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**CULTURAL EVOLUTION IN BIRD SONG, IN
THEORY AND IN CHAFFINCHES (*FRINGILLA
COELEBS*)**

Robert Francis Lachlan

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Abstract

This thesis examines the evolutionary relationships between culturally transmitted bird song and genetic predispositions for learning species typical song. Using spatially explicit simulations, I found that incompatibilities between birds with wide and narrow predispositions result in selection for wide predispositions. This hypothesis was supported by deterministic, analytical models, combined with simulations incorporating random perturbations. I called this the 'cultural trap hypothesis', since it may be an important factor in the maintenance of a role for learning in determining the song phenotype. Another proposed hypothesis for the evolution of song learning - cultural conformity - created a selection pressure for more restrictive predispositions. Other models examined the evolution of cultural conformity, and interspecific effects resulting from overlap in the predispositions of two species.

I recorded songs of chaffinches to try and test these models, and some of their underlying assumptions. I found considerable variation in levels of cultural diversity between areas, in accordance with a neutral interpretation of the cultural transmission of chaffinches and the ecology of the populations. In Scottish chaffinch populations, I estimated the cultural mutation rate to lie between 0.005 and 0.06. From my simulation studies of the cultural trap hypothesis, I predicted that higher levels of cultural diversity should increase the selection pressure for less restrictive genetic predispositions. I therefore compared isolated populations of chaffinches on the Canary Islands. In accordance with the theory, there was less diversity in some coarse scale, and organisational features of song that may reflect differentiation in genetic predispositions on islands with lower cultural diversity. However, in a third test, using a computer method to compare vocalisations that I developed, I found no patterns of differentiation between the islands consistent with the cultural trap hypothesis, leaving the question of whether there is genetic variation in song organisation in the Canaries unresolved.

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Declarations

(i) I, Robert Lachlan hereby certify that this thesis, which is approximately 46,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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(ii) I was admitted as a research student in September, 1996 and as a candidate for the degree of PhD in September 1996; the higher study for which this is a record was carried out in the University of St. Andrews between 1996 and 1999.

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(iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St. Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Chapter 1 Introduction

1.1 Preamble

This thesis concerns two areas of research that have both been in vogue in evolutionary biology in recent years: communication and cultural evolution. Both have developed a strong theoretical pedigree, but curiously studies combining the two are rather thinner on the ground (except for the series by Feldman & Aoki; e.g. Aoki, 1989). This is peculiar because two of the classic and best studied examples of cultural transmission, bird song and human language, are forms of communication. However, although the empirical field of linguistics and research on bird song have generated unprecedented quantities of data (see Pinker, 1994; Catchpole & Slater, 1995 for recent reviews), neither bird song learning nor human language have a strong theoretical framework. While theories from evolutionary biology and cultural evolution have been applied to these two cases, the full weight of a combination of recent advances in cultural evolution and communication theory has not been brought to bear on either. For language, this is understandable, since empirical research has produced a bewildering diversity of facts and controversies. In bird song, however, while considerable diversity in almost all aspects of organisation and function exists, a few key issues have emerged. It therefore seems appropriate to try and fuse the powerful theory with the compendious set of data.

In this chapter, I aim to introduce the key concepts that are central to nearly all of the rest of the thesis, although I have attempted to write each chapter to be understood independently of the whole. These concepts can be divided between the theoretical field of cultural evolution and the empirical field of bird song research.

1.2 Cultural evolution

Darwin's theory of evolution by natural selection is now often closely associated with genetics, due to the brilliant neo-Darwinian synthesis by population geneticists such as Fisher (1930). However, the theory can be boiled down to three

principles that do not necessarily require genes. First, information must be transmitted between individuals. Second, there must be some source of novel variants of these traits. Finally, some variants must be more successful than others at surviving and reproducing themselves in other individuals, so that these traits become adaptations. The term 'universal Darwinism' was invented by Dawkins (1976) to encapsulate the notion that evolution through selection is more widespread than just the case in which genes are the carriers of the information, a notion that had been partially developed by numerous writers since and including Darwin (Plotkin, 1993). Universal Darwinism has been a useful tool in understanding processes as diverse as the immunological response (Burnet, 1959; Jerne, 1985), and human thought (Plotkin, 1993). However, the most developed application of this approach has been in the study of culture. In the next sections, I shall illustrate how culture meets the requirements of evolution, focusing on examples of culture in animals other than bird song.

1.2.1 Cultural Transmission

Principally, there are two sources of information that may be used during the ontogeny of behaviour: genes and learning. Cultural transmission refers to a subset of the latter called social learning. Social learning occurs when one animal learns a behaviour pattern as a result of observing another performing that act. This definition includes a range of psychological processes (Whiten and Ham, 1992). Some are cognitively advanced, such as teaching (when the 'tutor' intends to transmit information for the benefit of the receiver), or imitation (the acquisition of the 'form' of a behaviour pattern through observation alone). Others are very simple. Local enhancement occurs when one individual is attracted to one location by the presence of another and, simply as a result of being in that place, is more likely to learn a behaviour pattern that the other had been carrying out than it would be otherwise.

While humans are the most extensively "cultural" animals, examples of cultural transmission are widespread throughout the animal kingdom (Heyes, 1994, Heyes & Galef, 1996). Experimental approaches have revealed that many animals that live in groups socially learn preferences for food types (rats: Galef, 1988; phytophagous insects: Thorpe, 1939, Papaj & Prokopy, 1989), food locations

(guppies: Laland and Williams, 1997; rats: Laland and Plotkin, 1990), feeding techniques (pigeons: Lefebvre and Palameta, 1988; black rats: Terkel, 1995; Japanese macaques: Kawai, 1965), predator identity (fish: Mathis *et al.*, 1995; blackbirds: Curio *et al.*, 1978), and mate preferences (guppies: Dugatkin and Godin, 1992, 1993; fallow deer: Clutton-Brock *et al.*, 1989; isopods: Shuster & Wade, 1991; sage grouse: Gibson *et al.*, 1991; quail: White & Galef, 1999 a, 1999 b), as well as showing vocal learning (see below).

The rules of cultural transmission are more relaxed than for genes. Whereas genes are transmitted only between parents and offspring in many species (i.e. vertical transmission in the useful scheme introduced by Cavalli-Sforza & Feldman, 1981), cultural transmission can also occur between members of one generation (horizontal transmission), or between unrelated individuals from different generations (oblique transmission). In humans and animals examples of all three have been documented. For humans, a survey that attempted to discover which was the more prevalent suggested that vertical transmission was predominant (Cavalli-Sforza *et al.*, 1982). In animals, it has often been suggested that horizontal transmission is the most common mode (Galef, 1988; Lefebvre & Palameta, 1988; Laland *et al.*, 1993, 1996). However, this may reflect a bias towards studying foraging behaviour in group living animals. Examples of vertical transmission have been described, notably the pine cone feeding techniques of black rats (Terkel, 1996), and sexual imprinting - effectively copying the mate choice of your parents (Laland, 1994). In primates, Coussi-Corbel & Fragaszy (1995) suggested that social learning was 'directed' by several factors, one of which was age.

