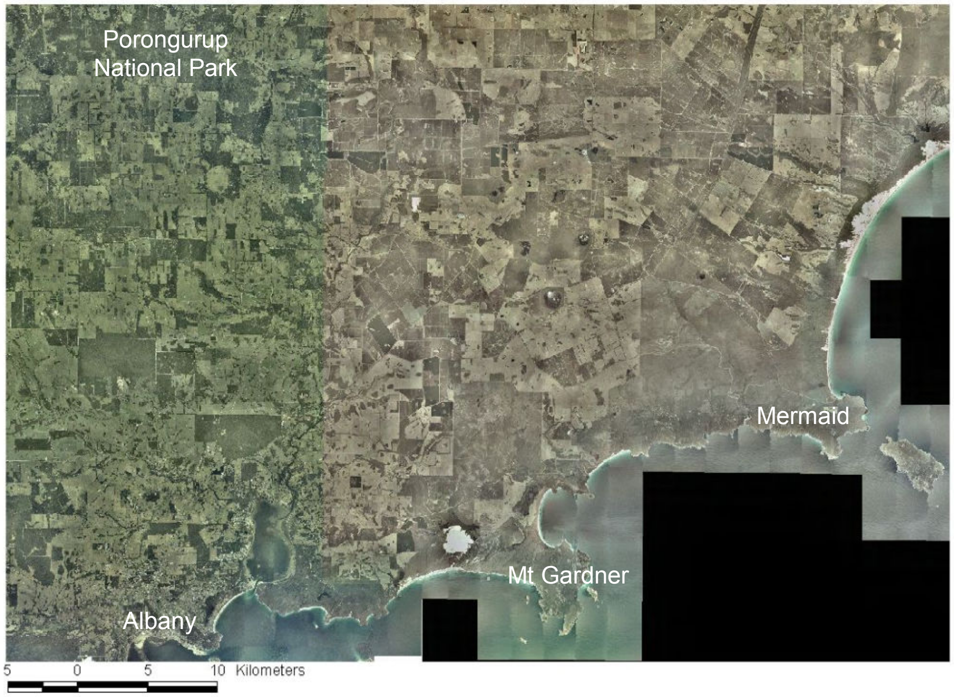


Figure 6.1: Location of the source population at Mermaid Point, the release site at Porongurup National Park and the nearby town of Albany.

Translocation (capture, holding and release) methods are described in Danks (1994) and Comer and Danks (2006). Male scrub-birds were captured using a modified mist-net and playback to lure them into the net. Playback territorial songs were either from the individual itself or from a neighbour within hearing distance to avoid introducing any new song types. Mist-net lines had been cleared in territories 3, 12, 27, 18, 22, 23, 24, 25, 29, 35, 34, 39, 26, 17 (see Figure 6.2). These territories were chosen for ease of access and suitability of the location for a net-line. Capture of males from these territories was opportunistic – wind speed and direction and cloud cover played a big role in which territories were targeted for capture as both wind and sun made the net more visible, decreasing the likelihood of a successful capture. Table 6.2 lists the dates and territories at which captures took place, as well as the names given to the birds.

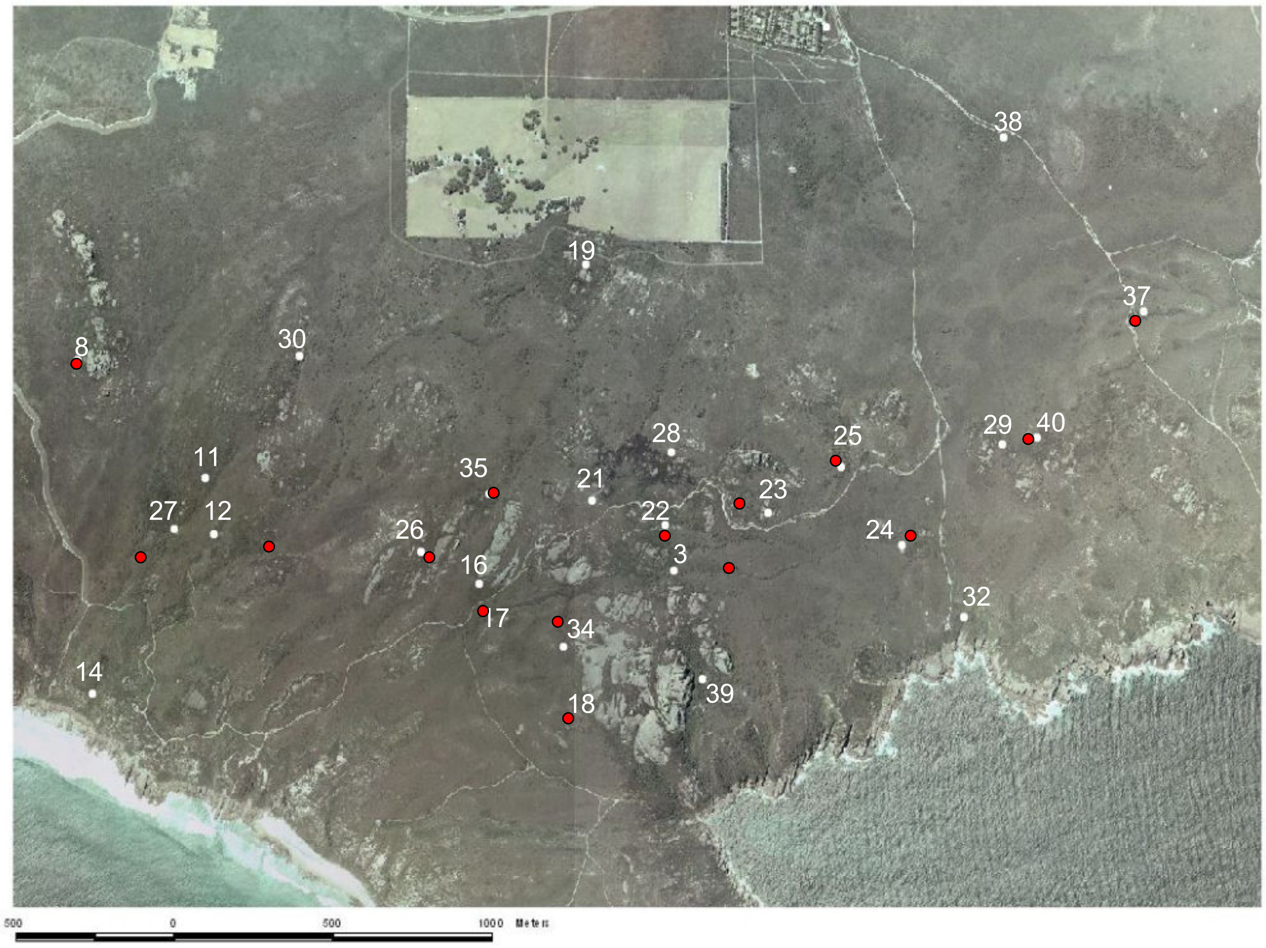


Figure 6.2: Location of the net-lines (red dots) in the Mermaid Point area. White dots represent territories occupied in 2006.

Table 6.2: Capture and release details for the eight males translocated.

Territory number	Date Captured	Name	Released	Release site
25	22 June	Togo	29 June	Millinup Pass
23	22 June	Pele	29 June	Spearwood Gully
17	22 June	Mendez	29 June	Millinup Pass
27	25 June	Harry	29 June	Spearwood Gully
24	17 July	Zizou	3 August	Millinup Pass
29	19 July	Niko	3 August	Millinup Pass
27	25 July	Fabio	3 August	Millinup Pass
23	31 July	Fred	3 August	Spearwood Gully

After a bird was removed from its territory, checks were made of that territory as often as possible to determine when replacement by another scrub-bird took place. Any new bird singing in that territory was recorded and his songs compared to those of the original territory owner as well as the surrounding territorial males. Further recordings of males in the area to monitor song groupings were conducted on 4 July, 15 July (also used to update the songs used for the second round of captures) and 17 August.

The captured males were held in the aviaries at Two Peoples Bay for varying lengths of time (Table 6.2) – the first group of four males was released at Porongurup National Park on 29 June, the second group of four on 3 August (Figure 6.3). The songs of males that sang in the aviary were also recorded and their songs examined for any changes in structure.

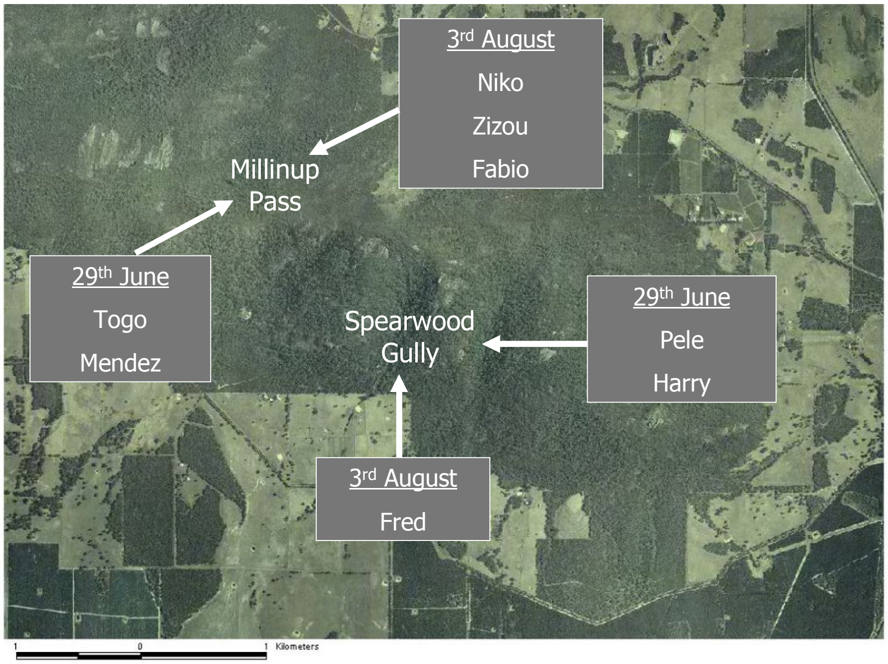


Figure 6.3: Release sites at Porongurup National Park showing where and when the eight scrub-birds were released.

After release, all males were radio-tracked, not only to follow their movements but also to allow confirmation of the identity of any singing scrub-bird. However the transmitters had been fitted with the wrong antennas (manufacturer error) and the fine wire became tangled easily, either snapping the antenna and reducing the range to 10-20m, or pulling the transmitter off entirely. Once the transmitters were off, the only practical method of monitoring the birds was listening for any singing.

For the first week after both releases the birds were radio-tracked daily and any singing was recorded. After the initial week, time was spent listening for singing on at least a weekly basis at first, reducing to a fortnightly basis by September. Any singing was recorded, and the resulting spectrograms compared visually (see Chapter 2) to the original pre-capture songs of all birds released in that area and to the songs of any other males singing at the release site. In addition, pre- and post-release repertoire size and song complexity were compared for each bird.

Recording the songs of the translocated birds was at times challenging. Sound transmission in forest is reduced so the resulting spectrograms were of poor quality unless recording distance was 40m or less. However, the scrub-birds were initially quite wary after their release and approaching them too closely often resulted in them either going quiet or switching to alarm calls or short song. Also, the birds were singing infrequently so the number of songs recorded per bird was generally low. This small sample size of their songs was unsuitable for a more detailed statistical analysis, even if recording quality had been adequate.

6.3 Results

6.3.1 Capture site (Mermaid)

Song groupings in the Mermaid area differed from the discrete song groups found at Mt Gardner and Bald Island (Chapters 4 and 7 respectively) in that there was overlap in song sharing between song groups (Table 6.3). However, it was still possible to split the birds into song groups as shown by the shading in Table 6.3 and mapped in Figure 6.4.

Table 6.3: Mermaid song sharing, June 2006. Each column represents a different song type and a “1” indicates the presence of that song type in an individual’s repertoire. Grey has been used to highlight blocks of shared songs that reflect song groupings.

	Song Type																															
Terr. No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
18	1	1	1	1	1	1				1																						
26							1		1	1	1	1	1	1	1	1																
35							1	1	1	1	1	1	1	1																		
17							1		1	1	1	1	1	1		1																
34							1		1	1	1	1		1		1	1															
19							1			1	1	1	1	1																		
22										1	1	1					1	1	1													
28										1	1	1						1	1													
23										1								1	1	1	1											
39																		1	1	1	1	1										
25																				1	1		1	1	1	1						
24																				1			1	1	1		1	1				
29																		1											1	1	1	1
37																		1											1	1	1	1

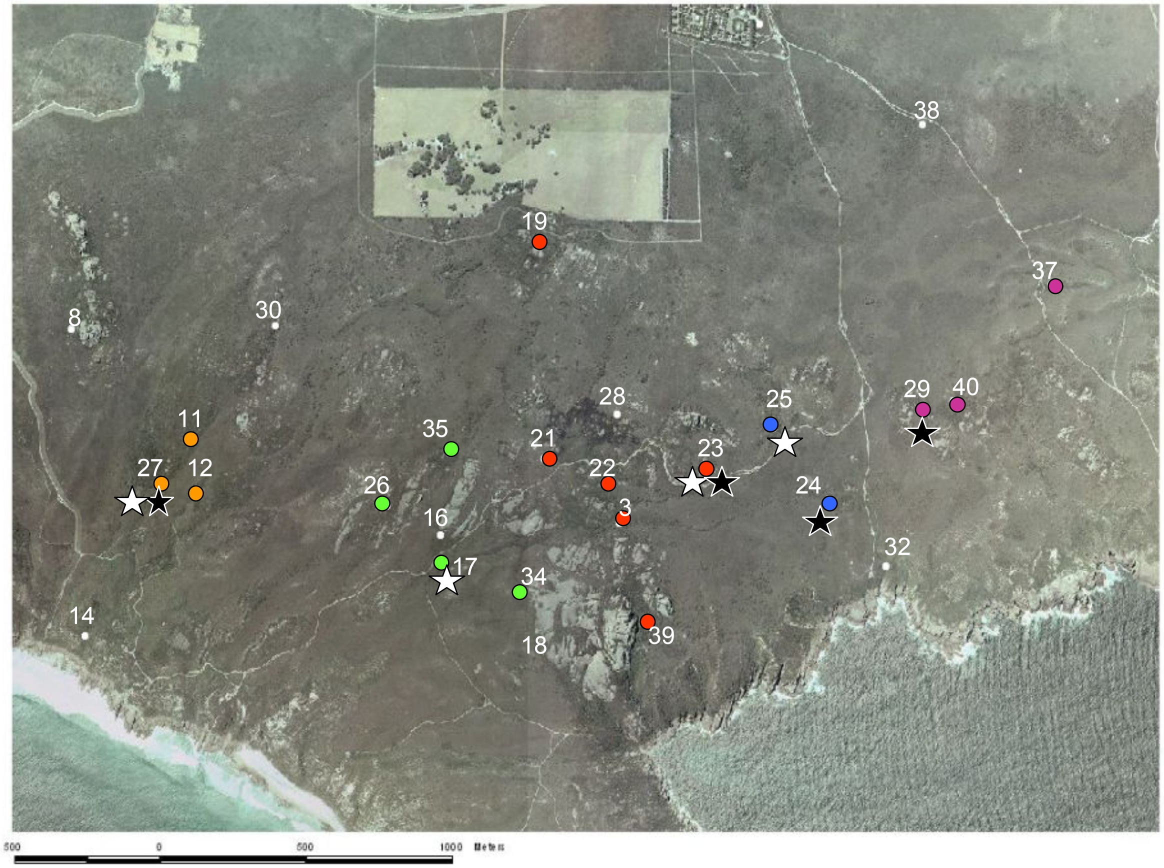


Figure 6.4: Song groupings in the Mermaid capture area. Dots the same colour represent birds that share songs (i.e. belong to the same song group). White stars show the locations that birds were captured for the first release, black stars show the locations of the second round of captures.

