HABITAT MATCHING AND CULTURAL CHANGE IN CHAFFINCH SONG

James Michael Williams

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by

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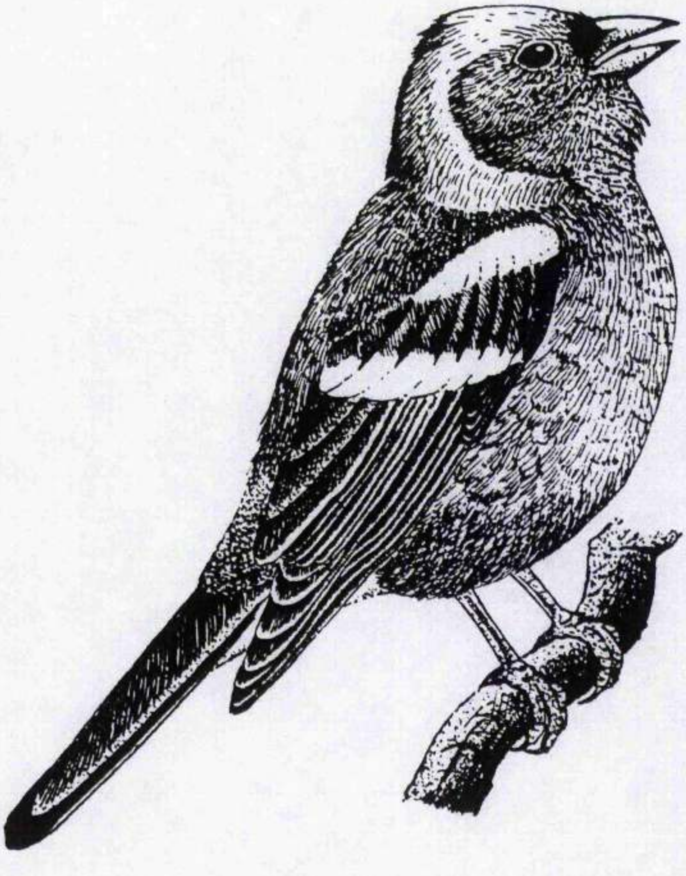

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Abstract

The acoustic adaptation hypothesis was reviewed. This predicts that the sounds used by birds singing in a dense habitat should be of lower frequency than those in a more open habitat, and that sounds should be spaced out more in time in denser habitats to avoid degradation by reverberations. These predictions were tested by recording chaffinch (*Fringilla coelebs*) songs in open scrub, coniferous plantations, and a natural Scots pine forest, but the results obtained gave little support to the predictions made.

Transmission of white noise and the songs of blue (*F. teydea*) and Canary Islands chaffinches (*F. c. tintillon*) through laurel and Canarian pine forests on Tenerife revealed a sound window of less excess attenuation than expected in both habitats at frequencies of 2-3kHz. The song of the blue chaffinch appears to be better adapted for transmission through both habitats.

Computer simulations of the formation of dialects by random copying of the songs possessed by neighbours predicted a strong effect of both the number of neighbours available to learn from, and the repertoire size, upon the songs' longevity and the number of birds sharing a particular song type. If the song type which was commonest amongst those sung by neighbours was learnt, larger groups of birds were found to share song types. At low copying error rates these groups approached the size of those described for the white-crowned sparrow (*Zonotrichia leucophrys*).

A computer program which uses the dynamic programming algorithm to compare objectively shapes digitised from sonagrams was developed and tested with syllables from chaffinch songs.

Chapter 1

Introduction

While this thesis is concerned primarily with chaffinch song, it is divided into three rather separate studies. The first investigates whether the song of the chaffinch (*Fringilla coelebs*) is adapted for transmission through the habitats in which it is sung. The second part builds on an earlier study by Goodfellow & Slater (1986) and uses computer simulations to examine the patterns of song sharing that can result from birds learning their song(s) from neighbours. The third part explores use of a pattern recognition technique called dynamic programming to compare shapes of bird song elements digitised from sonagrams. Each part will be introduced in turn: this introduction simply provides an introduction to the thesis as a whole.

The chaffinch is a small granivorous passerine bird which has been studied a great deal. There is an extensive literature on its ecology and behaviour, and particularly on the details of the learning and organisation of its song (see Chapter 3). In addition, as it is a very common bird which lives in a number of different habitats, it is a good species with which to study the acoustic adaptation hypothesis. One reason why it is of interest to test the hypothesis with chaffinch song from different habitats is that Jenkins & Baker (1984) found that some chaffinch song types in dense coniferous woods in New Zealand possessed an elaborate endphrase, which they suggested might be an adaptation to the transmission characteristics of these woods.

The literature about the acoustic adaptation hypothesis is reviewed in Chapter 2, and the literature about chaffinch song is reviewed in Chapter 3. A number of predictions made from the hypothesis have been tested by recording songs from open scrub, coniferous plantation woods, and natural Scots pine forest around Loch Garten in Speyside. The results of these tests are presented in Chapter 4. A worked example of the statistical analysis (ANOVA model) used is given in Appendix 1. In Chapter 5 the results of transmission experiments with white noise and the songs of two chaffinch species (the blue chaffinch *F. teydea*, and the Canary Islands chaffinch *F. c. tintillon*) in the laurel and Canarian pine forests on Tenerife are presented. Details of unusual syllables and song types recorded are compared with those in the literature in Chapter 6.

Computer simulation is a valuable tool for investigating the predictions of a theoretical model. The simulations presented are an extension to previous work (Slater *et al* 1980, Goodfellow & Slater 1986) which showed that small groups of birds singing the same song type could arise through random copying from the neighbours around them. Since the existence and formation of dialects or song neighbourhoods by birds is a subject of some controversy (Baker & Cunningham 1985), it is of theoretical interest to know how the number of neighbours available to learn from and the repertoire size may affect the sharing of songs between birds. The effect of the random learning process following various different rules was also investigated. The simulation studies are presented in Chapter 7. These have been published (Williams & Slater 1990, 1991).

Much of the work that is done on song learning involves an assessment of which of several potential tutors a tutee may have learnt from. The problem of classifying shapes from sonagrams also arises when an attempt is made to categorise the elements in songs. There are difficulties in comparing shapes objectively as variation can occur on both the time and frequency axes at the same time. A review of the methods used to analyse birds' sounds by computer (Williams & Slater in press) is presented in Chapter 8. A computer program using a pattern recognition technique (dynamic programming) has been implemented and tested with a small set of shapes digitised from sonagrams of chaffinch songs in an attempt to arrive at an improved technique. Chapter 9 is an account and assessment of the dynamic programming technique.

The conclusions from the studies presented are summarised in Chapter 10.

Chapter 2

Bird song and habitat matching: a review

The Acoustic Adaptation Hypothesis predicts that birds' songs should be adapted to transmit through the habitat in which they are sung. Since sound is a propagating waveform it will be scattered by obstacles in the transmission path. High frequencies, with a shorter wavelength than low frequencies, will be obstructed by smaller objects. It is therefore predicted that lower frequencies will transmit better through a dense habitat. Temporal distortion may also occur; signals in dense habitats should be separated more in time to reduce the effect of reverberations.

2.1 Factors affecting sound propagation

Much theoretical and empirical work has been carried out to answer questions about the transmission of sounds from such diverse sources as aircraft and lighthouses. Studies have concentrated upon the effect of vegetation and landforms in masking noise, especially from traffic (e.g. Embleton 1963, Aylor 1972a, 1972b, Cook & Van Haverbeke 1974, Allen & Dickinson 1977, Yamada *et al* 1977, Carlson *et al* 1977). Many abiotic and biotic factors can affect sound transmission. The most important are probably humidity, temperature, turbulence, ground attenuation, and habitat type (Ingard 1953, Wiener & Keast 1959, Harris 1963, 1966, 1971, Evans *et al* 1971, Bazley 1976, Piercy *et al* 1977, Michelsen 1978, Wiley & Richards 1978, Richards & Wiley 1980). These factors act by affecting the relative importance and effect of the processes that govern sound propagation, namely geometric spreading, absorption, scattering (diffraction), reflection, and refraction (Lyon 1973, Michelsen 1978, 1983, Wiley & Richards 1978).

General expressions for the attenuation of sound in air have been derived by Evans & Bazley (1956), Bass *et al* (1972), Evans *et al* (1971), and Bazley (1976). These rely on accurate and detailed micrometeorological measurements and this limits their usefulness for most field investigations. The factors and processes affecting sound propagation do not always act in a linear fashion, and the potential interactions make the transmission of sound a complex subject.

Increasing temperature causes sound to travel faster. A temperature gradient (with lower temperatures higher in the atmosphere as normally occurs above the earth's surface), will therefore cause sound waves to be refracted upwards. A shadow zone may develop, in which a receiver at a distance from the source will not be able to hear that source. This effect is tied to attenuation by the ground. A shadow zone caused by a temperature gradient can be broken up by wind. In inversion conditions, where the temperature gradient is reversed, sound may be refracted back down, and therefore travel further than otherwise expected. Birds singing under these conditions should be heard from further away than normal.

There is a peak of attenuation of sounds at around 5 - 20 % relative humidity (Harris 1966, 1971); less attenuation occurs at higher humidities, but the effect is both frequency and temperature dependent. More attenuation occurs for higher frequencies, and the peak of attenuation for lower relative humidities occurs at higher temperatures.

The wind, especially eddies caused by turbulence, is extremely important in determining attenuation (Richardson 1950, Ingard 1953, Mokhtar & Mahrous 1955, Brown & Clifford 1976). Higher frequencies are attenuated more than lower ones as a result of increased gustiness (Ingard 1953). The magnitude of the wind's effect will depend on the position of the source and receiver relative to its direction (Wiener & Keast 1959). This is because air velocity increases with height, so sound is refracted back down towards the ground in the downwind direction, and away from the ground in the upwind direction (Brenowitz 1986).

Sound is lost to the ground because it behaves as a porous absorbent medium. The extent to which the ground effect is important will depend to a large degree upon the substratum over which transmission occurs (Aylor 1972a, Martens 1977), and the roots of trees and other plants may affect the soil's porosity (Piercy *et al* 1977). Sound waves are also reflected from the ground, and the interference of the reflected and direct waves will depend upon the heights of the source and receiver (Embleton *et al* 1976). This interference mainly affects frequencies below about 1kHz (Wiley & Richards 1982, Brenowitz 1986); if this is linked with the attenuation by absorption and scattering (which increases monotonically with increasing frequency) the result is the "sound window" first observed by Morton (1975).

Roberts *et al* (1981) considered the ground effect unlikely to be important to the transmission of birds' songs when the sound source and receiver are between one and ten metres above the ground, over distances less than about 100m, and using frequencies greater than 500 Hz. Over longer distances (100m-300m), the most efficient frequency range should be from 1-2.5kHz to 6-10kHz (Roberts *et al* 1983). Their model (Roberts *et al* 1979, 1980) is however too simple (Martin 1981), because the attenuation which occurs is different for each plant community.

Empirical investigations on sound transmission have been carried out in various habitats. Linskens *et al* (1976) determined the acoustic properties of eight semi-natural plant communities. Each was found to have its own acoustic climate due to the species composition and soil. The season the experiments were done in was also found to be important. In general most attenuation was at low and high frequencies throughout the year, and this was attributed to soil and foliage characteristics.

Leaf area density, leaf width, and canopy breadth in a *Phragmites* reedbed were discovered to affect the transmission of random noise (Aylor 1972b). In contrast, little difference was found in the attenuation patterns of hemlock, pine and mixed deciduous brush habitats for transmission at frequencies of 2-10kHz (Aylor 1972a). The ground effect was found to be important for frequencies between 200 and 1000Hz.

In order to investigate the effect of foliage without the confounding factor of varying wind speeds (and other environmental factors), Martens (1980) used model forests in an anechoic chamber. The foliage acted as a noise amplifier in mid frequencies, but as a filter at high frequencies. The acoustic properties were determined by the species present, and there was a correlation between the maximum size of the plant leaves and the frequency at which filtering started. A correlation of attenuation and total biomass was also found.

Obstacles such as ground cover in the transmission path both scatter and absorb sound (Embleton 1963, Burns 1979, Martens & Michelsen 1981). The relative importance of these processes will depend upon the species present (Wiener & Keast 1959), as the vegetation acts as "a three dimensional diffraction grating" (Michelsen & Larsen 1983). The height of playback and the frequency of a transmitted tone were, however, found to affect transmission more than the habitat by Marten & Marler (1977); lower frequencies carried better, and a monotonic relationship of more attenuation with increasing frequency was observed when transmission was above about 2m. In addition, the patterns of excess attenuation were similar in open fields, mixed deciduous forest with and without leaves, and coniferous forests. The pattern of attenuation was also similar in secondary forest in Panama (Marten *et al* 1977).

2.2 The transmission of birds' songs

From the variety of the results described above it seems that a definitive study of sound transmission in diverse habitats is not possible because the results are always site specific, due to the fact that the number of possible factors affecting the transmission is large, and their interaction complex. Several studies have investigated the possible link between habitat acoustics and the sounds that birds use. Some have been purely observational, a few others have transmitted sounds experimentally, either white noise and tones of various frequencies, or birds' songs. It is undoubtedly true that songs attenuate and degrade as they are transmitted through the environment, but it is more difficult to prove that communication between birds is affected. Some studies (reviewed in McGregor 1991), have suggested that some bird species may be able to use the degradation imposed by propagation through the habitat to assess the likely distance away of a conspecific.

Effective communication requires both the detection and discrimination of a signal (Wiley & Richards 1978, Richards & Wiley 1980). The range over which a signal can be distinguished is limited by attenuation and degradation. Attenuation is the result of spherical spreading, degradation is the complex distortion which occurs as sound is transmitted through a habitat. This distortion can arise in several ways, for example, by attenuation in excess of that expected by spherical spreading, from reverberations, and from amplitude fluctuations. The amount of excess attenuation observed may depend upon the frequencies used, and each habitat is thus likely to have its own pattern of attenuation. Reverberations are a result of the scattering of sound by vegetation. Amplitude fluctuations are caused by turbulence. In practice of course, none of these processes occur in isolation, so the pattern of degradation of sounds produced by birds (and other organisms) varies considerably both within and between habitats.

Since both scattering from vegetation and atmospheric turbulence mainly affect frequencies greater than about 2kHz, in forests more attenuation will occur provided there is little wind present (Wiley & Richards 1982). However, in open habitats amplitude fluctuations can be severe, thus the distortion of a sound signal due to scattering of higher frequencies in forests is at least partly matched by distortion due to a greater micrometeorological heterogeneity in open habitats.

The relationship of the magnitude of amplitude fluctuations to the frequencies used and the distance over which sounds are transmitted is difficult to estimate as the low frequency amplitude modulation (AM) imposed upon the signal is irregular. Information in the signal which is contained in slow AM (< about 50Hz) is likely to be masked (Richards & Wiley 1980).

The relationship of reverberations to frequency is also complicated; though more occurs at higher frequencies it will be affected by the density and size of the foliage present, and by the directionality of the sound. Less reverberation occurs for more directional sounds, but there is little evidence of the use of directional sounds by birds. Some of the high frequency calls used by the black-capped chickadee (*Parus atricapillus*) are more directional than others (Witkin 1977), and Larsen & Dabelsteen (1990) suggested that blackbirds (*Turdus merula*) might be able to make the "seee" alarm call more directional by controlling the beak opening angle, and thus the sound pressure level of the noise.

It is common to observe that birds change perch position both within and between song bouts. This may be a behavioural adaptation to enhance the transmission of the sounds produced, as the bird's body can act as an acoustic shadow to high frequencies (Hunter *et al* 1986, Larsen & Dabelsteen 1990). Support for this hypothesis is provided by the observation that there was more variability in direction of singing in mockingbirds (*Mimus polyglottos*) early in breeding season (Breitwisch & Whitesides 1987) and that mated males sang into their own territories to a greater degree. Another strategy is to use a song or call that contains an alerting component, thereby facilitating detection of the sound; this was suggested as the function of the tonal element at the start of the song of the rufous-sided towhee (*Pipilo erythrophtalmus*) (Richards 1981), and for the alarm call recorded in the song of collared flycatchers (*Ficedula albicollis*) in an area of sympatry with pied flycatchers (*F. hypoleuca*) in Sweden. The alarm call may have been incorporated into the collared flycatchers' songs to enhance the species specificity of the signal (Wallin 1987).

Given the expectation of reverberations in dense habitats and amplitude fluctuations in open habitats it might seem that there is no clear reason to expect systematic differences in the optimal frequencies for long range communication in different natural environments. Nevertheless a number of studies across a variety of species have suggested that habitat has an effect upon the song structure. Some of these studies have been across several genera, others have investigated the acoustics relevant to a single species, or to a group within a genus.

Unfortunately, those studies (Chappuis 1971, Morton 1975, Lemon *et al* 1981, Cosens & Falls 1984a, Sorjonen 1986b) which have attempted to investigate the effect of habitat upon song across a number of genera are probably flawed by the phylogeny of the species studied, as the samples included some close relatives, all of which may have similar adaptations. Other possible confounding factors are body size (Wallsläger 1980, Ryan & Brenowitz 1985) and power output (Calder 1990); larger birds produce sounds with a lower emphasised frequency, and birds with larger territories may produce louder sounds. However, these studies probably also suffer from the problem of including closely related species.

2.2.1 Woods and forests

One of the first of the studies of sound transmission and bird song (Morton 1975) discovered that there was less excess attenuation (attenuation in excess of that expected from spherical spreading) than expected between approximately 1.5kHz and 2.5kHz at low levels in tropical monsoon forest in Panama. Estimates of the emphasised frequency of a variety of bird species in the habitat averaged 2.2kHz, and these songs were predominantly tonal. No evidence of a "sound window" was found in grassland or forest edge habitats. Transmission experiments at higher levels in the forest revealed that the sound window disappeared at heights above about 15 feet, suggesting that it may be the result of the interaction of frequency dependent attenuation and attenuation by the ground (Martin & Marler 1977, Martin *et al* 1977, Roberts et al 1979).

The large sample size (85 species in the upper and lower forest) in Morton's study suggests that the relatedness of some of the species used may be a confounding factor. Re-analysis of Morton's song data (Ryan & Brenowitz 1985) with data for nonpasserines, suboscines and oscines separated suggests that, although there are confounding relationships of frequency with body size, and to some extent with phylogeny, lower frequency sounds are produced by birds in the low forest habitat.

Lower emphasised frequencies have also been found for species in the dense undergrowth of tropical rain forest than in more open savannah habitat (Chappuis 1971), especially for small species using sounds with a relatively high pitch. Species were matched for family across the habitats, but the sample sizes within each group were very uneven. A strong selection pressure against frequencies greater than 1.5kHz was suggested by the results.

The helmeted hornbill (*Rhinoplax vigil*), a species of tropical and montane forest in Borneo uses loud calls which have the sound energy concentrated into low frequency (500Hz-1.5kHz) harmonics (Haimoff 1987). These calls appear to be well structured for transmission through the forest as they are audible at distances of up to 2-3km at some times of day.

Differences in the songs of great tits (*Parus major*) were found to be at least partly related to differences in the acoustic transmission of forests and more open parkland woods across Europe (Hunter 1978, Hunter & Krebs 1979). Attenuation tests showed that higher frequencies were attenuated more in the forests, however these included both coniferous and deciduous sites: the predictions of the hypothesis for these habitats are different. No link with climate, body size, perch height or acoustic competition was found. However, forest birds had larger territories, and it is not known for certain if songs from the forests have better acoustic transmission properties; woodland birds may sing louder or concentrate more energy at less attenuated frequencies. In addition the results of the attenuation tests were not considered to be very reliable (Hunter 1978). Another possible complicating factor is that Chappuis (1969) discovered a cline of pitch of birds songs with latitude; lower pitched sounds occurred further south, in the great tit as well as various other species.

The motif parts of blackbird (*Turdus merula*) song, thought to be important for long distance communication (Dabelsteen 1984) and species recognition (Dabelsteen *et al*

1989), have energy concentrated in the (low frequency) fundamental harmonic and are usually sung from high perches. More attenuation of thrush nightingale (*Luscinia luscinia*) song occurred in an open habitat in windy weather than when it was calm (Sorjonen 1983). More attenuation also occurred in a dense deciduous forest than in an open scrub, and elements with high frequencies and a wide frequency range were degraded most.

The songs of Carolina wrens (*Thyrothorus ludovicianus*) recorded in Florida and Maryland were found to be less degraded after transmission in their own area than in the other one, but both sets of songs were degraded equally when transmitted in an area foreign to both (Gish & Morton 1981). The songs of some Darwin's finches (*Geospiza* spp.) on different Galapagos islands were suggested to be adapted to the acoustical conditions of each island as the structure of the songs were found to be related to the transmission of different frequencies through the scrub and wood habitats on these islands (Bowman 1979).

Northern cardinals (*Cardinalis cardinalis*) singing in three stands of pine and hardwoods of different ages in Eastern Texas used different syllable types, and sang songs of different duration and complexity (Anderson & Conner 1985). A wider range of frequencies was used in the sapling stand, compared with the ranges in the pole and sawtimber stands. Where the canopy was not closed large amounts of frequency modulated sounds were used. This is somewhat suprising as Brenowitz (1986) suggested that frequency modulated sounds could be used to reduce degradation due to reverberations.

Summer Tanagers (*Piranga rubra*) live in different wooded habitats in the southeast and southwest of America. Songs in the denser eastern habitat were found to have lower maximum frequencies and a reduced frequency range (Shy 1983). The use of a narrower frequency range allows energy to be concentrated, it should therefore transmit further. The scarlet tanager (*P. olivacea*), a close relative, lives in more homogenous woods, the structure of its songs was not related to the tree density.

2.2.2 Grass and marsh habitats

The ground effect has been found to limit the low frequencies usable by grassland birds, with strong attenuation of frequencies less than 2kHz (Cosens & Falls 1984a). A decrease in the magnitude of the effect occurs with increasing height. Over a marsh habitat no ground effect was observed, and the minimum and emphasised frequencies used by a sample of species were lower than in the grassland habitat.

Higher frequencies were associated with field habitat and lower for forested habitat in the white-throated sparrow (Wasserman 1979). Waas (1988) suggested that the observed decrease in pitch with increased vegetation density of songs which had a low pitched note followed by one of higher pitch from open to mixed forests to boreal forest in this species might be an artifact as the birds sing above about 2m. Songs should therefore not be affected by the ground effect and as low a frequency as possible should be used in all habitats. Whilst this is true, if systematic differences occur between habitats, birds' songs can be expected to differ between the habitats. In addition, the study's statistics are inappropriate as a nested rather than a crossed ANOVA should have been used for the comparison of biomes and habitats, and only one song type was investigated; ignoring the observation that some song types are commoner in one habitat than in another seems strange, as those song types may be better adapted for the habitat(s) in which they are found.

Comparisons of the propagation of song sparrow (*Melospiza melodia*) song over fields and water (Shy & Morton 1986) suggested that they are locally adapted for transmission over about 30m, but no difference was observed at 60m. The accenting and buzzing songs used by yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) differ in the note structure, amplitude and frequency of maximal amplitude (emphasised frequency). After transmission through a marsh habitat the buzzing songs showed a shift in energy distribution, but the accenting songs did not. Results of behavioural experiments supported the hypothesis that the buzzing songs are used for short distance communication and the accenting songs over longer distances (Cosens & Falls 1984b).

The attenuation of pure tones was found to be frequency dependent with a strong increase above 5kHz in the habitats of three *Acrocephalus* warbler species (Jilka & Leisler 1974). A comparison of the songs and locations used led to the conclusion that the great reed warbler (*A. arundinaceus*) used the song posts at the top of the vegetation which are theoretically optimal, but that the reed warbler (*A. scirpaceus*) sang in non-optimal positions within the middle of the vegetation where transmission would only be over short distances. The sedge warbler (*A. shoenobaenus*) used song flights to escape the stronger attenuation found in its habitat as a result of the ground effect. Differences within reed-beds may also occur between seasons, Heuwinkel (1990a) found more attenuation of the songs of several *Acrocephalus* warblers in tests in the summer than in the spring.

The display of the blue-black grassquit (*Volatinia jacarinea*) combines both acoustic and visual elements. Males leap 30-45cm from their perches in tall grass and emit a high pitched buzzy trill. Wilczynski *et al* (1989) found that the leap enhances the display, as calls from above the grass could be distinguished from the background noise further away than those transmitted through the top of the grass in an open field habitat. The small difference in attenuation observed could be important as territories are small (mean diameter about 25m).

A correlation of higher frequencies with higher song posts was observed for 19 species of Parulid warblers (Lemon *et al* 1981). There was also a correspondence of song complexity with the usual singing height; songs sung at higher positions were associated with fast frequency sweeps, whilst those at lower positions had more element types. The distance over which songs were transmitted was environment, and thus the form of the song learnt by the tutee.

2.3 Acoustic interference

Although, in most cases, birds should sing using the lowest frequencies possible, this may not be appropriate in all cases. In environments with large amounts of low frequency background noise such as near waterfalls, birds' songs and calls might be expected to be of higher pitch than usual. Some evidence for this prediction is provided by Martens' (1990) study of birds living near Himalayan torrents. The birds avoided low frequencies (< 2kHz) and had loud calls and songs concentrated in a frequency range of 4-6.5kHz. Songs were often whistles perhaps as a mechanism to concentrate the energy present to transmit it further. It should be noted that the study lacked a control, i.e. songs from the same species away from the torrents were not studied. Further evidence that noise interferes with acoustic communication comes from the study by Heuwinkel (1990b) of song in dippers (*Cinclus cinclus*). He showed that song does not transmit further than about 5m, and argued that it serves for intrapair communication rather than for long distance communication. The song may show some adaptation for transmission as it has a high emphasised frequency (about 5kHz) in relation to body weight.

Other habitats are not without background noise of course and sounds from the wind and from other species can mask signals. For example, Bremond (1978) found that a not found to be maximised, but may be adapted for transmission to the bird's mate. Evidence for differential use of perches when singing has also been found for some European species; for example, the corn bunting (*Emberiza calandra*) maximises the transmission distance of its song by choosing higher song posts in the middle of the day than in the morning or evening (Moller 1986), and perches used by stonechats (*Saxicola torquata*) for singing were significantly higher than those used for foraging (Greig-Smith 1983).

Studies on the song of the rufous-collared sparrow (*Zonotrichia capensis*) have shown that a loose association of the trill rate and density of the habitat occurs (King 1972, Nottebohm 1975). Grassland populations showed a faster trill (20-110ms interval) than those in forests (75-280ms interval). The association remained consistent for over 10 years (Handford 1981). An association with the original vegetation, before conversion to agriculture took place, explained about 45% of the variation in trill rate (Handford 1988). This result is perplexing, but may suggest that although birds' songs can change over a few years as a result of cultural evolution, adaptive properties, such as improved transmission qualities, are more stable, and are likely to lag behind changes in the environment. These results conflict with Hansen's (1978, 1979) opinion that song learning might be part of the mechanism whereby songs become adapted to transmit through the environment. The distance between the tutor and tutee would be crucial in determining how clearly the song propagated through the noisy environment hampered communication for wrens (*Troglodytes troglodytes*). Brenowitz (1982a) concluded that the frequency range of the song of red-winged blackbirds (*Agelaius phoeniceus*) was adapted to transmit over long distances as it occupied a relatively quiet part of the frequency spectrum of the noise in their environment. The active space (the distance at which a receiver could perceive the signal over the background noise) was calculated as about 190m for this species in the absence of wind. This approximates to the diameter of two territories (Brenowitz 1982b).

Some of the effects of acoustic interference can be avoided by singing when others are silent (e.g. Cody & Brown 1969, Ficken *et al* 1974, 1985, Wasserman 1977, Popp *et al* 1985, Sorjonen 1986a, Popp 1989). Alternatively, songs may change as a result of interference. Lehtonen (1983) reported a decrease in the length of great tit songs over about 30 years in the Helsinki region, Finland. In the 1950s songs mainly consisted of three phrases, but by 1981 the commonest songs were of two phrases. The decrease was most noticable in noisy, sparsely wooded, urban areas. The song community (species present) was found to have a strong effect on the song length for a variety of European passerines (Sorjonen 1986b). Population density, avifaunal complexity, and habitat structure may all be important factors in determining the amount of background noise in a habitat (Kroodsma 1985).

Considerations of acoustic interference suggest that birds should not sing at the same time as others, either of their own or other species, so why is there a prominent peak of singing activity early in the morning ? The dawn chorus may occur for several reasons, including, female fertility and mate guarding (Mace 1987a, 1987b), variability in energy expenditure overnight (McNamara *et al* 1987), and that microclimatic conditions for acoustic transmission are often optimal at this time (Henwood & Fabrick 1979). These explanations are not mutually exclusive (Cuthill & Macdonald 1990).

2.4 Summary

Some studies have failed to find a link between habitat and song structure (e.g. Payne 1978, 1987, James 1981, Shy 1983) however, notwithstanding these negative results, it is obvious from the large number of studies cited above that the environment does impose constraints upon the time-frequency structure of many birds' songs. These may be minimised (Richards & Wiley 1980, Brenowitz 1986) in several ways:

(i) by producing the lowest possible frequency;

(ii) signalling from above the ground;

(iii) amplifying the dominant or fundamental frequency;

(iv) avoiding rapid syllable repetition in forest habitats, and slow repetition in open habitats due to the effect of amplitude fluctuations;

(v) emphasising frequency modulation in the signal, as this is less degraded by both reverberations and amplitude modulations;

(vi) singing at times of day when there is low ambient noise;

(vii) avoiding signalling at the same time as neighbours;

(viii) using species-specific patterns of sound such as a particular frequency range or time structure;

(ix) by incorporating redundancy into the signal produced.

In brief, a bird should avoid singing near the ground; should sing when the environmental conditions are as stable as possible, such as at dawn; and for long distance communication, should use as low a frequency as the body size will permit.

Chapter 3

Chaffinch song and acoustic adaptation

The chaffinch (*Fringilla coelebs* L.) is a small seed eating passerine. In the British Isles it is largely sedentary, but migrations occur on the European continent; some of these birds winter in Britain (Witherby 1938). The behaviour and ecology of the species have been comprehensively described by Marler (1956a) and Newton (1972). Song is used by males for both intrasexual and intersexual communication (Goodfellow 1988). Females rarely sing.

A song consists of two to four phrases of repeated syllables followed by a terminal flourish (see Figure 4.1). In some songs an unrepeated "transitional" syllable occurs between phrases. Songs usually last between two and three seconds, and are followed by a gap of a few seconds before the next is sung (Marler 1952). Within a song type, defined as a unique sequence of trill and endphrase syllables, there can be much variation in the number of repetitions of a given syllable both within and between birds (Slater & Ince 1979, pers. obs.).

Between one and six song types are learnt in about the first year of life (Marler 1956a, Thorpe 1954, 1958a, 1958b). Mimicry of other species is rare. The songs produced depend on auditory experience (Nottebohm 1968, see Slater 1989 for a review of bird song learning). A slight tendency for the birds to respond more strongly in a territorial situation to a stranger's song than to a neighbour's was noted by both Pickstock & Krebs (1980), and

Slater (1981), but the evidence appears to be against chaffinches using song repertoires as a cue to assess density of resident birds as Krebs (1977) suggested for the great tit (*Parus major*). There are methodological difficulties with this (Beau Geste) hypothesis (Slater 1978), and Dawson & Jenkins (1983), who tested it on chaffinches, concluded that they did not follow the predictions made.

The chaffinch tends to sing one song type several times (Marler 1956a found an average of 5.3 songs per bout) before switching to another (Brooks-King 1940, Hinde 1958). These sequences of song are cyclical (Slater 1983a); a bird tends to sing each song type in turn before beginning the first one again. Some transitions between song types are more common than others, so the order of singing song types tends to be fairly fixed. Within a bird different song types can vary markedly in how frequently they are sung (Nurnberger *et al* 1989, Goodfellow & Slater 1990).