1.2.2. Cultural variation

The existence of variants of human culture almost requires no description here, as it is apparent in almost any human belief or skill. Among the more quantifiable aspects of human culture, variations in language have provided an especially fruitful field of study. As with species in biology, linguists have constructed taxonomies of languages. These indicate that languages change through the incorporation of numerous small variants. The similarity of this system to genetics

extends to genetic and linguistic changes being quite highly correlated (Piazza *et al*, 1995).

In animal populations, field studies have also revealed considerable amounts of variation. Whiten *et al* (1999) collated information on the foraging techniques of chimpanzees from several field stations across Africa, and found large amounts of variation between sites, and suggested that many of these traits were culturally transmitted. Other primatological studies have observed the spread of behaviour patterns through groups and populations, notably in the Japanese macaque, where the spread of food washing (Kawai, 1965) and stone handling (Huffman, 1996) through groups have been recorded. In other taxa, a famous example is the spread of milk bottle-top opening by blue tits through Britain (Fisher & Hinde, 1949; Lefebvre, 1995).

1.2.3 Cultural adaptations

To date, only one experiment has measured the adaptiveness of a socially learned trait in a natural population. As part of the study of food processing by black rats in Israel, Terkel (1996) compared the energetic costs of two different modes of removing seeds from pine cones. In this study, a clear difference in the effectiveness of the two techniques was found. Importantly, both were clearly more efficient than techniques developed by rats using individual learning alone - such rats could not survive on pine cones alone. This suggests that social learning has led to the evolution of an adaptive feeding technique.

In studies of social learning using tasks set by the experimenter, it has also been shown that social learning can provide a clear advantage over individual learning alone (Laland & Plotkin, 1990, 1992; Giraldeau & Lefebvre 1986, 1987).

Despite this relative lack of direct support, it seems exceedingly likely that other culturally transmitted traits, such as opening milk bottle tops to obtain cream or

fishing for termites with sticks, are also adaptive. Galef (1995) makes the point that the psychological basis of social learning means that animals should still only learn behaviour patterns that are reinforcing in some way. This is a form of selection, and should promote adaptive behaviour most of the time.

1.2.4 Culture as an evolutionary system.

As culture fulfils the general requirements for evolution, it has attracted considerable theoretical interest (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). These studies adopted the methods of population genetics, and showed formally how culture can evolve. More detailed models have examined the pattern of diffusion of a trait through a population, for example, how different patterns of transmission may have important effects on the diffusion of information through populations (Boyd and Richerson, 1985; Laland *et al.*, 1993). As yet, only in a couple of instances have these models been used to examine the diffusion of a trait through a natural population. Lefebvre (1995) successfully modelled the spread of milk-bottle top opening through the population of British blue tits, although he concluded that a mixture of cultural and individual learning processes led to the observed spread of the behaviour.

Once the evolutionary nature of culture had been established, interest turned to its evolutionary causes and consequences.

1.2.5 The evolution of culture: culture as an adaptive trait

The adaptiveness of cultural transmission itself was first considered by Pulliam and Dunsford (1980), and Lumsden and Wilson (1981) (see Boyd and Richerson, 1983 for a comparison of these works). Lumsden & Wilson used a very simple model of cultural evolution, in which individuals chose one of two behaviours, on the basis of genetic preferences, which they called epigenetic rules (see also Alexander, 1990; Mundinger, 1995). As they ignore cultural diffusion (any individual can equally choose either behaviour), they found that genes which increase the

probability that an adaptive behaviour is adopted will be selected. They then describe a process of "genetic assimilation" in which genes which decrease the uncertainty in choosing the correct behaviour will spread, until the cultural aspect of the behaviour is lost. An analogous attempt to model the adaptiveness of cultural evolution was carried out by Cavalli-Sforza and Feldman (1983), who compared various types of cultural transmission (vertical and oblique), against a genetic (haploid) trait, which provided the same information as the cultural trait. They found that the genetic trait would always win such a competition, because of the assumed lower levels of accuracy of cultural transmission. However, this very simple model incorporates some stringent assumptions. It provides no possibility for individuals to avoid making costly learning mistakes, and it assumes a constant, homogeneous environment.

The approach taken by Pulliam and Dunsford (1980) was very different. Their analysis was based on a consideration of the different ways animals can discover whether a given behaviour is adaptive or not. They suggested that trial and error learning involved a cost, in that the outcome of the first trial could not be evaluated by the individual. Learning socially from other individuals (especially experienced, or successful individuals) can thus be seen to be a way of avoiding these costs.

Boyd and Richerson (1985, 1988), in an influential set of models, reconciled these two approaches, and provided a general result. They compared the success of a culturally inherited trait against an individually learned trait, making use of a Bayesian learning algorithm to provide a realistic simulation of animal learning. They considered this first analysis to be a model of how culture may have evolved - i.e. individual learning preceded social learning. Their models suggested that cultural evolution will be more efficient than a system of individual learning whenever (1) the error rate of individual learning is substantially greater than that for social learning, and (2) the environment is reasonably predictable. They analysed, in a similar way, the success of cultural evolution versus genetic evolution, and this provided analogous results. Cultural evolution will succeed over genetic evolution whenever (1) the error rate in social learning is low, and (2) the environment is not predictable. Thus cultural evolution is predicted to be optimal over a range of intermediate conditions of

environmental fluctuations (which may be either temporal or spatial: Boyd and Richerson, 1988).

1.2.6 The consequences of cultural evolution for genetic evolution.

If culture is an evolutionary system itself, then its own evolutionary 'interests' should exist, and, *prima facie*, these may be as powerful as those of the genes. As a result, the interactions between genetic and cultural evolution have attracted considerable theoretical attention (Feldman & Cavalli-Sforza 1976, 1984; Lumsden and Wilson, 1981; Boyd and Richerson, 1985, 1988; Feldman and Zhivotovsky, 1992; Laland, 1992; Feldman & Laland, 1996). The basis of this idea is that the acquisition of a cultural trait (for example, including a certain plant in the diet) is likely to change selection pressures on genetic loci (such as those affecting the ability to digest chemicals in that plant). This change in the selection pressures might act to increase the speed of genetic evolution, or to 'shield' genes from selection, if traits can be obtained culturally instead of genetically. Laland (1992) concluded that cultural evolution is likely to act more frequently to decelerate genetic evolution than to accelerate it.

A controversial branch of this field (that we shall see is particularly relevant to this study) has been the interaction between culture and those genetic aspects of behaviour that bias the acquisition of cultural traits. Lumsden and Wilson (1981) considered this in conjunction with their analysis of the adaptiveness of social learning. The models, and underlying assumptions used by Lumsden & Wilson, however, have been widely criticised (Maynard-Smith and Warren, 1982 Boyd and Richerson, 1985). The models are not true models of gene-culture co-evolution in that culture is not modelled as a true evolutionary system; it is not considered to be able to direct genetic evolution. Differences between populations are considered to be purely genetical, rather than genetic and cultural.