In total eight male scrub-birds were captured from five different song groups (Figure 6.4, Table 6.4). At least one bird was taken from each of the five song groups in the area, and three of the song groups had two birds taken, although none were captured from the same song group in the same round of captures.

Table 6.4: Song group origin (refer to Figure 6.4 for locations of songs groups and captures).

Song Group	Territory captured	
	1st release	2nd release
Blue	25 (Togo)	24 (Zizou)
Red	23 (Pele)	23 (Fred)
Green	17 (Mendez)	
Orange	27 (Harry)	27 (Fabio)
Purple		29 (Niko)

All birds captured were replaced within a very short period of time (Table 6.5). These were the maximum times it took for them to be replaced, as it was not always possible to check the territory immediately afterwards. Replacement was rapid, averaging 1.6 days after capture (excluding the value of 17 days as this bird was more than likely replaced much faster than this). In all but one case the replacement bird sang the same songs as the original bird (example shown in Figure 6.5). In fact, two of the territories had two birds removed and in both cases they were replaced by a third bird, also singing the same set of song types. The only exception was territory 25 where the replacement bird sang the songs of the neighbouring song group.

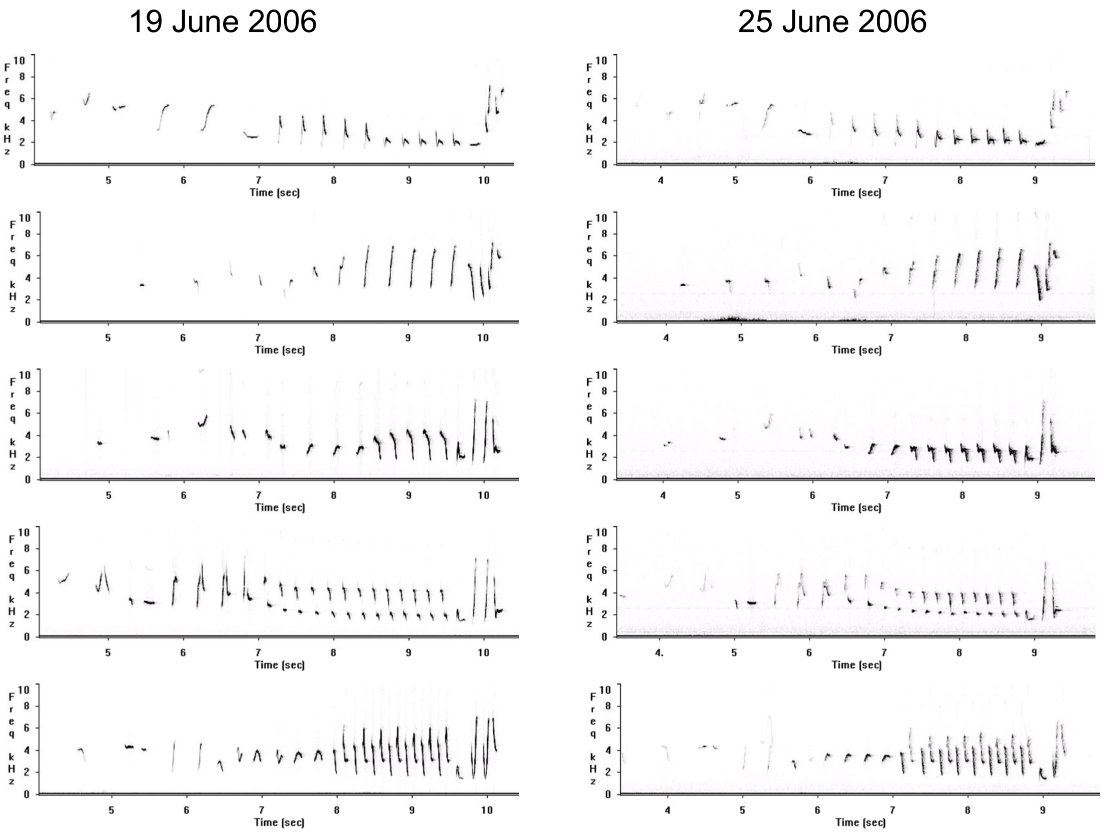


Figure 6.5: Repertoire of Pele recorded in Mermaid territory 23 prior to his capture (left) and the matching song types sung by the replacement male (right).

Table 6.5: Replacement of captured males – maximum time taken and songs sung by replacement male.

Territory No.	Captured	Replaced	Song Group
25	22 June 2006	4 days	neighbouring
23	22 June 2006	2 days	same
17	22 June 2006	2 days	same
27	25 June 2006	1 day	same
24	17 July 2006	1 day	same
29	19 July 2006	same day	same
27	25 July 2006	1 day	same
23	31 July 2006	within 17 days	same

6.3.2 Aviary

Of the four males captured in the first round only one bird, Mendez, sang in the aviary. The first bird captured in the second round of captures, Zizou, sang in the aviary until Fabio was captured eight days later. After Fabio was released into the aviary he and Zizou had a territorial and short song interaction that resulted Zizou going quiet and Fabio taking over as the singing bird within the aviaries.

6.3.3 Release Site (Porongurup National Park)

As mentioned in the methods, radio-tracking the translocated birds at the new site was not overly successful. All transmitters had either come off or were non-functional at the time each bird began to sing. Consequently, the identity of the singing bird could not be confirmed and assumptions had to be made based on the songs they were singing. This was not as big a problem as it could have been because in general enough of each bird's unique song characteristics remained at the time he began to sing to be reasonably confident in assigning his identity.

For example, before he was captured, Pele had five different song types in his repertoire. When he began to sing at Spearwood Gully three and a half weeks later he was only singing a single song type that on first glance appeared quite different and much simpler than any of his original songs. However, on closer examination one can see that the ending was identical to one of his pre-capture songs (Figure 6.6). The only other bird at Spearwood Gully at that point in time was Harry and none of his initial songs showed any similarity to this song type (Figure 6.7). The assumption could be made with a reasonable level of confidence that it was indeed Pele that was singing, not Harry.

With the exception of Fabio and Fred, all birds have been heard singing since their release at Porongurup National Park. Togo, Mendez and Harry all sang songs with clear-cut similarities to their pre-capture repertoires making their identification relatively straightforward. Matching Zizou's post-release songs to his pre-release songs was a little more complicated. There were no definite matches, although there were some similarities to Zizou's pre-release songs (Figure 6.8). However, none of the songs showed any similarity to any of the other birds in the area (Figure 6.9). In addition, the location of the singing was very close to where Zizou's transmitter signal was last picked up. These three factors combined provide strong inference that the bird was Zizou.

The songs of the sixth bird to sing after release (Millinup Pass) showed no similarities to any of the pre-release songs of any of the birds. Both Togo and Zizou were also recorded that day. When first recorded on 22 September he was only singing a single song type, suggesting that he had only just begun to sing again (as was observed with Pele at Spearwood Gully). This single song type matched one of the four song types that Zizou was singing when recorded that same day (Figure 6.10). Considering that while the transmitters were functional (5 days) Zizou and Niko generally stayed closer to each other than to any other bird and that they probably continued to do so, it is probable that Niko had heard enough of Zizou's songs to copy him. Also, the location of the singing was within 40m of Niko's release site – circumstantial evidence but nonetheless of potential significance. Therefore, Niko was the most likely identity of this particular bird.

Interestingly, each of the six birds that have been recorded singing at Porongurup National Park showed a substantial decrease in the number of different song types in their repertoire when they first began to sing again (Table 6.6). On average, repertoire size decreased by 67%. In particular, Pele and Niko were both only singing a single song type when they first began to sing, something that is usually rarely seen. Most of the birds have subsequently increased the number of song types in their repertoire since they first began to sing at the new site (Table 6.6).

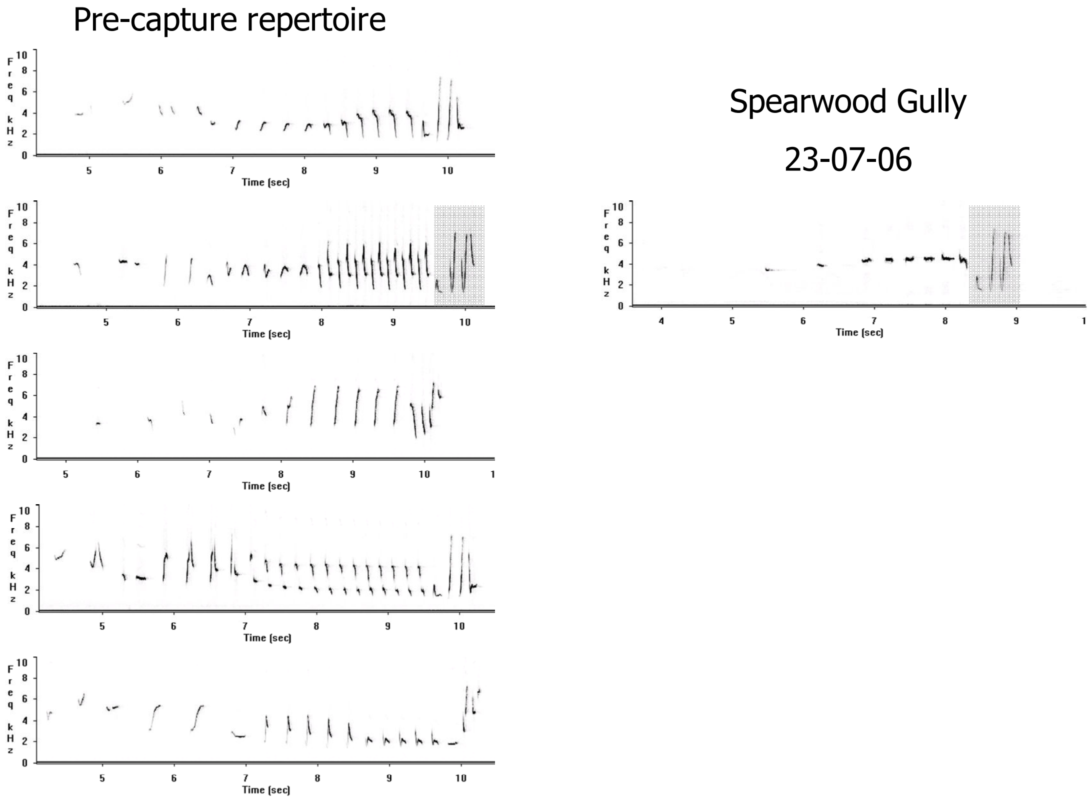
Table 6.6: Pre and post release repertoire sizes (number of song types). Fabio and Fred have not been heard since their release, however it is possible that they have moved away from the release sites and are singing in locations yet to be discovered.

	Pre-capture	Initial post-release	Maximal post-release
Togo	6	3	8
Pele	5	1	5
Mendez	8	3	7
Harry	11	6	5
Zizou	10	4	4
Niko	5	1	3
Fabio	11	-	-
Fred	6	-	-

On comparison of the post-release songs of all six birds that have sung, it was discovered that songs had become similar between three pairs of birds that initially had no song types in common. For example, Harry and Pele were taken to Spearwood Gully in the first release. Interestingly, first Pele sang within Spearwood Gully (23 July), then Harry was recorded singing from much the same spot five days later (28 July). The identity of the singing bird was determined by their songs as by this stage both transmitters were off. At no time were both the birds heard singing together. Shortly after the release of Fred, Pele had once again taken over as the singing bird within Spearwood Gully (4 August). Quite by accident it was discovered that Harry had moved and was now singing from a creek line on private property a little over a kilometre away (7 August) (Figure 6.11). This was discovered only three days after he was last recorded at Spearwood Gully.

When their songs were compared it was found that three of each of their five song types were now very similar. However, although the main body of all three songs was near identical, both birds retained their characteristic endings (Figure 6.13). It would be expected that their songs would have continued to become more similar until they matched exactly. Further sampling could have confirmed this but Harry was not heard after 18 August. Also, even if he had continued to sing from that location there was no guarantee that he could still hear Pele singing more than a kilometre away. At no time could I hear the other scrub-bird from either site, but scrub-bird songs are capable of carrying for that distance and scrub-bird hearing may be much more acute than ours.

At Millinup Pass the process of song convergence has been more complete. It has been noted between two pairs of birds – Togo and Mendez; and Niko and Zizou (Figure 6.12). Togo and Mendez were both part of the first release and about two months later two of their song types had become identical (Figure 6.14). Niko and Zizou were part of the second release at Millinup Pass, and after about two months three of their song types were very similar (Figure 6.15). Of particular interest is that Niko appeared to have copied the songs that Zizou had been singing for the previous two weeks. Zizou was first recorded singing on 7 September. On 22 September both Zizou and Niko were recorded. Niko was only singing a single song type, suggesting that he had only just begun to sing at the new site. Niko was recorded again on 6 October, singing the same song type, as well as an additional two song types. Both the original song type and one other matched two of the song types that were recorded from Zizou on 7 September and 22 September.

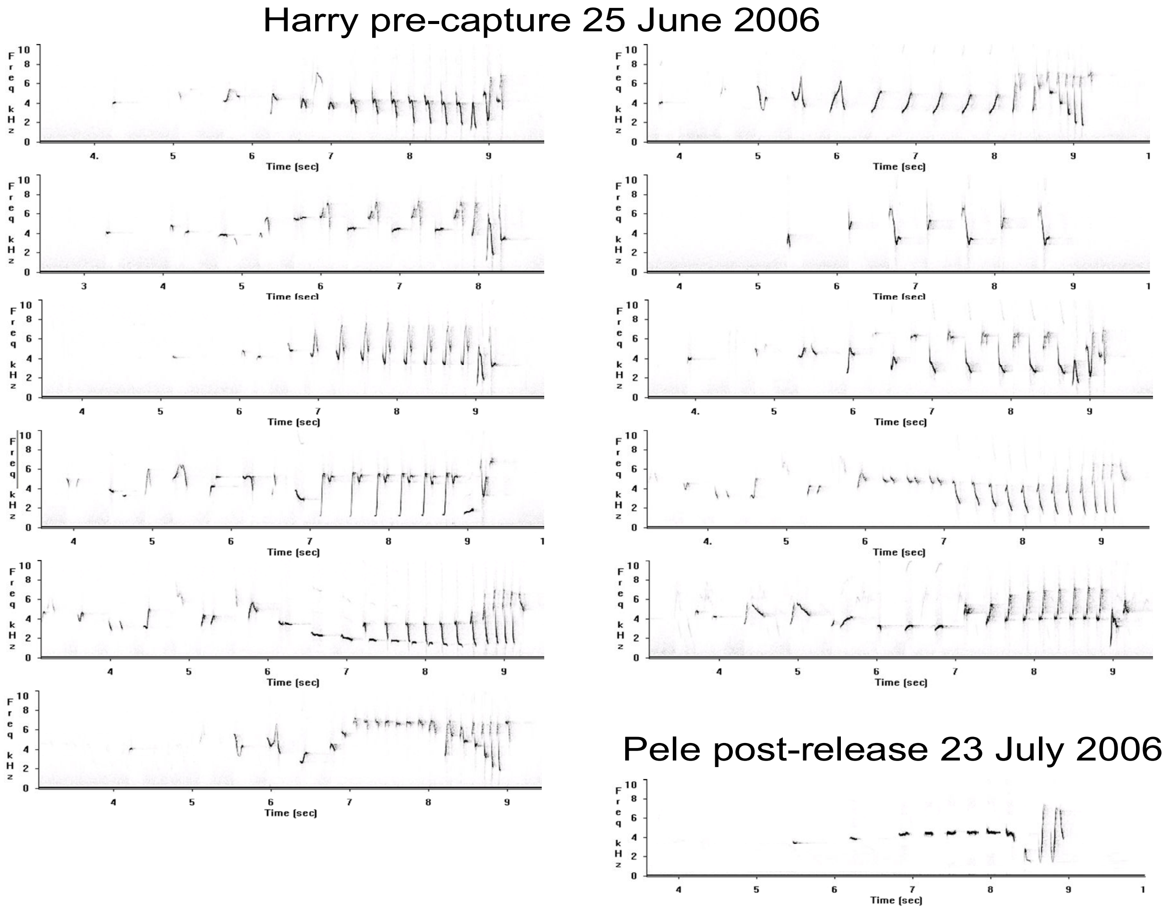


Pre-capture repertoire

Spearwood Gully

23-07-06

Figure 6.6: Pele's pre-capture repertoire compared with the single song type when he first began to sing at Spearwood Gully. Although this song appears quite different to any of the song types in his pre-capture repertoire it has an identical ending to one of the song types (highlighted in grey).