Some song types are used by many birds, others by a few, or even just one. The distribution of song types in a population can be fitted to that expected from a model of neutral alleles (Slater *et al* 1980), this suggests that songs are copied at random. Syllable variants in nineteen populations of chaffinches along a 200km transect in New Zealand also fitted a neutral model (Plunkett 1987).

Chaffinches share no more songs with their neighbours than would be expected by chance (Slater & Ince 1982), this may be because they learn some songs before they set up their territories. Hand reared birds are capable of learning songs both in their first spring, and in the previous summer. In addition, learning of additional songs may occur in the following spring even if some songs had been learnt the previous summer (Thielcke & Krome 1989). Chaffinches from widely spaced populations in France have similar syllables (Metzmacher 1982); possibly due to young birds learning in their winter quarters or on the spring migration.

Substantial individual differences are audible, these have led some authors to conclude that regional dialects exist (Metzmacher & Mairy 1972, Conrads 1979, 1986), and more sharing of syllables was found to occurr between nearer islands in the Canaries and Azores (Lynch & Baker 1986). However, chaffinch songs from populations in Sussex, Cheshire and Orkney were found to share structural features of time and frequency (Slater *et al* 1984). Since there is a large amount of variation within areas in the variables measured, as well as between them, the patterns found are better described as geographic variation. For species which have a number of song types (like the chaffinch) Goodfellow & Slater (1986) and Williams & Slater (1990) concluded from computer modelling that the existance of sharp dialect boundaries was unlikely.

Song types change over time; the songs present in an area alter due to inaccuracies in copying. Rare songs may die out because they are not copied (Ince *et al* 1980). While Conrads (1986) found little difference in the chaffinch songs in the Teutoberger Forest, Germany over an 18 year period, Ince *et al* (1980) found only 3 song types similar enough to be called the same over the same time span in Great Stanmer Wood, England. There is thus great variation in the possible stability of song types. This may be due to variation in the rate of miscopying of song types, and to variation in the rate of immigration of songs brought into the population by birds which have learnt their songs elsewhere. The combined rate of introduction of new song types by these proceses was estimated in Great Stanmer Wood to be less than 15%; that is, the probability of a new bird to the population singing a new song type (Slater *et al* 1980). The copying accuracy, calculated as 100 - rate of introduction of new song types, for this population was therefore 85%.

Estimates of the accuracy of copying whole songs in New Zealand are much lower: Jenkins & Baker (1984) estimated 60.3% (from one population), and Plunkett (1987) calculated it to be only 45% from nineteen populations. New songtypes may also be formed by recombining syllables, this has been recorded both in Britain (Slater & Ince 1979), and in New Zealand (Jenkins & Baker 1984).

The lower New Zealand estimates may reflect a greater bias towards song type formation by syllable recombination, and/or under estimation due to incomplete sampling of the size of repertoires of birds, and the fact that not all the birds in the New Zealand sites were recorded. The patterns of geographic variation for groups of syllables were modelled by Lynch *et al* (1989), who suggested that the transmission within and between populations of these "memes" depends upon the number of syllables linked together. The balance of the processes of miscopying songs and immigration may vary between populations, especially if migration of birds occurs in one place but not another, or if dispersal distances differ for any reason.

It is the object of the present study to investigate the effect of habitat upon the time-frequency structure of chaffinch song. That habitat may affect song in the chaffinch is suggested by the songs of chaffinches in New Zealand (Galbraith 1977, Jenkins & Baker 1984). The species was introduced there about a century ago; although most song types are similar in terms of the number of phrases and endphrase syllables to those described in Britain, about 10% of New Zealand song types were found to be unusual. In some of these songs the syllables have become elaborated, and the pitch altered.

The trill part of New Zealand songs is commonly simpler, and the end phrase more complex, possibly because elaborate end phrases should degrade less from reverberations in the dense coniferous forests where New Zealand chaffinches are typically found (Jenkins & Baker 1984). In Europe chaffinches more often live in mixed deciduous woods (Glas 1960), or at least earlier studies have been in such woods; their songs may not be adapted to the transmission characteristics of coniferous woods.

The following predictions of the acoustic adaptation hypothesis were tested by recording songs from coniferous woods and open scrub habitats:

1) The frequencies used in a dense habitat (coniferous wood) should be lower than in an open scrub habitat.

This is because high frequencies will be scattered more by obstructions in the transmission path. This can be tested both with the maximum frequency found on sonagrams, and with the frequency at which most energy is concentrated. The latter measure is the frequency of maximal amplitude measured on a power spectrum of a song or a part thereof.

2) Given (1) and that the minimum frequency should be as low as possible in all habitats, the range of frequencies used should be smaller in the coniferous woods than in the open scrub.

3) The effect of reverberations, which interfere with the transmission of the amplitude structure of sounds, is greater in dense habitats. It should be minimised by spacing sounds out in time more in the coniferous woods than in the open scrub. In addition, the effect of irregular amplitude fluctuations, which are expected to be more common in open habitats, will lead to selection for sounds in this habitat which are only separated by short gaps. This combined effect can be measured as the gap between syllables, or as the ratio

$$\frac{\text{duration of syllable}}{\text{syllable cadence}}$$

The cadence is the sum of the duration of the syllable and the gap between successive syllables.

The methods used to record, measure, and analyse songs are given in chapter 4.

Chapter 4

Is chaffinch song adapted for transmission through the habitats in which it is sung ?

Chapters 2 and 3 have reviewed the literature on the acoustic adaptation hypothesis and on the song of the chaffinch. The predictions made from the hypothesis at the end of chapter 3 are tested below on chaffinch songs recorded in Scotland.

4.1 Habitat descriptions

Recordings were made from two main habitat types: open scrub, and coniferous woodland. In addition, recordings were made in the Abernethy forest around Loch Garten, which is an area of ancient Scots Pine (*Pinus sylvestris*), to enable comparison between natural coniferous woodland and with plantations. To examine whether background environmental noise might have an influence on song structure, songs were recorded from an area of mixed deciduous woodland in the gorge of the Birks of Aberfeldy, a set of waterfalls and rapids. Songs were recorded in an open deciduous area near Dunkeld for comparison with the Aberfeldy sample. Map references below are given to four figure accuracy only as recordings were made over a larger area than is implied by a six figure reference.

4.1.1 Open scrub

These sites were characterised by an open aspect and, especially where gorse (*Ulex europaeus*) was present (Foret Hill, Largo Law, and St Andrews Links), by a lack of vegetation over about 1.0-1.5m in height. Chaffinches are scarce in very open areas, so the sample size was increased by recording in some rural villages and hedgerows (Logie, Gauldry and Kingsbarns). Those birds which lived in the gorse areas usually sang at the tops of the bushes, or in any trees (usually elder *Sambuccus niger*) which were present. The paucity of birds in this habitat is possibly because trees are very important to them: Goodfellow (1988) showed that the size of territories of chaffinches was negatively related to the density of mature and semi-mature trees. Recordings were made at five open sites.

(i) Foret Hill and Logie (NO 3920 & 4020).
(ii) Gauldry (NO 3723)
(iii) Kingsbarns (NO 5912)
(iv) Largo Law (NO 4204)
(v) St Andrews Links and Kinkell Braes (NO 4918 & 5215)

4.1.2 Coniferous woods (plantations)

In general these woodlands are characterised by their greater density of vegetation (mean density 6.6-8.2 trees/5m^2) compared to the open sites, and a lack of ground flora apart from some bracken (*Pteridium aquilinum*), mosses and grasses. The ground cover was rarely more than half a metre high, and in no case was it more than a metre. Often the ground was covered with just a carpet of needles, and sometimes small branches. It was impossible to obtain clean recordings of songs in the very densest of woods, as it was not possible to get close to the birds without disturbing them, therefore recordings were mainly made in slightly older woods which had been brashed and thinned. The trees present were sitka spruce (*Picea sitchensis*) at Dunkeld, Paddockmuir, and Priorwell wood, and lodgepole pine (*Pinus contorta*) at St Ford Links, Tentsmuir and St Michael's wood. Recordings were made at six sites:

(i) Dunkeld (NN 0342)
(ii) Paddockmuir (NO 2120)
(iii) Priorwell wood (NO 3523)
(iv) St Ford Links (NO 4600)
(v) St Michael's Wood (NO 4423)
(vi) Tentsmuir (NO 4829)

4.1.3 Loch Garten (NT 9617)

This is a large area of mature Scots pine woodland. It is more open (mean density 2.3 trees/5m^2) than the plantation woods, and has a ground flora of heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), with various herb, grass and moss species. The ground cover was usually between 25cm - 75cm tall. Some regeneration of the pines was noted, but these young trees were mainly small (up to 3m). Recordings were made between 1st - 4th May 1990. Since all the recordings at Loch Garten were counted as being from the same site the assumption that variation between areas within the general area did not occur had to be made.

4.1.4 Aberfeldy & Dunkeld

Recordings were made in the immediate vicinity of the waterfall and rapids at Aberfeldy (NN 8547) by following the path to the waterfall at the top of the gorge. The trees were mainly beech (*Fagus sylvatica*) and birch (*Betula* sp.), with a small amount of ground cover, mainly of herbs, grasses, and dead leaves. Recordings were made on the 6th April 1988.

The Dunkeld (NN 0343) sample was recorded in an open area of deciduous woodland, mainly beech, birch and sycamore (*Acer pseudoplatanus*), beside the road from Dunkeld to the Loch of the Lowes. As with Aberfeldy, the ground cover was mainly herbs and grasses. Recordings were made on the 1st June 1988.

4.2 Recording equipment and methods

The songs were recorded using either a Sony Walkman Professional (WM-D6C) or a Marantz CP430, in most cases using a Sennheiser MD 400 supercardoid microphone in an Atherstone 50cm fibreglass parabolic refector. In conditions where the wind speed was greater than about Beaufort force 2 a windshield (Rycote Ltd) was used over the parabola. A few of the songs at Tentsmuir were recorded using a gun microphone (Sennheiser MKH 816 in a tubular shock mount) and the Marantz recorder, and the songs at Loch Garten (plus a few of those at Largo Law) were recorded with a Telinga Pro III parabolic reflector (60cm diameter) and mono microphone, with the bass filter switched off, connected to the Sony Walkman recorder. All recordings were made on Type I (normal) tape (TDK D60, Sony H60, Maxell UR60).

In all cases recordings were made as close as possible to the singing bird (estimated <30m, modal distance about 10 - 15m), with a minimum of intervening vegetation. Recordings were made between 05:30 and 11:00 BST on clear days with a minimum of wind (_ Beaufort force 3), and no rain. An attempt was made to record as many song types as possible by recording from as many different birds as possible. This was achieved by moving from one to another if two or more were countersinging or, if not, moving about 100m between recording birds. This distance is approximately the diameter of a territory: Marler (1956b) calculated mean territory size as 6700 m^2. Songs were recorded until the bird either flew off, stopped singing, or I estimated that it had cycled through its song types. No attempt was made to record all the birds at a site. Recordings were made between 9th March - 2nd July in 1988, and 17th March - 16th June in 1989.

4.3 Sonagraphic analysis

A survey of the song types possessed by each bird was made by viewing them with a Unigon 4512 real time FFT analyser and SC1 waterfall display screen, and making a catalogue of sonagrams. In 1988 and 1989, a Kay Elemetrics 7800 Digital Sonagraph was used, but in 1990, a new machine, a Kay Elemetrics DSP 5500 became available. After the initial survey, a representative song for each song type was chosen for the measurements. The songs actually analysed were chosen visually on the basis of having minimal background noise and degradation.

Two sonagrams (wide and narrow band) were made for each song type. Measurements for time variables were taken from wide band (300Hz filter width) sonagrams, and for frequency variables from narrow band (45Hz filter width) sonagrams. All sonagrams were made using the 0-8kHz range, and settings (especially the print darkness) were standardised to ensure that the sonagrams were as far as possible directly comparable. With the sonagrams prepared by the 7800 Sonagraph, a program written in Turbo Pascal 4, in conjunction with a graphics pad (Cherry Mk III) connected to a Zenith 159-13 PC, was used to digitise points and convert them to time and frequency measures. Points were digitised with an accuracy of ± 0.5mm, this distance equates to ± 4ms, and ± 40Hz. The DSP 5500 sonagraph allows measurement of variables using cursors on the screen, so measurements taken in 1990 used this facility. The time cursors are moved in steps of 3ms when a two second time base is used for display of a sonagram.

4.3.1 Definitions of the parts of a song

The definitions below describe the terms used for the measurements taken, and are based on those of Slater & Ince (1979), and Slater *et al* (1984). They are shown in graphical form in Figure 4.1.

Element : a continuous trace on a wide band sonagram.

Syllable : a group of elements (sometimes, given the definition of a phrase below, a syllable was defined as just one element). There is usually no repetition of elements within a syllable, but see section 6.3 for more details.

Phrase : a sequence of repeated syllables.

Transitional syllable : a group of elements which is not repeated.

End phrase (flourish) : the terminal part of the song which contains no repeated syllables. There is one syllable type (Figure 4.1) which when present is always found at the end of the song. Though this syllable type may be repeated it is defined as being part of the flourish, as it can occur after more than one unrepeated syllable.

Song type : a unique sequence of syllables and end phrase

4.3.2 Measurements taken

Within each song type I measured the last syllable in the first phrase, and the first syllable in subsequent phrases. This is because in the first phrase it is often very difficult to measure the first syllable, as birds usually start singing quietly, and increase the amplitude of the song as the first phrase proceeds. This can be seen in Figure 4.1: the syllables in the first phrase become better defined as the phrase proceeds. However, since there is variability both within and between birds in the number of repetitions of a syllable within a phrase (see chapter 6 for more details), it is better to measure the first syllable, and this was done for phrases subsequent to the first.

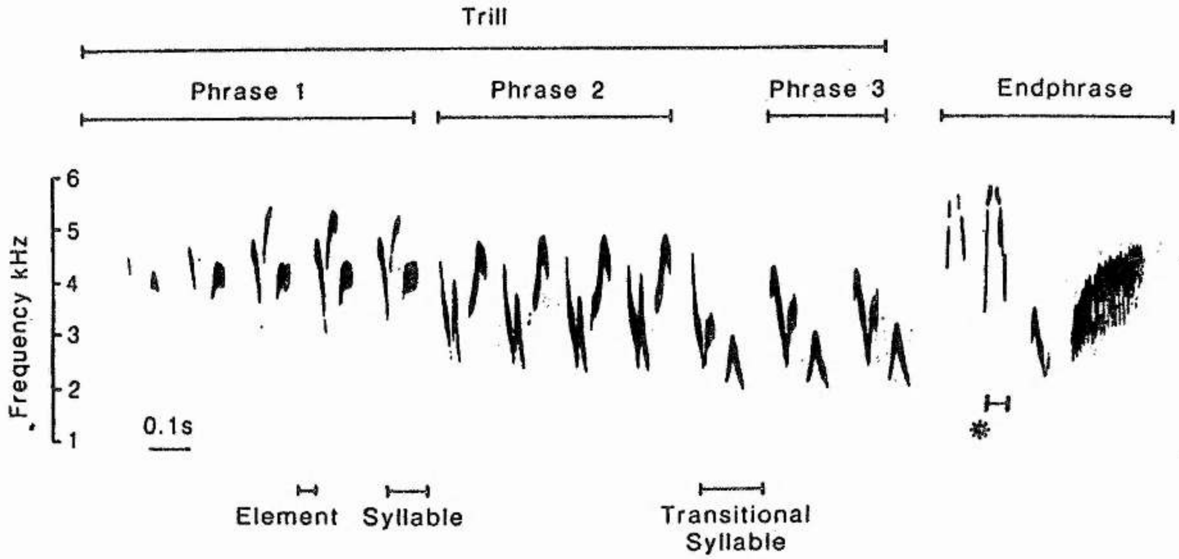


Figure 4.1 A sonagram of a chaffinch song. Note that phrase 1 becomes better defined as it is sung, and that the syllable type marked * only occurs in the endphrase part of the song.

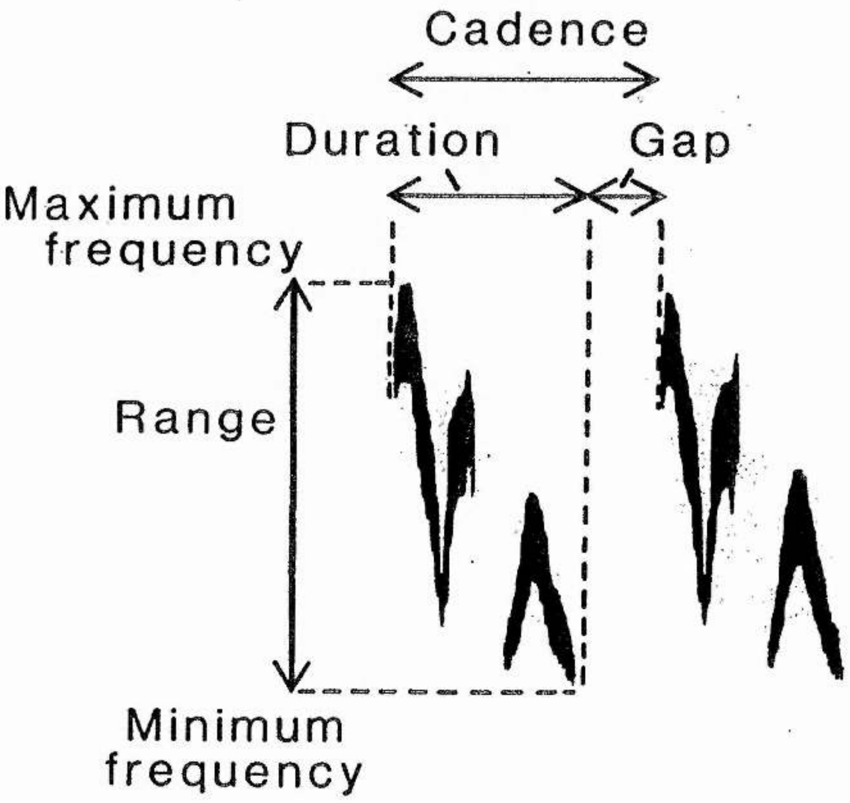


Figure 4.2 Measurements taken for each phrase.

The following features were measured:

(a) for each song type :

(i) the number of phrases.

(ii) the number of transitional syllables.

(iii) the number of elements in the flourish.

(iv) the frequency of maximal amplitude (see below).

(b) for each phrase and for the end phrase (Figure 4.2):

(v) maximum frequency : the highest frequency discernable on a narrow band sonagram.

(vi) minimum frequency : the lowest frequency discernable on a narrow band sonagram.

(vii) frequency of maximal amplitude (FMA): the frequency into which most energy is put. When two (or more) frequencies had the same amplitude the highest frequency was used. Since the prediction tested is that the frequencies in dense habitats should be lower this is a conservative way of testing it. The FMA was measured using a 1024 point (29Hz) power spectrum of the duration of the syllable or end phrase with the DSP 5500 Sonagraph. The frequency cursors are moved in steps of 20Hz on this scale power spectrum. This variable was also measured for the whole song (iv above).

(viii) duration : the time occupied by a syllable, excluding the interval between syllables. For the flourish it is from the start of the first element in the end phrase to the end of the last one, including the gaps between elements.

(ix) cadence : the time between the same point on successive syllables. This is effectively the duration

(above), plus the time gap between syllables. It is measured between the penultimate and ultimate syllables in the first phrase, and between the first and second syllables in other phrases. Since the flourish is not repeated, this variable cannot be measured for it.
From these were derived the following measures:

(x) range : maximum frequency - minimum frequency.

(xi) the ratio $\frac{\text{duration}}{\text{cadence}}$

(xii) gap : cadence - duration.

Maximal and minimal frequencies (and therefore range) were not measured for songs analysed in 1990. In addition it was not always possible to measure the time variables for all song types as the first phrase was occasionally ill defined.

4.4 Statistical analysis

Only one song for each song type was chosen because learning is extremely accurate, and therefore any other bird singing the same song type does so with the same time-frequency structure. In addition, as many song types are not shared, it would not be possible to assess the inter-bird variability in these song types, and this would complicate the statistical analysis. Since the appropriate level of variation to test between habitats is the variation between song types within a habitat, measuring the variation within song types (either within or between birds) is unnecessary.

A total of 44 song types were recorded from the open habitat, and 77 from the coniferous plantation habitat. A further 32 song types were recorded from the natural Scots pine forest at Loch Garten. These were classified by the number of phrases present (Table 4.1). Data were collected for each phrase of the song types, and therefore more measurements were made on longer songs. Exploratory data analysis revealed that within each length of song differences between the phrases occurred, and the data for the different phrases could not therefore be pooled. It would also be inappropriate to pool the data from the different length songs, so analyses were performed on the two, three and four phrase songs separately.

To analyse the data from the trill part of the songs a mixed model ANOVA design with crossed and nested factors was used (see Appendix 1). The factors involved were :

(i) *Habitats*, the general areas, are fixed.

(ii) *Sites* are the locations from which song types were recorded. These are nested within habitats and are assumed to be a random sample of the possible sites within each habitat.

(iii) *Types* are the different song types recorded from sites in each habitat. They are nested within both habitats and sites and are also assumed to be random, as no effort was made to record all song types within each site, and song types were unique to each site.

(iv) *Phrases*, which are the number of sequences of repeated syllables in songtypes (see section 4.3.1) are fixed. This factor is crossed with habitats, sites and types.

The analysis has the following sources of variation:

H	Habitats
S(H)	Sites within Habitats
T(SH)	Types within Sites within Habitats
P	Phrases
H*P	Habitats * Phrases
S(H)*P	(Sites within Habitats) * Phrases
T(SH)*P	(Types within Sites within Habitats) * Phrases

The degrees of freedom for the ANOVA tests may be less than expected from Table 4.1 due to missing data. Only song types for which data for all phrases were available were analysed as it was found that missing cases biased the sums of squares calculated.

Few four phrase songs were recorded, and most of these were single examples at a particular site, so it would not be possible to assess the variation between sites against that within sites. However, 5 four phrase song types were recorded at two of the sites, and fortuitously these were one site in each of the open scrub and coniferous plantation habitats. Comparisons between the four phrase songs were therefore restricted to this sub-sample so that the variation between habitats could be assessed against that within habitats. Since the habitats are represented by only one site each, the analysis was simplified, and the sites factor omitted.

The analysis for the end phrase data was somewhat simpler as each song type possesses only one flourish. The ANOVA used was a simplification of the model used to analyse the trill part of the songs, with the factors : Habitats, Sites within Habitats, and Types within Sites. Once again no error for the Types within Sites exists, so F values and probabilities were calculated for only the Habitat and Sites factors. The Sites MS was tested with the

Types MS, and the Habitats MS with the Sites MS. An identical analysis was used for the data on the frequency of maximal amplitude averaged over the entire song. The end phrase, and song FMA, data for four phrase songs were analysed with a one way ANOVA on the habitat factor.

Eleven song types were recorded at Aberfeldy, 7 possessed three phrases, but the sample included only 3 with two phrases and one with four phrases. At Dunkeld a sample of 3 two phrase and 12 three phrase song types were recorded. The comparisons between the sites were therefore made with just the three phrase song types since the samples of two and four phrase song types were too small. The ANOVA model used to analyse the trill data was the same as that for the four phrase song types, and a one way ANOVA on the habitat factor was used to test differences in the end phrase and song FMA data.

4.5 Results

4.5.1 Number of song types recorded

There was a significant association between length of songs and habitat (Table 4.1; Chi-squared=14.27, 4 df, p=0.007). The association for just the open and coniferous plantation habitats was not significant (Chi-squared=1.82, 2 df, p=0.30) indicating that the Loch Garten sample is the unusual one: shorter songs were commoner there, and no four-phrase songs were recorded.

TABLE 4.1

Number of song types of different lengths recorded in the different habitats.

	Number of Phrases		
Habitat	2	3	4
Open	12	23	9
Coniferous (plantations)	21	47	9
Coniferous (natural)	18	14	0

4.5.2 Trill part of the song

4.5.2.1 Frequency variables.

For the frequency variables (FMA, maximum frequency, and frequency range) both the habitat and sites factors were not significant for any of the song lengths. The F values and associated probabilities are presented in Tables 4.2-4.4.

TABLE 4.2

F values and probabilities for the frequency of maximal amplitude of syllables in the trill part of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	2.18	2,8	0.18	0.19	2,9	0.83	0.63	1,8	0.45
S(H)	0.77	8,42	0.63	0.78	9,73	0.63	-		
P	12.98	1,8	0.007	70.14	2,18	0.000	8.68	3,24	0.000
H*P	0.31	2,8	0.74	1.67	4,18	0.20	3.13	3,24	0.045
S(H)*P	2.07	8,38	0.06	1.35	18,140	0.17	-		

TABLE 4.3

F values and probabilities for the maximum frequency of syllables in the trill part of the song

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.04	1,7	0.85	1.12	1,8	0.32	0.32	1,7	0.86
S(H)	2.20	7,21	0.08	1.72	8,50	0.12	-		
P	38.42	1,7	0.000	12.59	2,16	0.001	5.85	3,21	0.005
H*P	0.02	1,7	0.90	0.03	2,16	0.97	3.91	3,21	0.023
S(H)*P	1.41	7,19	0.26	0.71	16,97	0.78	-		

TABLE 4.4

F values and probabilities for the frequency range of syllables in the trill part of the song

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.01	1,7	0.91	0.23	1,8	0.65	0.00	1,7	1.00
S(H)	2.37	7,21	0.06	1.18	8,50	0.34	–		
P	0.39	1,7	0.55	10.31	2,16	0.001	2.21	3,21	0.12
H*P	0.03	1,7	0.87	0.34	2,16	0.72	1.02	3,21	0.40
S(H)*P	1.22	7,19	0.34	1.46	16,97	0.13	–		

There is a significant decrease between the start and end of the trill for the FMA (Figure 4.3) and for maximum frequency of all lengths of songs. A significant difference between the phrases was only observed for frequency range for three phrase songs. A significant interaction of habitats and phrases can be seen for the four phrase songs for the FMA and maximum frequency. The interaction means that a different pattern of mean frequency with phrase was found in the different habitats.

4.5.2.2 Temporal variables

There was no significant difference between the sites (Tables 4.5 and 4.6) for all song lengths for the temporal variables (duration/cadence and gap between syllables). A significant difference between habitats was found for the gap between syllables (Figure 4.4) and duration/cadence (Figure 4.5) for three phrase songs. As with the frequency variables, the phrase measured was very significant (except for the duration/cadence for the two phrase songs). The significant effect of position of phrase in the song on the

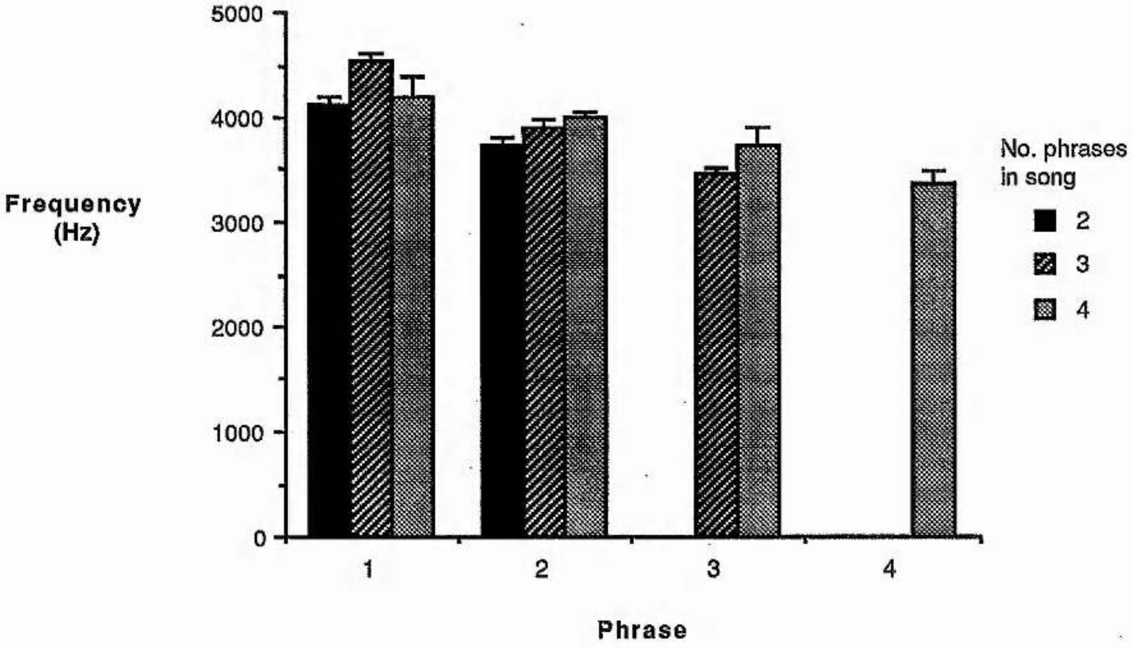


Figure 4.3 Frequency of maximal amplitude for the trill part of the song. Bars are means ± SE.

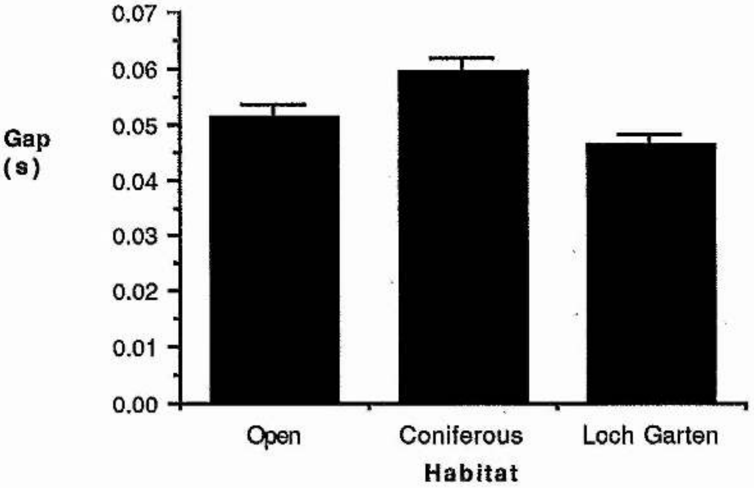


Figure 4.4 Gap between syllables for the trill part of the song. Bars are means ± SE.

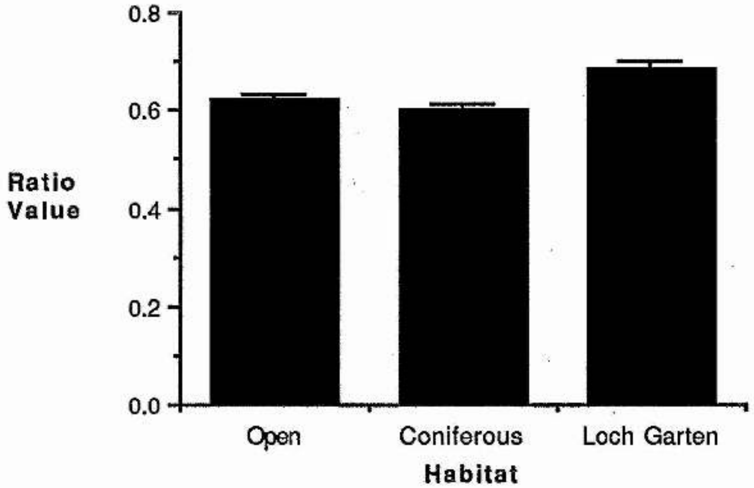


Figure 4.5 Duration / cadence for the trill part of the song. Bars are means ± SE.

duration/cadence ratio appeared due to a low ratio for the first phrase of the songs, and a higher ratio for later phrases. This fits with the shorter gap between syllables in later phrases (Figure 4.6).