Boyd and Richerson (1985) produced a separate synthesis of cultural evolution, which has been more widely accepted by social scientists. It incorporated an evolutionary model of culture. They coined the phrase "dual inheritance system" to

emphasise the equal weight they gave culture and genetic evolution. They also examined several interactions between behavioural genetics and cultural evolution. Most closely approximating the concept of Lumsden & Wilson's epigenetic rule was their "biased transmission". This term gave greater flexibility, and, importantly, they put forward processes to support their concept. "Direct bias" would result from individuals experimenting with different cultural traits, and selecting one on the basis of some internal (typically genetic) preference. "Indirect bias" would result from individuals selecting cultural traits, based on an evaluation of the tutor. Finally, "frequency-dependent bias" results from individuals selecting the cultural trait that is most, or least common in a population. Boyd & Richerson (1985: pp147-152) also developed a model examining the genetic modification of direct bias under natural selection. They found that, in their deterministic models, with vertical cultural transmission, biased transmission was not favoured. However, if an element of random cultural variation was incorporated, reflecting copying error for example, then biased transmission was selected for. Similarly, spatial variation in a cultural trait, or habitat-specific selection, favoured direct bias as a local adaptation, as long as there was only limited migration.

1.2.7 Empirical evidence for gene-culture co-evolutionary theory.

More specific models have been developed to investigate particular instances of cultural evolution. In general, these have been designed in contemplation of human cultural processes. Boyd and Richerson (1985) have produced a series of models to investigate aspects of the evolution of human cooperation, based on a model of group selection (which can be obtained if society-level punishment is applied). Aoki (1986), and Feldman and Cavalli-Sforza (1989) have investigated the coevolution of the cultural trait of dairy farming, and the genetic trait of lactose absorption. Lactose absorption by adults appears to have evolved as a response to the cultural evolution of dairy farming. Cavalli-Sforza *et al.* (1993) took a historical approach, and compared the demic expansions of *Homo sapiens* with archaeological data on cultural advances. Aoki and Feldman (1991) examined the existence of assortative mating, arising as a result of a culturally inherited trait (sign language) and a genetic one (recessive hereditary deafness). Durham (1991) described the coevolution of

farming practices in some populations in West Africa and sickle cell anaemia. In this case, the culturally transmitted farming techniques led to an abundance of malaria carrying mosquitoes, and hence a higher level of sickle-cell anaemia than in neighbouring populations. Laland (1994) examined the evolution of sexually selected traits under a gene-meme coevolution system. Finally, Laland *et al.* (1995) produced a variety of possible interactions between cultural evolution, and sociobiological hypotheses, such as sex ratios. The studies of Kirkpatrick and Dugatkin (1994), and Aoki (1989) stand out in that they are not explicitly aimed at human evolution. Kirkpatrick and Dugatkin's (1994) study of sexual selection and mate choice (following experiments on mate choice copying by guppies by Dugatkin and Godin, 1992,1993) found that sexual selection can be imposed by a cultural mating preference, but that mate choice copying is unlikely to promote male trait diversity, as had been hypothesised. I shall return to the model of bird song learning developed by Aoki (1989) later.

1.2.8 Summary

Cultural transmission appears to be a widespread, if not common, aspect of animal behaviour, occurring in a variety of taxa and circumstances. Cultural transmission gives rise to an evolutionary system. The theoretical evolutionary implications of this cultural evolution, that have been mostly focused on human behaviour, may apply equally, if not better, to the cultural transmission of animal behaviour. Moreover, theoretical studies suggest that cultural evolution may be an important factor in shaping the pattern of genetic evolution in those species where it is found. However, there have been few empirical studies of gene-culture interactions to date, and these have been restricted to humans and are only correlative. There is therefore a need for an experimental example which explicitly investigates the models of the interactions between genes and culture.

1.3 Bird song learning as a cultural trait.

Bird song learning is a classic example of cultural transmission in animals (Catchpole & Slater, 1995). In this section, I shall place it within a cultural

evolutionary framework. To do this, I will begin by applying the concepts of transmission, variation, adaptation, and finally evolution, to the literature from this field.

1.3.1 Song learning by birds - cultural transmission.

The modern interest in bird song learning was initiated by Thorpe's (1961) pioneering ethological work, and his use of sound spectrograms. He showed that chaffinches (*Fringilla coelebs*) learned their songs by copying those of other individuals, or, in an experimental situation, from tapes of song. Individuals reared from the nestling stage in isolation (so-called Kaspar Hauser birds) produced songs that resembled those typical of their species, although they lacked the precision, and some of the details of normal song. It was subsequently discovered that this relied on individuals being able to hear themselves, as deafened birds produced no recognisable song (Nottebohm, 1968). This work provided the 'template' model of learning. This model postulated that individuals possessed a genetic predisposition (or 'template') to learn species-typical songs. Further evidence in favour of this model came when the songs of other species were played to young chaffinches. Given no choice, the young birds were able to learn the heterospecific song. However, if they had a choice between a chaffinch song and a heterospecific song, the conspecific song was chosen. This is a classic example of what Boyd & Richerson (1985) referred to as a direct bias. Subsequent work replicated Thorpe's general results in other species: white-crowned sparrows (Marler & Peters, 1977); song sparrows, and swamp sparrows (Marler & Sherman, 1985). One of the more spectacular results used different breeds of the canary (Mundinger, 1995). In this study, Mundinger found that a breed that had been artificially selected (for about 200 years) for certain features in their songs and a breed whose song resembled those of wild canaries both preferred to learn the songs of their own breed.

The template model of song learning is still the most strongly supported theory of the ontogeny of bird song. The only alternative, the action-based model, was provided by Marler & Nelson (1992). In this model, birds first learn a number of songs, and then select a subset of these to form their adult repertoires.

Song learning has been shown to be taxonomically restricted. Other experiments have shown that species from other taxa produce normal song even when deafened (e.g. Barbary Doves: Nottebohm and Nottebohm, 1971; flycatchers: Kroodsma, 1984). Song learning has been demonstrated in three monophyletic groups (Sibley & Ahlquist, 1990, Kroodsma & Baylis, 1982) the oscines (songbirds); the psittaciformes (parrots); and one of the families of the apodiformes (hummingbirds). Moreover, evidence from laboratory studies, and from patterns of variation recorded from the field (see below), suggest that song learning is ubiquitous within the oscines. The ubiquity of social learning of bird song, as opposed to individual learning, is slightly less clear-cut. Patterns of geographical variation (Mundinger, 1982) in which songs are shared within a local geographical area suggest that culture is predominant in most species. However, two recent experiments on species with large individual repertoires of songs, the grey catbird (Kroodsma *et al*, 1997) and the sedge wren (Kroodsma *et al*, 1999) found that normal repertoires were developed without cultural transmission.

In many ways, bird song learning is an ideal subject for evolutionary models, since it fortuitously matches many of the assumptions included in standard modelling procedure. For example, one area of the development of song which has been the subject of much research is the timing of learning (Slater *et al*, 1988). Except for a very few exceptions (e.g. canaries), song learning is restricted to a time window, typically in early adulthood or as juveniles. The concept of a "critical period", dictating absolutely when song was learned, however, has been gradually replaced with the more flexible "sensitive period", which is more responsive to environmental fluctuation. However, it still appears that song learning only occurs once during the life-span of an individual, and that selection occurs after the trait has been acquired. This is also how most models of cultural transmission are constructed, for the entirely different reasons of mathematical clarity and tractability.