Harry pre-capture 25 June 2006

Pele post-release 23 July 2006

Figure 6.7: Harry’s pre-capture repertoire in comparison to the single song type that Pele first sang at the release site. Note that Pele’s song shows no similarity to any of Harry’s song types.

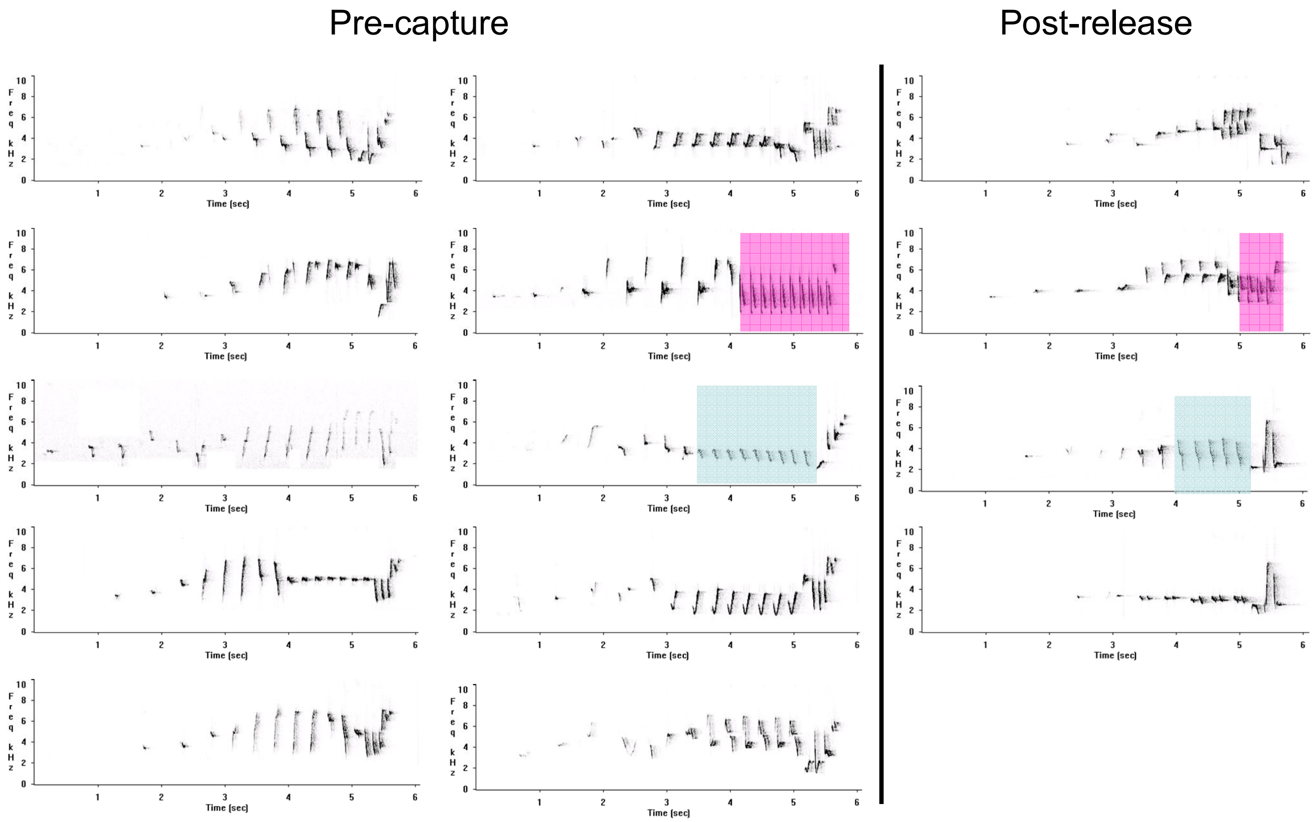


Figure 6.8: Zizou’s pre-capture and post-release songs with similarities highlighted.

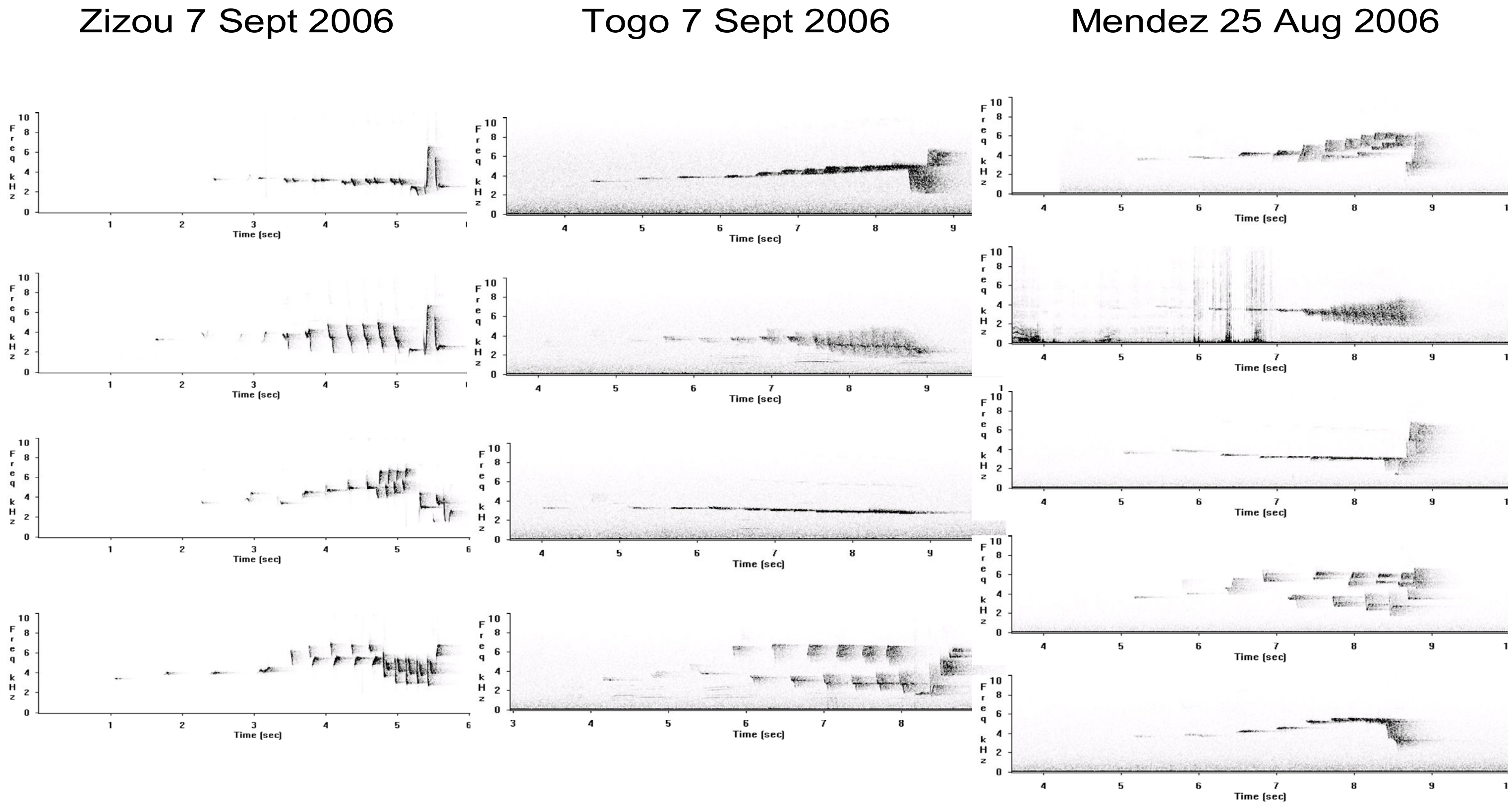


Figure 6.9: Zizou’s repertoire of 4 song types (left column) showed no similarities to the repertoires of the other two birds that had sung at Millinup Pass (centre and right columns).

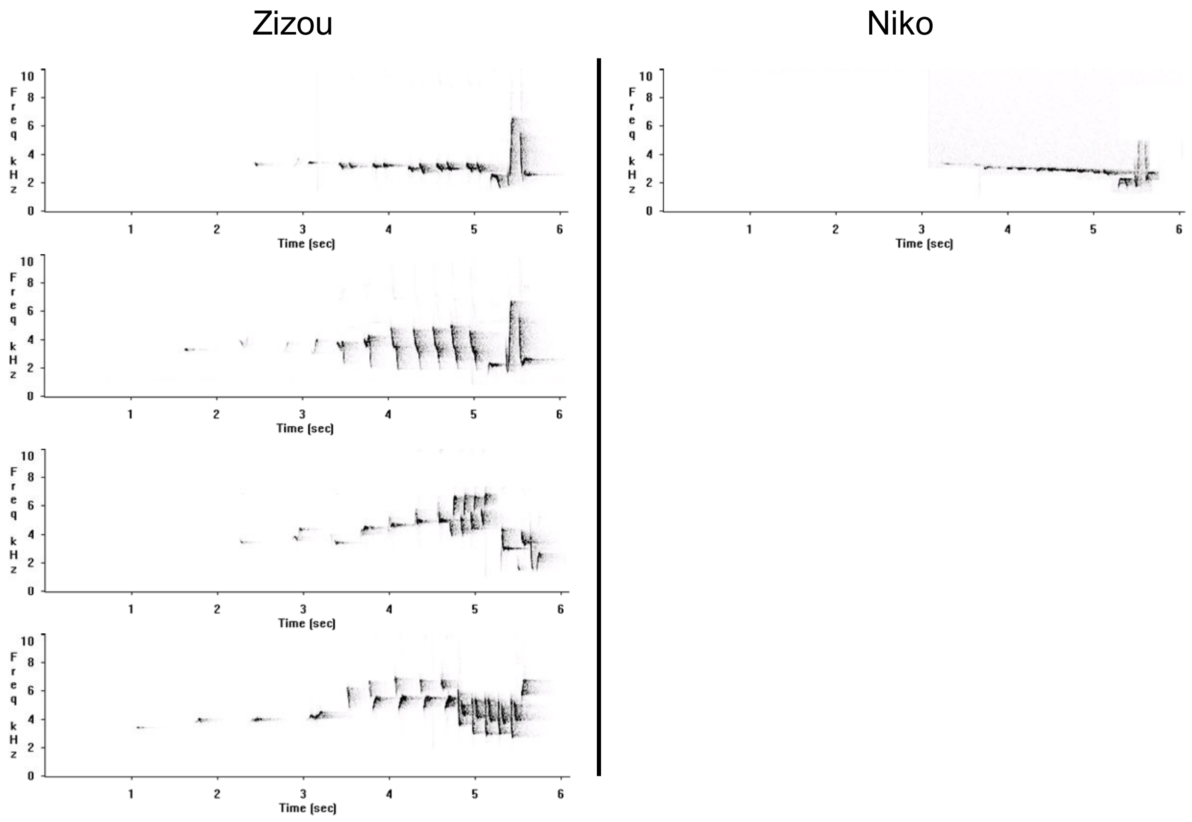


Figure 6.10: Post-release repertoires of Zizou and Niko. When Niko first began to sing he was only using a single song type which matched one of Zizou's song types (both shown in the top row).

Figure 6.11: Locations and dates of where Harry (red dots) and Pele (blue dot) have sung in the Spearwood Gully area.

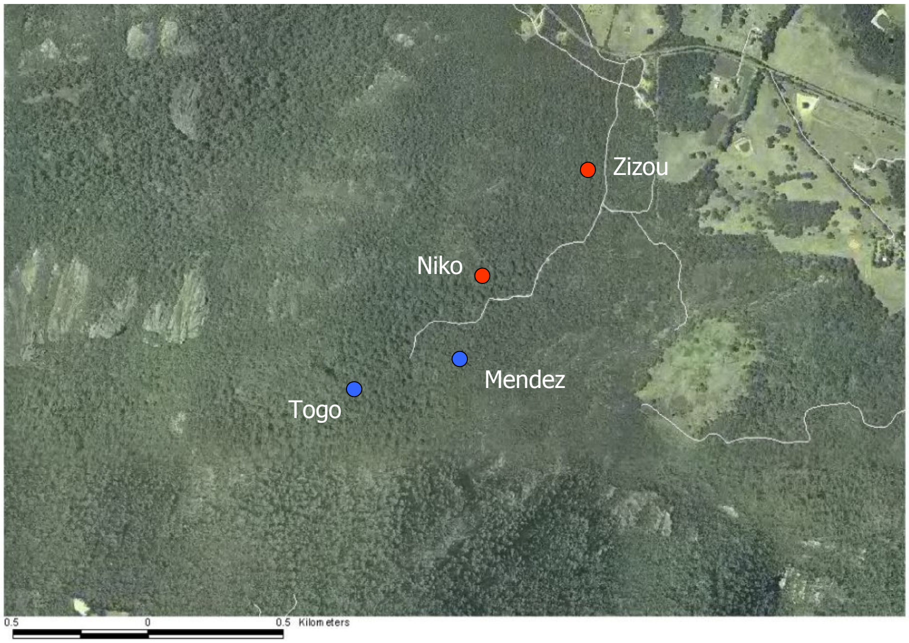


Figure 6.12: Locations of singing birds at Millinup Pass. Dots of the same colour indicate birds in which vocal convergence has been observed.