Several of the interaction terms were found to be significant (Tables 4.5 & 4.6), but no clear pattern emerged. Why these interactions should be significant and others not is unclear. These interactions indicate that the pattern of variation found between the phrases was different at different sites or between the different habitats.

TABLE 4.5

F values and probabilities for the ratio duration/cadence for the trill part of the song

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	3.00	2,8	0.11	4.48	2,9	0.045	0.29	1,6	0.61
S(H)	1.48	8,42	0.19	1.70	9,70	0.11	–		
P	2.93	1,8	0.13	21.99	2,18	0.000	6.45	3,18	0.004
H*P	0.08	2,8	0.93	1.32	4,18	0.30	4.33	3,18	0.018
S(H)*P	3.46	8,38	0.004	0.90	18,134	0.58	–		

TABLE 4.6

F values and probabilities for the gap between syllables in the trill part of the song

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.70	2,8	0.53	7.99	2,9	0.010	0.55	1,6	0.49
S(H)	0.57	8,42	0.80	1.02	9,70	0.43	–		
P	12.83	1,8	0.007	75.33	2,18	0.000	11.66	3,18	0.000
H*P	0.29	2,8	0.76	5.24	4,18	0.006	2.54	3,18	0.09
S(H)*P	3.30	8,38	0.006	0.94	18,134	0.53	–		

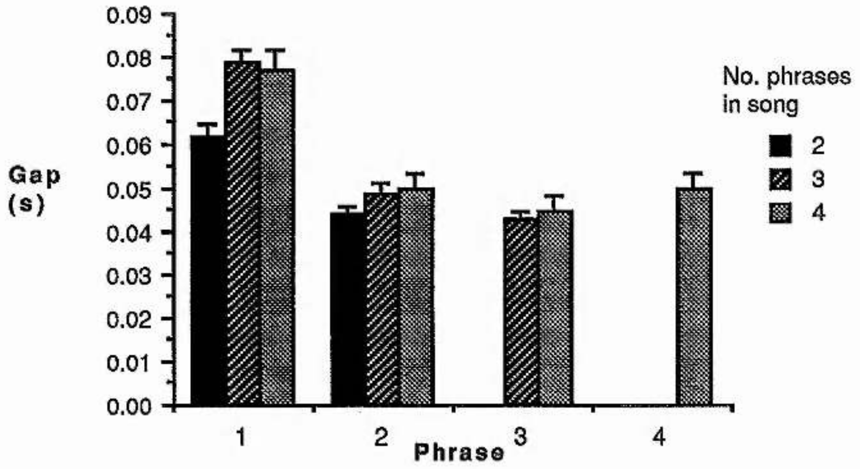


Figure 4.6 Gap between syllables for the trill part of the song. Bars are means ± SE.

4.5.3 End phrase part of the song

A significant difference (Table 4.7) between habitats was found for the frequency of maximal amplitude of the terminal flourish of two phrase songs (Figure 4.7). There was no significant difference between habitats factor for the other song lengths, and for the maximum frequency (Table 4.8) and frequency range (Table 4.9) variables. A significant difference between sites was only found for the maximum frequency and frequency range of three phrase songs. This indicates there is sometimes more variation within habitats than between them. The duration of the end phrase (Table 4.10) was not significantly different between either the habitats or the sites for all song lengths.

4.5.4 Frequency of maximal amplitude for the whole song

No significant difference between either habitats or sites within habitats (Table 4.11) was found for the FMA averaged over the whole song (trill + end phrase) for two, three or four phrase songs.

TABLE 4.7

F values and probabilities for the frequency of maximal amplitude of the end phrase part of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	10.34	2,8	0.006	2.26	2,9	0.16	0.03	1,8	0.88
S(H)	1.16	8,40	0.34	1.40	9,72	0.21	-		

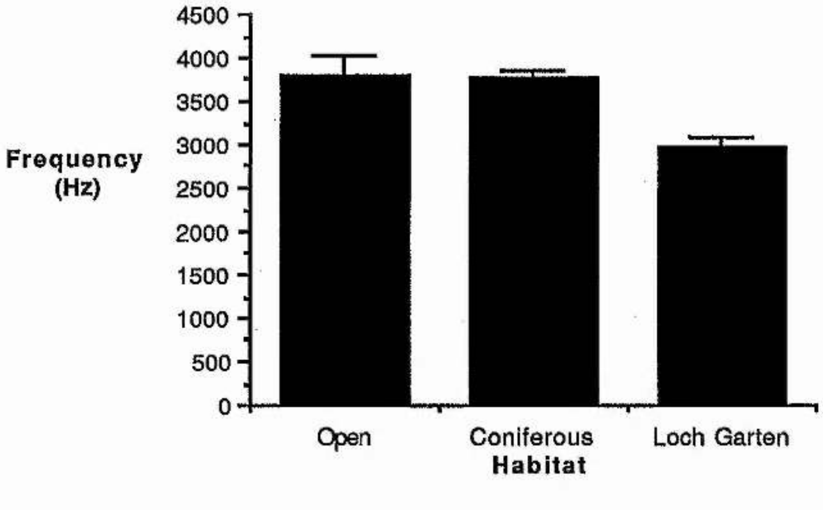


Figure 4.7 Frequency of maximal amplitude for the end phrase of 2 phrase song types. Bars are means ± SE.

TABLE 4.8

F values and probabilities for the maximum frequency of the end phrase part of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.88	1,7	0.38	0.07	1,8	0.81	0.45	1,8	0.52
S(H)	1.14	7,20	0.38	2.64	8,55	0.016	-		

TABLE 4.9

F values and probabilities for the frequency range of the end phrase part of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.45	1,7	0.53	0.21	1,8	0.66	0.01	1,8	0.94
S(H)	1.24	7,20	0.33	2.52	8,55	0.021	-		

TABLE 4.10

F values and probabilities for the duration of the end phrase part of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	1.89	2,8	0.21	0.15	2,9	0.87	0.00	1,8	0.96
S(H)	0.44	8,40	0.89	1.37	9,72	0.22	-		

TABLE 4.11

F values and probabilities for the frequency of maximal amplitude of the whole of the song.

	Number of Phrases								
	2			3			4		
Source	F	df	p	F	df	p	F	df	p
H	0.78	2,8	0.49	0.48	2,9	0.63	0.19	1,9	0.67
S(H)	1.07	8,40	0.40	0.72	9,72	0.69	-		

TABLE 4.12

F values and probabilities for frequency variables measured from the trill part of three phrase songs recorded at Aberfeldy & Dunkeld.

	FMA			Maximum frequency			Frequency Range		
Source	F	df	p	F	df	p	F	df	p
S	1.94	1,15	0.18	1.40	1,14	0.26	5.06	1,14	0.041
P	23.77	2,30	0.000	1.80	2,28	0.18	12.08	2,28	0.000
S*P	3.43	2,30	0.046	0.97	2,28	0.40	0.48	2,28	0.63

TABLE 4.13

F values and probabilities for temporal variables measured from the trill part of three phrase songs recorded at Aberfeldy & Dunkeld.

	Duration Cadence			Gap between Syllables		
Source	F	df	p	F	df	p
S	1.00	1,14	0.34	0.01	1,14	0.94
P	6.38	2,28	0.005	9.47	2,28	0.000
S*P	2.44	2,28	0.11	1.45	2,28	0.25

TABLE 4.14

F values and probabilities for variables measured for the end phrase part of three phrase songs from Aberfeldy and Dunkeld

Variable	$F_{1,15}$	p
FMA	0.00	0.98
Maximum frequency	0.18	0.68
Frequency range	0.22	0.64
Duration	1.10	0.31

4.5.5 Aberfeldy & Dunkeld

4.5.5.1 Trill part of the song

A significant difference between the sites was found for the frequency range (Table 4.12), but not for any of the other variables (Tables 4.12 and 4.13). The phrases factor was significant for all the variables except maximum frequency, and a significant interaction of phrase with site was found for the frequency of maximal amplitude.

4.5.5.2 End phrase part of the song and whole song FMA

No significant difference between the two sites was found for any of the variables (Table 4.14) measured from the end phrase. The frequency of maximal amplitude of the whole song (trill + end phrase) was not significantly different between the two sites ($F1,15=1.24$, $p=0.28$).

4.6 Discussion

The overall impression gained from these results is that the chaffinch songs recorded do not follow the predictions made by the acoustic adaptation hypothesis. Some significant results were found, but there is no consistant pattern across the different length songs. The phrases factor was very significant for the trill part of the songs. This indicates that the decreasing frequency and gap between syllables with increasing phrase number are important parts of the syntax of chaffinch song regardless of habitat.

The significant interactions of phrase and either sites or habitat do not form any clear pattern and are therefore difficult to interpret. For the four phrase songs, the habitat factor is the same as the site factor as there is only one site in each habitat, thus the significant habitat * phrase interaction (for FMA, maximum frequency, and duration/cadence) may be a site effect. It may also be due to the small sample size for the four phrase songs. The habitats * phrases interaction for the gap between syllables for three phrase songs is attributable to the Loch Garten sample, where, unlike the other two habitats, the gap measure for the third phrase is greater than that for the second phrase. The significant sites * phrases interaction for two phrase songs for the duration/cadence and gap between syllables variables results from a decrease in these variables between phrases at some sites, and an increase between phrases at other sites. Thus no particular pattern between phrases is followed for these shorter songs.

Significant differences between habitats were only found in three cases: (i) the duration/cadence for three phrase songs, (ii) the gap between syllables for three phrase songs, (iii) the frequency of maximal amplitude for the end phrase of two phrase songs. The first case is only just significant and, given the large number of tests performed, some would be expected to be significant by chance. The other two cases might also be due to chance but are much more significant, and are therefore more difficult to explain, especially since the habitat factor is not even close to significance for the other song lengths for those variables. In both cases the same pattern between habitats is found for the two and three phrase songs (the four phrase song sample is too small and cannot be considered as no four phrase songs were recorded for Loch Garten).

For the gap between syllables the mean for the Loch Garten sample is the lowest, that for the coniferous plantations sample the highest. This is only partly in line with the predictions made as the gap is smaller for the less dense woods, but the gap for the open scrub habitat was expected to be the smallest. The differences between the means observed are only of the order of a few milliseconds, and it is difficult to believe that these are adaptive. A Tukey HSD* *post hoc* test (Daniel 1991) was applied to the data, but none of the pairwise differences were significant. An HSD* test was used as the sample sizes for the habitats differed. This test is more conservative than either the usual Tukey HSD test or the Newman-Keuls test, but those tests could not be applied because of the different sample sizes of the means compared. The sample size used for each mean (gap between syllables) was the number of song types recorded for the habitat, as, since only one site was sampled at Loch Garten using the number of sites would be inappropriate.

Considering the end phrase FMA, the frequency for the open scrub habitat sample is the highest, and that for Loch Garten lowest. Again these data are only partly in line with predictions, as it was expected that the FMA for the open habitat should be greater than that for the coniferous woods, but that the Loch Garten sample should be intermediate between the open and plantation samples. A Tukey HSD* *post hoc* test on the mean end phrase FMA for each habitat revealed that the Loch Garten sample had a lower pitch than both the open and coniferous plantation samples ($p<0.05$), but no difference was found between the open and coniferous plantation samples. As with the data for gap between syllables, the test was used with the minimum number of song types of the two means compared as the sample size, because the Loch Garten sample was pooled, so the number of sites for that habitat was one.

A significant difference between the Aberfeldy and Dunkeld sites was found for the frequency range used in the three phrase songs. The greater range of frequencies used at Aberfeldy (mean 2258Hz) than at Dunkeld (mean 1715Hz) shows that the noise of the waterfall at the Birks of Aberfeldy may have an effect, but as with the duration/cadence ratio for the trill part of three phrase songs, this result may be due to chance as it is only just significant. It is also contrary to that predicted, as a higher minimum frequency would be expected in areas with low frequency interference, such as noise from running water, and this would lead to a lower expected frequency range at the Aberfeldy site.

The song of the chaffinch does not therefore appear to follow the predictions made from the acoustic adaptatioon hypothesis. It is interesting that Galbraith (1977) suggested that chaffinches in dense habitats in New Zealand use sounds with a greater frequency range than those in more open habitats; this is also contrary to the predictions of the acoustic adaptation hypothesis.

These results contrast sharply with those from studies of several other species (see Chapter 2), including the great tit (Hunter 1978, Hunter & Krebs 1979), summer tanager (Shy 1983), and thrush nightingale (Sorjonen 1983), which have found an association of habitat and song structure. Part of the difference may be that this study has been over a small geographic area, whereas that of, for example, Hunter (1978) investigated great tit song over the whole of Europe. However, this cannot be the entire answer as Anderson and Connor (1985) found differences between the songs used by northern cardinals in three stands of timber of different ages within a few kilometres of each other.

The lack of significance in the chaffinch results may be a result of the species' abundance. Chaffinches are amongst the commonest of British birds, occurring in 99% of farmland and 100% of woodland Common Birds Census plots in 1988 (Marchant *et al* 1990). Considerations of acoustic transmission may therefore approach irrelevance, as suggested for the rufous-collared sparrow (Handford 1988). In addition, a radio-tracking study of foraging chaffinches (Hanski & Haila 1988) showed that they use large areas outwith their nominal territories, which can include a variety of habitat types, thus birds may learn their songs in areas with different acoustic conditions to those in which they sing.

The heterogeneity of habitats in which chaffinches occur suggests that unless territories are set up in the habitat in which song types are learnt (as assumed by this study), it may not be an advantage to learn songs which are specialised for transmission through a particular habitat. There is much variation in tree density both within and between habitats, and the song structure observed may thus be a compromise. While it is possible to make predictions for the optimal structure of bird song when just open and coniferous habitats are considered, the situation becomes very much more complicated when mixed deciduous woods are considered. The density of these woods will depend crucially upon the species of trees and shrubs present, and it is likely that, as found by Liskens *et al* (1976) for eight communities, each will have its own acoustic climate depending upon the size and distribution of obstacles in the transmission path.

Nevertheless, it is interesting that the only result that is highly significant between habitats for a frequency measure is for the end phrase FMA (of two phrase songs). Bremond (1972) suggested that the trill and flourish parts of the song of chaffinches may have different functions, and concluded that the trill was used for species recognition. It does seem quite possible that the two parts of the song may have different functions, but I would suggest that, since it is the end phrase that is most audible over long distances (pers. obs.), it is this part that may be used for species recognition. Since the flourish usually contains at least one element with a substantial amount of frequency modulation it should be adapted for transmission over long distances in wooded habitats (Brenowitz 1986).

It is also interesting that the lowest frequency used in the end phrase of both two and three phrase songs was found in the Loch Garten sample. The frequencies observed for songs sung in open and coniferous plantation habitats were higher and similar to each other. This suggests that the songs may take a long time to become adapted for transmission through a habitat, thus the lack of difference between the habitats may be partly that the coniferous plantations are relatively recent (<100 years), so that songs may still be adapted for transmission through the previous habitat. For all the plantation conifer sites chosen this was probably more open. The original vegetation structure of agricultural land (80-200 years prior to current land use) explained 45% of the observed variation in trill rates of the songs of rufous-collared sparrows in Argentina (Handford 1988).

Whatever the explanation for the lack of adaptation found, it is clear that this study of microgeographic variation in song structure of the chaffinch in Scotland does not support predictions made from the Acoustic Adaptation Hypothesis.

Chapter 5

Transmission experiments with white noise and chaffinch songs on Tenerife

5.1 Introduction

The Canary Islands of Tenerife and Gran Canaria are the only places in the world where two chaffinch species occur. These are the Canary Islands chaffinch (*F. c. tintillon*) and the endemic blue chaffinch (*F. teydea*). The origins of the two species are somewhat uncertain, though a double invasion seems likely; the ancestors may have arrived from the Azores rather than the North African mainland (Grant 1980).

The songs are qualitatively different; that of the blue chaffinch has a few brief elements separated by long gaps and a complicated flourish which is repeated in most song types. The Canary Islands chaffinch has longer elements and the flourish is not clearly separated from the rest of the song (Lack & Southern 1949, Slater & Sellar 1986). Slater & Catchpole (1990) found that responses to song playback were greater to own species song than to that of the other species, and the responses to songs of British chaffinches (*F. c. gengleri*) were intermediate.

The simpler structure of the songs of the blue chaffinch was suggested by Lynch & Baker (1991) to be a result of colonisation by birds which had not learnt their songs, as they consider these songs to be similar to those produced by birds raised in acoustic isolation. The colonisation of an island group by a few birds could lead to a small syllable pool and thus affect the songs of descendants, as observed for the common chaffinches which colonised the Chatham Islands within the last centuary (Baker & Jenkins 1987). However, Grant (1979) considered that differentiation of chaffinches on Atlantic Islands occurred within the last million years. This would obviously be ample time for a new song tradition to build up, so it seems unlikely that the song of the blue chaffinch is a result of "withdrawal of learning" (Thielcke 1973), as the song would be expected to become more complicated over a period of time. A simpler explanation for the divergence between the songs is character displacement (Slater & Sellar 1986).

It is of great interest that these species inhabit, for the most part, different habitats; the blue chaffinch is restricted to Canarian pine (*Pinus canariensis*) woods at higher altitudes; the Canary Islands chaffinch is more widespread and is common in the lower altitude laurel (*Laurus* spp.) forest. The species coexist low in the Canarian pine forest where there is an understory of other trees and shrubs, but Slater & Catchpole (1990) and Lynch & Baker (1991) found the species were not interspecifically territorial.

The object of the experiments described below was to determine if a difference exists in the transmission characteristics of the Canarian pine and laurel forests, and to relate such differences, if present, to the characteristics of the songs of the two species. The work took place during a visit to Tenerife between 11th - 25th April 1989. Experiments in the Canarian pine forest were in the vicinity of La Montañeta, those in the laurel forest, adjacent to Erjos.

5.2 Methods

The general methodology of the experiment was similar to that used by Martin & Marler (1977). White noise was transmitted from a tape recording prepared in the laboratory from a signal generator, and re-recorded at distances of 1m and either 25m or 50m. Recording in stereo meant that differences in the micrometeorological conditions between repetitions of the transmission were controlled, as the recordings for each far distance were compared to those from the near microphone. This is necessary as the recordings at each site took approximately 45 minutes. The tape also contained 15s of silence, to detect if the amplitude of the background noise was similar to that of the transmitted sounds (a low signal to noise ratio), and of a 1kHz tone. The playback level was set to 85dB for the 1Khz tone by using a Lucas CEL 314 SPL meter (set to fast response, flat weighting, 60-100dB range). A tape of blue chaffinch and common chaffinch songs (Figure 5.1: three song types from each species, chosen from recordings made at close range (<10m, Slater pers. comm.) on a previous trip to Tenerife by Slater & Sellar in 1984) was also transmitted to investigate if these songs are less attenuated by transmission through their own habitat.

The sounds were transmitted from a polyplanar speaker attached to a Nagra DSM which acted as an amplifier to the tape in a Sony Walkman Professional WM-D6C (Figure

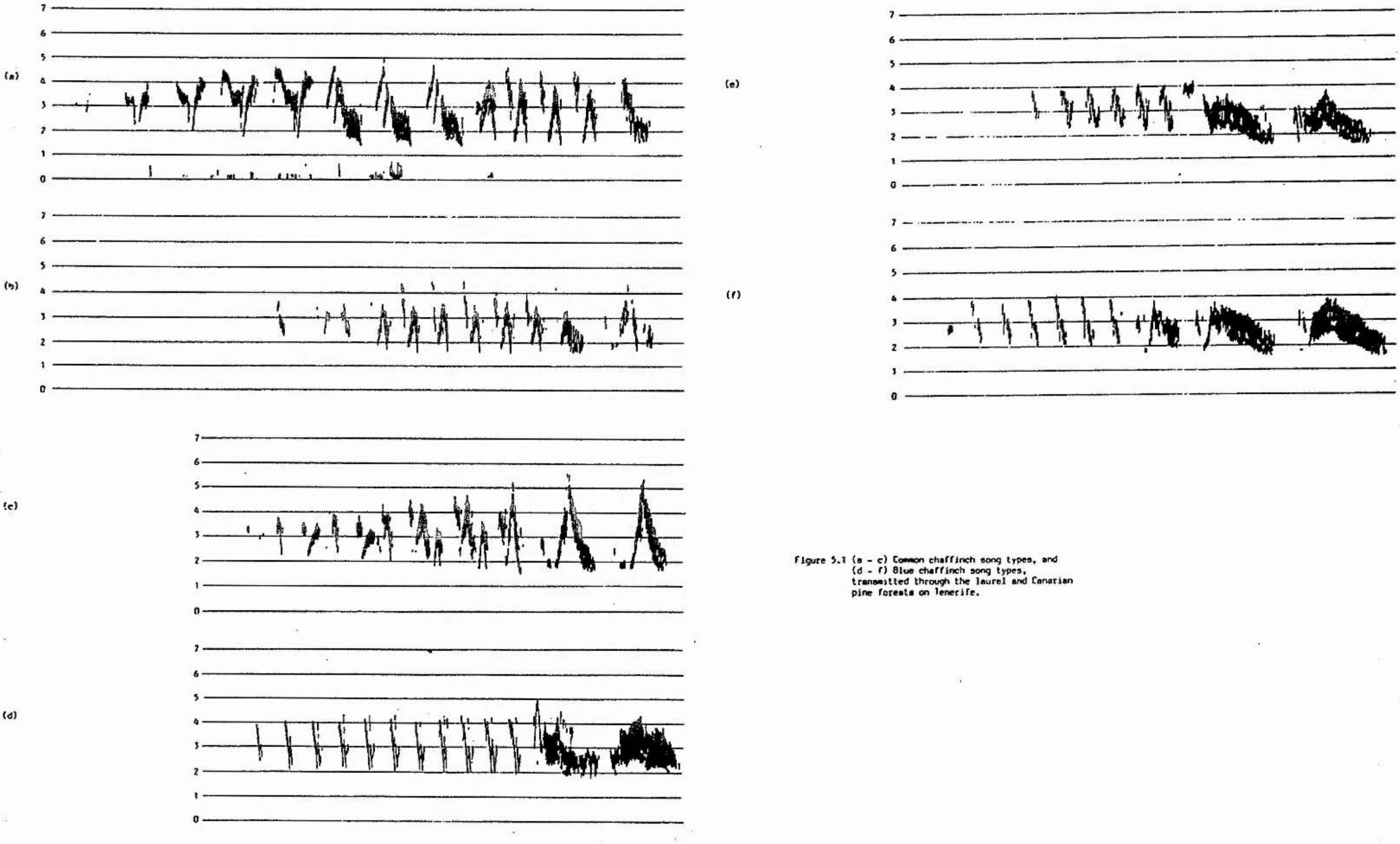


Figure 5.1 (a - c) Common chaffinch song types, and
(d - f) Blue chaffinch song types,
transmitted through the laurel and Canarian
pine forests on Tenerife.

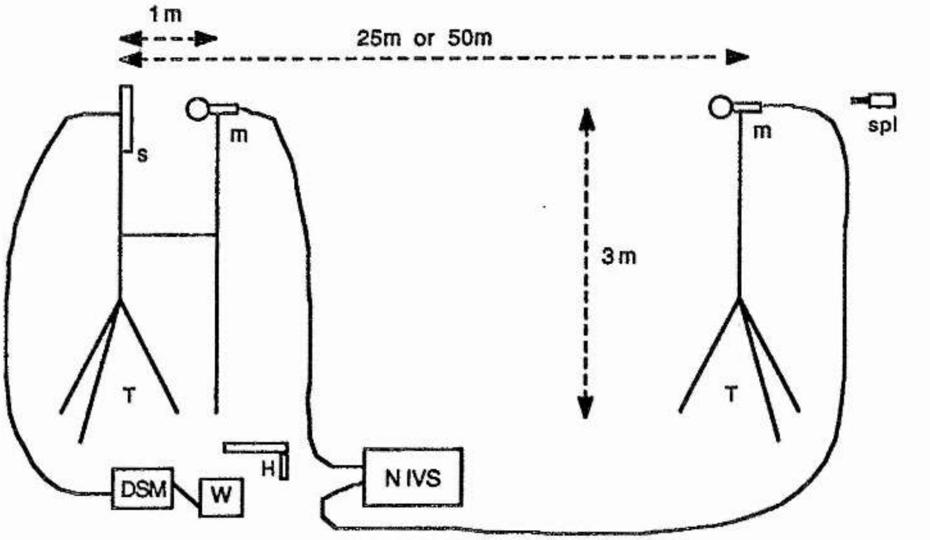


Figure 5.2 Transmission experiment equipment.
DSM = Nagra amplifier, W = Sony Walkman, N IVS = Nagra reel to reel tape recorder,
m = microphone, s = speaker, T = tripod, spl = Lucas SPL meter,
H = whirling hygrometer.

5.2). The speaker was supported on a guyed Velbon SEB-3 tripod, with an extension mounted on the central column, raising it to about 3m above the ground. A Beyer M69 N(C) microphone was mounted on a monopod attached to the tripod at a distance of 1m from the speaker at the same height. A second microphone (Beyer M69 N(C).2) was mounted at a height of approximately 3m at distances of either 25m or 50m from the speaker on a second tripod (plus extension column). These microphones (dynamic hypercardiod type) are equivalent when the speech/music switch on the M69 N(C).2 is set to the M position, and were chosen as they have a matched and very nearly flat frequency response between 0.5 and 10kHz. The microphones were not screened against wind noise. Recordings of the transmitted sounds were made on Agfa PE39 tape at 19.05cm/s with a Nagra IV-S, in stereo. The output of the reference microphone, at 1m from the source, was recorded with the left channel, and the output of the further microphone with the right channel. In order to maximise the record levels the right channel was set to maximum sensitivity (77dB), but it was necessary to set the left channel to 100dB or 110dB to avoid overloading. Equal lengths of cable were used on the two microphones and the microphones were used in the same position each time.

The experiment was performed at three sites in each habitat (laurel and Canarian pine). It is evident from the literature reviewed earlier (chapter 2) that the transmission of sounds through habitats is a complex subject, and that it is likely to vary greatly within a habitat, or even at a single place within a habitat. The experiment was therefore replicated three times for each site over each distance. The replications were with the far microphone positioned along the transmission line, and ± about 2m laterally from the first position.

The sounds recorded were analysed with a Kay Elemetrics DSP 5500 Sonagraph in stereo. For each channel a 1024 point (29Hz) power spectrum averaged over (the same) 10s of the noise or silence was calculated. The amplitude was measured at 500Hz intervals between 0.5 - 7.5kHz. These data are comparable between spectra as the input level from the Nagra IV-S to the sonagraph was kept constant at 95dB. A calibration experiment carried out prior to analysis showed that the record/playback level verniers on the Nagra IV-S tape recorder were linear, and that the input level of the sonagraph did not affect the amplitude found on the power spectrum. The right microphone was found to be slightly more sensitive than the left, the measurements from the right channel were therefore adjusted to take this difference into account.

Whilst measuring the power spectra it was observed that the frequency response of the polyplanar speaker was not linear. It was however consistent, and thus a difference between the amplitude at 1m, and 25 or 50m, can be calculated. Frequencies above 6kHz were transmitted at low amplitudes, and in several case the difference between the sound and silence at these frequencies was less than 3dB. Patterson & Gross (1972, p.179) recommend that such data be discarded, and therefore measurements for frequencies above 6kHz are not presented below. The few

(< 5) occasions where this occurred for frequencies below 6kHz were coded as missing data in the statistical analysis.

After allowing for the disparity in sensitivity of the two microphones at the frequencies measured, the difference in amplitude between the near and far microphones was calculated. When transmission occurs from a monopole source, the expected attenuation, due to spherical spreading, is 6dB per doubling of distance (Michelsen 1983). The expected attenuation for a particular distance can be calculated as $20 \log_{10} d$, i.e. 28dB for 25m; 34dB for 50m. The expected attenuation was subtracted from the difference in amplitude between the 1m and far microphones (allowing for the difference in recording level set for the microphones), and the remainder treated as excess attenuation. Statistically the data for each frequency measured cannot be viewed as independent as they came from the same power spectra. The analysis was therefore performed for each frequency separately.

The rerecordings of the birds' songs transmitted were analysed by measuring the frequency of maximal amplitude (FMA) on a 100 point (300Hz) power spectrum over the length of the song type (Table 5.1). The frequency cursors moved in steps of 80Hz on this scale power spectrum. As with the white noise analysis, sounds were input to the DSP Sonagraph in stereo, the input level from the Nagra IV-S was set at 95dB. If a power spectrum contained more than one frequency at the same maximal amplitude the highest frequency at that amplitude was recorded. The null hypothesis used for statistical analysis was that there should be no difference in FMA after transmission if the songs are adapted for transmission through their own habitat. The difference in FMA was therefore calculated by subtracting the frequency at 1m from that at the far distance.

TABLE 5.1

Time (s) averaged on power spectra for blue and common chaffinch songs transmitted on Tenerife.

Song Type	Blue chaffinch	Common chaffinch
1	2.00	3.15
2	2.45	2.50
3	2.42	2.52

At the beginning and end of the experiment temperature and humidity were measured with a whirling hygrometer. The number and circumference at breast height of trees along the transmission line were measured. The trees chosen were those along a 187cm wide transect between the playback speaker and the position of the far microphone at a distance of 50m. Few trees occurred in the transect at the Canarian pine sites, so extra trees in the immediate vicinity of the transmission line were also measured to bring the sample size for each site to a minimum of 20 trees. The average amplitude for the white noise and silence were measured with the SPL meter (set to the 30-70dB range, fast response, flat weighting), averaged by eye over the 15s transmission period at the far microphone position to provide a check that the sounds were received with a reasonable signal to background noise ratio when averaged over all frequencies.

The three sites in the Erjos laurel forest had a loam soil commonly covered with dead leaves and a sparse herb layer about 50cm - 1m tall. Typical species included *Erica arborea, Ranunculus cortusifolius, Genarium canariense, Hypericum glandulosum,* and *Crambe strigosa.* Mosses and lichens often occurred on the tree trunks. Though the transects over which transmission occurred were themselves fairly flat, this was because sites were chosen along the side of the steep slopes present. The canopy of the shrub layer was at about 8-10m, and up to about 25m for some of the larger trees. The weather in both habitats was often misty, and during the experiments the wind speed was mainly minimal (force 1 or less), across the axis of the transmission path.

At La Montañeta the soil was very stony with a large proportion of lava gravel. Many outcrops of lava were present and little vegetative ground cover was observed, though some bushes of *Erica arborea, Chamaecystus proliferus* and *Adenocystus viscosus* occurred, up to a height of 1.5m. Several species of lichen grew on the trees, sometimes quite densely. The ground was commonly covered with pine needles and cones, but this was not a deep layer as the needles are collected each year for packing bananas (Lack & Southern 1949). The trees present were larger and less densely packed than at Erjos, with a canopy height of 10-24m. Slopes were less steep than at Erjos, the ground was undulating. All sites in both habitats were situated within 50m of tracks used for access.

Time constraints encountered due to problems with importing the equipment needed for the experiment meant that all transmissions were made over a period of four days, and it was therefore not possible to control for the effect of humidity or temperature by only recording early in the day when these abiotic factors are most constant. However the experiment was partly balanced, as transmission occurred at about the same times within each habitat.

5.3 Results

5.3.1 Environmental measurements

The data for relative humidity (Figure 5.3) and temperature (Figure 5.4) show that higher humidities occured at Erjos during the transmission experiments, and that temperatures in the laurel forest are possibly more stable. Since experiments were performed over only four days and the measurements were instantaneous rather than part of a long term series it would be inappropriate to draw strong conclusions from these observations.