Another issue is that of the units of inheritance. One criticism that has frequently been levelled at the theoretical field of gene-culture interactions is the manner in which they divide culture into heritable units, a concept that was captured

by Dawkins' (1976) concept of the "meme". This problem has also been encountered many times by workers in the field of bird song learning, but bird song tends to be divided hierarchically into units from elements ('notes'), through to song types and repertoires. The resulting patterns of transmission are analogous to those of genes, chromosomes, and genomes. Cultural evolutionary studies of bird song have used a variety of different approaches (see Lynch, 1996; Payne, 1996 for two different methods). An objective method to determine exactly how birds organise their songs has been initiated by a recent study into how song sparrows organise their songs (Podos *et al.*, 1992). The authors used a statistical comparison of the variation of different potential "units" of song to determine the "minimal unit of production". They argued that song types appear to be the "probabilistic units of song production" for this species.

A final issue in cultural transmission is that of its mode. This again has been an issue that has received considerable attention (Catchpole & Slater, 1995). The results of studies based on patterns of geographical variation (e.g. Slater & Ince, 1982), and on marking and following individuals (e.g. Payne, 1996) have provided a fairly consistent answer: song appears to be transmitted obliquely from adult males that sing near to the territory that a young male establishes, or from a male singing near the bird's natal territory (though not necessarily the father). In fact, only two exceptions to this rule have been discovered: Darwin's finches (Grant & Grant, 1996), and zebra finches (Clayton, 1990; Zann, 1990) both exhibit some degree of vertical transmission.

1.3.2 Cultural variation in song.

For many cultural traits, individual, as opposed to social learning is an obvious source of new variants. However, bird song learning is a little more complex, since it is not well understood how individual variation in song arises. Current opinion on the roles played by individuals in changing songs is divided. This is illustrated by the terms used to describe this phenomenon: "cultural mutation" (Lynch & Baker, 1994, Lynch, 1996, Williams & Slater, 1990) suggests a mistake made during cultural transmission, whereas "improvisation" (e.g. Kroodsma, 1996, Payne, 1996) implies an

adaptive response in the production of novel song types, or at least true individual learning. Table 1 summarises the different causes of individual variation in song, and some of their possible consequences.

TABLE 1. Processes of individual variation in song acquisition.

Process	Amount of cultural transmission during process.	Possible effects of process on diversity and variety of songs within population.
" Improvisation ". Individual makes up new song type with little reference to possible models.	No cultural transmission – song is entirely novel.	Since song is novel, this is likely to increase song diversity and variety dramatically.
" Point mutation ". Individual makes up new song type, as a result of imperfect copying of possible model.	Some cultural transmission – only small elements of song are entirely novel.	Song diversity is increased. Song variety is increased less so, since some information is transmitted.
" Recombination ". Individual mixes up song-types of several models. e.g. Canary Island chaffinches (Slater & Sellar, 1986)	More cultural transmission – all information in song is present in models' songs. Only order of combination is entirely novel.	Song diversity may be increased if new song is a novel recombination. Little increase in song variety since nearly all information in novel song already exists.

Many field studies have revealed geographical variation in bird song that provides information about cultural variation in bird song. Mundinger (1982) catalogues hundreds of these cases (many more have been reported subsequently, including cases from non-oscine birds, such as the hummingbirds: Gaunt *et al.*, 1994).

Traditionally, geographical variation in song has been associated with "dialects", resulting from the mosaic or patchwork pattern of geographic variation found in some species (e.g. white crowned sparrows; Marler & Tamura, 1964; corn buntings: McGregor, 1980). This term has been implicitly associated with the idea that the pattern of geographic variation itself may be functional, for example, serving as a population marker (Baker & Cunningham, 1985). However, there is great variety in patterns of geographic variation themselves, from species such as the swamp sparrow, where many hundreds of individuals share song types (Balaban, 1988, a,b) to the case found in many species where there is a high turnover of song types, and geographic variation without dialects (indigo buntings: Payne, 1996; chaffinches: Slater *et al.*, 1980), indicating rapid temporal or spatial fluctuation. These findings are inconsistent with the hypothesis that song sharing reflects social organisation, and the use of the term 'dialect' itself has been criticised for this reason (e.g. Slater *et al.*, 1984).

An alternative view of cultural variation is that it is actually a functionless "epiphenomenon" resulting from patterns of learning, that may be influenced by song ontogeny, or ecological factors that affect which individuals a young male might learn a song from, and the likelihood that a mistake will arise during learning (Andrew, 1962; Slater, 1989; Williams and Slater, 1990). On the basis of the evidence set out above, this proposal should, at least, be viewed as the null hypothesis against which less simple theories must be tested.

1.3.3 Adaptations of socially learned songs

The function of song in male oscines has been clearly split into two categories (Catchpole & Slater, 1995), to attract females, and to repel rival males. Many aspects of song have been shown to be involved in these functions. For example, song rate, and song repertoire are both important sexually selected traits (e.g. Buchanan & Catchpole, 1997). Another essential role of bird vocalisations (including calls, as well as song) is in species recognition. This operates at a different level, in that it acts as a prerequisite for either of the key two functions. Males have been shown to respond more strongly to conspecific song (e.g. Bremond, 1976) than heterospecific song, as

well as to specifically learn species typical songs (Marler & Sherman, 1985; Mundinger, 1995), and females have also been shown to possess mating preferences for species specific song (e.g. Brenowitz, 1991).

In this review, I am concerned with the information that is culturally transmitted in song. This is, by the definition of vocal learning (Janik & Slater, 1997), the form or 'morphology' of the song. There is much evidence that this is important in species recognition (reviewed by Becker, 1982). It is curious that species identity is encoded by a cultural trait, as the error rate of a cultural trait is hugely greater than that for a genetic trait, especially in the many species which possess very small repertoires. From Ince *et al*'s (1980) calculation, from a population of chaffinches, which do not possess a large repertoire, a cultural "mutation" rate of 0.15 was estimated, 6 orders of magnitude greater than that for genetic mutations.

Two hypotheses have been postulated to explain this paradox. The "invariant features" hypothesis (Marler, 1960; Emlen, 1972) proposed that species recognition is encoded in the invariant aspects of song, song parameters that were identical throughout the species. Despite early support for this hypothesis, it has been challenged by the finding that not all invariant features of song are used to identify the species of a singer (Emlen, 1972), and by Nelson's (1989) finding for the swamp sparrow that there was no correlation between the accuracy of a feature of a song in predicting species identity, and its variability within a species.

The alternative hypothesis has been dubbed the "sound environment" hypothesis (Marler, 1960, Emlen, 1972, Bremond, 1976, Nelson, 1989). This hypothesis supposes the existence of a multi-dimensional "acoustic space". Species song should fall within certain bounds in this space, and individuals should use features which are most separated between species in this space, whether variable or not. Nelson's (1989) study of swamp sparrows supported this hypothesis over the invariant features hypothesis, although no absolute proof that the most reliable features are actually used by birds exists. Thus, the potential for confusion exists. Indeed observations seem to bear this out. For many species, occasional mimicry of heterospecific song has been reported on numerous occasions (Helb *et al*, 1985).

Clearly this represents a breakdown in species recognition. Moreover, it seems likely that maintaining the potential to sing a wide variety of songs would incur neural and physiological costs. Therefore the question of why social learning of bird song is so ubiquitous, even in species with small repertoires, remains a mystery.