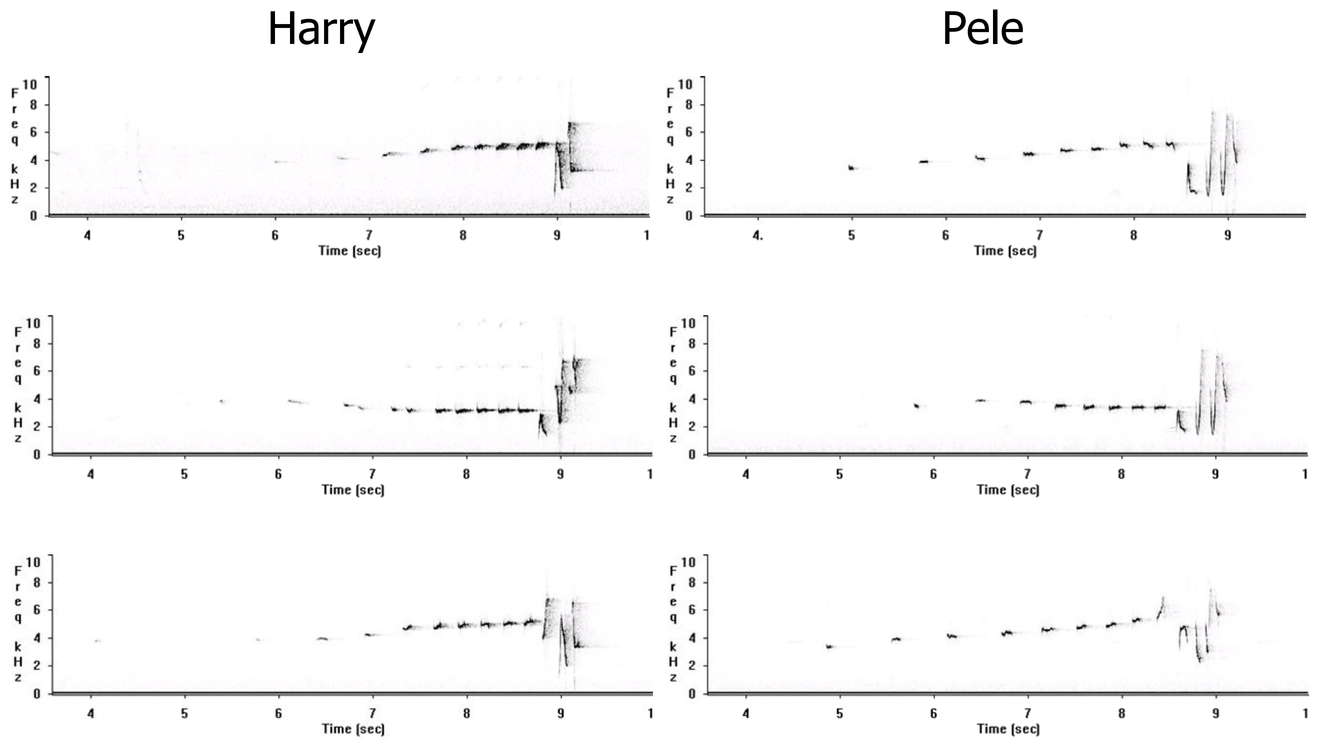


Figure 6.13: Convergence in the songs of Harry and Pele. Similar songs have been placed on the same row. The main phrase of each of the three different song types is almost identical but each bird has retained its characteristic endings.

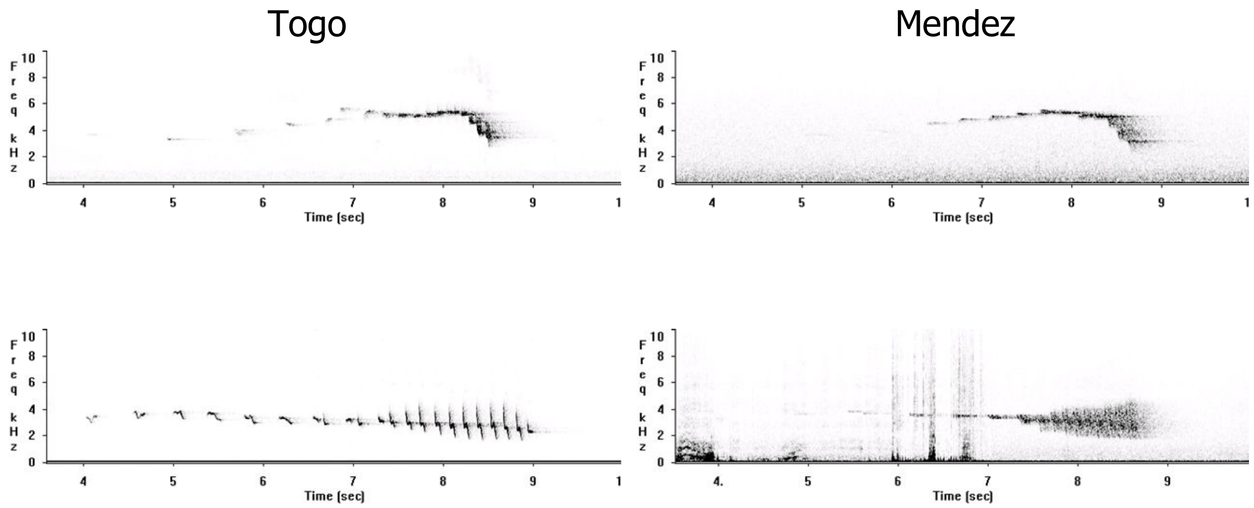


Figure 6.14: Convergence in the songs of Togo and Mendez. Similar songs are on the same row. Spectrograms of Mendez's songs are poor quality because sound transmission in the forest is reduced and it was impossible to get close enough to Mendez to get a good quality recording.

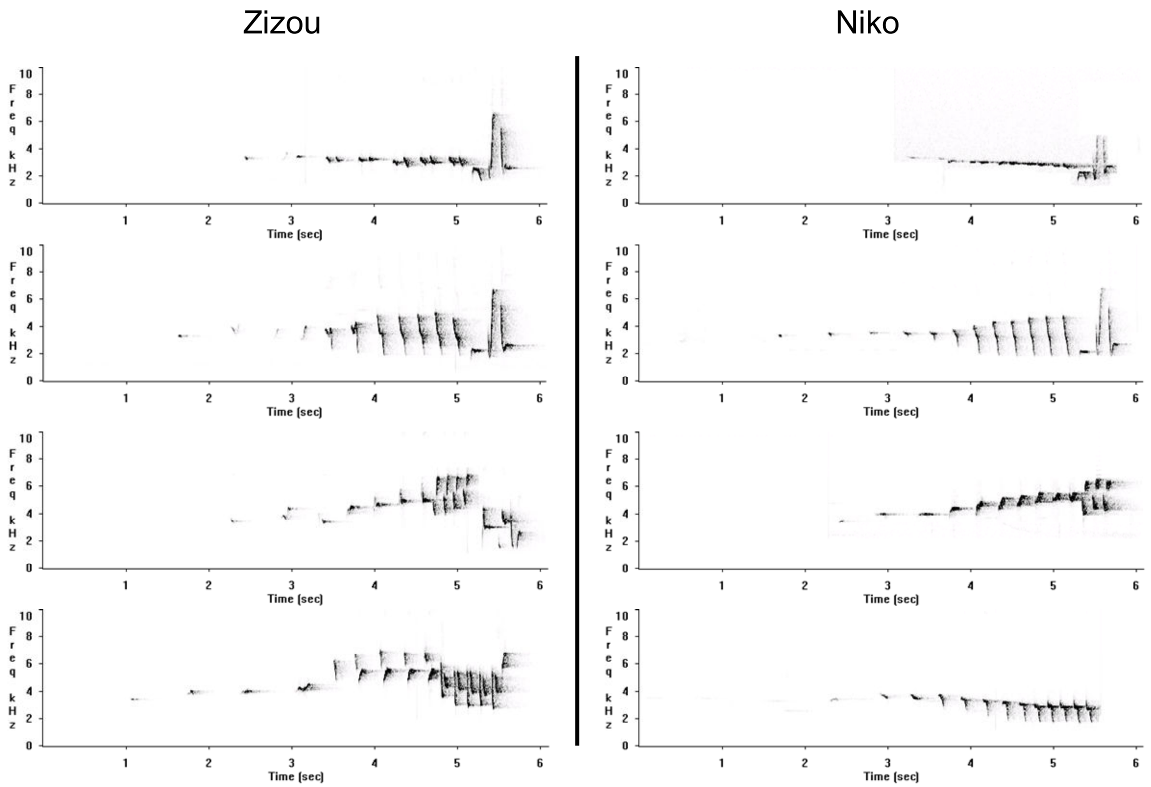


Figure 6.15: Post-release repertoires of Zizou and Niko. The songs in the top two rows are shared by both birds. The song in the third row is the same, except Niko's version omits the ending. The bottom row shows the remaining song type in each birds' repertoire which have no similarities to each other.

6.4 Discussion

The translocation of eight male Noisy Scrub-birds to Porongurup National Park offered a unique opportunity to study the effect that this process has on the songs of scrub-birds. More specifically, it allowed an in-depth look at the changes an individual made to the songs in his repertoire when removed from his original song group and subsequently released into an area where other males sing non-shared song types. The ability of scrub-birds to rapidly alter their songs and the fact that song sharing seems to be a widespread phenomenon means that birds are likely to have a preference for sharing songs with their neighbours and will alter their songs to do so.

This was the first time that song had been studied in relation to Noisy Scrub-bird translocations and it attempted to answer the following questions:

1) What effect does translocation have on song characteristics such as repertoire size?
2) Do scrub-birds have a preference for sharing songs?
3) Why do they share with some males and not with others?
4) How do they choose which bird to copy?
5) What would happen to their songs if several birds with no song types in common are put together?
6) How rapidly is a male replaced when he is removed from his territory?
7) Will the replacement male sing the songs of the original male?
8) Do song groups confer an advantage to their members?

Question 1 is addressed in the section below on the effects of translocation on song characteristics, questions 2 to 5 in the section on song convergence, questions 6 and 7 in the section on replacement of captured males, and the final question is addressed in the summary.

6.4.1 Effects of translocation on song characteristics

Since their release, only six of the eight males have been heard and recorded. Generally they have been singing only infrequently and recording quality at times was poor. This small sample of songs combined with the lack of clarity in some of the spectrograms meant that a more detailed analysis of song structure and song similarity (for example cross-correlations) was inappropriate.

However, despite this, some features such as song complexity and repertoire size could still be examined. One effect of translocation that was particularly apparent was the decrease in repertoire size post-release. On average repertoire size decreased by 67%. In particular, Pele and Niko both only sang a single song type when they first began to sing, something that is usually rarely seen. Presumably this reduction in repertoire size was a response to the stress of being in unfamiliar surroundings. In fact, most of the birds have subsequently increased the number of song types in their repertoire since they first began to sing at the new site.

6.4.2 Song convergence

Ideally, the process of song change in each of the birds would have been followed as it occurred to provide information about how a consensus repertoire was reached. Unfortunately not all of the translocated birds sang consistently, making it difficult to track the process of change. However, it was still apparent that the songs of birds, who initially had no song types in common, converged and in some cases became identical. The process of song convergence could either occur through the songs of one male being copied by others, or by two or more birds modifying their repertoires until their songs matched.

It was hoped to provide evidence that a dominant male was being copied by others to provide support for the theory that each song group consists of a dominant male and several other males copying his songs (Berryman, 2003). However, after release many of the birds only sang infrequently and it was difficult to tell which bird or birds initiated any changes. There was a strong suggestion that birds that initially had no song types in common altered their repertoires, with their songs becoming very similar, if not identical. So, it does appear that Noisy Scrub-birds do have a preference for sharing songs with their neighbours and will alter their songs to do so.

Several factors may provide evidence for copying the songs of a dominant individual. Firstly, although Harry and Pele never sang concurrently at Spearwood Gully and the process of song convergence was not apparent, there is some circumstantial evidence that, for a while at least, Harry was the dominant male within the area and that Pele copied his songs. Although Pele was the first bird heard to sing at Spearwood Gully (23 July), when the area was visited just five days later Pele was not heard but Harry was now singing from much the same spot. At what time during that five day interval Harry took over that area is unknown. However, considering that when Pele was first recorded he was very hesitant, singing infrequently and only singing a single song type it is likely that even if Pele had been singing for most of that 5 day period his song output and song variety would have remained low.

Between 28 July and 4 August Harry was the only bird heard at Spearwood Gully, indicating that he had taken over as the dominant territorial male within the area. By 6 August Pele was singing in Spearwood Gully and on 7 August Harry was discovered singing more than one kilometre away at Cockatoo Creek. Presumably Pele had remained quietly within the Spearwood Gully area during the period that Harry was singing there.

On comparison of their songs it was found that three of each of their five song types had become very similar in the main phrase, with each bird retaining its characteristic endings. These three song types had been present in Harry's repertoire since he first began to sing at Spearwood Gully. If the assumption is made that prior to resuming singing on 6 August, Pele only sang for at most a few days and that his song output and variety was low, then it is likely that Harry's songs provided the model for Pele to copy. So although Pele later reasserted himself as the dominant bird within Spearwood Gully, it does appear as though Pele may have copied the songs of the dominant bird at the time, namely Harry.

The second piece of evidence that a dominant bird may be copied by others was seen in the case of Zizou and Niko. These two birds were part of the second release at Millinup Pass. Prior to Fabio and Fred being captured, Zizou and Niko were held in the aviaries for six days during which time only Zizou sang. Zizou appeared to be the dominant bird, Niko made no song challenge during this time. Zizou was first recorded singing at Millinup Pass on 7 September. On 22 September both Zizou and Niko were recorded. Niko was only singing a single song type, suggesting that he had only just begun to sing at the new site. Niko was recorded again on 6 October, singing the same song type, together with an additional two song types. Both the original song type and one other matched two of the song types that were recorded from Zizou on 7 September and 22 September.

Assuming that Niko had only just begun to sing on 22 September, Zizou had been singing for at least 15 days prior to this. While radio-tracked, Zizou and Niko tended to stay closer to each other than to any other birds. If they continued to stay close then Niko would have had ample opportunity to learn Zizou's songs in the 15 days before he began to sing. Considering that Zizou seemed to be the dominant bird within the aviaries, this provides additional, albeit circumstantial, evidence that the songs of a dominant scrub-bird are copied by others.

Vocal convergence occurred in the three pairs of scrub-birds within 1-2 months. Vocal convergence has also been observed in several other species. In Black-capped Chickadees, call convergence occurs in winter flocks (Mammen and Nowicki, 1981). In an experimental flock, significant convergence of the 'chick-a-dee' call occurred within 1 week, with birds converging on a common mean rather than copying a particular individual (Nowicki, 1989). Vocal convergence has also been demonstrated in Budgerigars. Males introduced to an all-male flock will learn the call within 2-4 weeks (Bartlett and Slater, 1999), males average 2 weeks to imitate the contact call of the female they are paired with (Hile *et al.*, 2000) and experimental flocks of female Budgerigars will converge on a common call type within 4-7 weeks (Hile and Striedter, 2000). In contrast to the Noisy Scrub-bird, vocal convergence in both Black-capped Chickadees and Budgerigars occurred through individuals all modifying their calls rather than copying a particular individual as is possibly happening in the scrub-birds studied. The rate of vocal convergence in scrub-birds also appeared to be slightly slower, although this may be a product of sampling methods and the fact that the scrub-birds were singing unreliably and infrequently.

6.4.3 Replacement of captured males

Replacement of male Noisy Scrub-birds removed from their territories has been observed in past translocations. Of 65 males removed between 1983 and 1992, only 3 were not replaced and replacement sometimes occurred within hours or days but more often within weeks (Danks, 1994; Danks *et al.*, 1996; Danks and Smith, unpublished.). In one territory, over a four day period, three scrub-birds were removed and replaced by new males (Danks *et al.*, 1996). Also, the removal of a series of territorial males and their replacement by a very young bird suggests that the replacement males are already resident within the area (Danks and Smith, unpublished). However, there was no direct evidence for this.

The songs of replacement males have the potential to indicate what area they originated from. The songs of replacement males could potentially fall into one of four categories:

1) Shares song types with the original male (i.e. belongs to the same song group)
2) Shares song types with neighbouring male/s belonging to a different song group from the original male
3) Possesses song types from more than one of the surrounding song groups
4) Has a repertoire of song types that does not match any of the birds within the immediate area

Any of the first three options would indicate that the replacement bird had been present in the area for sufficient time to have learnt those particular songs accurately. The fourth option suggests that the bird has come from further afield, or that he has created his own repertoire of unique songs.

All birds captured were replaced within a very short period of time. Seven of the eight males were replaced with birds singing the same song types, and the remaining bird sang the songs of the neighbouring song group. This suggested that they were birds that must have been present in the area without singing for some time to have learnt the songs with that degree of accuracy. This confirms the presence of sub-dominant, non-singing males resident in the area.

6.4.4 Summary

The major role that translocation plays in Noisy Scrub-bird conservation means that any information that has the potential to increase understanding of the processes involved and possibly increase success is very important. Potentially one could have tested whether belonging to a song group conferred an advantage during translocation. If one group of males had all been taken from the same song group and the other group all taken from different song groups it could possibly have had some effect on translocation success.