More trees were observed within the 187cm x 50m transects at Erjos (mean 34.0) than at La Montaneta (mean 12.7). The difference was just short of significance between the two habitats (one way ANOVA $F_{1,4}=7.61$, $p=0.051$), probably due to the small sample sizes. A highly significant difference between both habitats and sites within habitats (Figure 5.5) was found for the mean circumferance at breast height (habitat $F_{1,156} = 79.80$,

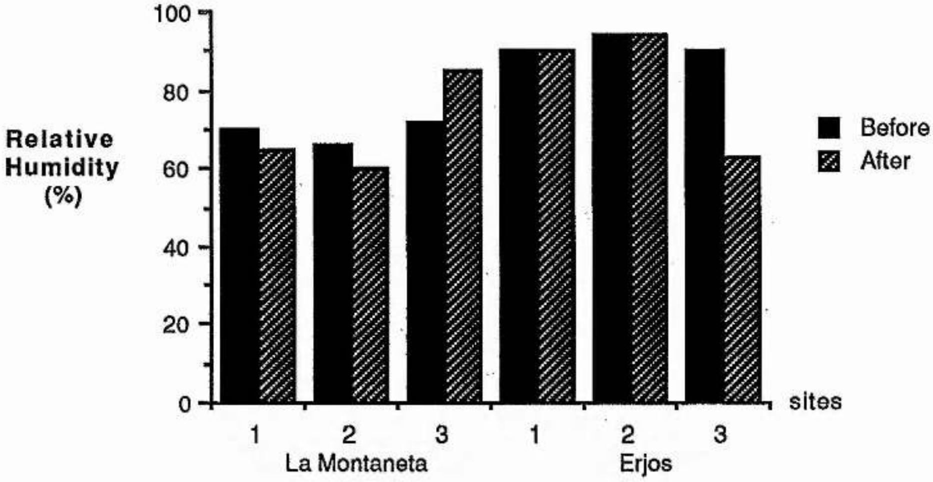


Figure 5.3 Humidity before and after the transmission experiments. Bars are individual measurements.

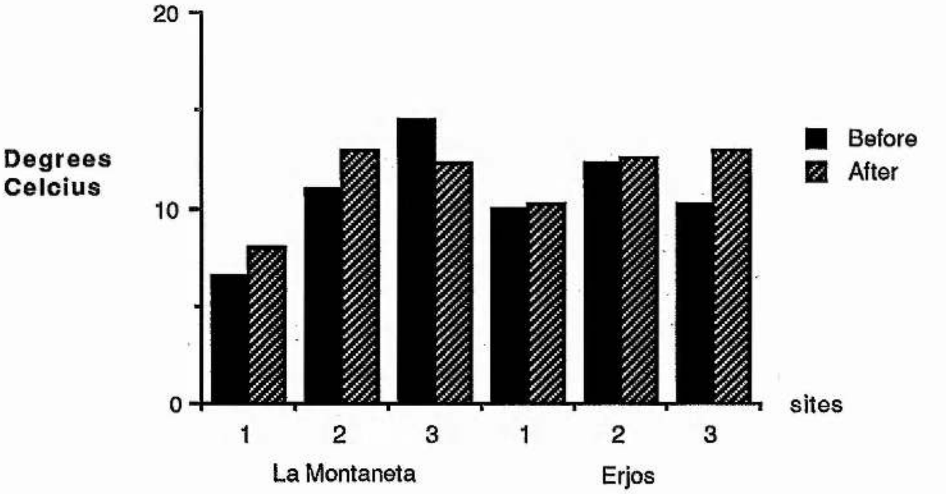


Figure 5.4 Temparature before and after the transmission experiments. Bars are individual measurements.

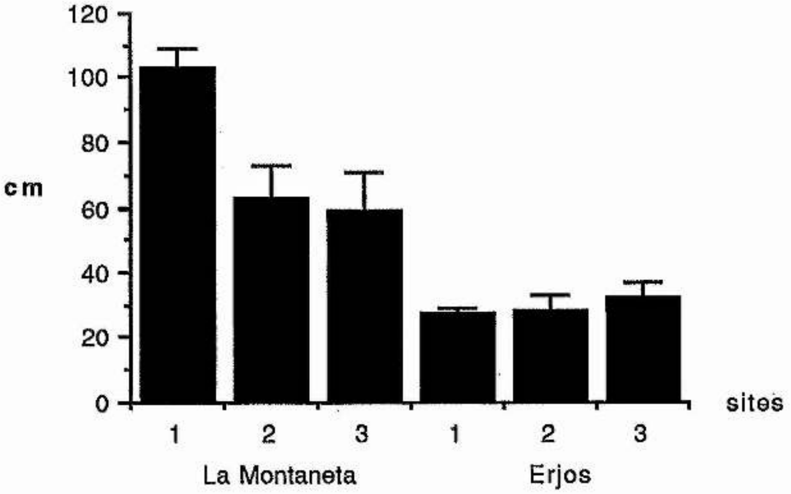


Figure 5.5 Tree circumferences.
Bars are means ± SE.

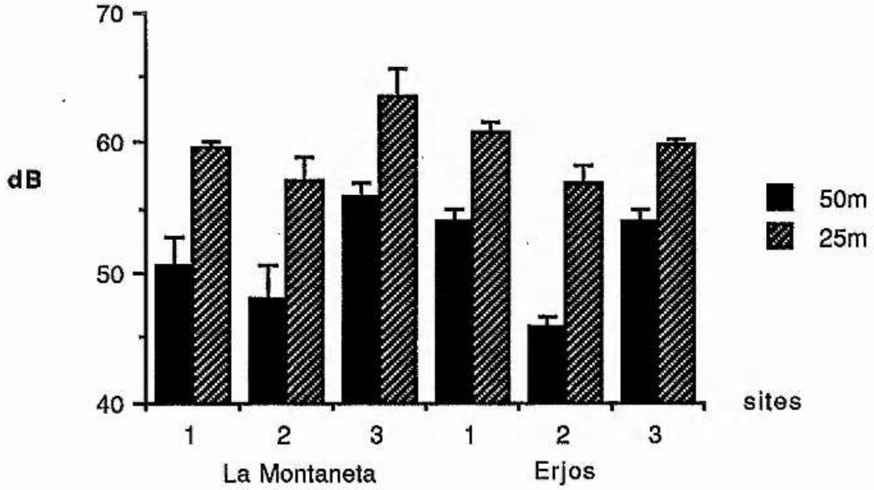


Figure 5.6 SPL for all frequencies.
Bars are means ± SE.

$p<0.001$; sites within habitat $F_{4,156}=6.21$, $p<0.001$). This indicates that though the laurel forest is denser, much variation between the different sites within each habitat was found.

In all cases the SPL measured over the 15s transmission of white noise at the far microphone position was more than 3dB greater than the SPL for the silent portion of tape. Analysing the SPL measurements for the white noise data (Figure 5.6) with a one way ANOVA for habitat and sites within habitat was not significant over both 25m and 50m for habitat (25m $F_{1,12}=0.16$, $p=0.711$; 50m $F_{1,12}=0.00$, $p=0.953$), but highly significant for sites within habitat (25m $F_{4,12}=12.76$, $p<0.001$; 50m $F_{4,12}=21.26$, $p<0.001$). There is thus much variation within habitats in the transmission of all frequenciees of white noise.

5.3.2 White noise

The data for one of the sites in the Canarian pine forest at La Montañeta had to be discarded as unreliable due to an equipment failure. The remainder of the data was analysed with a one way ANOVA over sites for each frequency measured over both of the distances. For transmission over both 25m and 50m a consistent pattern of more attenuation at the Erjos (laurel forest) sites was observed, but, probably because of small sample sizes, none of these differences were significant. The data for each of the sites within the habitats were therefore pooled, and the data sets for the two distances combined. This is a reasonable step as the attenuation expected for the 25m and 50m distances has been removed. Re-analysis of the data with a two way ANOVA for each frequency measured (both factors of habitat and distance fixed) revealed a significant difference between the habitats at frequencies of 0.5, 1.0, 3.5, 4.0, 4.5, 5.0, and 5.5kHz (Table 5.2). The distance factor and interaction were not significant for any of the frequencies. The pattern of attenuation at different frequencies is consistant for the two distances (Figures 5.7 and 5.8), except that slightly more attenuation occurs over the 50m distance.

5.3.3 Bird songs

The data were analysed with a two way crossed and nested ANOVA. The factors involved were habitat, species, sites nested within habitats, and song types within species. All factors were regarded as fixed as they were manipulated by the experimenter. After transmission over 25m a significant difference between the two species, and for the interaction between the species and sites within habitat, was found (Table 5.3).

TABLE 5.3

F values and probabilities for the transmission of six chaffinch songs (3 from each of the blue chaffinch and common chaffinch) over 25m in three sites in each of the laurel forest and Canarian pine habitats.

Source	d.f.	F	p
Habitat	1,72	0.01	0.926
Sites within Habitat	4,72	1.36	0.255
Species	1,72	6.54	0.013
Song types within Species	4,72	1.79	0.140
Habitat * Species	1,72	0.03	0.861
Habitat * Song types	4,72	1.57	0.191
Species * Sites	4,72	3.69	0.009
Sites * Song types	16,72	1.22	0.272

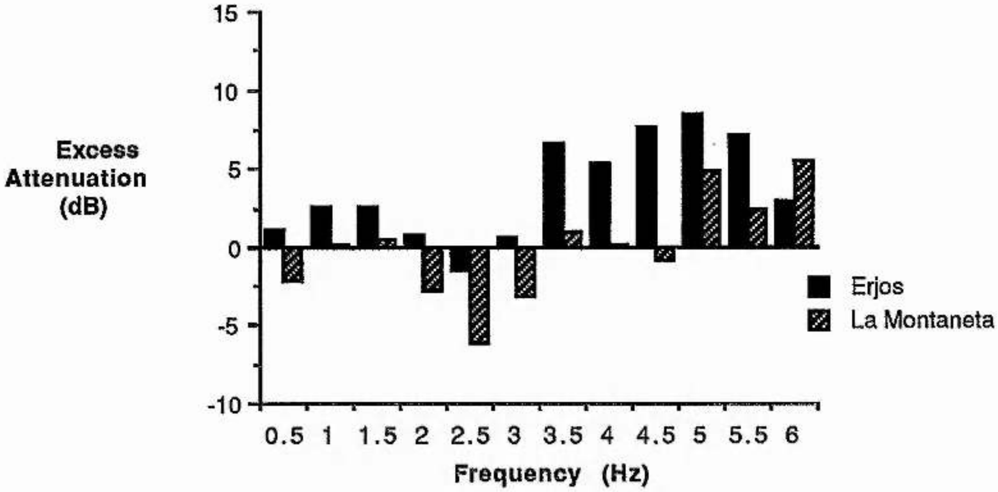


Figure 5.7 Transmission of white noise over 25m. Bars are means of the repetitions at three sites for Erjos and two sites for La Montaneta.

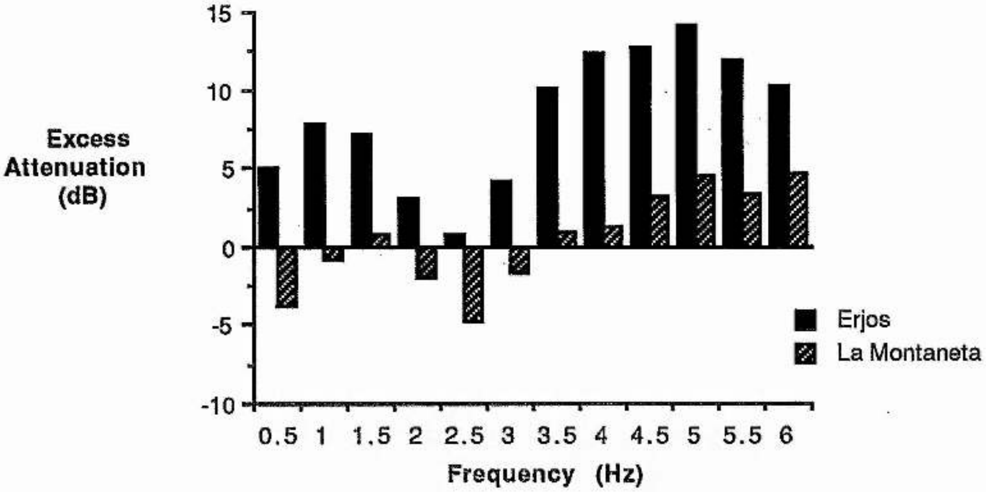


Figure 5.8 Transmission of white noise over 50m. Bars are means of the repetitions at three sites for Erjos and two sites for La Montaneta.

TABLE 5.2

F values and probabilities for the transmission of white noise in Canarian pine and laurel forests over 25m and 50m at La Montañeta and Erjos on Tenerife. All the F values have 1,26 degrees of freedom (except [1] 1,25 d.f. and [2] 1,24 d.f, both due to missing data).

Frequency (Khz)	Habitat	Distance	Interaction
0.5	5.62 p=0.025	0.18 p=0.673	1.14 p=0.295
1.0	5.62 p=0.025	0.85 p=0.364	1.82 p=0.188
1.5	2.92 p=0.099	0.95 p=0.338	0.71 p=0.406
2.0	2.91 p=0.100	0.38 p=0.541	0.09 p=0.772
2.5	3.30 p=0.081	0.43 p=0.516	0.03 p=0.859
3.0	3.03 p=0.093	0.82 p=0.373	0.14 p=0.716
3.5	5.96 p=0.022	0.32 p=0.574	0.32 p=0.574
4.0	11.02 p=0.003	2.74 p=0.110	1.40 p=0.248
4.5	9.93 p=0.004	2.62 p=0.117	0.02 p=0.884
5.0	10.47 p=0.003	1.65 p=0.211	2.08 p=0.161
5.5[1]	4.79 p=0.038	0.91 p=0.348	0.39 p=0.537
6.0[2]	0.30 p=0.588	1.29 p=0.268	2.04 p=0.166

A more complicated pattern was found for the data for 50m; all factors and interactions were significant (Table 5.4) except sites within habitat and the interaction of species with sites within habitat. The significant interactions are complex, but indicate that individual song types of each species have different transmission characteristics at different sites within each habitat

TABLE 5.4

F values and probabilities for the transmission of six chaffinch songs (3 from each of the blue chaffinch and common chaffinch) over 50m in three sites in each of the laurel forest and Canarian pine habitats.

Source	d.f.	F	p
Habitat	1,72	16.36	<0.001
Sites within Habitat	4,72	2.01	0.102
Species	1,72	8.00	0.006
Song types within Species	4,72	9.19	<0.001
Habitat * Species	1,72	13.00	0.001
Habitat * Song types	4,72	3.72	0.008
Species * Sites	4,72	2.01	0.101
Sites * Song types	16,72	2.84	0.001

More attenuation occurs for common chaffinch song in both habitats over a distance of 25m (Figure 5.9). Over 50m, most attenuation occurs for the common chaffinch in its own habitat. There is little difference in the FMA change for blue chaffinch song over both 25m and 50m in both habitats. It thus appears that the song of the blue chaffinch is well adapted to transmit through both the habitats investigated, but that of the common chaffinch does not transmit as well in either its own habitat or through the Canarian pine habitat.

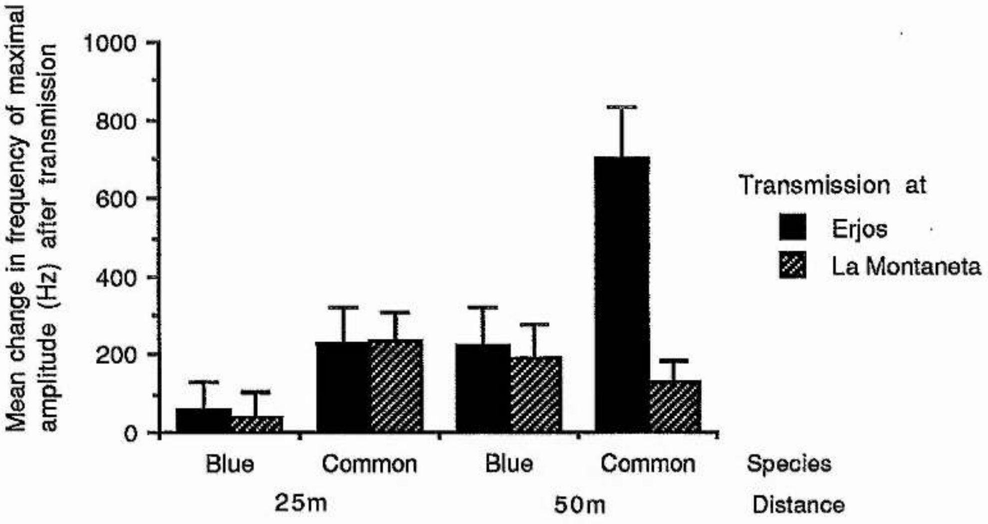


Figure 5.9 Transmission of blue and common chaffinch songs. Bars are means ± SE.

5.4 Discussion

Although statistical tests of the temperature and humidity data have not been presented, because of small sample size, it was observed that these factors varied less in the laurel forest at Erjos. The higher humidities observed at Erjos are probably the result of a temperature inversion often observed at around 1000m (Fernandopulle 1976). A quantitative analysis of the wind was not carried out, but the Canarian pine forest, since it is at higher altitude, is likely to be more exposed to the north west trade winds.

It is interesting to note that the average SPL recorded for all frequencies (Figure 5.6) of the white noise at 25m for all sites in both habitats is less than that expected purely from spherical spreading (65db), yet at 50m, for two of the sites at Erjos, and one at La Montañeta, the SPL recorded is greater than that expected by attenuation by spherical spreading alone (51dB). This may be due to the SPL measurement incorporating more background noise at the 50m distance; more bird sounds were noted on the tapes for the longer distance.

A significant difference was found for the SPL meter measurements between the sites (within habitats) over both distances, but not between the habitats. This variation within habitats may be partly due to the position of the SPL meter with respect to the trees. The SPL measurements were taken at the far microphone position, and for two of the replicates recorded at 25m at La Montañeta this microphone was located with a tree less than 3m in front of it. This was noted to decrease the SPL received, particularly for the 1kHz tone used for setting the playback level.

This suggests that if pure tones are used in birds' songs standing waves may interfere with communication, and that the sound pressure level heard for different frequencies will depend upon the position of the receiver. This may be one reason why many bird species use frequency modulated signals, as standing waves will not be set up for warbling tones. The variation in SPL may also be partly due to the significant difference in circumference of trees at the different sites within the habitats.

The laurel forest at Erjos was observed to be both denser, and to contain smaller tree trunks than at La Montañeta. Given this, the results for the transmission of white noise over both 25m and 50m are consistent with the acoustic adaptation hypothesis; higher frequencies are attenuated more than low ones, and more attenuation occurs in the denser habitat. The transmission characteristics of the different frequencies are complex. A sound window of less excess attenuation was observed for frequencies between 2-3kHz in both habitats (Figures 5.7 and 5.8). This is more marked for transmission over 25m, and is particularly evident at La Montañeta. The differences observed between the habitats when white noise was transmitted may be dependant upon a number of factors (reviewed in chapter 2) including the microclimate at the time of transmission, therefore these results should be interpreted with a certain amount of care as they are from only three sites within each habitat.

The sound window observed was unexpected as transmission was at a height of about 3m: the interference of the sound waves reflected from the ground with those transmitted directly between the source and receiver should be small when transmission occurs at heights above about 1-2m (Marten & Marler 1977, Roberts *et al* 1981). Less attenuation occurred at all the sites at La Montañeta: it should be noted that the transmission at these sites was carried out under very low wind conditions. It is likely that repeating the transmission experiment under more windy conditions would produce a different attenuation profile.

The results for transmission of the songs of blue and common chaffinches are less clear-cut. For transmission over 25m there is less change in the frequency of maximal amplitude for blue chaffinch songs in both habitats, but the habitat factor is not significant. The significant interaction of species with sites within habitat at 25m indicates that more change is observed at some sites than others for the two species' songs. After transmission over 50m the difference in the FMA is significant for both species and habitat. A significant difference is also found for the transmission of the different song types (within species), and for the interactions of habitat with species, habitat with song types, and sites with song types. These interactions imply that different song types of the two species transmit differently at different sites within the two habitats. The interaction of species and sites is not significant at 50m; this is a confusing result given that this interaction was significant at 25m.

A highly significant difference in the maximum frequency in the songs of blue and Canary Islands chaffinches was found by Slater & Sellar (1986). The mean maximum frequency for blue chaffinches was 4.4kHz, and for Canary Islands chaffinch was 5.8kHz. The blue chaffinch songs transmitted may therefore be attenuated less because they use lower frequencies which are in the same range as the observed sound window. In addition, since the song of the blue chaffinch contains more frequency modulated sounds than that of the common chaffinch it may be well adapted for transmission through a dense habitat. The songs of the common chaffinch may be attenuated more because they use a greater range of frequencies, and the higher frequencies are attenuated more.

From the above results it can be concluded that the song of the blue chaffinch is better adapted for transmission through both habitats, particularly over short distances, but that there is substantial variation in the transmission characteristics of both species' songs over longer distances. The song of the common chaffinch appears not to be particularly well adapted for transmission through either habitat. This may however be related to the variation within habitats in the vegetation density and microclimate (temperature, humidity etc) observed. The finding, that two closely related species can differ in the transmission characteristics of their songs' structure, is similar to that found for the summer and scarlet tanagers studied by Shy (1983).

Besides a difference in the microclimate of the two habitats, the ground surface is qualitatively different; at Erjos it is a moist loam, at La Montañeta a stony gravel. The soil porosity is one of the factors which can affect the amount of sound absorbed. Peak attenuation was found to be at lower frequencies for a soil which had more and larger pores (Aylor 1972a), thus more attenuation by the soil at La Montañeta might be expected. This may be altered by the number of large stones at the surface, which would reflect sound rather than absorb it. Given these complex acoustics it is suprising that the blue chaffinch sometimes sings on the ground (pers. obs.), as the signal would not be expected to transmit very far.

The minimum frequency for blue chaffinch song (1.4kHz) is slightly higher than that for the Tenerife chaffinch (1.3kHz), but both are lower than that for British chaffinches (1.6kHz; Slater & Sellar 1986). It is likely that attenuation by the ground is not therefore acting as a selective force. Since the males which sing on the ground are also foraging, it may be that communication in this case is to their mate rather than as a territorial signal to other males. A qualitative impression gained while recording blue chaffinches was that they may sing at lower amplitude than common chaffinches (Slater pers. obs.), this suggests that the species may transmit their songs over equal distances, but that the blue chaffinches save energy. However, how chaffinches perceive the sounds they hear is unknown.

It is important to stress that this study was limited by time constraints and the results reported should be regarded as preliminary. Further research on the songs used by the two species in the different habitats might reveal whether subtle differences in the structure exist, such as in the amount of frequency and amplitude modulation present. Similarly, this study did not assess the degradation of the songs after transmission to examine the effect of amplitude fluctuations and reverberations in the two habitats. These distortions are likely to vary between the habitats, as reverberations are common in dense woods and amplitude fluctuations in more open areas due to the influence of turbulence (Wiley & Richards 1978, 1982, Richards & Wiley 1980).

A further difference in transmission characteristics might occur in the overlap zone where both species are present. This might predict a convergence of the sounds used by the two species, but species with very similar songs may minimise competition by differences in breeding times and foraging behaviour (Brown 1977). Character displacement (Slater & Sellar 1986) would predict that species specific signals should diverge so the songs should be more different here than elsewhere. This would make results difficult to interpret, as failure to find differences in the transmission characteristics of the songs could be due to conflicting selection pressures.

Chapter 6

Syllable morphology and sequencing

Variability in the morphology of the syllables sung, and in the sequence in which they are produced, is very common in the song of the chaffinch (and many other species). This variability is important as it colours how the songs are interpreted. The chapter is split into three parts, each of which illustrates an aspect of how songs may change as they are passed between individuals when learning takes place. Firstly, the issue of transitional syllables is addressed. These are unrepeated syllables found within the trill part of the song, and are important as their presence alters how the song can be described. Secondly, the number of syllables found in the end phrase part of the song is compared with data from New Zealand, as it was this measure which prompted Jenkins & Baker (1984) to propose that some of the song types recorded in coniferous forests in New Zealand might be well adapted to transmit over long distances. Thirdly, some of the more unusual syllable and song types recorded are described and comparisons made with examples in the literature, particularly with the songs of chaffinches in New Zealand recorded by Jenkins & Baker (1984), and Plunkett (1987).

6.1 Transitional syllables

In the trill part of some song types an unrepeated syllable type occurs between two phrases of repeated syllables. These unrepeated syllables were defined as "transitional" by Slater & Ince (1979). Dividing the 153 song types recorded from the open and coniferous sites, and at Loch Garten into those with and without transitional syllables, and testing for an association with habitat was non significant (Table 6.1 X^2=1.817 2 d.f. p=0.403).

TABLE 6.1

Numbers of song types posessing transitional syllables associated with the open and coniferous habitats

	With	Without
Open	11	33
Coniferous (plantations)	16	61
Coniferous (natural)	4	28

Transitionals can only occur after the first phrase in two phrase songs (by definition), but in three phrase and four phrase songs they can occur in two, or three, places respectively. Though there are more opportunities for transitional syllables to exist in longer songs no significant association of number of phrases in the trill part of songs and the presence of at least one transitional syllable was observed (Table 6.2 X^2=1.361, 2 d.f. p=0.506). This finding replicates that of Slater *et al* (1984). For three phrase songs more transitionals occur after the second phrase than after the first (Table 6.3 X^2=7.118, 1 d.f. p=0.008) but too few four phrase song types were recorded to analyse in this manner. Two song types were observed with two transitionals; one each from the open and coniferous plantation habitat types. These song types were only counted once in tables 6.1 and 6.2, and omitted from tables 6.3 and 6.4. All other song types which possessed a transitional syllable had only one.

TABLE 6.2

Numbers of song types possessing transitional syllables associated with the number of phrases in the song. The data for the different habitats have been pooled.

Phrases	With	Without
2	8	43
3	18	66
4	5	13

TABLE 6.3

Number of transitional syllables in three phrase songs occurring after the first or second phrase. The data for the different habitats have been pooled.

	After 1st phrase	After 2nd phrase
Observed	3	14
Expected	8.5	8.5

TABLE 6.4

Numbers of type I and II transitional syllables from Open and Coniferous habitats.

	Type I	Type II
Open	4	6
Coniferous (plantations)	3	12
Coniferous (natural)	1	3

Transitional syllables appear to be of two kinds (Figure 6.1): type I; syllables which are truely intermediate in form between the morphology of those in the

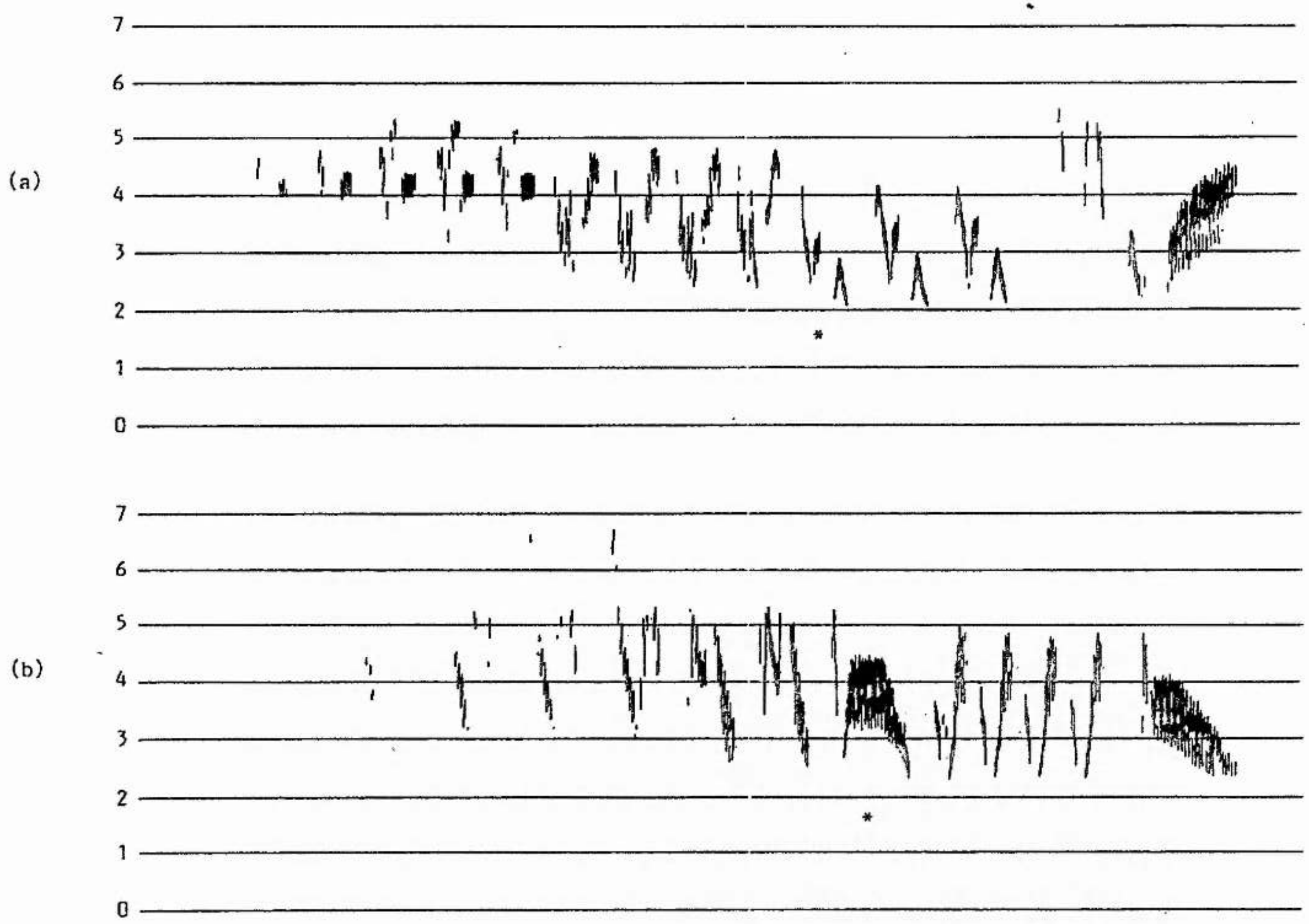


Figure 6.1 Types of transitional syllable. (a) Type I, the transitional is of intermediate form to the syllables in preceeding and succeeding phrases. (b) Type II, the transitional is of a different morphology to the other syllables. Transitional syllables are marked with a *.

preceding and succeeding phrases, and type II; those which are of completely different morphology.

Table 6.4 shows the result of classifying the 28 transitional syllables recorded amongst the songs from the open and coniferous habitats. There is no difference between the habitats in terms of the numbers of transitional syllables of each type that were observed (X^2=1.217, 1 d.f. p=0.544).

The second class of transitional syllables may in fact be better regarded as syllables which are not repeated rather than as those which are strictly transitional. Variation in the number of syllables within a phrase is common within song types, both within and between birds (discussed in detail by Slater & Ince 1979). Since the definition of a phrase has been a sequence of repeated syllables, reduction of this repetition means that syllables might in some songs be regarded as part of a phrase, and in others as transitional, as shown by phrase 2 of song type MO/E (Figure 6.2).