1.3.4 Cultural evolutionary studies of bird song.

Descriptions of geographical variation do not constitute true cultural evolutionary studies, since they provide no insight into how the patterns of variation were generated. The most logical way to resolve the controversy of what geographical variation represents is to carry out a process-oriented enquiry of how "dialect" patterns of variation might arise. A number of detailed investigations have focused on questions of the patterns of song sharing from a cultural evolutionary viewpoint by forging links between individual behaviour, and population-level results. The most extensive studies have been largely carried out using two species: the indigo bunting (Payne *et al.*, 1988; Payne and Payne, 1993; Payne, 1996, 1982), and the chaffinch (Ince, *et al.*, 1980; Slater *et al.*, 1981; Slater & Ince, 1979, 1982; Goodfellow and Slater, 1986; Williams and Slater, 1990, 1991; Lynch and Baker, 1986, 1991, 1993, 1994; Lynch *et al.*, 1989; Lynch, 1996). These studies have used a considerable number of techniques to explore the processes of bird song cultural evolution. However, all have used a neutralist model of song transmission - in other words song type frequencies are assumed to be controlled by the processes of mutation, immigration and drift, rather than selection. As described above, this is a reasonable null hypothesis to take for learned bird songs in most situations, due to the primary role of the socially learned information in species recognition.

The work of Payne, and his coworkers on the indigo bunting has focused mainly on the temporal stability of local song traditions. Their results are based on an ongoing long term (the first data come from 1965) study of two populations of indigo buntings in southern Michigan. By following the fate of individual song-types (or "themes"), several important statistics of cultural transmission of indigo bunting song have been deduced. A "half-life" of 3.8 years per song was calculated for 15 years of records, although the definition of song type was somewhat looser than that used in

other studies. In terms of song turnover, a few song themes lasted for 10 years or more, but most lasted only a few years. Payne (1996) suggests that the many new songs that were therefore recorded during this period were the result of cultural "immigration", songs that were learned by young males from outside the population, and entered the population when the young males acquired territories there. An alternative approach looked at song sharing between neighbouring males (Payne, 1982). Interestingly, Payne discovered that young males that shared songs with neighbours were more successful at breeding than those that did not.

Studies of chaffinch song have addressed both the question of temporal stability and that of geographic variation. Studies of a population of chaffinches in a wood in Southern England (Ince, *et al.*, 1980; Slater *et al.*, 1980) provided similar results to the studies on indigo buntings. Two sets of recordings of the songs in the wood, separated by 18 years, indicated that 3 of the 35 song-types present in the later sample were also present in the earlier one. This accurately matched a computer simulation of cultural drift of song, with a "cultural mutation rate" of 15%. It was not clear what proportion of the new songs generated at 15% were the result of immigration, as opposed to mutation. However, a parallel study that measured the mutation rate based on the amount of cultural diversity present within one year also provided an estimate of 15%. Another series of studies has focused on variation (Lynch *et al.*, 1989; Lynch and Baker, 1986, 1991, 1993, 1994; Lynch, 1996), within and between populations of chaffinches on the oceanic Atlantic islands, and along a cline in a recently introduced population in New Zealand. While the field of cultural evolution has progressed rapidly by borrowing theoretical "tools" from population genetics, these studies are notable in the extent to which they borrow from theories of genetic drift, an approach that was deliberately neglected in the classic theoretical studies of cultural evolution (Boyd and Richerson, 1985). From this theory, Lynch & Baker (summarised by Lynch, 1996) have shown that the cultural traits of song-types and elements behave similarly to neutral genetic alleles. For populations of chaffinches on Atlantic Islands (Canaries, Azores, and Madeira), estimates of within-population diversity fitted a neutral model, and between-population cultural differentiation was correlated with genetic differentiation, and appeared related to geographic isolation. Along a cline in New Zealand, differentiation of populations on

the basis of song was shown for some measures of song. This result differs from that of (Slater *et al.*, 1984) who found little or no differentiation in chaffinch song from three locations, spanning the length of the British Isles. An interesting aspect of this work was the effect of the length of culturally transmitted traits (Lynch & Baker used the term 'meme'). Chaffinch song is made up of a string of syllables. Lynch & Baker considered different lengths of memes, from one syllable in length to the length of the whole song. They found in both sets of studies that increased meme length led to greater variation, and less differentiation between populations. Lynch (1996) also re-analysed data in the literature to produce a comparative study of the neutrality of song-types. His correlation between expected and measured levels of song diversity over a wide range of 17 species was impressively strong, suggesting that the cultural evolution of song does indeed appear to be neutral. Finally, a set of computer simulation studies (Ince *et al.*, 1980; Goodfellow and Slater, 1986; Williams and Slater, 1990, 1991), which are based on a geographic matrix of "territories", have elucidated some further potential properties of cultural evolution of bird song. Parameters such as the cultural mutation rate, repertoire size, and the number of potential tutors that individuals listen to before learning their songs, have been shown to have dramatic effects on the geographic variation of song, showing that simple ecological effects, as well as differences in song organisation can create the variety between species that has been recorded.

Does this evidence that cultural evolution of song appears to be a neutral phenomenon support the view that geographic variation is a meaningless "epiphenomenon"? From the perspective of the bird, this would appear to be so, but by creating an evolutionary system in culture, we also have to consider the evolutionary viewpoint of the song-types themselves. Geographical variation might be seen instead as the result of competition between units of cultural inheritance. Such a culture-oriented viewpoint has already been used to explain geographic variation in song, in the case of habitat matching. There is some evidence (reviewed in Catchpole & Slater, 1995, Ch 4.) that song in a given area can be optimal for transmission through the habitat, and that habitat differences can predict aspects of song variation. This is considered to be the result of competition between features of different song

types. Those which transmit best are more likely to be heard by a young male, and are therefore more likely to be learned.

According to the simulation studies of bird song cultural evolution, patterns of geographical variation should be strongly affected by a number of parameters of cultural transmission that might obviously be affected by ecological conditions, or by aspects of song organisation. For example, one prediction is that the number of individuals that a bird hears, and could learn a song from, has a major effect on the existence of mosaic-type geographical variation - the fewer potential tutors, the more mosaic-like the pattern becomes (Williams and Slater, 1990). Probably, the number of potential tutors is affected strongly by the density of a species in a given population, the size of territories, the amount of suitable habitat, the transmission of sound in the habitat, the patterns of distribution of young birds, or the movement of birds relative to their territories. Similarly, the cultural mutation rate is proposed to play a pivotal role (Ince & Slater, 1980, Goodfellow & Slater, 1986). The cultural mutation rate may well be dependent on a number of factors, such as the length (i.e. number of elements) of the trait (Lynch & Baker, 1994, Lynch, 1996), the complexity of the trait, how many times the song is heard, which may be affected in turn by sound transmission, repertoire size, and aspects of social organisation.