However, the number of scrub-birds being translocated was so small that it would not have provided an adequate sample size. Site effects could potentially influence results as well. Also, measuring success would be very difficult given that the scrub-bird is such a cryptic species and that only males were translocated, therefore precluding assessment of reproductive success. The only practical measure of success is persistence of males, as indicated by singing. A lack of singing though, does not necessarily mean failure. Individuals may be present in the area without singing, or may have moved away.

The question of whether founder groups do better when composed of individuals that are familiar with one another has been investigated in Saddlebacks and North Island Robins (Armstrong, 1995; Armstrong and Craig, 1995). Survival, dispersal, pair bonding and reproductive success was evaluated in translocated groups of familiar and unfamiliar individuals. In both species there appeared to be no evidence that using familiar individuals increased translocation success.

Although it was impractical to demonstrate whether song group origin had an impact on the success of a Noisy Scrub-bird translocation, some interesting information was still gained. Noisy Scrub-birds have the ability to alter their songs relatively rapidly, with vocal convergence apparent within 1 to 2 months. Therefore, scrub-birds that initially have no song types in common have the capability to form new song groups within a short period of time. Consequently, any benefit that translocating males belonging to the same song group would provide, would probably be temporary and limited to the initial settling-in period. The following chapter investigates song sharing in an already established translocated population.

Chapter 7 –
Song Sharing on Bald Island

7.1 Introduction

The previous chapter dealt with the short-term effects of translocation on the songs of the Noisy Scrub-bird. The opportunity to study the longer-term effects of translocation on songs was provided by the population established on Bald Island.

Small, isolated populations of species, such as those found on islands, commonly show a reduction in genetic diversity, usually attributed to a founder effect or drift in small populations (Grant, 2001; Baker *et al.*, 2003). The question is, what impact does isolation have on cultural diversity? Translocated or naturally occurring island populations of birds provide an opportunity to study the impact that isolation has on vocal diversity.

The colonisation of an island by a bird species presents several potential ways in which there may be a loss in vocal variation. As with the loss of genetic diversity, vocal diversity may be reduced by a founder effect or drift in a small population, or it may occur through a 'withdrawal of learning' where the founding individuals colonise before they have fully learnt their songs (Baker *et al.*, 2003). Species in which a loss of vocal diversity in island populations has been observed include Singing Honeyeaters and Red-capped Robins on Rottnest Island (Baker, 1996; Baker *et al.*, 2006) and Chaffinches on Chatham Island (Baker and Jenkins, 1987). In these species it was suggested that a founder effect could account for the loss of vocal diversity. Conversely, some studies have shown that island populations have increased vocal diversity. For example, Western Gerygones on Rottnest Island have evolved a song with distinctly different syntax and commonly have a repertoire of two or more song types as opposed to a single song type on the mainland (Baker *et al.*, 2003, 2006).

Bald Island was chosen as a translocation site for Noisy Scrub-birds because of its close proximity to already occupied scrub-bird habitat, long unburnt vegetation (>100 years in some places) and the fact that it is predator free (Danks, 1994, 1997). Translocation to Bald Island, as with other scrub-bird translocations, extends the species' range and provides additional protection against wildfire, avian disease and, in this case, provides a predator-free environment (Danks, 1994).

Between 1992 and 1994, 11 scrub-birds (8 males, 3 females) were translocated to Bald Island (Danks *et al.*, 1996). Initial estimates suggested that the amount of habitat on the island was capable of supporting up to 20 territories (Gilfillan *et al.*, in prep.). By 1997 the number of singing males had exceeded the number of males released and by 1999 it had exceeded the predicted number of territories that the island was thought capable of supporting (Gilfillan *et al.*, in prep). Population growth has continued rapidly (Figure 7.1). By 2006 the population index had increased to 77 singing males. It has been suggested that the larger than expected population size is not just a result of low predation pressure and utilisation of non-typical habitat, but also as a consequence of the breeding colony of Great-winged Petrels supporting abundant invertebrates providing a good food source for the scrub-birds (Comer, 2003).

The small number of individuals released means that a founder effect could have quite an impact in this population, not only by only sampling a limited range of the genetic diversity but also by sampling a small proportion of the vocal diversity. If song learning is accurate and there is little improvisation or repertoire change, then there is the potential for a population to show a founder effect for quite some time (Baker, 1996). However, as demonstrated in the previous chapter, translocated scrub-birds are capable of rapidly altering their repertoires, both in terms of song structure and the number of songs in their repertoire. As a consequence of this vocal plasticity, songs will not be limited to the original sample of song types but will be subject to innovation, improvisation and modification, resulting in the production of song variation and cancelling out any founder effect.

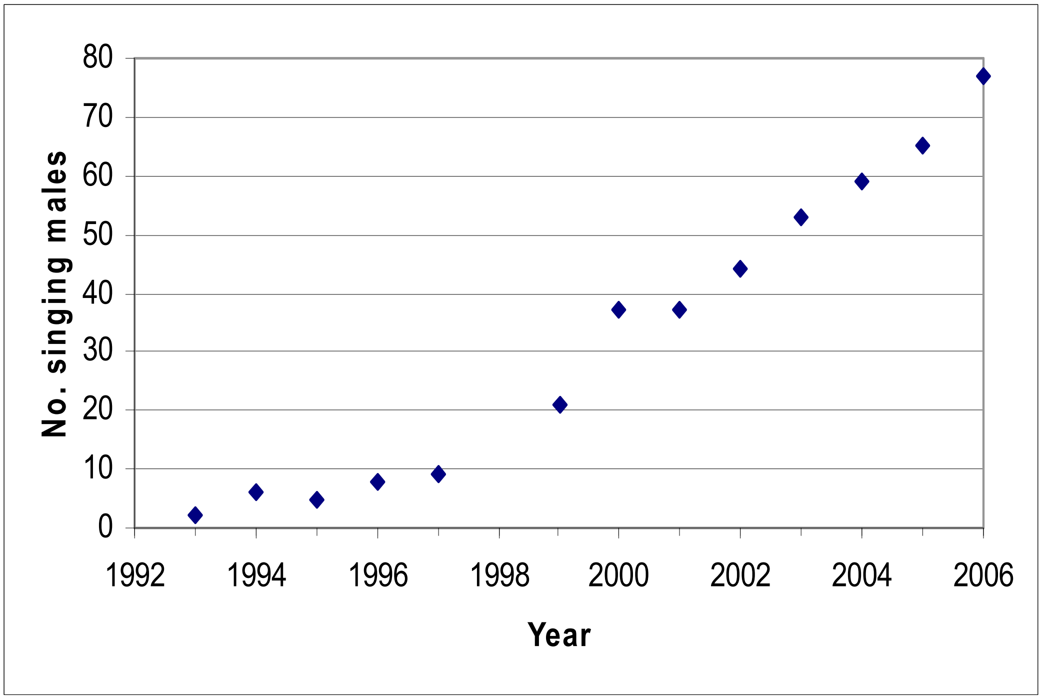


Figure 7.1: Number of singing males present on Bald Island.

The songs of the singing males on Bald Island were recorded in 2004, 2005 and 2006 in order to compare them with the patterns of song groupings observed on Mt Gardner. Although Mt Gardner was the source population for the birds translocated to Bald Island, the fact that there was a period of 10 years between the last release and the first sampling session of scrub-bird songs meant that there should have been more than sufficient time for any differences in song to have arisen.

Because repertoire change is a normal process in the Noisy Scrub-bird and territorial song appears to exhibit endless variety, it is difficult to tell whether the songs themselves are markedly different from those of the mainland birds. They do not sound appreciably different, and fit the syntax of normal territorial song. The more generalised measures of repertoire size, song group size and levels of song sharing were therefore deemed more practical measures by which to compare song characteristics.

The interesting aspect of Bald Island is that it is a completely closed system. Other than the initial releases between 1992 and 1994, no scrub-birds have been introduced to, or removed from the island. No natural movement of scrub-birds between Bald Island and the mainland (1.2km apart) could occur because they are poor fliers, incapable of sustained flight.

In addition, the study of Bald Island allowed another look at the effect translocation has on the songs of Noisy Scrub-birds, with the advantage that this was an established population in which the long-term effects of translocation on song could be studied. The aim of this exercise was to examine features such as repertoire size (reflecting vocal diversity), song group size and degree of song sharing in the Bald Island population and to compare these features with those from the source population at Mt Gardner. Because Noisy Scrub-birds are capable of rapidly changing their songs (Chapter 5) and will alter their songs to form song groups at a new site (Chapter 6), it was predicted that scrub-birds on Bald Island would show similar patterns of song sharing and vocal diversity to the Mt Gardner population.

7.2 Methods

Bald Island (Figure 7.2) is a 717ha island, 4.6km long and 2.3km at its widest point. It lies 1.2km off the coast. Sampling sessions on Bald Island were carried out during three trips; 21-24 September 2004, 2-5 August 2005 and 1-4 September 2006. In each of these sessions as many singing male scrub-birds as possible were recorded. In the 2004 sampling session, the songs of 33 out of a total of 59 singing males were recorded (56%); in 2005, 43 out of 65 were recorded (66%) and in 2006, 49 out of 77 were recorded (64%). The proportion of birds recorded was not higher due to the limited time on the island and infrequent singing of some birds, meaning that it was impossible to record them all. The size of the island, rough terrain and limited time meant that it was impossible to visit and record at every territory.

Recordings were analysed using the same methods as for the Mt Gardner population (see Chapters 2 and 4). Scrub-birds were named using the territory numbers from the annual census preceded by a “BA” (e.g. BA31).

Figure 7.2: Map of Bald Island. The numbered white dots represent the territories surveyed in the annual census.

The Bald Island sampling sessions were then compared to the results from Mt Gardner. An ANOVA with number of songs recorded as a covariate was used to look for differences in the individual repertoire size between Mt Gardner July 2005 and Bald Island August 2005. All Mt Gardner and Bald Island sampling sessions were not tested simultaneously as the data for each are dependent and therefore not suitable for a general ANOVA. Mt Gardner July 2005 and Bald Island August 2005 were selected as representative of each site. Also, because they were sampled at nearly the same time of year, and because in both July and August singing activity is high, there should not be any major confounding temporal effects. Song sharing was analysed using the same method as for individual repertoire size but without a covariate (as discussed in Chapter 4).

All Bald Island and Mt Gardner song group size data were analysed simultaneously with ANOVA. Data were first log-transformed to correct for correlations between means and variances. A planned comparison was also used to test the *a priori* hypothesis that there would be no differences in song group size between the two sites. Analysis comparing group repertoire size between the two sites was carried out using the same method.

7.3 Results

Tables 7.1 – 7.3 show the song types sung by each individual and how song sharing birds can be split into discrete groups. Figures 7.3, 7.4 and 7.5 map the boundaries of the song groupings present on Bald Island in 2004, 2005 and 2006 respectively. A combined map of these song groupings is shown in Figure 7.6. Most of the apparent change in song group boundaries is a result of incomplete sampling of territories each year.

Table 7.1: The song types present in each individual's repertoire in the September 2004 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU
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Table 7.2: The song types present in each individual's repertoire in the August 2005 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
68	1	1	1	1	1	1																				
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Table 7.3: The song types present in each individual's repertoire in the September 2006 sampling session. Each row represents an individual (identified by his territory number) and each column is a different song type. A "1" in a column indicates the presence of that song type in an individual's repertoire. The grey shading shows how individuals can be split into discrete song-sharing groups.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
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Figure 7.3: Song groupings present on Bald Island in September 2004. Territories at which songs were recorded are represented by a red dot. Red lines encompass the song-sharing males that comprise a song group. White dots show territories occupied in the 2004 census at which no songs were recorded.

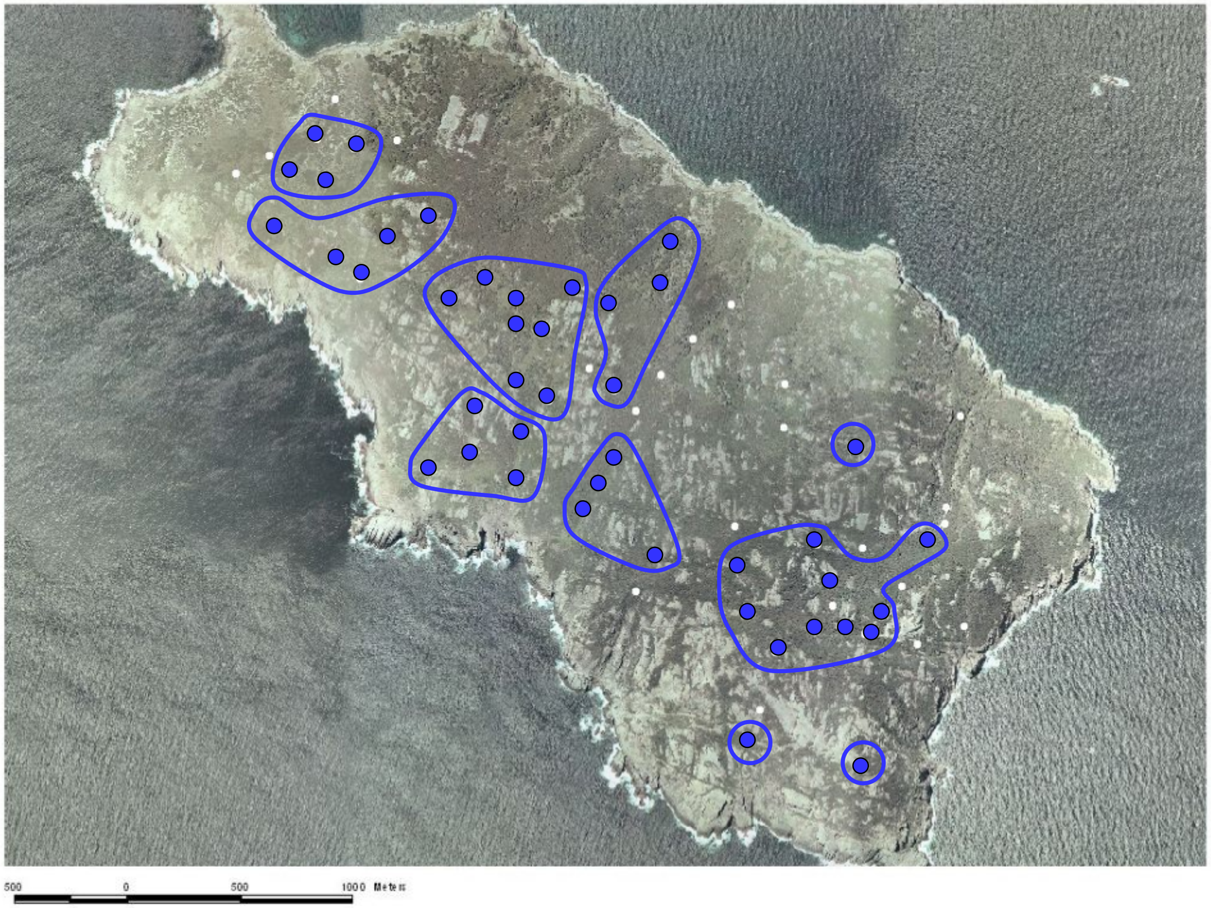

Figure 7.4: Song groupings present on Bald Island in August 2005. Territories at which songs were recorded are represented by a blue dot. Blue lines encompass the song-sharing males that comprise a song group. White dots show territories occupied in the 2005 census at which no songs were recorded.