An alternative interpretation of transitional syllables is that they may be syllables which have been copied from the song of another species. Helb *et al* (1985) describe a sonagram of chaffinch song (their figure 5) which they claim is partially a copy of greenfinch (*Carduelis chloris*) song. One of the syllables shown is in a position between two phrases and would be described as transitional using the definitions in chapter 4. The syllables in the greenfinch and chaffinch songs show a close similarity, but since the songs were recorded at

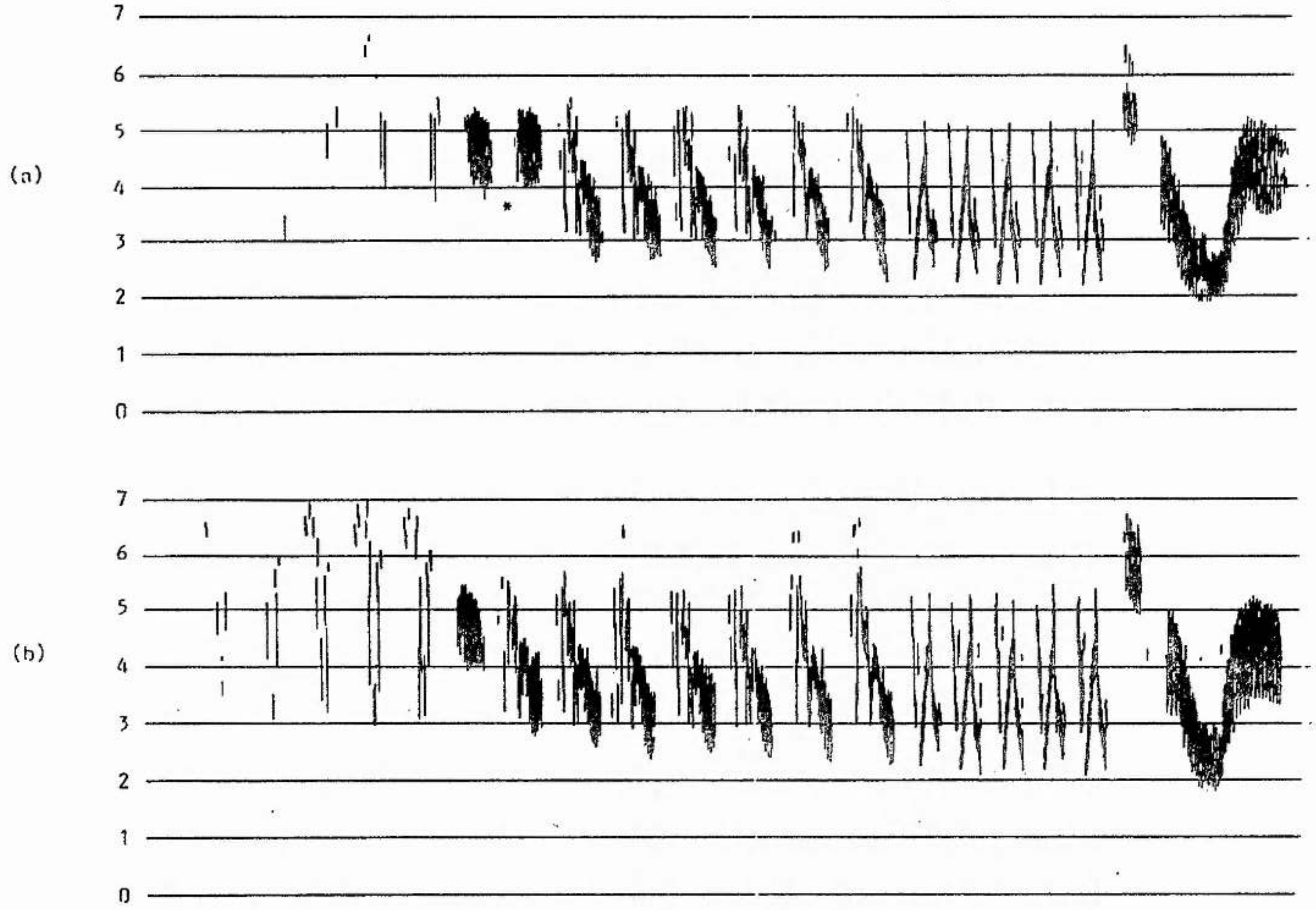


Figure 6.2 Phrase 2 (*) of song type MO/E (a) is reduced to a transitional sillable if it is not repeated (b).

different places in different years the evidence is far from conclusive.

Mimicry of other species song by chaffinches is rare, but does occur on occasion; documented examples include chaffinches singing songs including elements typical of the songs of lesser whitethroat (*Sylvia curruca*, Bromley 1946), dunnock (*Prunella modularis*, Hartley 1946), greenfinch (*Carduelis chloris*, Conrads 1977), nuthatch (*Sitta europaea*, Conrads 1979) and canary (*Serinus canaria*, Slater 1983b). In addition, Thorpe (1958b) demonstrated that young male chaffinches might learn tree pipit (*Anthus trivialis*) song in a tutoring experiment. Mixed singing in chaffinches was interpreted as due to the lack of a conspecific model during the sensitive phase leading to "a defect in normal song learning" by Helb *et al* (1985). The sounds imitated are usually similar to those produced by conspecifics,

6.2 Numbers of syllables in the end phrase

The end phrase or flourish part of a chaffinch song is defined as a sequence of unrepeated syllables following the trill portion. However, it has also been taken to include one particular syllable type which may be repeated (see Figure 4.1), because Slater *et al* (1984) observed that this syllable type is only ever found at the end of the songs in which it exists, and that it may be preceded by more than one unrepeated syllable type.

The syllables typical of the end phrase often include a substantial amount of frequency modulation, this may be important in reducing the degradation due to reverberations when transmission through a dense habitat occurs. Elaborate end phrases were described by Jenkins & Baker (1984) from some of the song types recorded in dense coniferous forests in New Zealand, and the New Zealand songs were found to have significantly fewer trill phrases and more end phrase syllables than a sample of published British song types.

Analysis of the Scottish songs recorded in this study showed that there was no difference in the number of end phrase syllables between songs recorded from different sites (within habitats) for two or three phrase songs (Two phrase songs $F_{8,40}=0.732$, $p=0.663$; Three phrase songs $F_{9,72}=0.836$, $p=0.586$). No significant difference was found between habitats (Two phrase songs $F_{2,8}=0.006$, $p=0.994$; Three phrase songs $F_{2,9}=0.084$, $p=0.920$; Four phrase songs $F_{1,8}=0.03$, $p=0.878$). Pooling the data for end phrases from songs of different lengths, no significant difference between sites (within habitats) ($F_{9,133}=1.003$, $p=0.441$), or between habitats ($F_{2,9}=0.878$, $p=0.448$) was observed.

A significant difference in the number of end phrase syllables was however found between the different lengths of song types pooled across sites and habitats ($F_{2,142}=6.23$, $p=0.003$). This is because shorter songs have more end phrase syllables (Figure 6.3).

The incorporation of trill syllables into the end phrase of some New Zealand chaffinch songs was interpreted by Jenkins & Baker (1984) as one of the reasons why some song types have very elaborate end phrases. The process has also been described by Slater & Ince (1979) for British chaffinches, and was observed in a few of the song types

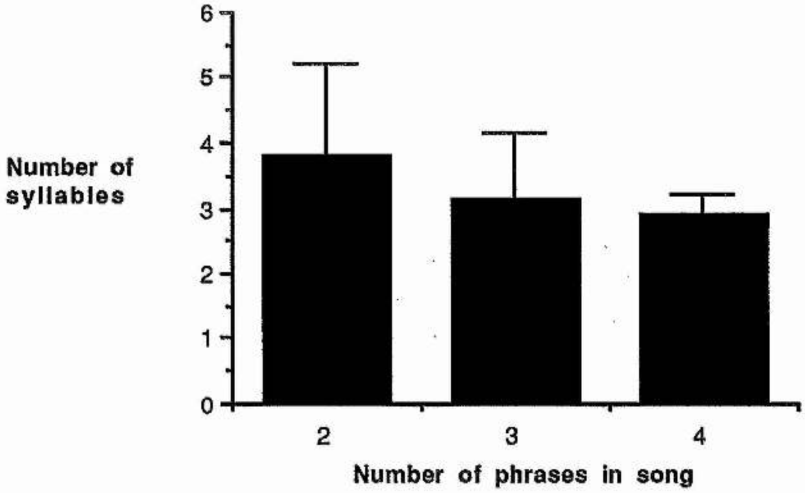


Figure 6.3 Number of syllables in the end phrase. Bars are means ± SD.

recorded in this study. It is exemplified by phrase 3 of song type TM/M (Figure 6.4). A comparison of syllables from 32 song types recorded in the Abernethy Forest around Loch Garten revealed little sharing of syllables between songs, and only two syllables were found which occurred both in the trill part of a song and also within an end phrase. It should be noted that the sampling at Loch Garten was neither complete nor exhaustive, and for this reason no measure of the amount of sharing has been calculated, yet it is clear that that unlike the examples discussed by Jenkins & Baker (1984) and Plunkett (1987), in Scotland syllables of the same morphology are only rarely found in both the trill and end phrase parts of the song.

6.3 Unusual song types and syllables

In general the form of the syllables sung by chaffinches is extremely stereotyped. However, slight alterations of a syllable may occur as a phrase is sung. These are generally at the start of a song. I interpret these alterations as the bird singing successive syllables with greater amplitude as the song begins (see figure 4.1 for an example).

A gradual decrease (or increase) in pitch from the first to last syllable of a phrase occurs in some New Zealand song types. Some of the songs recorded in Scotland showed a pitch decrease between the beginning and end of a phrase (Figure 6.5), but none had an increase within a phrase.

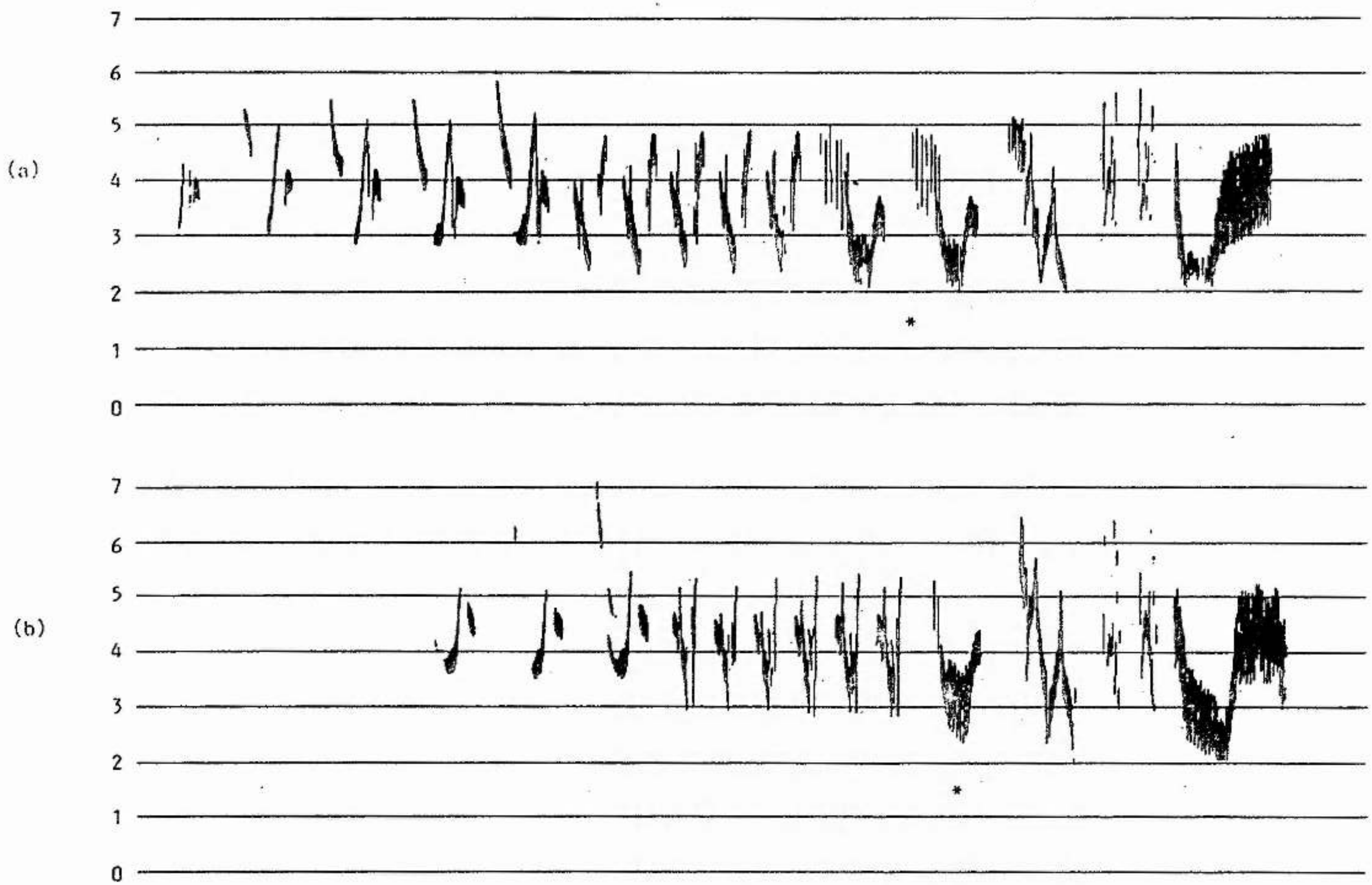


Figure 6.4 Phrase 3 of songtype TM/M (a), marked * is reduced to part of the endphrase (b).

Figure 6.5
Phrase 2 shows a decrease in pitch between the start and end of the phrase.

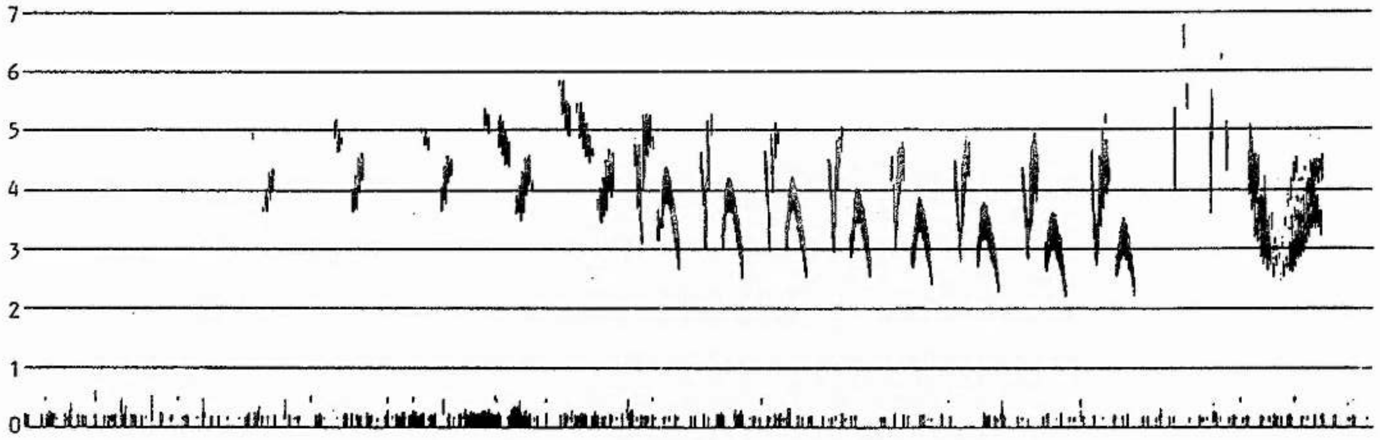
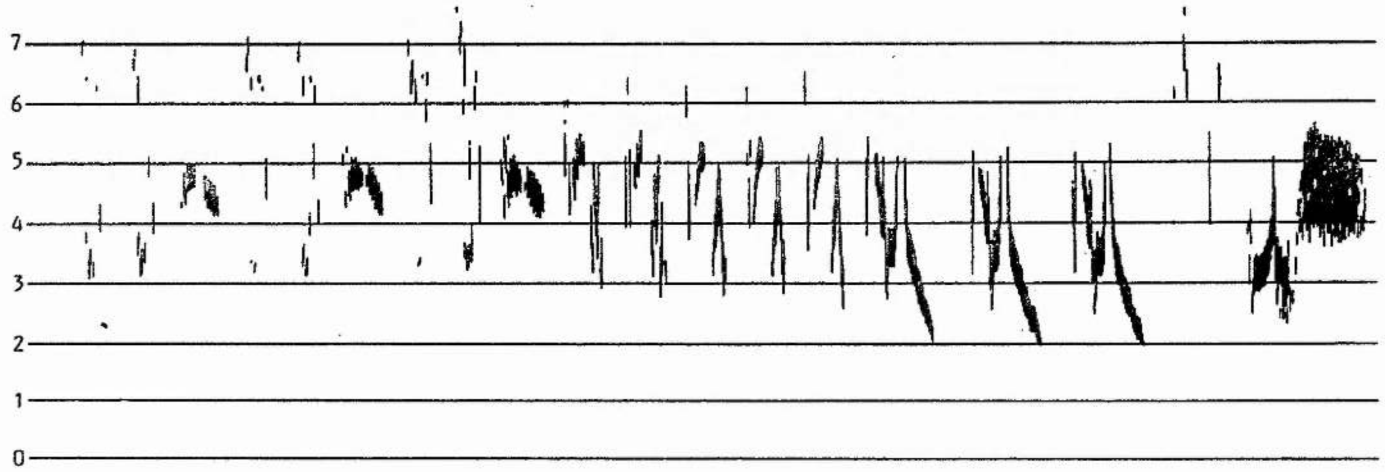


Figure 6.6
The first phrase of song type MO/D contains a complex arrangement of elements.



A further example of unusual syllable morphology was provided by syllable type MO/D1 (Figure 6.6). Syllables were defined (section 4.3.1) as a sequence of elements which are repeated. However, it is clear that repetition of a higher order occurs in this case.

Two somewhat unusual song types were recorded at Loch Garten. LG/Q (Figure 6.7a) is a song type with only one phrase. This is the only song type with one phrase which I have recorded, though Marler (1952), who described pitch variations within the trill portion of songs, also found a few songs with a single phrase, and Jenkins & Baker (1984) found songs with only one phrase to be common in New Zealand. A variant (LG/Qa; Figure 6.7b) was sung by another bird, and this was a conventional two phrase song. This illustrates the kind of change possible when songs are learned by imitation of a tutor. The birds singing LG/Q and LG/Qa did so repeatedly, and the recordings are sufficiently good to be sure that the first phrase of LQ/Qa was not missed.

Another song type (LG/D; Figure 6.8) had a very complicated end phrase. Unfortunately the recordings are poor, as the bird only sang a few times before either flying off or ceasing to sing (it was not observed). Attempts to rerecord the bird on other occasions were unsuccessful. Strictly, by the definitions used, this song type could be regarded as a three phrase song without an end phrase, the last phrase being very complicated. The syllables in the 'end phrase' are however of the type usual for this position in the song. This song type is again the

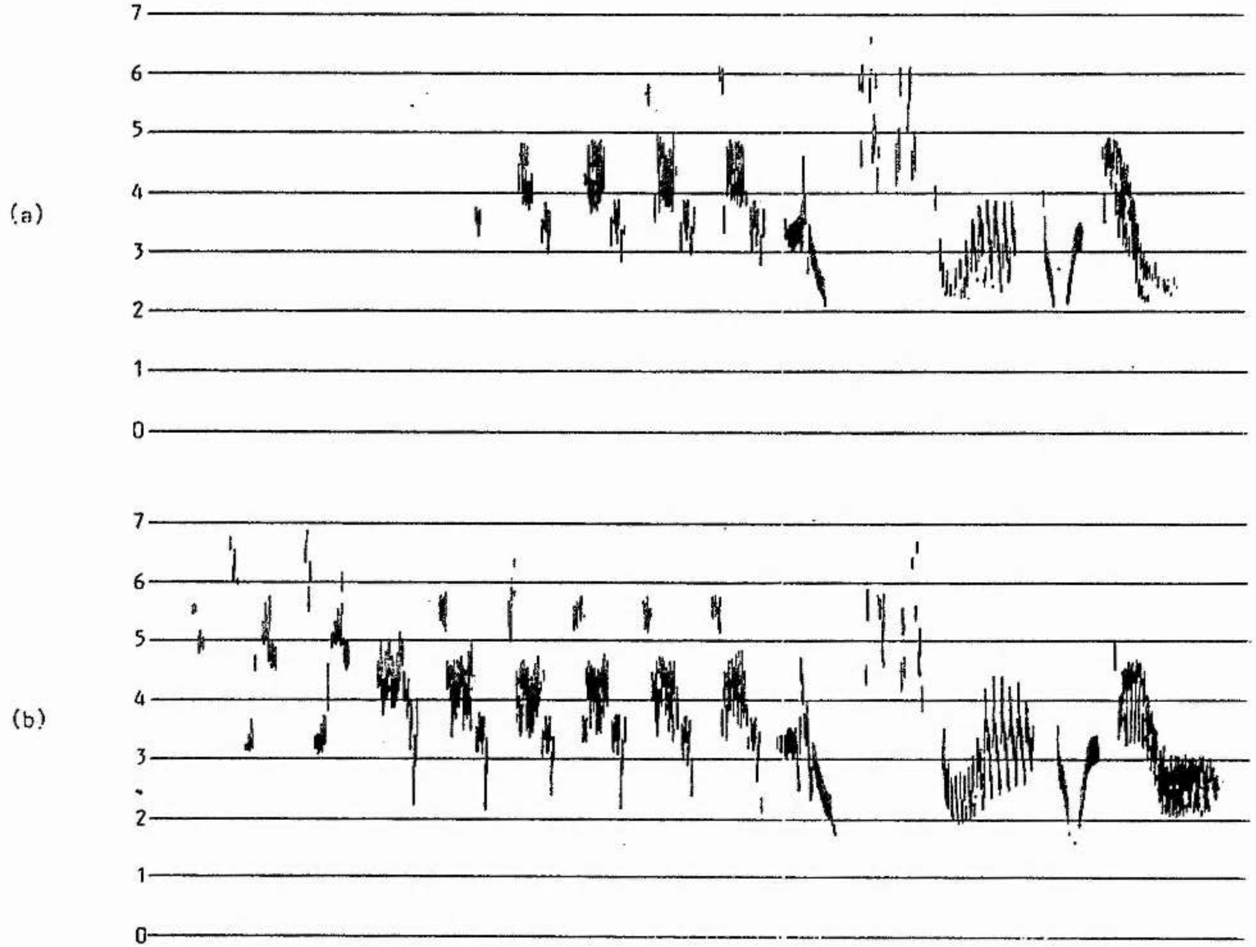


Figure 6.7 (a) Song type LG/Q has only one phrase in the trill part of the song.
(b) A variant, LG/Qa has two phrases in the trill.

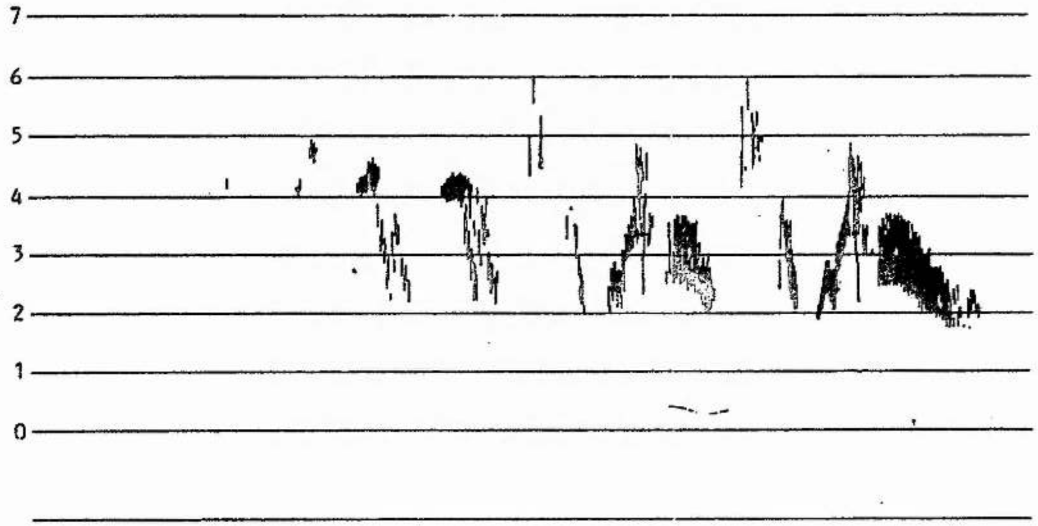


Figure 6.8 Songtype LG/D has a very complicated endphrase.

only one of its type that I have recorded, but Vere Benson (1951) and Marler (1956a) both report songs of this sort from Britain, and song types with a double end phrase were described for New Zealand chaffinches by Plunkett (1987).

Chapter 7

Cultural change in chaffinch song

7.1 Introduction

Learning plays a role in the song development of all songbirds studied to date (see review by Slater 1989). In many cases the copying of song takes place from neighbours when young birds first set up their territories so that birds on adjacent territories tend to share songs, while the songs of those further apart are less similar. While the learning can be remarkably accurate, there is good evidence from a number of studies that inaccuracies of copying may lead to new forms of song arising (e.g. Jenkins 1978, Slater & Ince 1979). These "cultural mutations" may be the reason why the songs present in a given area change with time, and why there are also differences in song between localities.

Much of the geographical variation in song is complex, especially in cases where each individual has a repertoire of several different song types and these are not all learnt as a package from one other bird. However, in some species dialect areas have been described in which groups of birds share the same song type or types and are separated from each other by more or less sharp boundaries. Whether or not this mosaic pattern has any functional significance is a matter of a good deal of controversy (see Baker & Cunningham 1985 and associated commentaries).

Each male chaffinch has 1-6 song types and these are usually learnt in the first thirteen months of life, either after hatching in the summer or the next spring when the bird itself starts to sing (Slater & Ince 1982). In a few cases learning may be later (Nurnberger *et al* 1989, Goodfellow & Slater 1990). All chaffinch songs share basic features but they differ in form both within the repertoire of a single bird and between birds, so that within a population a number of different song types are found. Some of these are shared by many birds, some are sung by only one bird.

Slater *et al* (1980) found that the frequency of song types in a population in Sussex fitted the distribution expected from a model of neutral alleles (Ewens 1972), and suggested that the songs in a bird's repertoire are learnt at random amongst those available and that different ones are often learnt from several different individuals.

Studies on other species, notably by Payne (1985; Payne *et al* 1981, 1988), also support the idea that transmission of songs from one individual to another is a random process, with changes through time and space accumulating by errors in transmission.

7.2 Review of computer simulations

7.2.1 Cultural evolution

Computer simulation is a powerful tool in helping us to think about complex biological problems. In earlier studies on song in chaffinches Slater *et al* (1980) employed it to examine whether the distribution of song types in a population might be accounted for by individuals copying from each other at random with occasional errors in copying leading to the creation of new song types.

In the Stanmer Great Wood population studied by Slater *et al* (1980) a total of 35 song types were sung by 42 birds. Of these, a few song types were sung by many birds and many were sung by only one or two individuals. Thus 22 birds sang the commonest song, but there were 21 songs each sung by only one bird. A simulation of the rate of miscopying required to produce the distribution of sharing between repertoires observed produced a best match to the field data with a rate of 15%. The results were the means of three runs, each started with all birds singing a single song type and run with a 40% annual mortality rate (data from the British Trust for Ornithology). Running the program for 100 cycles ensured that the outcome was independent of the starting conditions.

Ince *et al* (1980) went on to compare the 35 song types recorded in the same wood in 1978 with a sample of 22 that had been recorded there 18 years earlier. Only three types were similar enough to be considered as the same. Ten runs of a simulation based on these data were carried out using the 15% miscopying rate. These simulations predicted that a mean of 3.2 song types should be in common between the samples, a remarkably good fit to the data (Slater *et al* 1980).

Slater *et al* (1980) also found that the distribution of repertoire sizes of the chaffinches in Stanmer Great Wood did not match a zero truncated poisson distribution, as there were fewer large and small repertoires than expected. This may be due to birds learning the same song more than once, but using it as if it were two separate types. The size of repertoires was simulated, based on the idea that repertoires could be built up by drawing songs at random from those available, allowing the same song to be learnt more than once. An iterative technique where the observed mean repertoire size homed in on that in the Sussex population (2.9) was used. The simulation produced a repertoire size of 3.26, and this did not differ significantly from the field data. The simulation also predicted more large and small repertoires than were observed, but it is possible that repertoires are built at random in this way.

7.2.2 Dialects

The issue of whether song dialects exist and what their function(s), if any, might be is a complex and controversial one. The main problem is one of definitions; the term "dialect" is used in several different senses. If clear dialects exist it should be possible to distinguish easily between individuals in different populations or subpopulations. Sharp dialect boundaries with such clear differences have only been described for a few species, and it is perhaps not surprising that these all have small repertoires of only one or two song types. Examples are the white-crowned sparrow (*Zonotrichia leucophrys*, Baptista 1975), European redwing (*Turdus iliacus*, Bjerke & Bjerke 1981) and corn bunting (*Emberiza calandra*, McGregor 1980, McGregor and Thompson 1988).

Some authors have argued that chaffinch song shows dialects (Metzmacher & Mairy 1972, Conrads 1986), but Slater *et al* (1984) rejected this hypothesis as they found great variation within areas as well as some sharing of features between them. Such differences between areas are better referred to as geographic variation.

Goodfellow & Slater (1986) used a computer simulation to explore the possibility that dialects might arise as the result of random copying of song types. A 10 x 10 matrix was used, and the simulation was run over 300 'years' with birds able to learn a single song type from one of up to four neighbours next to them. The simulation started with all birds singing the same song type. The mutation rate of 15% arrived at by Slater *et al* (1980) and a mortality rate of 40% were used. If a new bird had no pre-existing neighbours to copy from it made up a new song type. A simple mosaic of shared songs resulted (see Figure 6 in Slater 1989) with small groups of birds (up to 8 or 10) sharing a song type.

The size of the groups varied with the error rate used (see Figure 1 in Goodfellow and Slater 1986), but in no case, even with extremely accurate transmission, were groups approaching the size of those described for white-crowned sparrows found. When the simulation was started with the birds in one half of the matrix singing one song type, and those in the other singing another, a stable border could be achieved provided error and mortality rates were low. A random process might thus account for small song neighbourhoods, such as those described by Payne and his co-workers in the indigo bunting (*Passerina cyanea*) and the village indigobird (*Vidua chalybeata*), but not for the large dialect areas found for some other species such as the white-crowned sparrow.

7.3 The influence of repertoire size and numbers of neighbours

The simulation by Goodfellow & Slater explored the simple situation of all birds having one song and each of them having four neighbours, from one of whom they copied. This idea is extended below to examine the consequences for song distributions of birds having different repertoire sizes and different numbers of neighbours. This simulation is thus more likely to be relevant to birds, such as the chaffinch, which have a small repertoire of song types not necessarily all learnt from the same bird, and which may vary in the number of birds from whom they can copy according to their breeding density and the structure of the habitat.

7.3.1 Methods

The simulation took the form of a computer program written in Turbo Pascal 4 and run on a Zenith Model 159-13 computer (see Williams 1990 for more details). It used a population of 169 'birds' arrayed in a 13 x 13 matrix. Each run started with all the birds singing the same song types (numbered 1,2,...), the number of songs present being the size of the repertoire for that run. Every 'year' all birds had a fixed chance of 'dying' and being replaced. Those that died were chosen at random. For chaffinches a realistic mortality rate is 40% (i.e. 60% of birds survive each year, see Goodfellow & Slater 1986) and all the simulations used this figure. The birds that did not die continued singing the same songs as before, and the new ones learned songs from neighbours.