1.4 Why do oscines learn their songs?

Boyd & Richerson (1985, 1988) have made the prediction that, under normal circumstances, social learning should be an adaptive strategy only over an intermediate range of conditions. However, the restricted taxonomic distribution of bird song learning suggests that other factors may be at work. While parrots and hummingbirds have not been so extensively studied, bird song learning has been recorded in hundreds of species of oscines. Within this group, the variety and range of bird song learning is incredible. There are large variations in repertoire size, patterns of delivery, and patterns of learning that overlap to a large extent with sister-taxa, especially the suboscines, that do not learn their songs (Kroodsma, 1996). Importantly, the function of song also varies considerably. In some species, female choice for large repertoires has led to repertoires of over 300 song types per bird. In

others, repertoires are limited to one or a few song types. Some species sing a wide variety of sounds, and may even mimic other species of birds, or even inanimate sounds, while other species are restricted to a fixed number of potential song elements (measured as around 100 for the swamp sparrow, Marler & Sherman, 1985; Balaban, 1988 a).

1.4.1 Functions of bird song learning.

Except for two cases, interspecific mimicry, which appears to be maintained as a sexually selected trait (Eens, 1997), and the maintenance of large repertoires, also thought to be through sexual selection (Buchanan & Catchpole, 1997), there have been no strong hypotheses for why birds learn their songs. However, interspecific mimicry occurs in very few species, and while large repertoires are more common, there are many species whose males possess small repertoires - often of only one song type.

Slater (1989), Kroodsma and Byers (1991), and Catchpole & Slater (1995) describe the extant hypotheses for song learning in species with small repertoires that do not mimic: (1) As an efficient mechanism of transferring large amounts of information. This seems plausible for species with large repertoires, however the error rates endemic in cultural transmission preclude this from explaining why species with short, simple songs learn them. (2) Social adaptation between males sharing songs. Song sharing is seen as a form of communication that allows vocal matching between males, especially neighbours. This may have fitness consequences through increased abilities to recognise and locate neighbours. As we have seen, the fact that patterns of song sharing are variable, and neighbours often do not share songs at above random frequencies (Slater & Ince, 1982), suggesting that this cannot explain song learning in all songbirds. (3) Learning allows genetic adaptation. This hypothesis is based on the assumption that dialect boundaries represent population boundaries, and that potentially costly hybridisation between populations is avoided. Again, we have already seen that there is little evidence that such phenomena are widespread. (4) Finally, Hansen (1979) proposed that cultural transmission allows individuals to choose songs that will transmit best in their given habitat. This has some empirical

support, although this is not found for all species. Catchpole & Slater conclude: 'the effect is not often a striking one, and it seems unlikely that this advantage of song learning would account for its widespread occurrence'. In fact, none of these theories possess the necessary generality to explain why bird song learning is so widespread. As cultural evolutionary theory has been used to investigate adaptiveness, it is reasonable to consider a new evolutionary explanation for song learning, based on cultural evolutionary theory, as I shall do here.

First, however, I should point out that this has been attempted before (Aoki, 1989). Aoki used a modelling technique standard to the field of gene-culture coevolution, deterministic analytical modelling, with no role for geographical variation in song, which unfortunately enforced stringent assumptions, which have led to it being rejected by researchers studying bird song learning (e.g. Kroodsma, 1996). As we have seen, in nearly all species of oscine studied, young males learn their song(s) from local adult males, with very limited, or no, preference for learning from fathers. In Aoki's (1989) model, though, one necessary assumption was that a substantial degree of vertical transmission must occur. Similarly, there is little evidence that females show preferences to mate with males singing a particular song type, as long as it is not abnormal (i.e. females impose only stabilising selection). Such a female preference was again a necessary precondition of Aoki's model. The only strong evidence of this phenomenon has been the brown-headed cowbird (West and King, 1985, 1986, 1988), which is unusual in that it is a brood parasite. Another putative example of female choice for certain song types that is often quoted is that of the white-crowned sparrow (Baker and Thompson, 1985). However, this result has been challenged by more recent experiments, (Baptista and Morton, 1988) which have shown no female preferences for particular song types at dialect boundaries.

1.5 Conclusions.

The aim of this literature review was to introduce the twin themes of song and culture with which this thesis is predominantly concerned. In the remaining chapters, I shall describe my attempts to apply gene-culture coevolutionary theory to bird song. This application has focused on one particular evolutionary puzzle, why do birds use

song learning? As described above this is a major unanswered question in the study of bird song. However, I hope that by illustrating the parallels between song learning and other examples of cultural transmission, this issue will also be of interest more generally to cultural evolutionary theorists. Among the wealth of empirical data that has been collected on bird song, our understanding of the roles of genes and culture in song ontogeny stands out. Although models with direct bias have been modelled, bird song is one of the only cases where the nature of this bias is at all well understood. Perhaps as a result of this lack of knowledge, previous models on the adaptiveness of culture have modelled the interaction in the most general way possible - without any definition of the nature of the genes underlying culture.

The thesis can also be divided between theoretical and empirical approaches. Chapters 2-4 are mathematical models, while the remainder describes preliminary attempts to justify and test these models. A successful evolutionary investigation requires both a strong theoretical ideas, and solid empirical facts. I hope this introduction has demonstrated that there are few potential investigations into the relationship between genes and culture whose prospects are as bright as those into bird song in these respects.

Chapter 2 The maintenance of vocal learning by gene-culture interaction: the cultural trap hypothesis

2.1 Abstract

Vocal learning has evolved in several groups of animals, yet the reasons for its origins and maintenance are controversial, with none of the theories put forward appearing to apply over a broad range of species. The theory of gene-culture coevolution is applied to this problem taking the specific case of the maintenance of song learning in birds. The interaction between genes underlying the filter for recognising and learning conspecific song, and the culturally transmitted songs themselves, sets up an evolutionary force that may maintain a role for vocal learning. I evaluated this hypothesis using a spatial simulation model. My results suggested that a wide range of conditions that maintain a role for vocal learning exists. Song learning may persist due to an evolutionary trap even though the average fitness in a population of learners may be lower than in a population of non-learners.

2.2 Introduction

Vocal learning is an impressive, and well-studied example of cultural transmission in non-human animals (Catchpole & Slater 1995). It seems to be ubiquitous in songbirds (Kroodsma & Baylis 1982), but does not occur in their closest relatives, the suboscines, and appears to have evolved separately in two other avian groups: hummingbirds and parrots, and four groups of mammals (see Janik & Slater, 1997). However no widespread functions for learning have been found. Questions about the evolution of song learning can be divided into those about its origin and those about its maintenance. In this paper I address the latter. While learning clearly facilitates the generation of large repertoires, thought to be sexually selected (e.g. Buchanan & Catchpole, 1997), many species of songbirds have relatively simple songs, with a single type or a small repertoire and no single clear reason has emerged to explain why learning is beneficial for them.

The development of song in oscine birds has been extensively studied: young males of most species produce normal songs only when exposed to conspecific song during a sensitive phase in ontogeny, and the resulting songs are usually a very precise copy of the tutor's. This system results in complex, and varying, patterns of cultural evolution (Lynch 1996; Payne 1996), and thus in geographic and temporal variation. Song learning results in several costs. Heterospecific song learning, although occasional, has been reported for many species (Helb *et al.* 1985). This is likely to hinder species recognition, as aspects of song known to be important in species recognition are learned in many species (Becker 1982). There is also the risk that a suitable tutor may not be available. The song then developed (isolate song) is discriminated against by the females of many species (Searcy 1992). Finally, song learning requires considerable investment in time before fully crystallised song is produced. To counter these costs, there must be selection maintaining learning. Specific functions for learning have often been proposed (e.g. habitat matching, Hansen, 1979; assortative mating, Nottebohm, 1972; and neighbour matching, Payne, 1982). However, while these hypotheses have been supported in some species, none apply to all. Indeed there are species such as the chaffinch (*Fringilla coelebs*) for which none of the existing hypotheses apply (Slater, Lachlan, & Riebel, *in press*), yet which require song learning for normal song development.