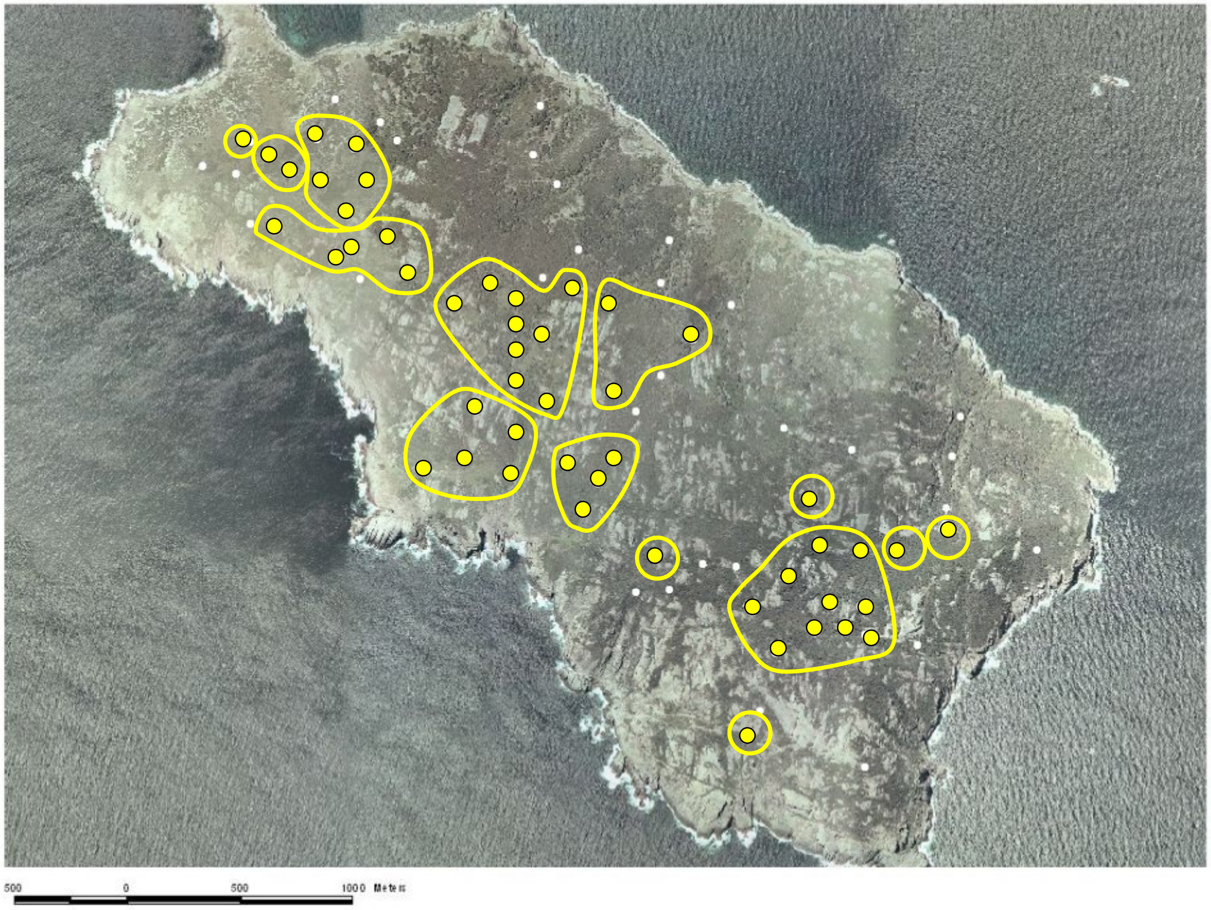

Figure 7.5: Song groupings present on Bald Island in September 2006. Territories at which songs were recorded are represented by a yellow dot. Yellow lines encompass the song-sharing males that comprise a song group. White dots show territories occupied in the 2006 census at which no songs were recorded.

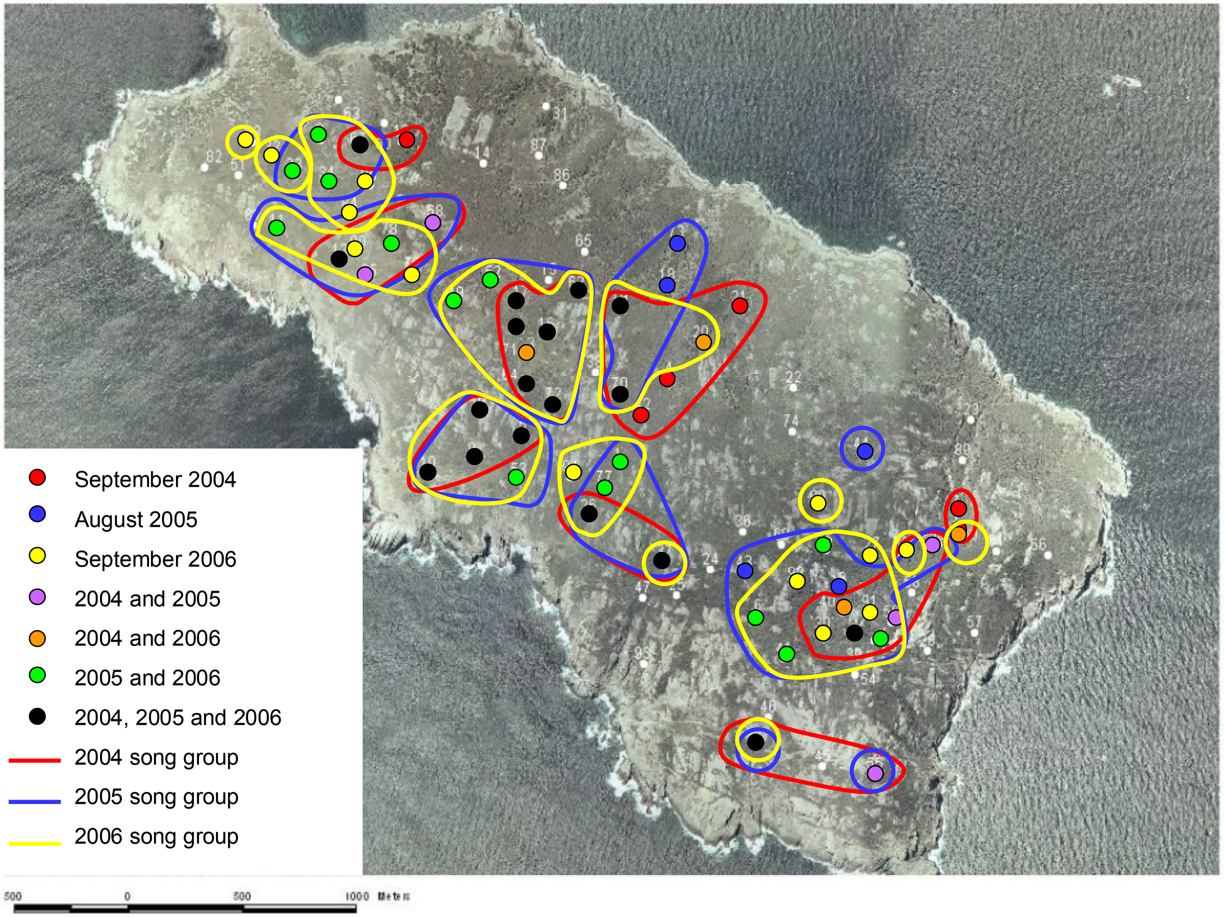

Figure 7.6: Combined song groupings for 2004, 2005 and 2006. White dots show territories not recorded in any of the sampling sessions.

Table 7.4 summarises the average values of repertoire size, song group size and song sharing for each of the three sampling sessions. Mean individual repertoire size was 5.4 song types per bird in both 2004 and 2005 and only slightly lower in 2006. Mean group repertoire size was larger than individual repertoire size in all cases. The degree of song sharing, as measured by the percentage of song types in a bird's repertoire shared with other birds, was similar in both 2004 and 2005 at 89.8% and 88.8% respectively, and lower in 2006 with 83.7% song types shared.

Table 7.4: Results of the Bald Island sampling sessions.

	Bald Island		
	Sep-04	Aug-05	Sep-06
No. birds recorded	33	43	49
Mean no. songs recorded/bird	10.7	10.2	11.0
Std error	0.86	1.04	0.98
Min no. songs recorded	4	1	1
Max no. songs recorded	31	29	31
Mean individual repertoire size (song types/bird)	5.4	5.4	5.3
Std error	0.25	0.33	0.27
Min individual repertoire size	2	1	1
Max individual repertoire size	9	9	9
No. song groups	9	10	14
Mean song group size (birds/song group)	3.7	4.3	3.5
Std error	0.65	0.94	0.81
Min song group size	2	1	1
Max song group size	7	10	10
Mean group repertoire size (song types/group)	8.1	7.9	7.6
Std error	0.99	0.92	0.76
Min group repertoire size	4	3	4
Max group repertoire size	14	11	12
Mean % songs shared with at least 1 other bird	89.8	88.8	83.7
Std error	3.32	4.09	4.67
Min % shared	25	0	0
Max % shared	100	100	100

A repeated measures ANOVA revealed no significant differences in individual repertoire size between the three sampling sessions ($F_{(2,34)} = 1.46$, $p = 0.296$). However, the covariate of number of songs recorded was significant for all three sessions ($p < 0.01$ in each). In many cases, only a small number of songs were recorded from a given individual. Where fewer songs were recorded, the bird had a smaller repertoire. A subsequent pair-wise comparison of each session (Table 7.5) confirmed that there was no significant difference in individual repertoire size between any of the sampling sessions. Once again, the covariate had a significant impact on the repertoire size for all sampling sessions ($p < 0.001$).

Table 7.5: Results of a pair-wise repeated measures ANOVA comparing individual repertoire size between each of the Bald Island sampling sessions.

	Sep 04	Aug 05	Sep 06
Sep 04		$F_{(1,22)}=1.092$ $p=0.307$	$F_{(1,21)}=0.084$ $p=0.775$
Aug 05			$F_{(1,30)}=2.396$ $p=0.132$
Sep 06			

The ANOVA testing all Bald Island sampling sessions showed no difference in song group size ($F_{(2,30)} = 0.40$, $p = 0.672$). Likewise, there were no significant differences in group repertoire size ($F_{(2,30)} = 0.098$, $p = 0.907$). A repeated measures analysis showed no differences in song sharing between any of the Bald Island sampling sessions ($F_{(2,36)} = 0.61$, $p = 0.548$). This was verified by a pair-wise comparison of each session (Table 7.6).

Table 7.6: Pair-wise comparison of song sharing between all Bald Island samples.

	Sep 04	Aug 05	Sep 06
Sep 04		$F_{(1,23)}$=1.660 p=0.210	$F_{(1,21)}$=2.219 p=0.151
Aug 05			$F_{(1,31)}$=1.640 p=0.210
Sep 06			

On comparing the Bald Island and Mt Gardner results (Tables 7.7 – 7.10) it can be seen that individual repertoire size was similar at between 5.0 and 5.5 song types per bird, with the exception of Mt Gardner September 2004 (Table 7.7). The overall average individual repertoire size was 5.4 song types per bird on Bald Island and 5.1 on Mt Gardner. There was no significant difference in individual repertoire size between Mt Gardner and Bald Island in the 2005 sampling sessions ($F_{(1,67)}$ = 0.0004, p = 0.983). The covariate had a significant impact on the repertoire size ($p< 0.001$).

Mean group repertoire size varied more widely (Table 7.8), with Mt Gardner values (overall average 6.5 song types per group) generally lower than those observed on Bald Island (7.9 song types per group). However, the overall ANOVA revealed no significant differences in group repertoire size between the two sites ($F_{(6,68)}$ = 1.18, p = 0.328). The planned comparison showed that there was no appreciable difference in group repertoire size ($F_{(1,68)}$ = 3.86, p = 0.053). Although the result was not significant, the sample size was small and the p-value was low. Therefore this result may be unreliable and would be worth investigating further.

Table 7.7: Mean individual repertoire size (number of song types per bird).

Bald Island	September 2004	5.4
	August 2005	5.4
	September 2006	5.3
Mt Gardner	May 2004	5.5
	July 2004	5.0
	September 2004	4.6
	July 2005	5.4

Table 7.8: Mean group repertoire size (total number of song types per song group).

Bald Island	September 2004	8.1
	August 2005	7.9
	September 2006	7.6
Mt Gardner	May 2004	5.4
	July 2004	6.8
	September 2004	6.2
	July 2005	7.6

The overall ANOVA showed no significant differences in mean song group size (Table 7.9) between any of the Mt Gardner and Bald Island samples ($F_{(6,68)} = 0.59$, $p = 0.735$). The planned comparison was also non-significant ($F_{(1,68)} = 0.68$, $p = 0.413$).

There was no significant difference in song sharing between Mt Gardner and Bald Island in the 2005 sampling sessions ($F_{(1,68)} = 0.20$, $p = 0.657$). Song sharing amongst members of a song group (Table 7.10) varied with no apparent trend. The combined average for Bald Island was 87.5% and 88.1% for Mt Gardner.

Table 7.9: Mean song group size (number of birds per song group).

Bald Island	September 2004	3.7
	August 2005	4.3
	September 2006	3.5
Mt Gardner	May 2004	3.3
	July 2004	3.9
	September 2004	2.3
	July 2005	3.1

Table 7.10: Mean % songs shared with at least one other bird.

Bald Island	September 2004	89.8
	August 2005	88.8
	September 2006	83.7
Mt Gardner	May 2004	95.7
	July 2004	89.6
	September 2004	81.3
	July 2005	86.0

7.4 Discussion

The translocated population on Bald Island provided an opportunity to study the long-term effects of translocation on the songs of the Noisy Scrub-bird. More specifically, it showed that the song group phenomenon observed on Mt Gardner also occurred on Bald Island and allowed comparisons to be made between the two sites of repertoire size, song group size and the degree of song sharing. It was predicted that the Bald Island population would show similar patterns of song sharing to the Mt Gardner population and the results seemed to support this.

Overall, there appeared to be no major differences between Bald Island and the source population at Mt Gardner in repertoire size and patterns of song sharing. Of particular interest was whether there was a decrease in vocal diversity (measured by repertoire size) in the island population. Differences in both individual repertoire size and group repertoire size were not statistically significant between Bald Island and Mt Gardner, indicating that vocal diversity was not reduced in Noisy Scrub-birds on the island over the time period of this study. It would also be of interest to investigate whether the diversity of syllables used within song types on Bald Island was similar to the mainland.

Baker *et al.* (2006) suggested that an island situation with a good food supply, low predation pressure and high population density, with no opportunity for dispersal, may result in increased male competition, polygyny and extra-pair matings. Such a situation could cause sexual selection to act on songs, producing more elaborate vocalisations. Population density is higher on Bald Island and may account for the slightly larger repertoire size. It is unlikely that this increase in repertoire size will continue indefinitely because at some stage the scrub-bird population will reach the carrying capacity of the island. Also, repertoire size was relatively consistent over the three years of the study, indicating that it is likely to be stable in the longer term.

The reduction of vocal diversity seen in some island populations of songbirds (e.g. Baker and Jenkins, 1987; Baker, 1996) is thought to occur through a founder effect, drift or withdrawal of learning (Baker *et al.*, 2003). As discussed earlier, founder effect is unlikely to have much of an impact on a translocated population of Noisy Scrub-birds because of their vocal plasticity. Likewise, drift is also unlikely to have much of an effect as it already occurs in scrub-birds in the form of repertoire change (Chapter 5). Withdrawal of learning, where colonisation occurs before songs are fully learned, does not occur during scrub-bird translocations as only territorial males with fully developed songs are targeted for capture. Therefore it is not surprising that there has been no reduction of vocal diversity in the population of scrub-birds on Bald Island.