Chaffinches appear to learn the different songs in their repertoire by copying each from a single (possibly different) individual (Slater & Ince 1979, Slater *et al* 1980), this was managed in the program by making a list for each newcomer of the songs possessed by those of its neighbours that were not new (new birds could not learn from other new birds); the songs to be learnt were then chosen at random from this list of those available. Once a song type had been learnt, it could not be learnt again by the same bird, so that duplicates of the same song type within one repertoire were not allowed. The entire array was processed to determine which cells had become unoccupied before any of the new individuals were assigned song types.

In copying from neighbours there was also a chance that a 'mistake' would be made, and in this case a new song type was generated. For chaffinches the probability of miscopying a song type has been estimated at around 0.15 (Slater *et al* 1980), a figure which also includes the effect of new songs being introduced by immigration into the population. This 15% error rate also includes the probability of new birds copying from other new birds, a process which may occur in the wild, but is undetectable, and was not allowed in these simulations. The program was arranged so that birds could learn from up to eight neighbours (the four in the same row or column as themselves, plus the four diagonal to them; Figure 7.1), except at the edge. The number of neighbours could also be set at four and two to investigate the effects of number of neighbours on the sharing of song types. In the case of two neighbours the program joined columns so that a linear array of 169 cells was formed from the two dimensional matrix.

If a neighbour in a particular direction had also 'died', so that a cell could not learn from the cell next to it, then the program used the songs in the repertoire of the nearest neighbour in the same direction which had not died in its list of possible songs to be learnt. This is limited by the edge of the array, and is equivalent to a bird listening to another further away when the intervening territory was empty. In each simulation all the birds had the same repertoire size, but this was varied between simulations from one to six.

Mortality rate, song copying error rate, repertoire size, and number of neighbours were all parameters which could be varied in the program. Goodfellow & Slater (1986) examined the first two of these, while keeping the others constant. In the runs reported here the first two were kept constant so that the influence of varying the others could be examined. Initial tests established that an equilibrium was reached after a run of about 80 'years', and all the runs described here were over 100 'years' to ensure that such a stable state was achieved. If any of the songs placed in the array at the start was still present at

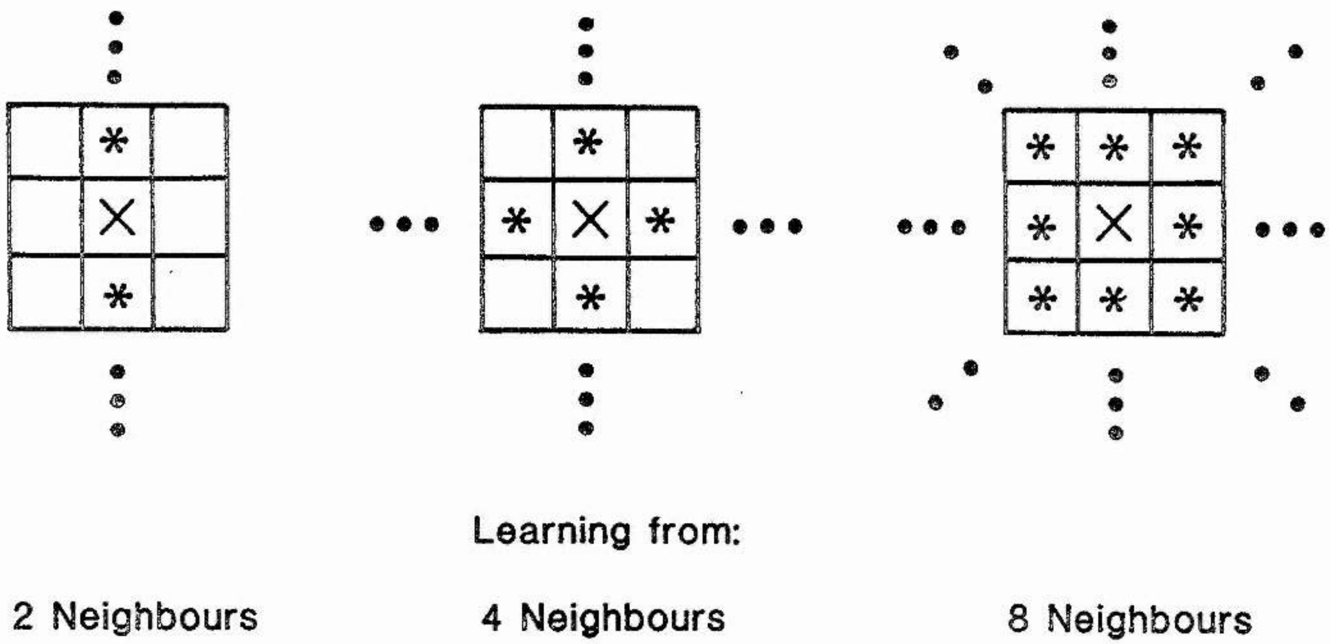


Figure 7.1 Locations of tutors from which birds can learn . A given cell (X) can learn from any of the cells marked *, or, if these are 'dead', from the nearest extant cell in the directions indicated by the dots.

the end of the run, then that run was rejected and another carried out.

Preliminary tests also showed that a matrix of 13 x 13 cells was sufficient to avoid edge effects, and thus all trials were for this size of matrix. However, birds on the edge have fewer neighbours and this is likely to affect the amount of song sharing between them. Measures of song sharing between neighbours (as described below) were therefore calculated only for those cells with the correct number of neighbours. Thus the first and last cells for runs with two neighbours, and the outer rows and columns for runs with four and eight neighbours, were used only for calculating the number of songs shared by the other cells and did not themselves contribute to the sharing coefficients that were calculated.

7.3.2 Analyses

The results for the ten runs at each repertoire size and each number of neighbours were subjected to several different analyses to assess the impact that changes in these variables had on various measures. For each of the runs statistics about the birds and song types present in the matrix were gathered every 'year' and these were later used, together with statistics calculated from the form of the matrix at the end of the simulation, to provide a report on the results of that run. The analyses carried out were as follows:

1) The mean longevity of all the song types which had both been generated and become extinct during a run was calculated. This set is arbitrarily bounded, but obviously

both the extant song types, and those song types used to seed the array cannot be used. An alternative might be to calculate the mean song longeivity of all song types which arose during the simulation by stopping the simulation to collect statistics, and then restarting it and allowing the extant (non seed) song types to become extinct. However, since an equilibrium was reached this is unlikely to be graetly different from the mean already obtained.

2) The number of birds sharing a song type was assessed in two different ways. For each run the mean number of birds sharing a song type was calculated over all the song types present, and the number of birds sharing the commonest song type was also worked out. The sharing was assessed from the matrix at the end of the run.

3) To get some idea of the realism of the simulation the distribution of the number of repertoires in which each song type occurred was calculated for one randomly chosen run of each type. This was compared with the data collected by Slater *et al* (1980) for chaffinches in Great Stanmer Wood, Sussex.

4) Songs that are shared between birds commonly exist in groups of adjacent birds, but can be split into several different groups. In order to test if this splitting was more likely to occur with larger repertoires or numbers of neighbours a fragmentation index was calculated. The index used was:

$$\frac{\text{number of groups for song types shared by two or more birds}}{\text{number of song types shared by two or more birds}}$$

5) The mean number of songs shared between a bird and its neighbours was measured in two ways:

(i) The Jaccard Similarity Index. This is a measure of the proportion of repertoire sharing that occurs. The index is calculated as : $a / (a + b + c)$, where a is the number of songs shared, and b and c are the number of songs that are not shared in the two repertoires being compared. The index was calculated at the end of each run for each neighbour of an individual and averaged to provide the mean value for that bird. These mean values were then averaged over the whole matrix to provide a value for the run.

(ii) The alternative measure was the number of songs shared with each neighbour, averaged to provide a value for the cell, and these values averaged for the run. The results for this measure will not be presented as they were virtually identical with those for the Jaccard Index.

Two way analyses of variance were calculated for the data from ten runs for each neighbour and repertoire size combination. The number of neighbours was regarded as a random factor, and the repertoire size as a fixed factor. All statistics were performed with Minitab, except for the Kolmogorov-Smirnov tests which were carried out using the PC-Calc spread-sheet. All the data presented in the Figures are the means of the ten runs.

7.3.3 Results

Figure 7.2 shows how the average number of years for which a song type lasted varied with repertoire size and number of neighbours. Although the differences are not striking, songs lasted longer with increasing repertoire size ($F_{5,10}$=13.6, $p<0.001$). The interaction was not

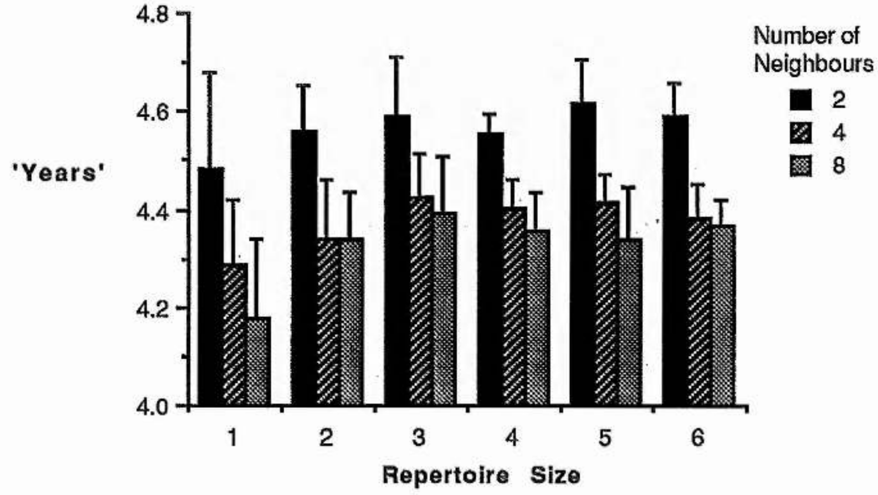


Figure 7.2 Mean song longevity.
Bars are means ± SD.

significant ($F_{10,162}=0.62$, NS), showing that the two effects were independent. The trend with number of neighbours was the opposite of that expected: songs lasted a shorter time with more neighbours ($F_{2,10}=142.4$, $p<0.001$).

The number of neighbours had a strong effect (Figure 7.3) upon the number of birds sharing the commonest song ($F_{2,10}=75.8$, $p<0.001$), while this increased only slightly with repertoire size ($F_{5,10}=4.8$, $p<0.05$). The interaction was not significant ($F_{10,162}=0.92$, NS). These results are in line with those predicted, as both larger repertoire sizes and greater numbers of neighbours would be expected to increase the probability of a song being copied between neighbours.

The expectation for the mean number of birds sharing a song type was the same as that for the number sharing the commonest type: that there would be an increase with both repertoire size and number of neighbours. However, while there was a rise with number of neighbours (Figure 7.4; $F_{2,10}=24.8$, $p<0.001$), there was no effect of repertoire size ($F_{5,10}=1.0$, NS). Again, there was no interaction ($F_{10,162}=1.6$, NS).

Table 7.1 also examines song sharing, but compares it with earlier data on chaffinches, where the number of birds in the population sharing each song type had been determined. It shows that some runs with two and with eight neighbours gave a significantly different distribution from these chaffinch data, but none of those with four neighbours did. This may stem from the fact that the four neighbour simulation was the most realistic one as far as

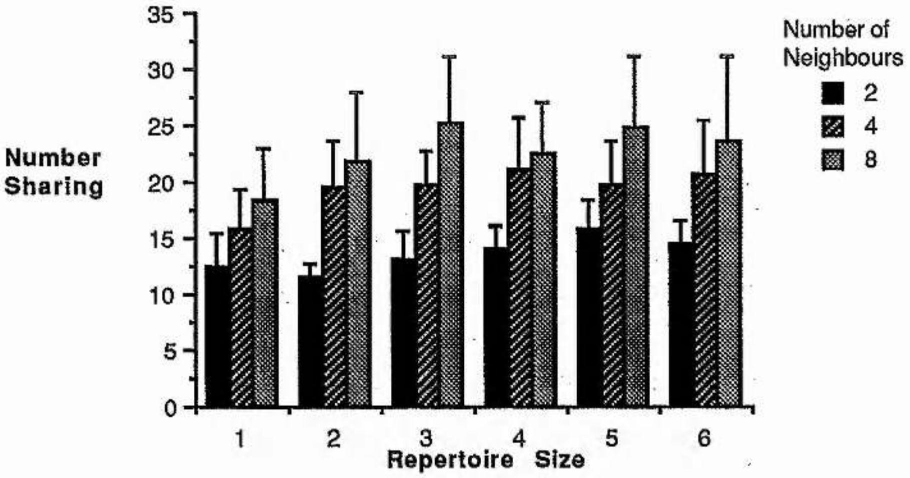


Figure 7.3 Maximum number of birds sharing a songtype. Bars are means ± SD.

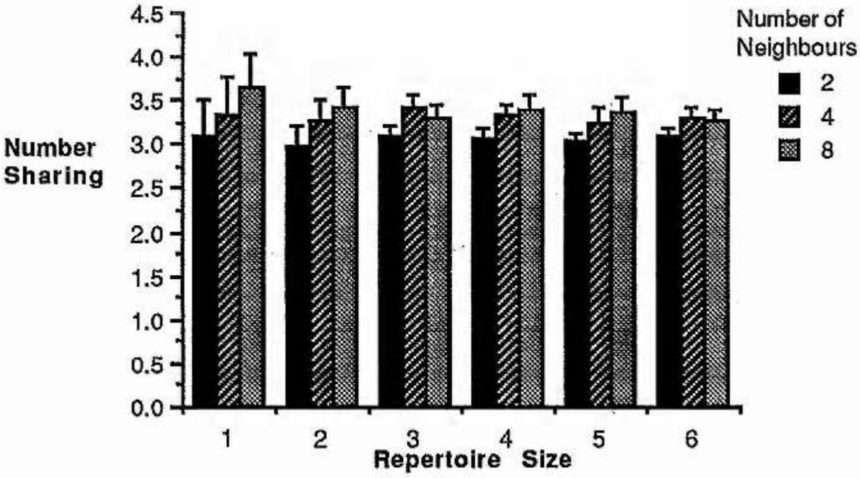


Figure 7.4 Mean number of birds sharing a songtype. Bars are means ± SD.

this particular group of chaffinches was concerned: taking the 36 individuals for which it was reasonably certain that all neighbours were known, the number averaged 4.14 (range: 2-9).

TABLE 7.1

Chi-squared values (Kolmogorov-Smirnov two sample test, 2 d.f.) for comparison of song type frequency distribution in a chaffinch population (studied by Slater *et al* 1980) and that found in simulations. The tests were carried out using one randomly selected run for each combination of repertoire size and number of neighbours.
(* p<.05, ** p<.01)

	Number of Neighbours		
Repertoire Size	2	4	8
1	5.90 NS	4.89 NS	4.65 NS
2	13.28 **	2.71 NS	8.51 *
3	5.96 NS	5.91 NS	4.95 NS
4	6.24 *	5.83 NS	7.19 *
5	10.16 **	4.92 NS	7.50 *
6	9.00 *	5.92 NS	3.97 NS

There was a slight but significant increase in the fragmentation index (Figure 7.5) with number of neighbours ($F_{2,10}$=160.6, p<0.001). However, there was no effect of repertoire size ($F_{5,10}$=0.85, NS), and no interaction ($F_{10,162}$=1.1, NS).

Turning now to the sharing of songs between neighbours, Figure 7.6 shows how repertoire size and number of neighbours affected the proportion of the repertoire shared (Jaccard index). Both larger repertoire size

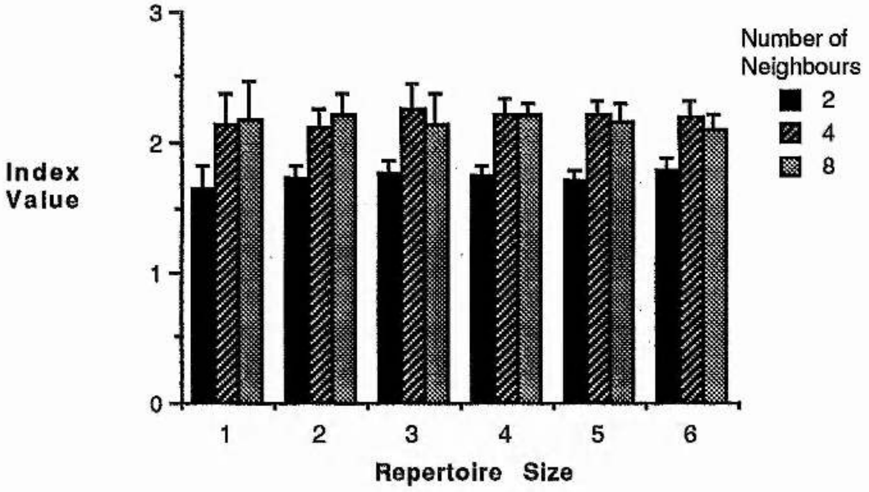


Figure 7.5 Fragmentation index.
Bars are means ± SD.

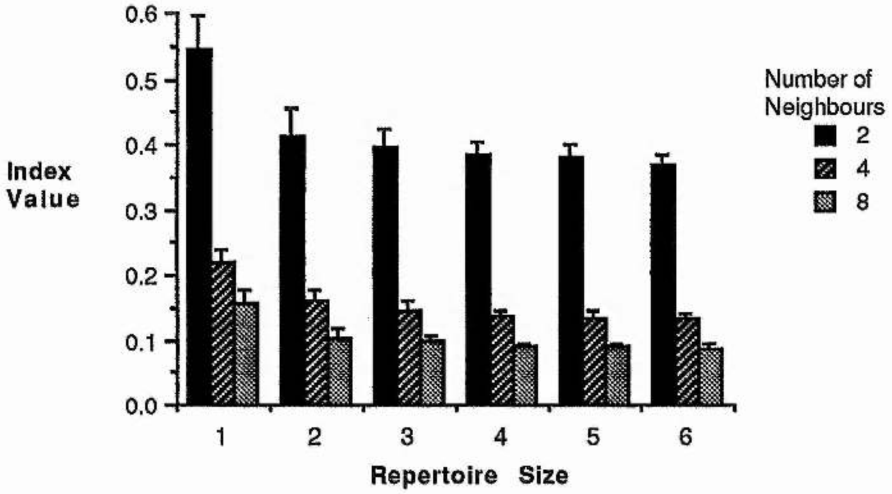


Figure 7.6 Jaccard index.
Bars are means ± SD.

($F_{5,10}=11.3$, $p<0.01$) and more neighbours ($F_{2,10}=362.5$, $p<0.001$) led to a significant reduction in the Jaccard Index. In other words, the larger the repertoire and the more neighbours the lower the proportion of the repertoire that was shared between neighbours. There was a strong interaction between the factors: the effect of number of neighbours was stronger at large repertoire sizes than at small ones ($F_{10,162}=10.1$, $p<0.001$). The results detailed above are summarised in Table 7.2.

TABLE 7.2

Summary of results of simulations with varying numbers of neighbours and repertoire sizes.

	Effect Of Increased	
	Repertoire Size	Number of Neighbours
Mean Song Longevity	Rise	Fall
Number with commonest song	Rise	Rise
Mean number with a song	No change	Rise
Jaccard Index	Fall	Fall
Fragmentation Index	No change	2 low, 4 & 8 higher

Finally, the simulations also illustrate how, as the repertoire size increased, the pattern of sharing of songs between neighbours became more complex. This is shown in Figure 7.7, where the distribution in the population of the six song types possessed by a particular bird are

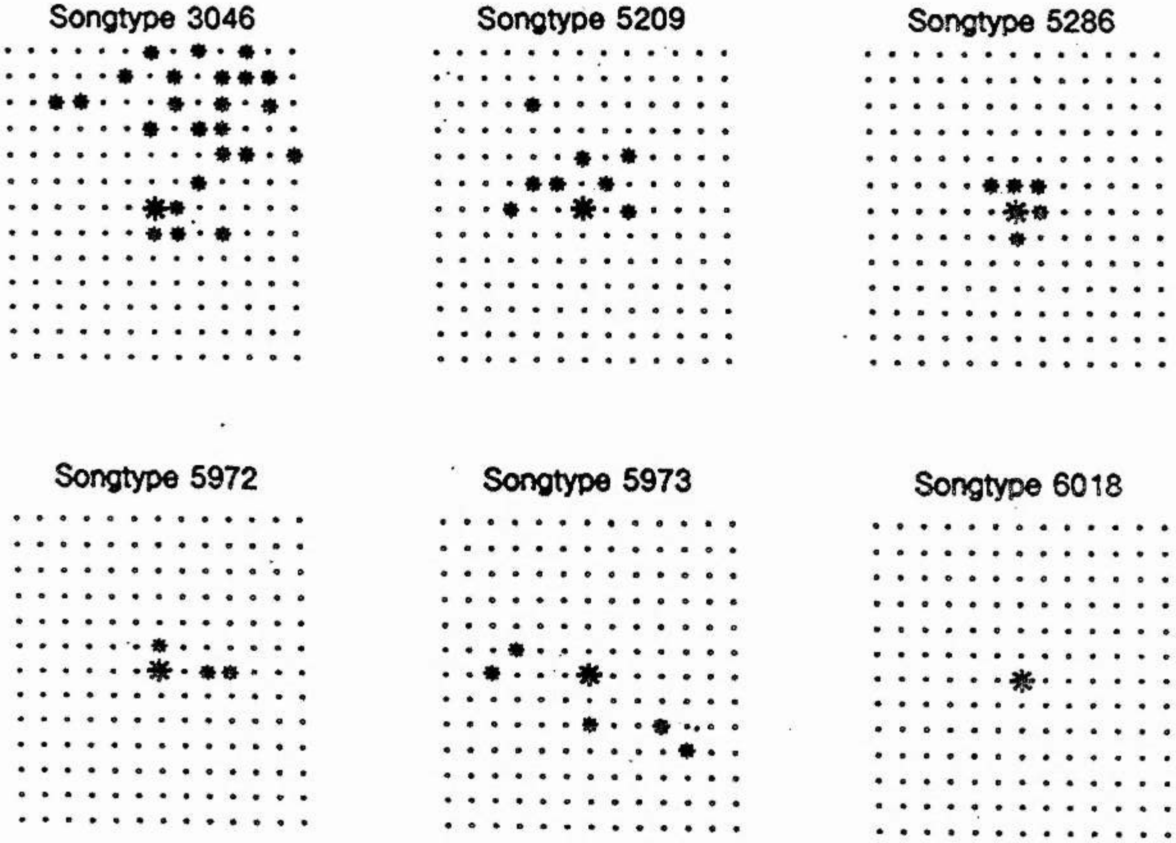


Figure 7.7 Distribution of the six songs in the repertoire of cell 7,7 (large star) to show the complex patterns of sharing between repertoires. Each map is for one song type, with stars indicating cells in which it was found. These data are from a run with a repertoire size of six and with eight neighbours.

illustrated, and suggests that the existence of sharp dialect boundaries between groups of birds in which individuals have a small repertoire size is very unlikely, unless all the song types are learnt as a package. This seems likely for the corn bunting, though McGregor (1980), and McGregor & Thompson (1988) detail a few instances where learning must have been from more than one male.

7.4 *Rules for choosing song tutors*

The simulations by Goodfellow & Slater and those described above suggest that random learning of song types may lead to small groups of birds singing the same song as each other but would not explain cases where large numbers of birds share song features. Using a modified version of the program described above, the effect of different learning conditions on song sharing was investigated.

7.4.1 Methods

The simulations reported above (and by Williams & Slater 1990) used the entire repertoire of each neighbour in the list of possible songs to be learnt. Thus, with a repertoire size of one, and with four neighbours to learn from, the first song chosen was nominally one of four possibilities. However, if any of the songs are shared, then this changes the probability that this song will be learnt. If, for example, song 45 is in the repertoire of three neighbours, but song 67 is only in the repertoire of one, then song 45 has a three times greater probability of being learnt.

The modified program compared this unequal probability of learning a song type with the following alternatives:

(i) Each song has an equal probability of being learnt. This was managed by only adding songs to the list of those which could be learnt if they were not on it already. In this case, with a repertoire size of one, the program would make a random choice between songs 45 and 67, even though three neighbours sang the former and only one the latter.

(ii) Learning the rarest song present; in this case song 67 would be chosen.

(iii) Learning the commonest song; here song 45 would be chosen.

In situations (ii) or (iii), if there was no single rarest or commonest song, then the program made a random choice between the songs which were equally rare or common. To simplify the comparisons being made, all runs of this simulation were carried out with a repertoire size of one and with four neighbours. As before, a 13 x 13 matrix, 15% error rate and 40% mortality rate were used. The simulation was run for 300 years. The simulation was run for longer due to the tendency for the song type used to seed the array persisting past 100 years when the commonest song was being learnt.

Ten runs for each of the learning situations were carried out and analysed with Minitab using one way analyses of variance.

7.4.2 Results

Mean song longevity is low when learning the commonest song, and high when learning the rarest (Figure 7.8). This is probably because it is difficult for a new song to spread into the simulation when the commonest is being learnt, but when the rarest is being learnt, just as a song is about to die out it becomes the rarest, and is therefore likely to be chosen for learning. The differences are significant ($F_{3,36}$=94.04 p<0.001). A Newman-Keuls *post-hoc* test revealed that all pairwise comparisons were signifiantly different (p <0.01).

The maximum number of birds sharing a song type is much larger when the commonest song is learnt (Figure 7.9). The difference is less when the mean numbers shared are compared, but both results were significant: maximum shared $F_{3,36}$=14.07 p<0.001; mean shared $F_{3,36}$=6.94 p=0.001. Newman-Keuls *post-hoc* tests on these results showed that all pairwise comparisons were significant for the mean number of birds sharing a songtype (P <0.01), but that only comparisons with the situation when the commonest song type was learnt were significant (p <0.05) when the maximum number sharing a song type was considered. In line with the pattern of sharing of songs, the proportion of the repertoire shared between neighbours, as measured by the Jaccard index (Figure 7.10), is significantly greater when the commonest song is learnt ($F_{3,36}$=32.24 p<0.001). All pairwise comparisons were significant (Newman-Keuls test, p <0.01).

There is a significant difference in the fragmentation index between the learning situations (Figure 7.11;

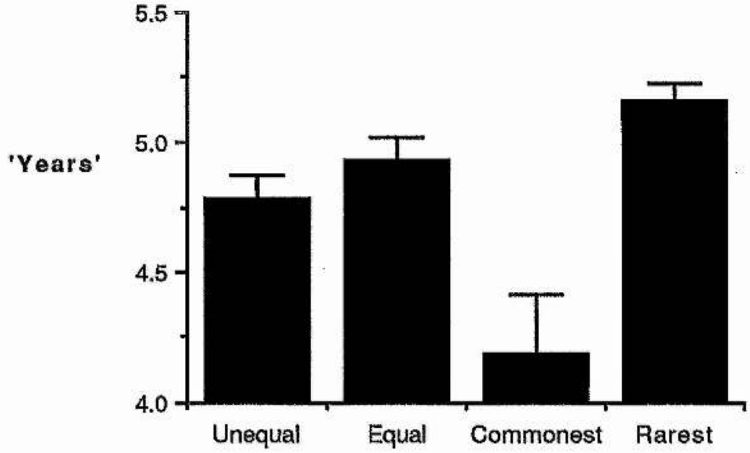


Figure 7.8 Mean song longevity.
Bars are means ± SD.

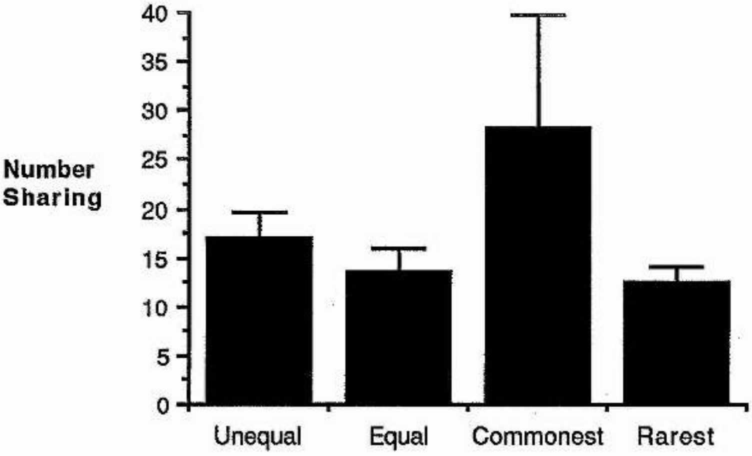


Figure 7.9 Maximum number of birds sharing a song type.
Bars are means ± SD.

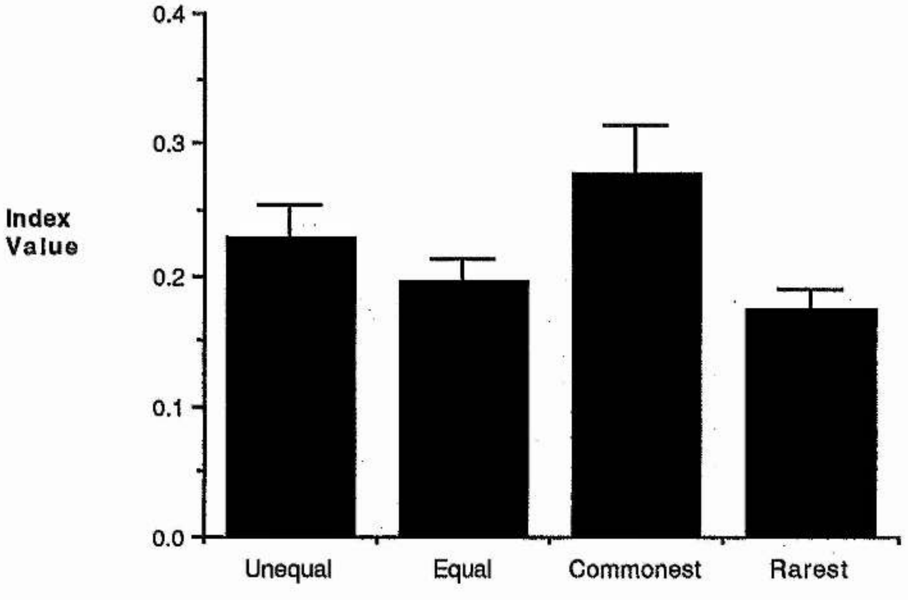


Figure 7.10 Jaccard index.
Bars are means ± SD

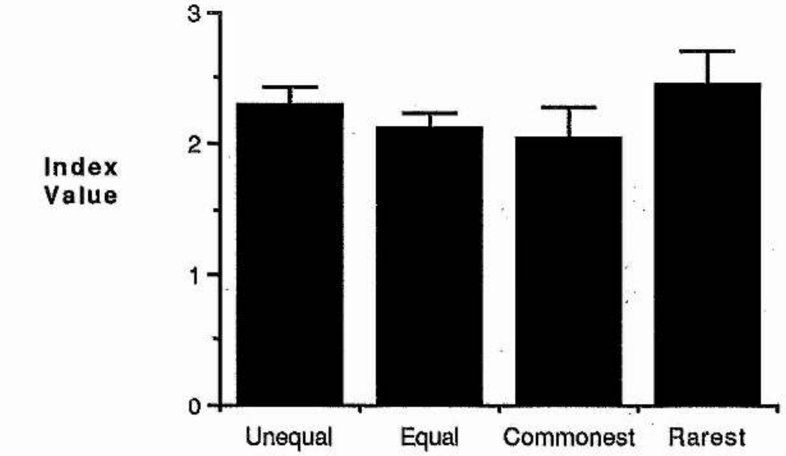


Figure 7.11 Fragmentation index.
Bars are means ± SD.