Gene-culture coevolution (Feldman & Cavalli-Sforza 1976; Boyd & Richerson 1985; Laland *et al.* 1993) examines the active role that cultural transmission can play in genetic evolution. Aoki (1989) provided the only previous attempt to apply this theory to the function of song learning. However, his model is highly restricted because it requires vertical transmission of song from father to son, for which there is evidence in only a very few species (see Catchpole & Slater, 1995). In most species that have been studied, learning appears to occur after independence, notably from territorial neighbours (Payne 1996).

In this paper, I describe a novel hypothesis to explain the how the roles of genes and culture in song might have evolved, and I then evaluate it using a simulation model. First, I introduce the theoretical framework on which the hypothesis is based.

2.3 A framework for investigating the evolutionary contest between genes and culture in song.

A realistic theoretical framework is important in the process of evaluating alternative evolutionary hypotheses, especially in complex situations, such as the interaction of genes and culture.

Fig. 2.1a suggests the nature of the interaction between genes and culture in song learning. In my model, I have simplified song variation to one dimension, the 'combined song variable'. Song learning occurs as males pick one value on this dimension. A genetic predisposition to learn certain songs exists (Marler & Sherman 1985; Mundinger 1995). This acts as a filter, normally ensuring that only species specific songs are learned. Within these limits, there is no preference for any particular song over any other. This pattern of neutral transmission of songs has empirical support (Lynch, 1996; Payne, 1996). Males can learn songs outside these limits, but their tendency to do so decreases progressively as the songs become more unusual. Again, this is based on empirical data: hand-reared birds can be trained to sing heterospecific song in the absence of conspecific song; and occasional heterospecific learning ('mixed singing') has been recorded for many species (Helb *et al.*, 1985).

Whereas species that socially learn their songs typically have a wide range of different song types, those that do not have highly stereotyped songs. In terms of a genetic predisposition, song learners might be represented by Fig. 2.1 a. In contrast, Fig. 2.1 c illustrates a situation where the genetic predisposition has become so narrow that only one type of song is preferred. At a population level, this situation is indistinguishable from one in which song is genetically predetermined. All individuals sing the same song, and culture plays no role in determining the phenotype. If cultural transmission was being outcompeted by genetic transmission, one might expect, therefore, that the width of the filter would become progressively narrower, until the situation in Fig. 2.1 c was reached. Conceivably, this could happen in one step. However, this is unlikely for such a complex system as song

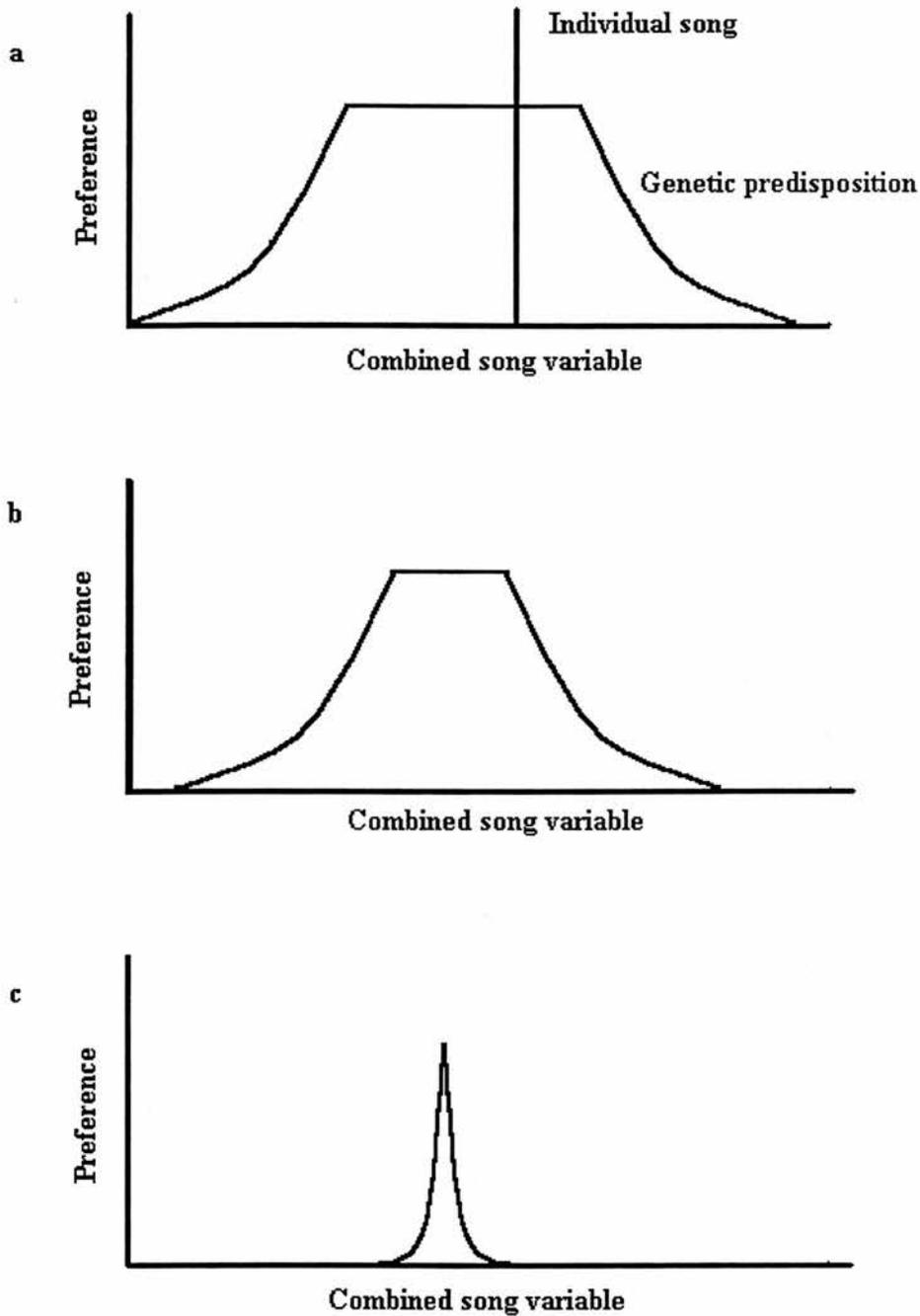


Fig.2.1. a: The relationship between the genetic filter and learning. The filter leads to variations in the preference of males to learn different songs. Males pick one value in this distribution, an example being shown by the vertical line, as a result of learning. a-c: The effects of learning would disappear if progressive narrowing of the filter took place.

learning, that must involve the actions of many genes. However, mutations in single genes could be the basis of narrowing or widening of this predisposition. My conclusion from this consideration is that when reduced widths of the predisposition are favoured, the role of culture is being eroded at the expense of genetic transmission. Therefore, to assess whether cultural transmission is favoured, the relative success of genes that either narrow or widen the genetic predisposition should be measured.