Noisy Scrub-birds are capable of changing both the structure of their songs and the number of songs in their repertoire within a matter of weeks (see Chapters 5 and 6). Therefore it can be assumed that even though the Bald Island population was derived from the population on Mt Gardner, sufficient time had elapsed for any potential differences to develop. The observed similarities in song groupings and repertoire size were confirmation that the patterns of song groupings in the Mt Gardner sub-population were not an isolated phenomenon. It appeared that translocation had no lasting effects on the songs of the Noisy Scrub-bird, with apparently normal repertoire size, song sharing and song group patterns present in the Bald Island population. Therefore, at least in terms of vocal diversity, translocation of a small number of founders appears to have no long-term detrimental effect. The following chapter examines the findings of all aspects of this study and discusses their significance in terms of the possible social system of the Noisy Scrub-bird.

Chapter 8 –
Overview of Findings and General Discussion

The main aim of this study was to investigate the patterns of song sharing and repertoire change in the Noisy Scrub-bird. It was hoped that this would provide information that might indicate the social system of this otherwise very secretive species. Of particular interest was the impact of translocation on the songs of Noisy Scrub-birds. This allowed male scrub-birds that did not share any songs to be combined at a new site to study the development of song sharing groups. The Noisy Scrub-bird is rarely seen and very little is known about its social structure or mating system. Because singing plays a major role in the monitoring and management of this species, it would be useful to have a more complete understanding of what this singing signifies and how it relates to the social system.

This chapter is structured by first presenting a summary of the empirical results in relation to the aims of this study, followed by a comparison with other species. Next, a speculative model that may explain Noisy Scrub-bird song groupings and repertoire change based on the dominance scenario suggested by Berryman (2003) will be developed, and a series of predictions based on that theory will be explored to ascertain if the Noisy Scrub-bird conforms to them. This section also suggests future work that could be carried out to test these predictions. Finally, the relationship between songs and social systems will be discussed, as well as the implications of this in terms of the management of the Endangered Noisy Scrub-bird.

8.1 Major findings

Chapter 3 – Territoriality and Radio-tracking

Aims:

- To confirm that the same individual sang from the same location each day.
- To compare territories mapped by radio-tracking and those mapped by using the locations of singing males and to compare this with the annual census, as well as the territories mapped by Dr Graeme Smith in the 1970s and 1994.

Findings:

The assumption that the same individual sang from the same location each day appeared to be valid. Territories were non-overlapping and, in areas where birds' movements are well-known, there should be little chance of confusing the identity of singing birds.

The number of territories identified using the locations of singing males in the Tick Flat study area was approximately half the number of singing males detected in the same area during the annual census. Although this does indicate a level of error inherent in the census methods, it is important to remember that this reflects an index of the population. As long as census methods remain consistent, population trends should still be robust and meaningful.

The locations of territories varied very little between 1994 and 2005. Territory size reported by Smith (1985a) for the 1970s data was much larger than during the 2005 study. However, the method used by Smith to calculate territory size was not stated. Smith's 1994 data (unpublished) were used to calculate territory size using the same method as the current study and yielded smaller territory sizes, smaller in fact than those found in the current study. The Tick Flat area is long unburnt and it may be possible that, as the vegetation ages, it becomes less suitable for scrub-birds, forcing them to increase the area over which they forage and which they defend vocally.

Chapter 4 – Song Sharing on Mt Gardner

Aim:

- To investigate patterns of song sharing on Mt Gardner, focussing on the extent of song sharing, repertoire size, song group size, and the stability of song groups over time.

Findings:

Groups of up to 10 territorial males shared the same set of song types. The average repertoire size was 5.1 song types per male and the mean level of song sharing between members of a song group was 88%.

Song groupings on Mt Gardner were discrete. Members of a song group shared most, if not all, of their song types. Males from different song groups had no song types in common. Some change in the boundaries of song groups occurred as groups split or merged, or as birds on the periphery changed their songs to match with a neighbouring song group.

Chapter 5 – Repertoire Change on Mt Gardner

Aims:

- To track the changes in the songs of male scrub-birds over time and to quantify repertoire turnover and song persistence.

- To identify which individual introduced changes to the shared songs of members of a song group.
- To investigate song type matching and song rate to determine if this indicated which male was dominant.

Findings:

Repertoire change was rapid and, with the exception of one individual, was found in every individual studied in the Mt Gardner population. It occurred simultaneously in all members of a song group, with birds making the same changes to their shared songs. The source of repertoire change was mainly modification of existing song types with occasional divergence of a single song type into two distinct song types, as well as some innovation providing new song types. The average life of a song type was approximately six months. Although some song types persisted for the entire 16 month sampling period, they were continually being modified and a year later would no longer have been recognised as the same type without their continuity being monitored.

It was not possible to identify which individual introduced changes to the shared songs because of problems with recording. High quality recordings are necessary for the detailed analysis required to identify small structural changes in songs. Because this study was carried out in winter, no periods of suitable weather extended for the required number of sampling days. However, this approach still has potential in the future.

Song type matching occurred less often than expected by chance. It was hoped that song matching might indicate the dominant male within a song group.

Although the degree of song matching varied amongst the three individuals studied on Tick Flat, there were no indications of dominance among them.

Song rate varied between three focal males. There appeared to be a positive relationship to body weight, although the sample size was too small to draw any definite conclusions. Further investigation might indicate that song rate is correlated with body weight and thus could provide an honest signal of male quality.

Chapter 6 – The Effect of Translocation on the Songs of the Noisy Scrub-bird

Aims:

- To investigate the effect that translocation had on the songs of eight male scrub-birds that initially did not share any songs. It was predicted that these males would rapidly alter their songs so that they shared with their new neighbours.
- To identify if the songs of a particular male were copied or if the songs of two or more individuals converged on common songs.
- To study the replacement of males that had been removed from their territories. To measure how quickly they were replaced and to compare their songs to the original territory owner.

Findings:

Recombining scrub-birds that shared no song types at a new site during a translocation resulted in these individuals modifying their songs so that they shared with each other within a one to two month period. There was some suggestion that the songs of the dominant individual were copied, although this needs further investigation to confirm it.

Removal of eight males from their territories resulted in rapid replacement by males singing the same set of song types, with the exception of one individual who sang the songs of the neighbouring song group. This appears to indicate that subdominant males are present in the area.

Chapter 7 – Song Sharing on Bald Island

Aims:

- To study a population of scrub-birds that was established by translocation between 1992 and 1994 in order to determine if translocation had a long-term effect on their songs.
- To compare repertoire size, song sharing and song group size between the Bald Island and Mt Gardner scrub-bird populations.

Findings:

Observation of the population on Bald Island confirmed that there were no appreciable long-term effects of translocation on the songs of translocated Noisy Scrub-birds. Song group size, repertoire size and levels of song sharing were similar to those found in the Mt Gardner population.

8.2 Comparisons to other species

The Noisy Scrub-bird seems unusual in the discreteness of song groupings and the rapidity of repertoire change. However, song sharing groups that change their songs over time are also found in other species (e.g. Village Indigobird, Payne, 1985, Payne and Payne, 1997; Yellow-rumped Cacique, Trainer, 1989). The presence of continual repertoire change in the Noisy Scrub-bird indicates that males are capable of learning new songs throughout their life (i.e. they are open-ended learners, *sensu* Catchpole and Slater, 1995). For other species to be capable of repertoire change similar to that seen in the scrub-bird, they too are likely to be open-ended learners. It is these species that will be compared and contrasted to the Noisy Scrub-bird. Song sharing groups are given various names in the literature, including song groups (Jenkins, 1977), song neighbourhoods (e.g. Payne, 1985; Gaunt *et al.*, 1994) and dialects (e.g. Trainer, 1989, Kroodsma, 2004). For the purposes of this chapter, these terms will be used interchangeably.

The European Starling is an open-ended learner (Chaiken *et al.*, 1994) that has a complex pattern of song sharing. Some song themes are species-specific, others are shared amongst members of a social group, while some are individual-specific. Consequently, the size of the dialect area varies for each theme (Adret-Hausberger, 1982; Hausberger, 1997). Over a three year period, 12% of 34 song types from the same area could not be recognised (Adret-Hausberger, 1986), although there is evidence that within a stable social situation, songs change very little over time. Young starlings learn their songs from adults that they interact with socially, not aggressively (Hausberger, 1997). The pattern of song sharing and repertoire change in the European Starling differs from the Noisy Scrub-bird because song groupings are not discrete units for all song types, and repertoire change is much slower and results from social instability.

The Thrush Nightingale is another song sharing species, with neighbouring males sharing more songs than non-neighbouring males (Sorjonen, 1987; Griessman and Naguib, 2002). Once again, this species lacks the discrete song groupings with clear-cut boundaries that are seen in the Noisy Scrub-bird. Repertoire change is also present in the Thrush Nightingale, with the repertoire of a male more similar to the songs of a neighbour than to his own songs from the previous year (Sorjonen, 1987). The rate of change was not stated.

Interestingly, the suboscine Three-wattled Bellbird has song dialects resulting from song learning. Generally, suboscine birds have innate rather than learned songs, although the bellbird is an exception to this rule (Kroodsma, 2004, 2005). Three dialects have been described and in some areas young males are bilingual, singing the songs of the two neighbouring dialects, although in adulthood they discard one of the songs. Within each dialect there is a process of gradual change to the songs over time, with all adults making the same changes to their song (Kroodsma, 2004, 2005). The fact that this species usually sings just a single song type means that dialects are discrete by default, unlike the Noisy Scrub-bird where the entire set of about six song types needs to be shared to result in discrete song groups. Although the exact rate of song change was not stated, it was probably slower than that observed in the scrub-bird.

The Saddleback sings up to four song types and these song types may be shared by groups of up to twenty males (Jenkins, 1977). Unlike Noisy Scrub-bird song groups, Saddleback groups may overlap, with males at the boundaries singing the songs from adjacent groups. Young males did not usually sing the songs of their fathers, but rather the songs of the territorial neighbours where they settled (Jenkins, 1977). In contrast to the Noisy Scrub-bird, Saddleback song types were fairly stable over time, although adult males were capable of adopting new song types (Jenkins, 1977).

Perhaps the patterns of song sharing most similar to those observed in the Noisy Scrub-bird are found in the Yellow-rumped Cacique and the Village Indigobird. The Village Indigobird is a brood parasite with no social bonds within the family. Each male has up to 24 song types and all of these song types are shared with up to twenty neighbours (Payne, 1985; Payne and Payne, 1997). These song groups (called song neighbourhoods in this case) are usually discrete, although in some cases males have been recorded singing the songs of two or more groups. However, these males seemed to be in the process of dispersing to different song groups and adjusting their songs accordingly (Payne and Payne, 1997). Within a song neighbourhood, all males made the same gradual changes to their song types. Within four to five years all or most of the songs were unrecognisable. Male Village Indigobirds are polygynous and breed in a dispersed lek. Males at the centre of the arena usually gain about half of the matings. A successful male often leads the process of song change, with his songs copied by the surrounding, less successful males (Payne, 1985; Payne and Payne, 1997). Apart from the slower rate of repertoire change, Village Indigobirds have similar patterns of song sharing to Noisy Scrub-birds.

Yellow-rumped Caciques have repertoires of five to eight song types shared by all members of a breeding colony. These songs differ from songs at other colonies (Trainer, 1987). Repertoire change occurred as all members of the group made the same gradual changes to their song types and as dispersing males introduced new song types. 78% of song types were distinct from those present a year earlier, with 45% apparently derived from earlier songs, and 17% were possibly introduced by dispersing males (Trainer, 1989). These patterns of song sharing and repertoire change are quite similar to that of the Noisy Scrub-bird, although the proportion of song types introduced by dispersing scrub-birds is probably low if the assumption that territory holders have a long tenure is valid. The rate of song change in the cacique is somewhat slower too; in the scrub-bird most songs are substantially different within six months.

It has been suggested for both the Village Indigobird and the Yellow-rumped Cacique that successful males are copied by other males (Payne, 1985; Trainer, 1989). In fact, Trainer (1989) proposed a very similar situation to the dominance scenario suggested for the Noisy Scrub-bird.

8.3 Predictions of the dominance scenario

Noisy Scrub-bird song groupings are remarkably discrete and cohesive, even in the presence of continual repertoire change. Berryman (2003) suggested that within each song sharing group of Noisy Scrub-birds there was a dominant male that was copied by all the other members of the song group. It was proposed that this dominant male had songs that were more attractive to females, and that neighbouring birds gained an advantage by copying his attractive songs. The dominant bird continually made changes to his territorial songs and was copied by all the other males in the song-sharing group. The aim of this project was to further explore song sharing and repertoire change in the Noisy Scrub-bird, with the hope of providing evidence to support the dominance theory.

The secretive nature of the Noisy Scrub-bird combined with the difficulty of capture and the need for non-intrusive study due to its Endangered status, mean that direct evidence to support the dominance scenario is difficult to obtain. A series of predictions about Noisy Scrub-birds can be drawn from the proposal, however, and each of these will be examined in turn and discussed in relation to the results of this study:

1) *If male song acts as both a signal of relative dominance to other males and as an indicator of male quality to females, then some aspect of song should reflect male and/or territory quality.*

Possible song cues that may signal male quality include song rate, amplitude, repertoire size, and song sharing. For direct evidence to support this prediction, playback trials would be needed to measure both male and female responses to songs that were manipulated to alter various song characteristics. However, this was outside of the scope of this project.

Some evidence of a relationship between Noisy Scrub-bird song and male quality was obtained as part of the repertoire change investigation (Chapter 5), where song rate was examined. Song rate varied between the three focal males, and when compared to body measurements appeared to be positively related to body weight. However, the small sample size was insufficient to determine any real relationship. This would need further investigation, however this would be very labour-intensive, as a large sample of songs over a period of at least several days would be required to provide an accurate measure of average song rate.

Gil and Gahr (2002) reviewed how a male's singing behaviour may provide an indicator of his quality in terms of direct material benefits and indirect genetic benefits. Song characteristics that may reflect male quality include repertoire size, specific song content (song sharing, dialects, special syllables, song frequency), timing of singing, performance related traits (song rate, length, amplitude), and countersinging patterns. Costs and constraints that may affect these song characteristics include energy and time budgets, physical and developmental constraints, social aggression, predation, age and experience, neural costs (developmental costs, maintenance costs, trade-offs in brain space, endocrine costs), and immunocompetence costs (Gil and Gahr, 2002).

Song rate (number of songs per unit of time) is probably the most likely indicator of male and/or territory quality in the Noisy Scrub-bird. Singing takes up time and energy that could otherwise be spent on activities such as foraging. Therefore, a male with a high song rate is either high quality himself and efficient at foraging, or has a high quality territory with good food resources, reducing the time spent foraging (Gottlander, 1987; Catchpole and Slater, 1995; Lambrechts, 1996; Oberweger and Goller, 2001). It has been suggested that song rate indicates male and/or territory quality in a number of species, including Pied Flycatchers

(Gottlander, 1987), Willow Tits (Welling *et al.*, 1997) and Blackcaps (Hoi-Leitner *et al.*, 1995).

The effect of food availability on song rate has been demonstrated in several species, where provisioning of food resulted in an increase in song rate and a decrease in the time spent foraging (Ipswich Sparrow, Reid, 1987; Pied Flycatcher, Gottlander, 1987; Alatalo *et al.*, 1990). Other studies have shown that song rate correlates with various aspects of male quality. For example, song output of male Barn Swallows was reduced by the presence of parasitic mites (Moller, 1991) and song rate was positively correlated with a male body condition index in the Willow Warbler (Nystrom, 1997). A high song rate in male Willow Tits was associated with more intense nest defence and a greater input into feeding nestlings (Welling *et al.*, 1997). Song rate may therefore be used by both males and females in assessing male quality. Song rate in the Ochre-bellied Flycatcher correlated positively with the number of visits by both males and females to a male's territory; muted males had higher rates of intrusion and the majority quickly lost their territories (Westcott, 1992). Village Indigobird males that sang more were also more successful in gaining matings (Payne and Payne, 1977).