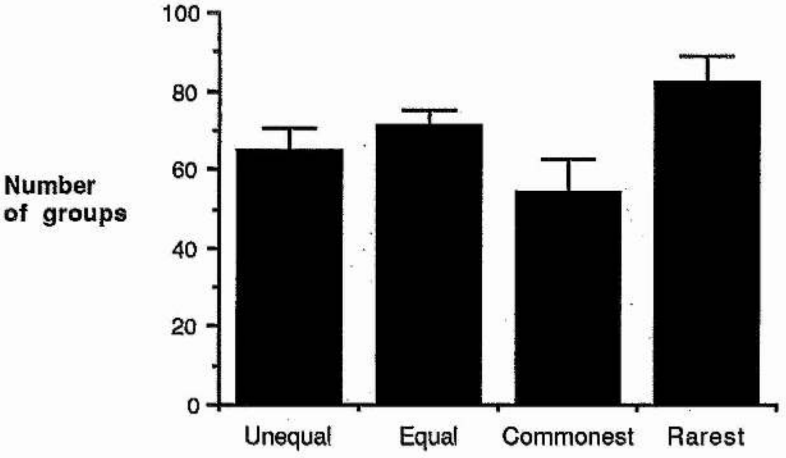


Figure 7.12 Number of groups (of birds sharing song types)
Bars are means ± SD.

$F_{3,36}=9.06$ $p<0.001$). All pairwise comparisons were significant (Newman-Keuls test, $p<0.01$). This may be because there are more groups when the rarest song is being learnt (Figure 7.12, $F_{3,36}=33.37$ $p<0.001$). Newman-Keuls *post-hoc* tests showed that there was a significant difference between the mean group size for the rarest and commonest songs being learnt ($p<0.01$), for the rarest and unequal learning situations ($p<0.05$), and for the equal and commonest leaning situations ($p<0.05$). The other pairwise combinations were not significant.

7.5 Large groups and learning the commonest song

Having found that large groups of birds sharing a single song type could be produced by learning the commonest song type the effect of varying the rate of miscopying while learning the commonest song was investigated. This is comparable to the work that Goodfellow & Slater (1986) did with random learning.

7.5.1 Methods

Ten runs each for mutation rates of 1% and from 2.5% to 25% at 2.5% intervals were performed. A repertoire size of one, and four neighbours to learn from were used. When the commonest song is learnt and the matrix is seeded with all birds singing the same song, that song type can last for a very long time. Therefore, for this investigation of the effect of mutation rate each bird started with a different song type. Since song types had therefore to spread rather than just remain extant it did not matter if any of them persisted for the entire simulation. Nevertheless, runs were over 500 'years' to try as far as possible to ensure that an equilibrium had been reached. In fact, when the mutation rate was very low (1-5%), the song types at the end of the simulation were very often a selection of those present at the start. A 20 x 20 matrix was used to increase the population of birds in anticipation of large groups at low mutation rates.

7.5.2 Results

With a very low mutation rate, very large groups of birds sharing the same song type can occur (Figure 7.13). The maximum number sharing actually approached the number of cells in the matrix for mutation rates of 1%. As suspected from the simulation of different learning conditions, the mean song longevity (which is calculated only for songs which arise during the simulation, not for any of the songs used to seed the matrix, or those extant at the end), is very low for very low mutation rates. This is probably because it is rare that new songs get established when the commonest song type is learnt.

The mean song longevity increases with increasing mutation rate (Figure 7.14), but decreases at rates greater than about 15%. This may be because at mutation rates above this it is difficult for a large group of birds singing the same song type to become established. The mean song longevity is an underestimate of the length of time that songs actually persist for low mutation rates because it does not include those songs which remain extant throughout the simulation.

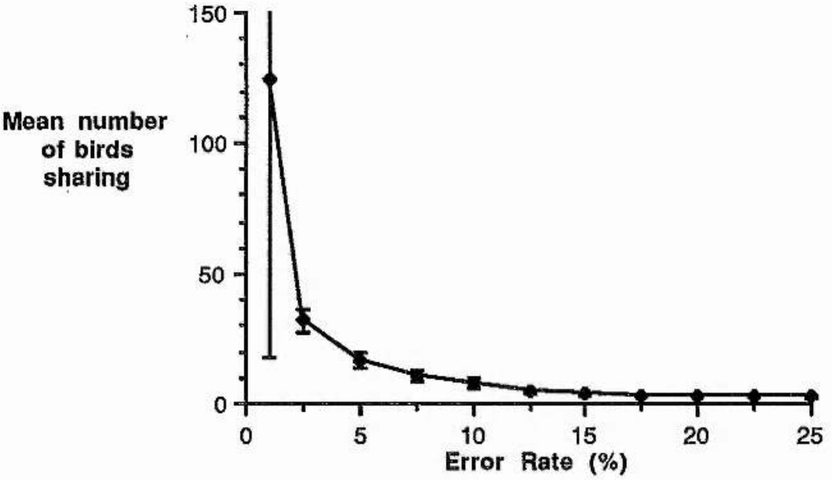


Figure 7.13 Song type sharing when the commonest song type available is learnt. Points are means ± SD.

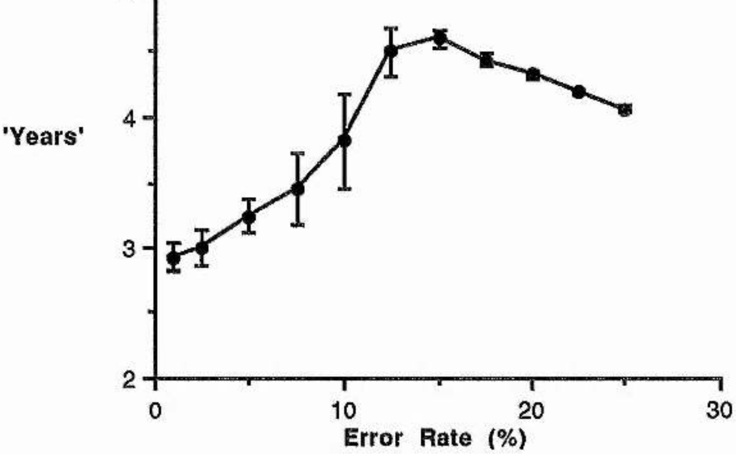


Figure 7.14 Mean song longevity when learning the commonest song type available. Points are means ± SD.

7.6. *Discussion*

The results suggest that both repertoire size and number of neighbours are likely to have strong influences on the distribution of song types in a population. With an increased repertoire size or number of neighbours, more birds in the simulated population were found to share any one song, although the effect of repertoire size on numbers sharing was very slight. A lower proportion of songs were shared between neighbours when repertoire sizes were large, and the amount of sharing was also reduced with more neighbours. Song longevity increased with repertoire size, this presumably being linked to the fact that more birds shared any one song so that individual song types were less prone to extinction. However, songs lasted less long on average in the simulations with more neighbours. This may relate to the fact that birds with more neighbours have more copying options and there are therefore more chances for a particular song to go uncopied and so become extinct.

In general the most unexpected result of the simulations was the magnitude of the effect of the number of neighbours from which a bird can copy on the various results. The simulation assumed that each of a bird's song types has an equal probability of being learnt by a new neighbour. In other words, birds do not preferentially learn particular songs. However, despite this, commoner songs are more likely to be passed on. When a bird 'dies', and a new one then learns from the neighbours around it, the list of possible songs it can learn is the total of the repertoires of those neighbours. Although doubling the number of neighbours can double the number of possible songs that can be learnt, the effect of this will depend upon how many songs are shared between neighbours.

This effect of neighbours is one that may have an influence on song distribution and sharing in the wild. For example, in large areas of continuous habitat birds may commonly have four or more neighbours, whereas in areas where the habitat occurs in strips, such as along hedgerows or streams, the number of neighbours is likely most often to be two. The simulation makes a number of predictions which it may prove possible to test where habitats differ in structure in this way.

The comparison of the data on the frequencies of different chaffinch song types with the distributions generated by the simulations hinted that number of neighbours may influence song type frequencies. The match to the data was generally better with four neighbours than with two or eight, and four neighbours was the most appropriate figure for the population from which the data were collected. On the other hand, comparison with these chaffinch data suggested that repertoire size is unlikely to be important in affecting the frequency of different song types. Although chaffinches average 2-3 songs in their repertoire, there is nothing in the simulations to suggest that variation in this factor might affect the distribution of song types in the population. In other words, there is no suggestion that simulations with realistic repertoire sizes give a better fit to the data than those with greater or smaller ones.

A feature of these simulations is that a new bird was not allowed to learn the same song type twice, even if that type existed in the repertoire of more than one neighbour. Slater (1983a) suggested that chaffinches may sometimes learn the same song type more than once and this may lead the apparent repertoire size to be smaller than the real repertoire size. In various simulations in which the effect of such a possibility was tried, I found that allowing multiple-learning had rather little influence on the results.

Another, more general, point is worth making. The results of these simulations are very much more complex than those reported by Goodfellow & Slater (1986). As soon as birds have repertoire sizes greater than one, and can copy parts of their repertoire from different individuals, the distribution of song types in the population takes on a complex pattern, with overlapping ranges and no sharp boundaries shared by different types. These simulations suggest that this is not because individual song types take on a different distribution where there are repertoires: the fragmentation index used was found not to vary with repertoire size. But, as Figure 7.7 illustrates, the simple fact that the different songs of the same bird may occur with very different frequencies and distributions can lead to complex overlapping patterns. It is thus not surprising that simple mosaic patterns of song distribution have only been described for species with one or two song types. Payne's (1985) work on indigobirds, which have about 23 song types, might seem to contradict this, but the song types were probably transmitted together, making the situation analagous to the one song type case.

These results, as well as making predictions which can be tested on real populations, indicate that both repertoire size and numbers of neighbours may have important consequences for the distribution and persistence of song types. Even relatively simple simulations such as these can lead to complex patterns of song sharing not dissimilar to those found in wild populations of songbirds. In the light of these findings, it seems doubtful whether it is necessary to propose functional explanations for geographical variation in song and for song dialect boundaries (see Wiens 1982, Waser 1985). In cases where many birds share a song type it may, however, be necessary to propose that copying is exceptionally accurate. It may also be necessary to propose that special processes are in operation where groups of birds are separated by sharp dialect boundaries which remain in the same location over long periods of time (see McGregor & Thompson 1988). But, in the white-crowned sparrow, the species over which there has been most controversy, it even appears that the size and location of dialect areas differ depending on which part of the song is used to define them (Baker & Cunningham 1985; Baptista 1985). Given such problems of interpretation, and the complexity of the results discussed above, there is clearly a need for more field data collected over longer periods. At present there is little evidence to suggest that geographical variation in song is other than an epiphenomenon of vocal learning.

In the simulations investigating the effect of imposing a simple rule on the song type to be learnt, only small groups of birds were found to share songs when these are learnt at random from the neighbours surrounding them unless the accuracy of copying is assumed to be extremely high. If the commonest song present amongst neighbours was learnt, rather than one being randomly chosen, then large groups could be formed when copying accuracy was high. The song longevity also depends on the learning conditions.

The results suggest that the number of song types to which birds are exposed and whether or not they follow a simple rule such as 'learn the commonest song' can have a crucial effect upon the distribution of song sharing that is observed. Sharp and stable dialect boundaries are possible if copying is very accurate, as was found by Goodfellow & Slater (1986). Given the controversy over the size and location of white-crowned sparrow dialects, it will be very interesting to discover just how accurate copying between individuals is in this species, and whether they do copy at random or not.

Another interesting data-set on which these simulations may shed light is that on the song sharing of Darwin's medium ground finches (*Geospiza fortis*) on the Galapagos Islands. Gibbs (1990) found that the frequencies of different song types changed during the course of several years. The commonest type became progressively rarer while the other three became more common. It appeared that birds possessing the rarer types both survived longer and had greater breeding success. These results are perplexing, but they do suggest that, in this population, a rule such as 'learn the rarest song' might have some advantage. As has been shown here such a rule could have a dramatic effect on the distribution of songs within the population.

Much remains to be found out, and there is great diversity in the patterns of song sharing in the songbird species that have been studied to date. The data of Gibbs (1990) are exceptional in that they suggest that certain song types may be copied in preference to others. Random copying processes with a low error rate seem able to account for most of the results described for other species. While there may be a diversity of patterns of song distribution in wild populations, these simulations have shown that differences in features such as repertoire size, number of neighbours, accuracy of copying, and how the bird to be learnt from is chosen can all have an impact. The diversity and complexity of song distributions do not necessarily imply diverse and complex underlying mechanisms.

Chapter 8

Computer analysis of bird sounds

This chapter reviews the literature about the use of computers to analyse bird vocalisations as an introduction to the assessment of the dynamic programming algorithm presented in chapter 9.

8.1 Introduction

Early descriptions of bird songs were limited to graphic plots of the relative pitch and duration of notes, or to using onomatopoeic descriptions (for example, Marler 1952, Thorpe & Lade 1961), processes that did not allow detailed and precise comparisons. The invention of the sonagraph (reviewed by Fant 1958 and Hinde 1969) revolutionised the study of vocal communication. It became possible to get a visual representation of the time-frequency structure of a sound, and to measure durations and frequencies accurately (see Marler 1969, and Beecher 1988 for a discussion of the limits of accuracy possible). Real-time spectrum analysers have also made a substantial impact (Hopkins et al 1974, McGregor 1989).

A disadvantage of using sonagrams is that they are complex. Hjorth (1970) suggested that simplified diagrams showing just a line drawing of the shape of the sound, such as those produced by the Melograph Mona, might be more appropriate for some uses. Although sonagraphic analysis is a great improvement on previous qualitative descriptions, early technical limitations impeded some investigations. One way round this was to modify the apparatus. Marler & Isaac (1960) installed a worm gear to their sonagraph's sectioning system so that power spectra could be obtained at 2.5ms intervals, to study shifts of energy within syllables in the song of the chipping sparrow (*Spizella passerina*). However, most users are less adventurous in altering such a complicated machine !

Over the past two decades computers have greatly increased in complexity and versatility and their cost has decreased (in terms of processing power). Indeed, signal processors are now often themselves computers. The latest Kay sonagraph, the DSP 5500 (reviewed by Catchpole 1990), is a very sophisticated microcomputer based sound analysis workstation. It even has the option of an interface to another computer for further analysis.

Techniques for the analysis of animal vocalisations are not as advanced as those for speech, but the use of microcomputers is now standard in many laboratories. Most of the computer programs devised have been application specific. For example, Soucek & Vencl (1975) described programs to calculate the transition probabilities between the syllables used by duetting white-crested jay thrushes (*Garrulax leucolophus patkaicus*). These programs could certainly be used to analyse transition probabilities between other behavioural events, however, the problems posed by one species often differ markedly from those of another. Unless programs are written in a very generalised form they are unlikely to be easily translated between species.

8.2 Fourier Analysis

Converting the sounds recorded on magnetic tape into a format that a computer can process requires the use of an analogue to digital (AD) converter. The sampling rate needs to be more than twice the maximum frequency the researcher is interested in (Nyquist's theorem). Thus, to analyse frequencies up to 16kHz, a sampling rate of greater than 32kHz is required. Failure to sample fast enough results in aliasing, whereby high frequency oscillations appear to be at lower frequencies because many of the peaks and troughs of the original signal are missed. After the signal has been digitised it is subjected to a discrete fast Fourier transformation (FFT) to resolve the frequency-time structure of the signal. Many computer packages and programming libraries contain algorithms for calculating FFTs, and the method has been well described in the literature (for example, Stanley & Peterson 1978, Gibson & McCabe 1981, Eddy & Bremner 1983, Kaplan 1983, Yost et al 1983).

FFT analysis was used by Zoloth et al (1980) and Clark et al (1983) to analyse and synthetise bird vocalisations, and by Goedeking (1983) to describe amplitude and frequency modulation in the calls of cotton-top tamarins (*Saguinus oedipus*). A related technique, that of zero-crossing analysis, has been used by some authors (for example, Scarr 1968, Staddon et al 1978, West & King 1986). At a time when FFT analysis was limited by hardware processing speeds this method provided a more rapid method of displaying frequency information than a sonagraph, but, with modern real-time methods, the technique has probably been superseded.

Fourier analysis is used to produce sonagrams. Several computer systems, varying widely in complexity and price, have been developed as alternatives to the sonagraph. Watts (1989) described a simple and inexpensive personal computer based sonagram system. Fast complex systems which can manipulate sounds for statistical analysis and sound synthesis have been produced by Clark et al (1987) and Richard (1991).

The synthesis of vocalisations, either *de novo*, or by modification of recordings from animals, is of obvious use in behavioural experiments. Playback tapes can be prepared from sampled sounds, cutting and pasting them together to form a sequence of stimuli within the computer's memory. The digitisation is then reversed (by applying an inverse FFT, and using a digital to analogue converter) and the resultant sound(s) are recorded on tape. This is likely to be more precise than dubbing. Many authors have used computers to synthetise sounds (for example, Aubin & Bremond 1983, Dabelsteen & Pedersen 1985a, b, and Weary et al 1986). These can then be used to investigate the effect of making small changes in a signal in a reliable fashion. The logical extension of this kind of experiment, whereby a computer is made to produce sounds in an interactive fashion, its output depending on the response given by the subject, is being developed (Bremond & Aubin 1989, Dabelsteen & Pedersen in press a, b). An alternative synthesis method, modulation analysis, was described by Dörrscheidt (1978).

8.3 Comparisons of Sounds

In many studies it is of value to arrive at an estimate of how similar sounds are to each other. This is often done by visually comparing sonagrams. Whilst the human brain is probably the best apparatus currently available for such work, the repeatability and objectivity of comparisons made in this way are frequently questioned.

To get round such problems, Bertram (1970) copied Indian hill mynah (*Gracula religiosa*) syllables from sonagrams onto a squared tracing paper grid, aligned traces to give the best fit along the time axis by eye, and then used the number of matching and non-matching squares to form a difference index. Grid overlays and coding techniques were also used by Koeppl et al (1978) and Miller (1979), in these cases in conjunction with multivariate statistical analysis. The application of multivariate techniques to the study of avian vocalisations was reviewed by Sparling & Williams (1978, but see the critique by Martindale 1980). By their very nature multivariate statistics involve the laborious task of taking many measurements before comparison. It would be better if a computer could be used for as much of the analysis as possible: for example, by digitising the sounds, filtering out background noise, and classifying the songs.

As Field (1976) points out, digitising sonagrams by hand is a slow business, and the use of a digitising tablet can speed the process up, as well as making it more accurate and repeatable. Though the use of an AD converter and FFT analysis is faster still, requiring the user to do little more than sample a section of tape, most recordings are, as a result of background noise, far from ideal. A digitising tablet and the human brain enable the user to capture just the part of the signal that is important to them. Chabot (1988) for example, used a digitising tablet and grid to trace the use of 16 frequencies on a logarithmic scale from sonagrams of the calls of humpback whales (*Megaptera novaeangliae*). The matrices produced were compared using the Jaccard similarity coefficient.

A slightly different approach was used by Pickstock et al (1980) who digitised sonagrams with an image analysis system, and compared the terminal flourish of chaffinch (*Fringilla coelebs*) songs by computing an index based on the area and length of perimeter of the shapes. A problem with grid based methods is deciding upon the grid size to be used; too coarse a grid will omit possibly important data, yet too fine a grid will result in redundant information.

A criticism levelled at much work on comparing sounds is that the form of a signal may not be fully described by individual measured features. For this reason, Clark et al (1987), after digitising swamp sparrow (*Melospiza georgiana*) songs with an AD conversion and FFT analysis, computed similarity values by cross correlating matrices as they were moved against each other along the time axis; the maximum correlation was the value used. A program to identify the constant and variable parts of syllables by averaging a set of sounds was also developed.

One of the difficulties with comparing sounds is that two copies of the same syllable may have subtle differences; they may vary in duration, frequency or in both dimensions simultaneously. Clark et al (1987) aligned their matrices to the best fit on the frequency axis before cross correlating on the time axis, but this method would not cope with slurring. Similarity indices suffer from the problem of comparisons of indices calculated from sets of matrices of different sizes. In addition, it is difficult to decide if weighting should be attached to the dimensions involved, particularly if information about the amplitude of the signal is included in the comparison.

Pattern recognition methods seem a promising approach to solving the problem of comparing disparate shapes. Many authors have used a variety of algorithms for computerised recognition of handwriting (for example, Fujimoto et al 1976, Burr 1980b, Mori & Masuda 1980, El-Wakil & Shoukry 1989, Cheng et al 1989, Plamondon & Lorette 1989). An example technique is elastic matching, which uses calculations of the amount of stretch needed to map shapes onto each other by matching points in an iterative fashion (Burr 1980a). Similar techniques could be applied to deciding if a syllable came from a library of known shapes. If a threshold similarity was not reached, the syllable could be either rejected, or the library expanded.

Another application is sequence comparison, to determine how similar sets of songs are. Bradley & Bradley (1983) used time warping to compare sequences in the songs of the savannah sparrow (*Passerculus sandwichensis beldingi*). The calculations involved finding the minimum change needed (by insertion, deletion and substitution of elements on the time axis) to match the sequences.

8.4 Conclusion

The methods used for analysing bird songs have come a long way since the invention of the sonagraph, and much work is in progress to further improve analytical techniques. Systems under development include those which will allow the automatic identification and measurement of the note structure of songs (Pavan 1988, Manzi et al 1988) and compensation for the influence of background noise by analysis of the amplitude functions of acoustic signals (Dabelsteen et al 1989, T. Dabelsteen pers. comm.). In addition, digital sound recordings are likely to become widely used (see Menne 1989 and Stoddard 1990 for reviews of techniques and equipment).

The techniques described require much computer time and memory. However, personal computers are now very powerful and can be used for applications which would have required a mainframe just a few years ago. Given the advances already made, and the possibilities that pattern recognition methods promise, objectively classifying and comparing sounds may soon be a practical proposition.

Chapter 9

Objective comparisons of song syllables: a dynamic programming approach

9.1 Introduction

Numerous approaches have been used to make the comparison of sounds objective. These methods are often time consuming and most researchers prefer to compare shapes of syllables on sonagrams by eye. Whilst the human brain is probably the best shape comparison tool currently available, the subjectivity of different observers and reliability of repeated comparisons are open to question.

Grid based methods have been used to calculate similarity indices and as a basis for multivariate statistics (Bertram 1970, Koeppl *et al* 1978, Miller 1979, Chabot 1988). Image analysis was used by Pickstock *et al* (1980), and Clark *et al* (1987) used cross-correlation to find the maximal similarity between two elements. All these techniques suffer from limitations (Williams & Slater in press), principally that subtle differences may occur in both the time and frequency dimensions, and that to compare shapes accurately the whole of the shape should be used, not just a subset of measured features.

A somewhat different approach is to use techniques derived for pattern recognition. A variety of algorithms have been used for shape comparison, for example in the fields of character and handwriting recognition (reviewed by Mori & Masuda 1980, Plamonden & Lorette 1989). These methods are often complex both mathematically, and in the computational resources required. Somewhat simpler methods may be adequate for the comparison of simple song elements and syllables from sonagrams.

Dynamic Programming (also called time warping) is commonly used for such tasks as word recognition and speech analysis (Sankoff & Kruskal 1983, Russell *et al* 1986). The basic algorithm works in one dimension, and is a technique which compares sequences by calculating a 'distance' between them. The algorithm can be interpreted in several ways (e.g. Sakoe & Chiba 1979) and extensions to the two-dimensional and n-dimensional cases have been made (Moore 1979) but these involve much more processing, and are therefore slow. It might seem that dynamic programming is an inappropriate technique to compare two dimensional shapes. However, if they can be converted to a one dimensional sequence (of some alphabet of primitives) the technique becomes applicable. Its attraction is that it has a good mathematical background, and can be defined with a short recursive equation. It is therefore simple to implement.

The technique is also called time-warping because in speech analysis the waveforms of two sounds are matched by stretching and compressing the time axis. The waveforms may be smoothed in some fashion, for example by filtering to remove background noise, before the comparisons take place. The application below applies the technique in a somewhat different (and less complicated) manner. Rather than directly comparing two sounds, digitisations of the shapes of syllables are made from sonagrams, and it is the sequence of directions traced round pairs of shapes which are compared.

9.2 The dynamic programming algorithm

The measure of distance calculated by dynamic programming is a function of the number of insertions, deletions and substitutions needed to convert one sequence (**a**), into another (*b*). Each operation is assigned a cost, and it is the sum of these costs which forms the calculated difference between the sequences. The object of the method is to minimise the overall cost. The algorithm below is (with minor modifications) that used by Bradley & Bradley (1983) to calculate differences between sequences of notes in the songs of the savannah sparrow (*Passer sandwichensis beldingii*)

The initial conditions imply that a pseudo-element is added to the start of each sequence, to provide a start point for the calculations. If more than one element is inserted or deleted at the same time, then the cost applied is the sum of the costs of inserting or deleting the individual elements.

Calculations are performed in a two dimensional matrix (Figure 9.1). The distance between subsequences is found for each matrix cell from cell (0,0) to cell (n,m). The algorithm operates by finding the portions of the sequences which are possible matches and the minimum cost to link these sebsequences. Since the algorithm calculates a complete pairwise comparison of elements in the sequences, the optimum alignment of the two sequences will be found.

The total distance calculated depends on the lengths of the two sequences compared. The overall similarity value calculated must therefore be normalised by dividing it by the sum of the lengths of the two sequences.

The algorithm is described recursively :

$$S^{\boldsymbol{ab}} = \frac{D^{\boldsymbol{a}\,\boldsymbol{b}}_{n\,m}}{n + m}$$

Where :

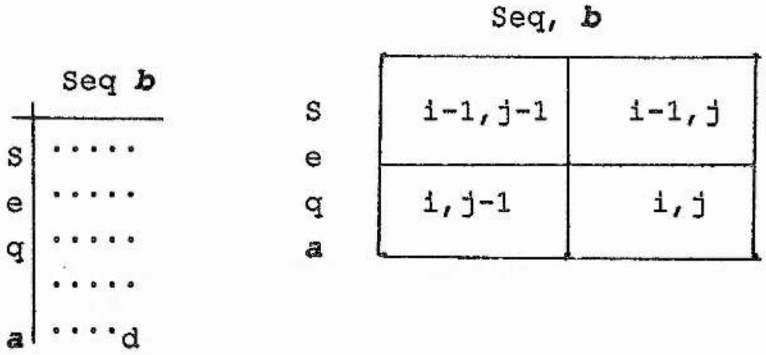
$S^{\mathbf{ab}}$ = the overall similarity of sequences $\boldsymbol{a}$ and $\boldsymbol{b}$,
$D^{\boldsymbol{a}\,\boldsymbol{b}}_{i\,j}$ = the distance between subsequences $\boldsymbol{a}_i$ and $\boldsymbol{b}_j$,

$$= \quad \text{Minimum} \quad \begin{bmatrix} D(\boldsymbol{a}_i,\boldsymbol{b}_{j-1}) & + \text{Ins}(j), \\ D(\boldsymbol{a}_{i-1},\boldsymbol{b}_j) & + \text{Del}(i), \\ D(\boldsymbol{a}_{i-1},\boldsymbol{b}_{j-1}) & + \text{Sub}(i,j) \end{bmatrix}$$

$$i = 1,2,\ ..\ n$$
$$j = 1,2,\ ..\ m$$

$\boldsymbol{a}_i$ = the subsequence $\boldsymbol{a}_1 \ldots \boldsymbol{a}_i$,
$\boldsymbol{b}_j$ = the subsequence $\boldsymbol{b}_1 \ldots \boldsymbol{b}_j$,
n = the length of sequence $\boldsymbol{a}$,
m = the length of sequence $\boldsymbol{b}$,
Ins(j) = cost of inserting element j of sequence $\boldsymbol{b}$ into sequence $\boldsymbol{a}$,
Del(i) = cost of deleting element i of sequence $\boldsymbol{a}$,
Sub(i,j) = cost of substituting element i of sequence $\boldsymbol{a}$ with element j of sequence $\boldsymbol{b}$,

With initial conditions :
$S(\boldsymbol{a}_0,\boldsymbol{b}_0) = 0$
$S(\boldsymbol{a}_0,\boldsymbol{b}_j) = \text{Sum}[\ \text{Ins}(j_k)\ ], \quad k = 1,2,\ ..\ j$
$S(\boldsymbol{a}_i,\boldsymbol{b}_0) = \text{Sum}[\ \text{Del}(i_k)\ ], \quad k = 1,2,\ ..\ i$



(A) (B)

Figure 9.1. (A) The matrix used for calculations. The matrix cells (˙) contain the cumulative distance to that point and (d) is the total distance between the sequences. (B) The distance to cell (i,j) of the matrix is found by taking the values for its predecessor cells [(i,j-1), (i-1,j), (i-1,j-1)] and finding which of the three terms below is the minimum.

1) the value in cell (i, j-1) + the cost of inserting element j from sequence ***b***.
2) the value in cell (i-1, j) + the cost of deleting element i of sequence ***a***.
3) the value in cell (i-1, j-1) + the cost of substituting element i in sequence ***a*** with element j of sequence ***b***.

9.3 Methods

To assess the technique, 17 elements of four different shapes (as assessed by eye) were digitised three times each from sonagrams of chaffinch (*Fringilla coelebs*) songs from sonagrams of chaffinch (*Fringilla coelebs*) songs prepared on a Kay Elemetrics 7800 Digital Sonagraph. The shapes were traced with a Cherry Mk III graphics pad connected to a Zenith 159-13 personal computer controlled by a Turbo Pascal 4 program. Points digitised with this graphics tablet have a definition of $^1/_{10}$th mm. Since this is unreasonably accurate, coordinates were divided by a factor of 10. This also facilitated plotting them on the computer's screen. The digitisation produces a sequence of points which together trace the outline of the shape (Figure 9.2). The program then calculates the orientation of the lines connecting adjacent points, and converts these to a linear sequence of codes based on those proposed by Freeman (1961).

The codes (Figure 9.3) have been reinterpreted here to mean a line in a particular orientation (Figure 9.4). The space around a point is envisaged as divided into a number of segments, the width of which depends upon the number of codes. Codes of 0-7 produce segments of 45°; i.e. $\pm 22.5^{\circ}$ to the vertices and diagonals. This may seem large, but is all that is needed if the next point is immediately adjacent. Smaller segments could also be used, with concomitantly more codes.

Freeman's codes were used to describe and compare handwritten characters by Fujimoto *et al* (1976) and El-Wakil & Shoukry (1989). A possible criticism of the method is that the length as well as the orientation of the lines between points may be important. This can be overcome by converting each line into a series of standard length

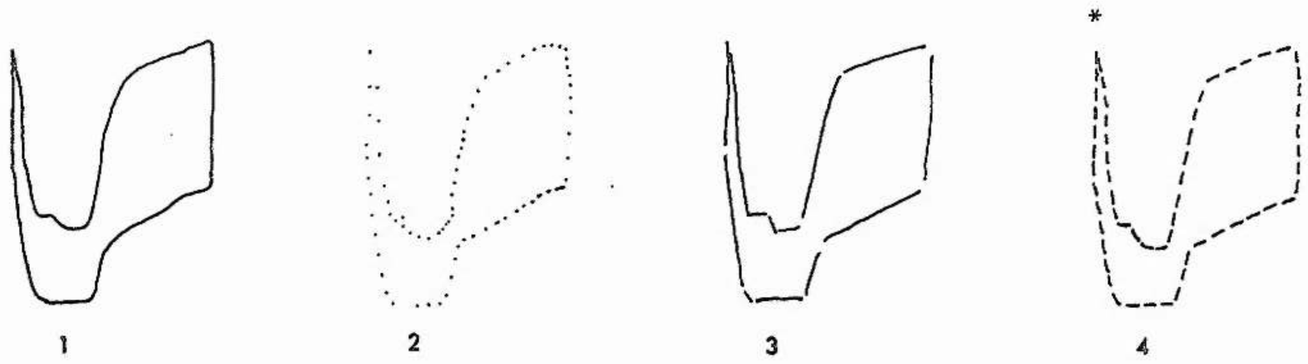


Figure 9.2 How the program works.
A shape (1) is traced on the graphics tablet to produce a dot image (2).
The dots are joined to produce lines in the same orientation (3).
The lines are then split into vectors of unit length (4) which are coded as shown in Figures 9.3 and 9.4. Starting at *, using codes of 0-7, and moving in a clockwise direction, this shape would be coded as:
666666666070022222222111116666666655555566644422222222222222

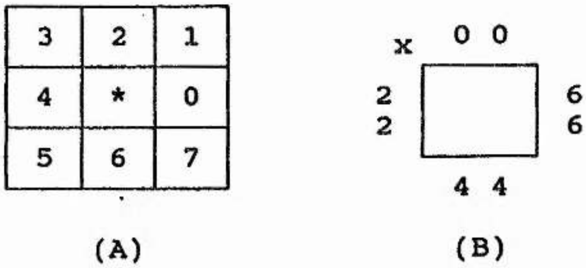


Figure 9.3. (A) Codes devised by Freeman (1961) to enable a compact description of line drawings by the position of the next pixel. From the current pixel (*), the next one is given by the direction moved; (B) this square would be coded 00664422 if coding is in a clockwise direction (starting at x).

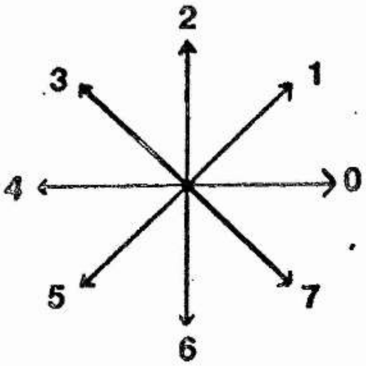


Figure 9.4 Freeman's codes interpreted as vectors of uniform length.

sections of the same orientation. The length aspect is then covered by the number of sections. The length used for each section was 1mm, since this is the smallest accuracy allowed if the coordinates digitised are divided by a factor of 10. The sequences of vectors of unit length can be compared by dynamic programming.

The value of the distance metric calculated is obviously very dependent upon the values set for the insertion, deletion and substitution operations. In order that the difference between different sequences is greater than zero (non-negative property) all costs must be greater than or equal to zero. Since the comparisons made are between sections of lines of unit length, the difference between them should be based on the difference in their orientation. The substitution costs are therefore calculated as (1). This calculation also fulfills the requirement that if the sequences are the same the overall distance between them will be zero (zero property).

(1) $\mathrm{Sub}(i,j) = |v_i - v_j|$ if $\mathrm{Sub}(i,j) <= \mathrm{halfseg}$
or $\mathrm{segments} - |v_i - v_j|$ if $\mathrm{Sub}(i,j) > \mathrm{halfseg}$

where v_i and v_j are the orientations of the i^{th} and j^{th} elements from sequences $\boldsymbol{a}$ and $\boldsymbol{b}$ respectively; segments is the number of codes (e.g. 8), and halfseg is segments / 2.

The symmetry property (that $D(\boldsymbol{a},\boldsymbol{b}) = D(\boldsymbol{b},\boldsymbol{a})$) requires that the insertion and deletion costs for an element are the same. This does not however mean that all elements need to have the same insertion, deletion, or substitution costs. Since substitution is often viewed as the combination of insertion and deletion, the substitution cost is often set to be greater than or equal to the combined costs of insertion and deletion. However, as a greater change of direction should cost more than a small one, setting the insertion and deletion costs relative to the substitution cost is inappropriate.

Whilst testing the program it was decided to allow insertion of an element only if it was the same as the previous element in sequence ***b***, and deletion only if it was the same as the last element in sequence ***a***. This was achieved by setting the insertion and deletion costs to be a nominal cost (= 1) for cases where the condition was true, and the cost to be greater than the substitution cost where the condition was not met. This forces the value calculated for a matrix cell in the minimisation to be the substitution unless an element is repeated in one of the sequences being compared. In addition, to calculate the insertion and deletion costs of several elements together, and thereby fill the first column and row of the calculation matrix, the cost of inserting or deleting elements at the start of a sequence was set equal to 1. Whether the triangle inequality (D(***a***,***b***) + D(***b***,***c***) _ D(***a***,***c***)) is met is crucially dependent upon the relative costs of insertion, deletion and substitution, and it is likely that it will not work if the symmetry property is violated.

The codes formed for the line sections will depend upon the start point of the digitisation, direction of shape tracing, and the size of the image. It is therefore essential to compare sonagrams prepared on the same scale, and to ensure that a consistant start point is used for all shapes. All the shapes described below were digitised from sonagrams with a 2.56 second timebase, and 0-8kHz frequency range. The start point of digitisation was taken to be that nearest the start of the sonagram, or if the shape began with a vertical line the start point was the top of that line. The start point was thus the top left of the shape, and points were captured in a clockwise direction. It is also important to compare sequences prepared with the same set of codes. For the first three analyses below codes of 0-7 were used.

The 17 shapes digitised consisted of four examples of each of four shape classes (Figure 9.5), plus an extra example of the downslur class. Two of the shape classes chosen were from the trill part of chaffinch song; (i) a downslur, and (ii) a chevron; the other two classes were chosen from the endphrase part; (iii) an ovoid, and (iv) a down and up slurred shape.

9.4 Analyses

(1) The difference between the first and second, and the first and third digitisations of each example shape was calculated for 16 elements (excluding the extra example of the downslur class). The difference between the second and third repetitions was not calculated as it will not be independent if the triangle inequalty condition is met. The data were analysed with a two way ANOVA for each shape class, with replicates as a fixed factor, and shape example a random factor.

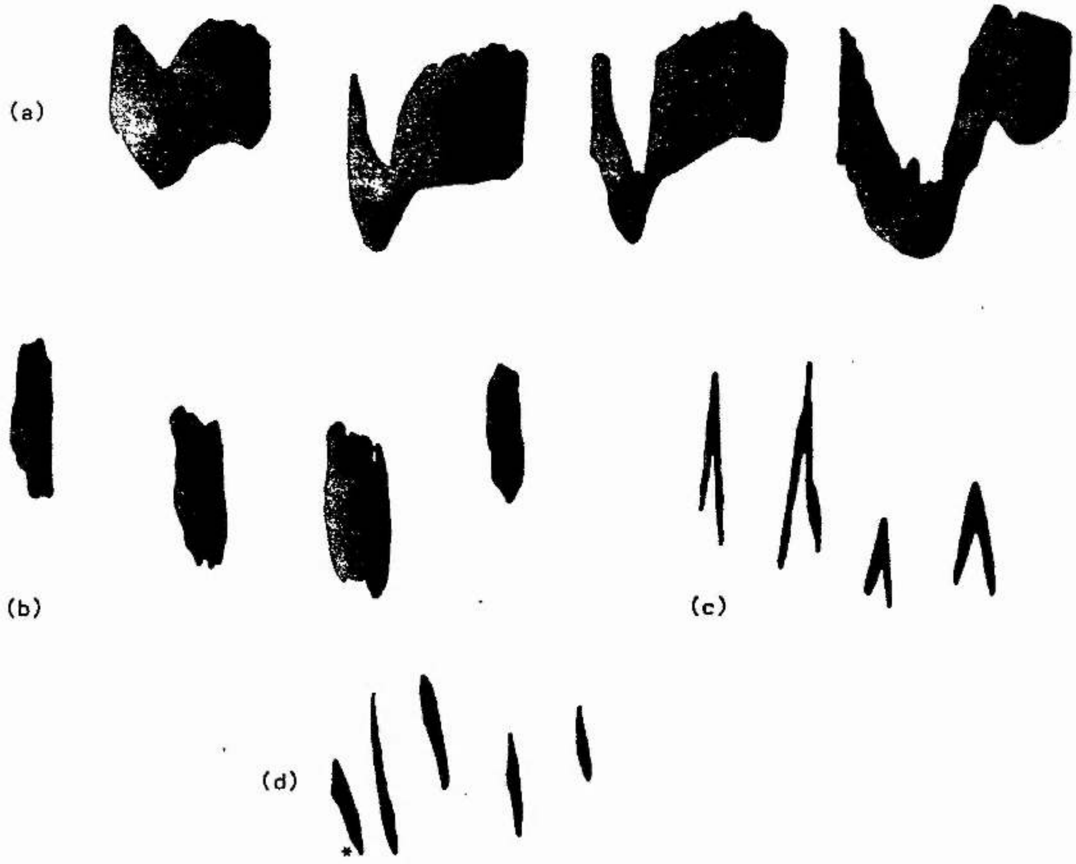


Figure 9.5 Shapes digitised to test the program.
The shape classes are: (a) down and up slur,
(b) ovoid,
(c) chevron,
(d) downslur.
The shape marked * was compared with the othrs.

(2) The first digitisation of the further example of the downslur class was compared with the first digitisation of the other 16 elements, to find if a shape could be identified. The data were analysed with a one way ANOVA on shape class. The downslur was chosen to compare with the others as it is the type with the most in common with the other shape classes.

(3) Repeatability of results was tested by repeating the second analysis with the two other digitisations of the same downslur. Each digitisation of the extra downslur was compared to each set of digitised shapes. The data were analysed with a three way ANOVA with shape set, digitisation and shape class as fixed factors.

(4) To test the effect of using different numbers of codes to describe the shapes, the stored coordinates for the first digitisation of each shape were reprocessed (with a subsidiary program) to produce descriptions with 16, 24, 32, 48, and 64 codes. For each set of codes the first digitisation of the extra example of the downslur class was compared with the first digitisation of the other shapes, and these data compared with those obtained when using 8 codes. A two way ANOVA was used, with both number of codes and shape class as fixed factors.

9.5 Results

The difference between the first digitisation and the second and third was not significant for each shape class (Ovoid $F_{1,3}$=1.25, p=0.345; Down-up $F_{1,3}$=1.71, p=0.282; Chevron $F_{1,3}$=0.43, p=0.559; Downslur $F_{1,3}$=3.23, p=0.170).

The differences between examples within each class were also not significant (Ovoid $F_{3,3}=8.84$, $p=0.053$; Down-up $F_{3,3}=3.86$, $p=0.148$; Chevron $F_{3,3}=8.30$, $p=0.058$; Downslur $F_{3,3}=2.51$, $p=0.235$). These statistics imply that a consistent distance is calculated when examples of the same shape are compared, and that individual elements can thus be digitised in a repeatable manner.

A highly significant difference was found when the downslur shape was compared with each of the 16 others in four classes ($F_{3,12}=17.10$, $p<0.001$). The mean normalised distance was smallest for the downslur shape class (Figure 9.6). All the differences between the mean distances for each group were significant with a Newman Keuls test at the $p<0.01$ level, except for the comparison between the downslur shape class and the ovoid shape class, which was significant at the $p<0.05$ level. This is a restricted test, but it indicates that identification of shapes is possible with the technique. It is reassuring that the distances calculated are the least for the shapes which were classified as the most similar by eye (i.e. the other members of the downslur shape class), and that a significant difference between all the shape classes was found.

The pattern of smallest mean distance for the downslur class was repeated when the effect of repeated digitisations was investigated. Shape class was significant ($F_{3,108}=175.07$, $p<0.001$), but neither the main effects of digitisation ($F_{2,108}=1.25$, $p=0.290$) or shape set ($F_{2,108}=0.86$, $p=0.427$), nor any of the interactions were

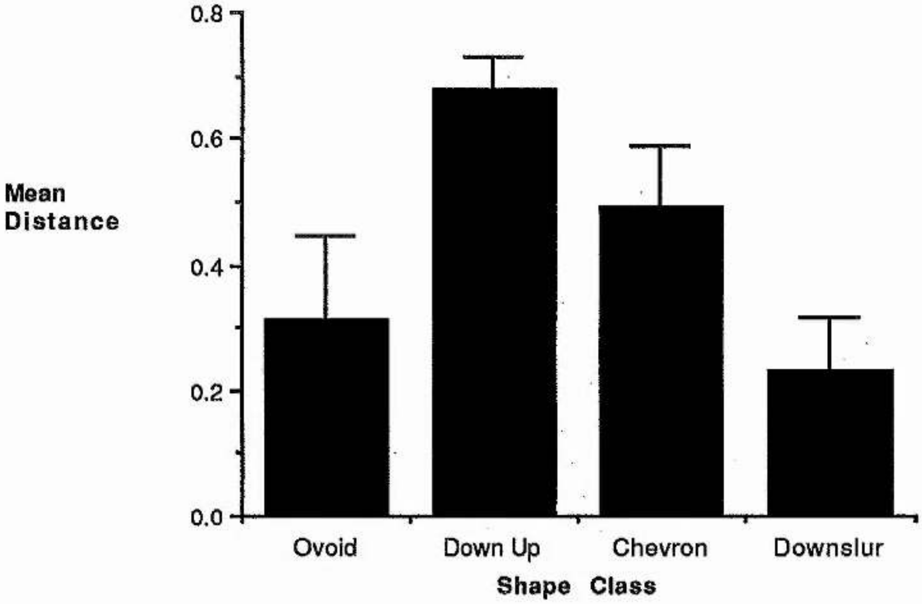


Figure 9.6 Mean distance between a member of the downslur class and other shapes. Bars are means ± SD.

significant (shape class * digitisation $F_{6,108}=0.23$, $p=0.966$; shape class * shape set $F_{6,108}=0.31$, $p=0.932$; digitisation * repeat $F_{4,108}=0.01$, $p=1.0$; shape class * shape set * digitisation $F_{12,108}=0.01$, $p=1.0$). This suggests that a consistent discrimination between a shape and others is possible.

There was a very significant effect of both shape class ($F_{3,15}=121.61$, $p<0.001$) and number of codes ($F_{5,15}=130.16$, $p<0.001$), but no significant interaction ($F_{15,72}=1.30$, $p=0.228$) when the effect of number of codes was assessed. As with the second analysis, the mean distance calculated for the downslur shape class is the least, and this is consistent across the different sets of codes (Figure 9.7). As the maximum number of codes allowed increases, the distances calculated increase. This is expected as finer discrimination should occur with smaller segments. However, the distances calculated are based on the differences in orientation, and further work on a series of degraded shapes and number of codes would be needed to find if the results are the effect of discrimination or purely the result of larger differences between the coded values.

9.6 Discussion

These results suggest that dynamic programming is a potentially useful technique to compare shapes digitised from sonagrams objectively and repeatably. Individual elements can be digitised in a repeatable manner. The mean distance calculated when comparing a further member of the

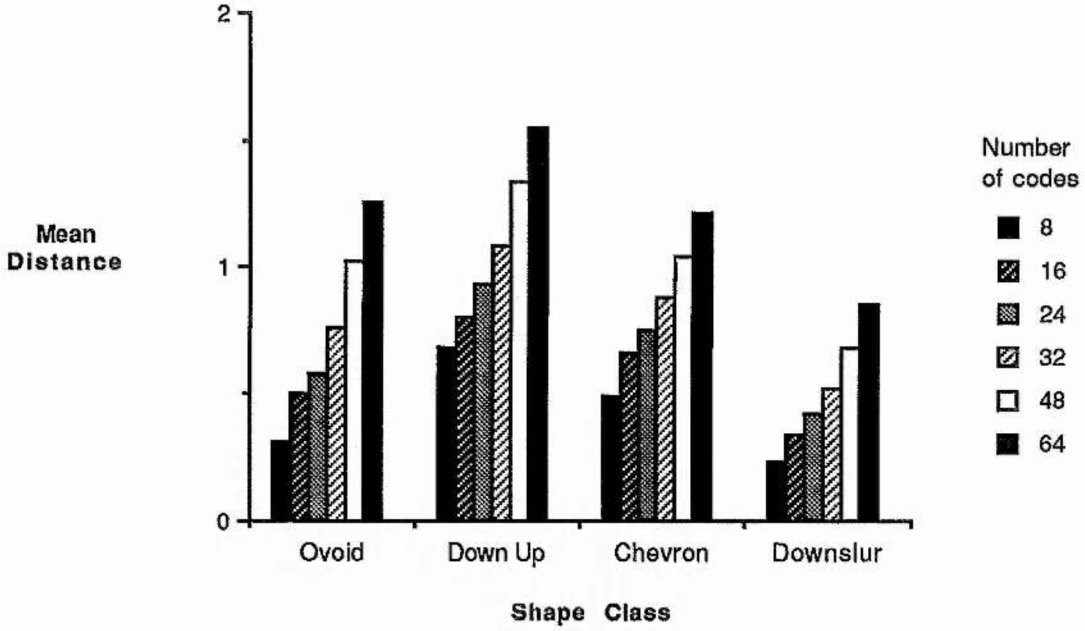


Figure 9.7 Effect of comparing shapes with different numbers of codes. Bars are means.

downslur class with four examples of each of four shape classes was found; the minimum distance was consistently to other members of the same shape class. This effect was found across both repeated digitisations, and when comparisons were made with different numbers of codes.

It might be suggested that the orientation of standard length vectors should be used rather than converting them to a series of codes, but codes allow smoothing of minor differences of direction in the outlines of the shapes traced. The amount of smoothing allowed can be controlled by the unit length chosen, and the number of codes used to describe the shape. Since the discrimination between shape classes occurred at all scales it may be that it is not necessary to be over accurate in the angles used, and that converting shapes to a series of codes between 0 and 7 is sufficient.

The consistent identification of a shape as a member of the same general class implies that it may be possible to set up a library of examples of shapes. Sounds could be identified by categorising them with that to which they showed the minimum distance after comparison with each of the examples. It might be necessary to set a threshold value above which a digitised element had to be placed in a new class rather than identified with a pre-existing one. Dynamic programming could also be used after elements were identified to find if sequences of elements, such as song types, were the same, as advocated by Bradley & Bradley (1983), who tried several methods to identify sequences of notes sung by the savannah sparrow.

The system implemented here suffers from several limitations. That it can only compare shapes digitised on the same scale is relatively trivial, though it might be a problem if a library of shapes was envisaged. This could be overcome by transforming all shapes to a particular size (e.g. 200 x 200 pixels), and normalisation of size would also have the advantage that averaging of shapes could be performed. Since the coordinates digitised are stored, the requirement to compare shapes which have the same set of codes is not a problem, as the coordinates can be reprocessed to form a new set of codes if required. Similarly, though the direction of digitisation affects the orientation of the lines between adjacent points, this can be overcome by using an abitrary rule, for example, tracing in a clockwise direction.

Starting the digitisation in the same place is a less easy problem, and is one of the reasons why input of shapes by a scanner or image capture system might be better. Edge detection techniques could be used to trace the shape. The disadvantage of using a scanner is that of how to detect background noise; and what to do with it. This would be even more of a problem if signals were digitised from tapes with an analogue to digital converter. Thus, though digitisation tablets are slow to use, they do have the advantage that the user can choose what to include.

A more severe limitation is that the method can (at the moment) only be used for simple shapes which can be described with a curve drawn without lifting the pen from the surface of the graphics pad. Complex sounds with harmonics could not be compared as each harmonic is distinct; each would need to be digitised separately. Since the harmonics also vary, potentially in a systematic manner, setting up comparisons would be very difficult. A more advanced program of the same sort as that described here might work, for example the techniques of elastic matching described by Burr (1979, 1980a). Alternatively, it may be possible to develop an expert system with a learning algorithm (such as a neural net), and "teach" a program to classify shapes. There is much interest and activity in this field of research as both computers and computing techniques become more sophisticated.

It is evident from the analyses described that the combination of pattern recognition techniques and statistics is a useful approach in making the comparison of sounds, described as shapes from sonagrams, more objective.

Chapter 10

Conclusions

The results presented in each chapter have already been discussed at the end of each of them. Here, the work will be summarised and further studies that might lead on from it will be proposed.

10.1 Tests of the acoustic adaptation hypothesis

The predictions made by the acoustic adaptation hypothesis (that sounds made by forest living birds should be lower in pitch and be separated more in time than those produced by birds in a more open habitat) were tested on a microgeographic scale by recording chaffinch songs from coniferous plantations, from open scrub, and from the natural Scots pine woods around Loch Garten. The results of statistical tests between habitats and sites within habitats (Chapter 4) upon both frequency and temporal measures were, to a large extent, not significant. The number of syllables in the end phrase, predicted by Jenkins & Baker (1984) to be greater in a denser habitat, was also found to be not significantly different between habitats (Chapter 6).

Given the lack of evidence for the transmission of sounds by chaffinches over a maximal distance, it may be that the song is instead optimised for transmission over some lesser distance, such as to a bird's mate. This would be much more difficult to test than if sounds are transmitted over a maximal distance, as it becomes much more difficult to make predictions from the acoustic adaptation hypothesis. Indeed, if the birds learn their songs, or sing, in more than one habitat, it may not be possible to make predictions at all.

A highly significant effect of the position of a phrase in the song (phrase number) for both the frequency and temporal measures was found for all lengths of songs. The gap between syllables, and the frequency of maximal amplitude, decrease with increasing phrase number, so that the song speeds up and gets lower in pitch as it proceeds. This appears to be part of the essential syntax of chaffinch song. A series of playback experiments with altered songs could be used to investigate the importance of the different features of the songs for species and individual recognition.

The lack of effect of habitat is quite surprising given the differences in structure and density observed between the habitats from which recordings were made. No tests of the differences in the transmission characteristics of white noise were made in Britain. It is, however, likely that these habitats, and/or sites within them, would affect propagating sounds in a different manner (Liskens *et al* 1976). This could be tested by repeating the transmission experiment performed on Tenerife in various habitats where chaffinches sing in Britain.

The lack of difference found between the habitats investigated may result from the fact that the chaffinch is one of the commonest British bird species. It probably exists in many areas in as high a density as that area will support. Under these conditions, most songs are likely to transmit well to the nearest conspecifics, so that there may be very little selection pressure to adapt songs to transmit over longer distances. The transmission characteristics of the habitats may not therefore be an important constraint (Handford 1988). In addition, if the selection pressure experienced is not for sounds to transmit over the longest distance possible, some sounds, which would otherwise be predicted to be selected against, may "survive" and be passed on by cultural evolution.

A test of the transmission characteristics of white noise and of the songs of the two chaffinch species on Tenerife (Chapter 5) revealed more attenuation of all frequencies in the denser laurel forest than in the more open Canarian pine forest. A sound window of less excess attenuation than expected was found at frequencies of 2-3kHz in both habitats. Whether this is an artifact of the methodology used is unclear. A sound window can be explained as an interaction of the monotonic trend towards more attenuation at higher frequencies with the ground effect. The latter arises because interference between direct and ground reflected waves leads to more attenuation of low frequencies. The existence of a sound window at heights of about 3m above the ground was unexpected as Marten & Marler (1977) found these windows disappeared at heights greater than about 2m. The same general pattern of attenuation was found in both the laurel and Canarian pine forests.

The blue chaffinch songs were transmitted with less distortion in the frequency of maximal amplitude over distances of 25m and 50m than the songs of common chaffinches in both of the habitats tested. These results should be viewed with a certain amount of caution, as only three song types were tested for each species, but they do nevertheless suggest that there are differences between the species' songs.

The song of the blue chaffinch appears to be better structured to fit the sound window observed. However, this does not take into account differences between the species' ecology. One of these, that blue chaffinches probably have a larger territory (Slater pers. comm., pers. obs.), would predict (as observed) that blue chaffinch song would transmit over long distances with less attenuation in both habitats. The sound window may be important if birds often sing on the ground, where the window would make a difference to the transmission of different frequencies, but since birds generally sing at above about 3m it may be of peripheral importance. The distance over which chaffinches transmit song (about 100-200m) may mean that the use of a sound window is unimportant compared to the case for some primates (Waser & Waser 1977, Waser & Brown 1984), where transmission may be over a kilometre or more. Transmission with minimal signal degradation would be expected to be more important over longer distances.

The transmission experiments were performed over only four days, and the results must therefore be regarded as preliminary. Much further work is possible as the experiment could be replicated at more sites, and a method to assess the degradation in amplitude structure of the songs should be developed. It would be interesting to investigate the acoustics of the overlap zone where both species are present, and to repeat the experiment with more songs of both species. Since the blue chaffinch occurs both on Tenerife and the island of Gran Canaria, it would also be interesting to investigate the acoustics of the habitats on this island too, as Bowman (1979) found differences between the acoustics of some of the Galapagos islands, and associated differences in the song structure of some of the *geospizine* finches.

10.2 Simulation studies of chaffinch song

The computer simulation studies carried out (Chapter 7) show that random processes are probably adequate to explain much of the variation in sharing of song types between individual birds, at least in chaffinches, but also perhaps in many of the other species that have been studied. Small neighbourhoods of a few birds singing the same song type appeared in many of the simulations, but as the repertoire size was increased the pattern of sharing of songs between neighbours became more complex. It appears that large dialect areas are unlikely to arise for species with a repertoire size of greater than one song type. Both the repertoire size and number of neighbours available to learn from were found to have an effect upon the amount of sharing of songs between individuals and the songs' longevity.

The results produce predictions of the amount of sharing which may be expected in the field with different numbers of neighbours. These predictions can be tested by mapping birds' territories and the amount of song sharing observed. Though the model used is quite specific to the data observed for the chaffinch, and changes in the values used as parameters are likely to change the results, it may be possible to use the program written to make predictions about song sharing in populations of other species.

If a simple rule, such as "learn the commonest (or rarest) song available", is added to the model the results change. The effect of learning the commonest song of those posessed by neighbours is particularly interesting, because at low error rates the size of the groups found approaches that observed in the wild for white-crowned sparrows. The accuracy of copying in this species is not known, and there are problems concerning the criteria for defining a dialect and thus in deciding on the sizes of the groups observed. Complex patterns of song distribution were produced in these simulations with a relatively simple model, and they leave little doubt that small groups of birds sharing the same song type could be produced by a random process. This suggests that the complexity of song distribution patterns which are sometimes observed in the wild need not imply complex underlying mechanisms.

10.3 Shape analysis of bird songs

The variation in the amount of repetition of syllables in birds songs observed (Chapter 6) is not just a methodological issue, because the definitions used alter the way that the phenomena are interpreted. The dynamic programming technique proposed for the analysis of shapes could also be used to analyse how variable the sequencing of different birds' songs are, and to find whether particular syllables occur in sequence more often than expected.

The trial of the dynamic programming algorithm (Chapter 9) demonstrates that it has the potential to be a useful technique, particularly when linked to statistical analysis, to identify an unknown syllable. The method is currently somewhat limited, but it is the first objective technique which can take into account variation on both the time and frequency axes at once when comparing shapes from sonagrams. Further work with simple shapes is planned to assess the similarity of song elements from different areas, and to test if a library of elements, against which an unknown shape can be tested, can be built up. Other computational techniques may also be used for shape recognition, and it remains to be seen which will prove to be the most useful in the long run.

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Appendix 1

Chaffinch song ANOVA

A worked example of the ANOVA model used to analyse the variables measured from the chaffinch songs (for testing the Acoustic Adaptation Hypothesis) is given below. It is a mixed model design with crossed and nested factors. The factors involved are :

(i) *Habitats*, which are the general areas, are fixed.
(ii) *Sites* are the locations from which song types were recorded. These are nested within habitats and are assumed to be a random sample of the possible sites within each habitat.
(iii) *Types* are the different songtypes recorded from sites in each habitat. They are nested within both habitats and sites and are also assumed to be random, as no effort was made to record all songtypes within each site, and song types were unique to each site.
(iv) *Phrases*, which are the number of sequences of repeated syllables in songtypes (see section 4.3.1) are fixed. This factor is crossed with habitats, sites and types.

The analysis has the following sources of variation:

Habitats
Sites within Habitats
Types within Sites within Habitats
Phrases
Habitats * Phrases
(Sites within Habitats) * Phrases
(Types within Sites within Habitats) * Phrases

The correct error for each of the main effects and interactions is calculated using the rules for expectations of mean squares (table below).

	H	S(H)	T(SH)	P	PH	PS(H)	PT(SH)
H	0	1	1	h	0	1	1
P	p	p	p	0	0	0	0
S	s	1	1	s	s	1	1
T	t	t	1	t	t	t	1

H : $pst\sigma^2_{H} + pt\sigma^2_{S(H)} + p\sigma^2_{T(SH)}$ (a)
S within H : $pt\sigma^2_{S(H)} + p\sigma^2_{T(SH)}$ (b)
T within S : $p\sigma^2_{T(SH)}$ (c)
P : $hst\sigma^2_{P} + t\sigma^2_{PS(H)} + \sigma^2_{PT(SH)}$ (d)
H * P : $st\sigma^2_{PH} + t\sigma^2_{PS(H)} + \sigma^2_{PT(SH)}$ (e)
S(H) * P : $t\sigma^2_{PS(H)} + \sigma^2_{PT(SH)}$ (f)
T(SH) * P : $\sigma^2_{PT(SH)}$ (g)

The appropriate error for : (a) is (b)
(b) is (c)
(d) is (f)
(e) is (f)
(f) is (g)

There can be no error for (c) or (g) as there are no terms which lack those sources of variance.

The worked example uses data for the frequency of maximal amplitude (see section 4.3.2) for two phrase songs. Only songtypes for which data for all phrases was available were analysed as it was found that missing cases biased the sums of squares calculated.

Since the nesting of both sites and types are unequal, the statistical package used (Minitab) could not calculate all the sums of squares required. The following procedure was therefore used.

(a) Calculate oneway ANOVAs for each factor and write down the sums of squares and degrees of freedom.

	df	SS
Habitats	2	1246577
Sites	10	3532331
Types	50	17882550
Phrases	1	4128141

(b) Calculate twoway ANOVAs for Phrases crossed with Habitats and Sites. The sequential sum of squares is required.

	df	SS
H * P	2	197258
S * P	10	2741542

(c) Calculate the (nested) sums of squares and degrees of freedom for Sites and Types by subtraction. The between Sites SS is the total of the Habitats SS and the Sites within Habitats SS, and the between Types SS is the total of the Sites within Habitats and Types within Sites SS. The degrees of freedom are also calculated by subtraction.

	df	SS
Habitats	2	1246577
S within H	8	2285754
Sites	10	3532331
S within H	8	2285754
T within S	42	15596796
Types	50	17882550

(d) Calculate nested and crossed sum of squares and degrees of freedom for (Sites within Habitats) * Phrases by subtraction.

	df	SS
H * P	2	197258
(S within H) * P	8	2544284
S * P	10	2741542

(e) Form an ANOVA table and calculate the sum of squares and degrees of freedom for (Types within Sites within Habitats) * Phrases by subtraction of the other sums of squares from the grand total sum of squares.

	df	SS
Habitats	2	1246577
S within H	8	2285754
T within S	42	15596796
Phrases	1	4128141
H * P	2	197258
(S within H) * P	8	2544284
(T within S) * P	38	5849740
Total	101	31848550

(f) Calculate Mean Squares for each source of variation (divide the sum of squares by its degrees of freedom).

	df	SS	MS
Habitats	2	1246577	623288.50
S within H	8	2285754	285719.25
T within S	42	15596796	371352.28
Phrases	1	4128141	4128141.00
H * P	2	197258	98629.00
(S within H) * P	8	2544284	318035.50
(T within S) * P	38	5849740	153940.52
Total	101	31848550	

(g) Using the appropriate error term calculate F values, and look-up probability values.

	df	SS	MS	F	p
Habitats	2	1246577	623288.50	2.181	0.178
S within H	8	2285754	285719.25	0.769	0.632
T within S	42	15596796	371352.28		
Phrases	1	4128141	4128141.00	12.980	0.007
H * P	2	197258	98629.00	0.310	0.742
(S within H) * P	8	2544284	318035.50	2.066	0.064
(T within S) * P	38	5849740	153940.52		
Total	101	31848550			