Catchpole (1982) suggested that in species in which males have little or no input into raising their offspring, females should ensure they choose a territory which has sufficient resources for them to raise their chicks alone. If song rate does reflect territory quality, then female Noisy Scrub-birds that select a male who sings frequently could also be selecting a good territory in which to raise a chick. A high quality territory will provide a female with better nesting locations and more plentiful food; both of which will increase the survival of the female and her offspring (Podos *et al.*, 2004).

Repertoire size and song sharing are unlikely to act as cues in the Noisy Scrub-bird because they are fairly uniform between the members of a song group and are therefore unlikely to show enough variation to distinguish between individuals. Song type matching is also a potential cue – in some species it appears to be an aggressive signal (Vehrencamp, 2000) and leader-follower rules can indicate dominance (Kroodsma, 1979). Amplitude too could provide a cue – a European Starling studied showed a 16% increase in oxygen consumption when its song increased by 16dB (Oberweger and Goller, 2001), suggesting that a male may need to be high quality or have a good territory in order to meet the energy demands of singing loudly.

2) *Each territorial male copies the songs of the most dominant male near him.*

This would involve each territorial male listening to the males around him and evaluating their relative dominance. He would then copy the most dominant of his neighbours. If he was more dominant than the males surrounding him, then he would sing his own unique set of song types.

This would explain why song groups were so discrete and had abrupt boundaries. It was observed that a bird either shared songs with a neighbour or he did not. In no instance was a male ever found to sing the songs of two or more song groups. It is easiest to envisage that each male only copies the songs of one male, rather than songs from all his audible neighbours. If songs from all neighbours were copied, then boundaries between song groups would be less distinct.

Direct evidence to support this prediction is difficult to obtain. Observations of the eight male scrub-birds translocated to Porongurup National Park (Chapter 6) suggested that the songs of a dominant individual may be preferentially copied. Further evidence could be obtained by conducting playback trials to either captive males or males that are naturally acoustically isolated from other territorial males. However, it would be necessary to know what characteristics of Noisy Scrub-bird song convey dominance or attractiveness. Within Village Indigobird song groups, there is evidence that the most successful male is copied by the others in the group and this successful male has a higher song rate (Payne and Payne, 1977; Payne, 1985; Payne and Payne, 1997).

3) *Repertoire change will occur simultaneously amongst all members of the song group. Within the song group there will be one individual who introduces all the changes to the shared song types.*

For all males within a song group to make the same changes to their shared songs there needs to be some method of reaching a consensus repertoire. The simplest explanation is that just one male within the group introduces all the changes to the songs. If more than one male was modifying the songs then it would make it very difficult for the group to stay as a cohesive song-sharing unit, particularly if two or more birds were modifying a particular song type in different directions.

The dominance scenario proposes that the cohesive repertoire change seen within a song group is the result of the dominant bird continually modifying his songs and the other members of the song group making the same changes to their shared songs in order to retain their mimicked attractiveness. If this is the case, then it would be expected that within each song group there will be one male whose songs are always slightly ahead of those sung by the rest of the group.

An attempt was made to test this proposition by recording three males intensively over nine days (Chapter 5). The aim was to measure features of the songs to quantify change and to identify how it varied amongst the males. However, inclement weather meant that the recording quality was not sufficient to allow such detailed comparisons to be made. It may be worth repeating this, although it is very labour-intensive and time-consuming. Evidence from the Village Indigobird showed that the successful male usually introduced changes to the song types of the group (Payne, 1985).

4) *The dominant male may have his songs type-matched more frequently by the other song group members as they check their songs against the model*

Song type matching was investigated in the three males that were recorded intensively. Although it did appear that one of them was matched more frequently, song matching seemed to be avoided to some extent, with it occurring less often than the level expected by chance. The presence or absence of a consistent leader in song matching would by no means prove or disprove the dominance theory. It would merely have provided circumstantial evidence that there was a song leader. This could either be a dominant male singing first, followed by other males to check their version of that song, or a subordinate male singing first, followed by a dominant male singing the correction, or song matching may have another function altogether. In the Marsh Wren, males show ritualised leader-follower rules during countersinging, with the subordinate male frequently matching the song types of the dominant male (Kroodsma, 1979).

5) *If the songs of the dominant male within a song group are more attractive to females then he should have greater mating success.*

Ideally, there is a need to observe which females mate with which males, but the Noisy Scrub-bird is so rarely seen that this would yield little information. To determine if there is variation in the breeding success between the members of a song group, the paternity of all the chicks within a song group or several song groups would need to be determined. However, this would require catching all the males and finding all the chicks within that area. Males are difficult to capture and there is no guarantee all nests would be found as they are well hidden. Also, this would be very time-consuming, intrusive and impractical. Evidence from the Village Indigobird shows that within a song group there is a successful male who obtains the majority of the matings (Payne, 1985; Payne and Payne, 1997).

Although it could be viewed that the members of a song group are, in effect, parasitising the dominant male's success, it is possible that the dominant male actually benefits from being copied. Having a group of birds repeating his attractive songs would increase the area over which these songs are broadcast and could potentially attract more females into the area. Once in the area, the females could then use other song cues to discriminate between the males.

As discussed earlier, it is likely that the dominant male within a song group continually changes his songs in order retain his attractiveness to females. Assuming that females are using song as a cue for mate choice, then the dominant male should have songs that are more attractive in some way. Song rate is a likely cue of male and/or territory quality, but the continual repertoire change within song groups suggests that song structure may also play a role in mate choice. If indeed it is the dominant male who is responsible for initiating all the modifications to the group's repertoire, then it is likely that part of his success lies in having songs that are slightly different to the rest of the group. The other members of the group would play a continual game of catch-up, modifying their songs to sound as similar to the dominant male as possible.

8.4 Relationship between song and social system

There is evidence that male Noisy Scrub-birds are opportunistically polygynous (that is, they may mate with more than one female), and there is no male input into breeding other than mating (Smith, 1985a; Danks *et al.*, 1996). The degree of polygyny and whether some males are more successful than others is unknown because of the difficulty of observing scrub-birds. It is possible that the song sharing of the Noisy Scrub-bird may indicate social system. Both the Yellow-rumped

Cacique and the Village Indigobird are polygynous and the patterns of song sharing and rapid repertoire change seem to be related to the high degree of social competition (Payne, 1985; Trainer, 1989; Payne and Payne, 1997).

There are some general characteristics of species that are polygamous. Polygamy tends to occur in species in which one sex does not participate in the care of offspring, where resources are unevenly distributed, if sexual receptivity of the other sex is asynchronous, and if the ratio of fertilisable females to sexually active males (operational sex ratio – OSR) is imbalanced (Emlen and Oring, 1977). All of these factors result in the potential for one sex to accumulate several mates. In the Noisy Scrub-bird there is no male parental care, resources are patchy because of variation in the distribution of suitable vegetation, the breeding period of females may extend from May to November (Danks *et al.*, 1996), and the OSR is imbalanced because presumably only the territorial males mate (there is evidence from removal of males (Chapter 6) that suggests there may be a large population of non-territorial males resident in the area). Therefore, the Noisy Scrub-bird appears to conform to the conditions that may promote the evolution of polygamy.

Polygamy occurs when an individual has several mates and polygyny refers to the form of polygamy in which individual males frequently control or gain access to multiple females. Emlen and Oring (1977) define several different types of polygyny: 1) Resource defence polygyny where males indirectly control access to females by monopolising critical resources, 2) Female (or harem) defence polygyny where males directly control access to females, and 3) Male dominance polygyny where monopolisation of females or critical resources is not economically feasible and females select their mates from aggregations of males. Male dominance polygyny was further divided into explosive breeding assemblages where both sexes converge for a short, synchronous mating period; and leks where female receptivity is less synchronised and males are sexually active throughout the entire period in which females are capable of breeding. Within stable assemblages, males compete for position or dominant status. Leks are characterised by a skew in male mating success (Foster, 1981, 1983). The patterns of song sharing and repertoire change in the Noisy Scrub-bird could suggest that male dominance polygyny, or more specifically a lek mating system is present. The song groupings observed in the Noisy Scrub-bird possibly represent a lek, with each lek identified by a shared set of song types.

Leks are mating systems in which males gather at a site to display to females. The males contribute no parental care to the offspring (Emlen and Oring, 1977; Foster, 1983; Reynolds and Gross, 1990). In a classical or clumped lek, males display in dense aggregations, whereas in a dispersed or exploded lek males display from fixed sites that, as the name suggests, are dispersed in space (Reynolds and Gross, 1990; Thery, 1992). In a dispersed lek, the emphasis is often on auditory rather than visual contact (Foster, 1983). If indeed the Noisy Scrub-bird is a lek-mating species, the lek would be considered to be dispersed because of the scattered nature of male territories. Beehler and Foster (1988) consider leks to be clustered in space. However, Noisy Scrub-bird territories show no such clustering and so by this definition are not a dispersed lek. Nonetheless, there is no reason why leks need be clustered in space if they can be identified by some other means. In the Noisy Scrub-bird, the presence of discrete groups of song sharing males could be used to identify each lek. Leks are not necessarily obvious spatially, but acoustically show discrete clusters of song sharing males. The close analogues to Noisy Scrub-bird song groupings, seen in the Village Indigobird and Yellow-rumped Cacique, also show lek or lek-like mating systems identified by song sharing, as does the Three-wattled Bellbird (Feekes, 1982; Payne, 1985; Kroodsma, 2004).

Lek mating systems potentially provide females with several benefits. Having an aggregation of males can minimise female assessment time, travel time and energy, and reduce the risk of injury from males or predation (Reynolds and Gross, 1990). A possible disadvantage of leks is that they increase the risk of disruption of mating by other males. Foster (1983) suggests that if disruption is high then selection will act to reduce this through dominance hierarchies and/or an increase in the spacing between males. She proposed that an equilibrium between forces favouring clustering and those promoting dispersion have resulted in the formation of dispersed leks. Accordingly, disruption is unlikely in the Noisy Scrub-bird as their territories are dispersed and non-overlapping (Chapter 3), and direct encounters with neighbours appear to be rare (pers. obs.).

There are two hypotheses regarding lek formation, the hotspot hypothesis and the hotshot hypothesis. The hotspot hypothesis states that leks form when males aggregate in areas where females are likely to congregate or pass through. The hotshot hypothesis focuses more on male-male interactions, with males clustering around a successful “hotshot” male (Beehler and Foster, 1988; Thery, 1992). The song groupings present in the Noisy Scrub-bird and the dominance scenario suggested to explain them, falls neatly into the hotshot category. The hotshot hypothesis, like the dominance theory, proposes that the successful, attractive male gains more matings, and also that the males clustered around him benefit by obtaining more matings than if they displayed alone (Beehler and Foster, 1988).

8.5 Management implications

The main aim of this study was to investigate whether the songs of the Noisy Scrub-bird could indicate the social system of this species. Although there is little direct evidence, it is suggested that the mating system of this species is possibly a dispersed lek, with each lek identified by a set of shared song types. It is possible that, within each lek, the mating success is skewed, with the dominant male gaining most of the matings as is predicted by both the dominance theory suggested to explain song groupings and the hotshot hypothesis of lek formation. It should not be assumed that each territorial male is contributing equally to the genetic pool of the next generation. It is perhaps important to consider that, in a translocation situation where there are only a small number of founders, a skew in mating success may result in only one or two of the males fathering offspring, further reducing the genetic diversity.

Probably the most important aspect of this study was the investigation of the impact of translocation on the songs of male scrub-birds. If song groups are functionally significant and confer an advantage to their members, then the choice of birds for translocation could be a major factor in the success of the translocation. The eight translocated males that were studied initially did not share any songs but within one to two months had altered their songs so that they shared. This vocal flexibility and the rapid change in songs to form new song groups means that translocation probably has relatively little impact on the function and success of their songs. Also, the major benefit of belonging to a song group is most likely related to an increase in breeding success. Because females are not released until a year after males are first released at the translocation site, the impact of translocation on mating success will be delayed until after males have had the opportunity to establish new song groups. Within a few months the translocated males had begun to share songs, so by the time females are released they should have well-developed song groups.

An additional benefit of monitoring the songs of translocated individuals was that it allowed ongoing identification of the individuals by their songs, particularly in the first few months. Although over time their songs changed and individuals began to share songs, in most cases identity could be assigned with a reasonable amount of confidence. This potential for identification exceeded expectations and was longer-lasting than radio-tracking. In two cases it permitted the detection of an individual taking over singing at a location where another had been singing previously. In the past, it would have been assumed that singing from the same location was all from the one individual.

Another finding that may affect management of this species is the observation that the number of singing males recorded on Tick Flat in the annual census was twice the actual number of territories present when mapped based on singing locations. While this does raise a concern that the census may be overestimating the number of territorial males, it is important to remember that this is just a population index and as long as census techniques remain consistent from year to year, population trends should be meaningful.

In the future, further insights into scrub-bird life could be provided by more song monitoring. For example, it would be interesting to translocate males all taken from the same song group to see what effect this has on their songs. Also, as suggested earlier, it could be useful to determine paternity for all the chicks in an area to see if breeding success is skewed. However, this is impractical due to the time-consuming and difficult nature of scrub-bird captures and nest-searching. It would also be very intrusive, especially for an Endangered species.

The great advantage of using song to investigate the Noisy Scrub-bird social system is that it is non-invasive with very little, if any impact on the birds being recorded. Scrub-birds are rarely seen so colour banding and direct observation of individuals, while extremely useful, is impractical because resighting of scrub-birds occurs so infrequently. Although direct evidence is difficult to obtain, song has yielded some clues to guide further investigation of their social system.

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Appendix 1 –List of Species Names

Barn Swallow	*Hirundo rustica*
Blackcap	*Sylvia atricapilla*
Black-capped Chickadee	*Poecile atricapillus*
Brown-headed Cowbird	*Molothrus ater*
Budgerigar	*Melopsittacus undulatus*
Cactus Finch	*Geospiza scandens*
Canary	*Serinus canaria*
Chaffinch	*Fringella coelebs*
Corn Bunting	*Miliaria calandra*
Eastern Phoebe	*Sayornis phoebe*
European Starling	*Sturnus vulgaris*
Golden Bowerbird	*Prionodura newtoniana*
Great Tit	*Parus major*
Great-winged Petrel	*Pterodroma macroptera*
Greenish Warbler	*Phylloscopus trochiloides*
House Finch	*Carpodacus mexicanus*
Indigo Bunting	*Passerina cyanea*
Ipswich Sparrow	*Passerculus sandwichensis princeps*
Marsh Wren	*Cistothorus palustris*
Medium Ground Finch	*Geospiza fortis*
New Zealand Robin	*Petroica australis*
Nightingale	*Luscinia megarhynchos*
Noisy Scrub-bird	*Atrichornis clamosus*
North Island Robin	*Petroica australis longipes*
Ochre-bellied Flycatcher	*Mionectes oleagineus*
Pied Flycatcher	*Ficedula hypoleuca*
Red-capped Robin	*Petroica goodenovii*
Rufous Scrub-bird	*Atrichornis rufescens*
Saddleback	*Philesturnus carunculatus*
Singing Honeyeater	*Meliphaga virescens*
Song Sparrow	*Melospiza melodia*
Stripe-backed Wren	*Campylorhynchus nuchalis*
Superb Lyrebird	*Menura novaehollandiae*
Three-wattled Bellbird	*Procnias tricarunculata*
Thrush Nightingale	*Luscinia luscinia*
Village Indigobird	*Vidua chalybeata*
Western Bristlebird	*Dasyornis longirostris*
Western Gerygone	*Gerygone fusca*
Western Whipbird	*Psophodes nigrogularis*
Willow Tit	*Parus montanus*
Willow Warbler	*Phylloscopus trochilus*
Yellow-rumped Cacique	*Cacicus cela*
Zebra Finch	*Taeniopygia guttata*