Even if wider genetic filters are favoured, the width of the filter cannot continue to increase indefinitely. It seems plausible that various costs to song learning might rise as the filter width increases. These costs include interspecific confusion, but possibly also metabolic costs associated with larger brains (only if wider filters entailed larger brains). This is likely to create stabilising selection, but to assess this, it is necessary to include a direct fitness cost to possessing a wider filter in some part of the test.

2.4 The ‘cultural trap’ hypothesis for the evolutionary maintenance of song learning

We have developed a hypothesis to explain the evolutionary maintenance of song learning within the framework described above. The cultural trap hypothesis is based on gene-culture coevolutionary theory, and is named because learning is maintained in an evolutionary trap formed by the interaction between genes and culture. While in most species only males sing, I assume that females also inherit filters, used to recognise songs as belonging to conspecifics who might be potential mates, using the same limits within the filter. This assumption seems reasonable since, under hormone treatment, females can be induced to sing (e.g. Pohl-Apel & Sossinka, 1984); they also possess many of the brain structures known to be involved in song learning (Nottebohm & Arnold, 1976). The most impressive piece of evidence for the shared genetic basis of song recognition between the sexes, however, is that the species specificity of females’ sexual responses to male song in canaries is removed by a lesion of the Higher Vocal Centre (Brenowitz, 1991). The HVC is part of both the learning and production pathway of song by males (Slater & Catchpole, 1995). However, it must be emphasised that the

assumption that the genetic basis of song recognition in males and females is the same is critical to the cultural trap hypothesis, and has not been subjected to a direct test as yet.

The hypothesis assumes a population in which all individuals learn their songs. Song learning is determined by a genetic filter of similar form to that in Fig. 2.1, and the only changes in fitness resulting from learning one song or another is imposed by female choice, which is also determined by the genetic filter. I assume an oblique mode of cultural transmission and that new song types arise through cultural mutation (random changes in the song). I compare the success of two alleles. The 'wide' allele causes the genetic filter to be wider than does the 'narrow' allele. There exist, therefore, four classes of individual in the model: males and females, each with wide or narrow allele. Males with the wide allele have the potential to learn songs outside the filters of narrow allele females. If they do so, they may not be recognized by potential mates. When that happens, both the male with the wide allele, and the female with the narrow allele will pay a cost resulting from a lost mating opportunity. Under normal circumstances, it might be expected that this would affect the success of both alleles equally.

My hypothesis compares the conditions when one or other allele is uncommon. This approach was introduced at the outset of gene-culture coevolutionary models by Feldman & Cavalli-Sforza (1976), and has been used in many subsequent models of this type (e.g. Aoki, 1989). When the wide allele is rare, males possessing that allele will be likely to copy songs from the more common narrow allele males, and will thus be recognised by all females present. But when the narrow allele is rare, it is likely that many of the common wide allele males will be singing songs that cannot be recognized by the narrow allele females, and these females will thus be selected against. I therefore predict that the narrow allele when rare will become extinct more frequently than the wide allele when rare. Overall, the wide allele should be more successful than the narrow allele, and under the terms of the framework outlined in Section 2.3, this is sufficient to promote song learning.

2.5 Description of the model

The aim of my model is to assess whether the cultural trap hypothesis outlined above is likely to generate a significant bias in favour of the wide allele in conditions that are realistic for bird song cultural transmission. We have used a spatial simulation model of cultural transmission (Williams & Slater 1990) which consisted of a grid, in which each location corresponded to the territory of one pair. Key to my hypothesis is the distribution of unusual songs. Since spatial dynamics are crucial to the cultural transmission of bird song (Slater, 1989; Lynch, 1996), my model therefore has to include them although I also discuss a simpler non-spatial model. We modelled only essential aspects of the life cycle (recruitment, reproduction and death), as well as processes of song learning. These were then iterated for each territory in steps corresponding to 1 year. The simulation was loosely based on data available for the chaffinch (*Fringilla coelebs*). Although this species has a repertoire of 1-6 song types (meaning each male sings between 1-6 distinguishable songs), a repertoire of 1 song type was imposed in this model, for simplicity. The simulations were conducted in 12 sets, labelled 'a' to 'm' in the text, Table 2.1 and in Fig. 2, in each of which variations in different parameters were examined. The list of parameters varied is given in Table 2.1. The iterated procedures, and sets of parameters that I tested were as follows:

1. Mortality. The probability of mortality was equal for all individuals. For set (f), the rate of mortality was varied from 0.05 to 0.5; for others it was kept at 0.4 (Goodfellow & Slater, 1986). In set (e), a fixed mortality cost was applied to all individuals possessing the wide allele. The value of this cost, which was added to the normal mortality rate (0.4) was varied from 0.005 to 0.02.
2. Male dispersal. An empty territory could be filled by one of the offspring of the previous year or earlier of a pair in another territory. Dispersal was not biased in any other way. In set (d), increased male dispersal was examined. Here, the maximum number of territories a male could cross in dispersal was varied from 1 to 4 territories. The probability of dispersing over a given number of territories was equal for all these distances. In a final condition, males could disperse from anywhere

Table 2.1 List of parameters varied in the simulations

Data Set	Parameter varied	Range parameter varied over	Default parameter value
a	dispersal (songs, females, and males combined)	1-4-entire population	1
b	song learning distance	1-4-entire population	1
c	female dispersal	1-4-entire population	1
d	male dispersal	1-4-entire population	1
e	mortality cost to wide allele	0.005-0.2	0
f	mortality rate	0.05-0.5	0.4
g	population (grid) size	200-1250	200
h	initial frequency of 'mutant' allele	0.01-0.5 (2-100 individuals)	0.2 (40 individuals)
i	cultural mutation rate	0.005-0.2	0.1
j	proportion of songs expected to be 'normal'	0.9-0.1	0.6
k	ratio narrow : wide of filter widths	0.9-0.2	0.6
m	probability of mating with male with recognized song	0.6-1.0	0.7

within the population. In all cases, every empty territory was always taken over by a new male, so that the population of males remained constant in size.

3. Song learning. Males learned song in their first year from any one of their neighbours. The computer sampled all neighbours, in random order, and the most preferred song was learned. When songs of equal attractiveness to a male were encountered, the first that was sampled was chosen. In set (b), increased song learning distances were examined. Here, songs could be learned from a varying maximum distance, from 1 to 4 territories, and the probability of learning songs from among these distance was set to be equal. In a further condition, songs could be learned from any male in the population. Preference for songs was governed solely by the genetic predisposition for song. The form of the predisposition, shown in Fig. 2.1a is described in equations 1-3. Equation 3 describes the central flat part of the graph, while equations 1 and 2 describe the curves on either side. These equations describe the preference, P , that a bird shows for learning a song with a value x as follows:

$$[1] \quad \text{If } x < \min \text{ then } P = \frac{\text{prop}}{\max - \min} \times e^{\frac{2 \cdot \text{prop} \cdot (x - \min)}{(1 - \text{prop})(\max - \min)}}$$

$$[2] \quad \text{If } x > \max \text{ then } P = \frac{\text{prop}}{\max - \min} \times e^{\frac{2 \cdot \text{prop} \cdot (\max - x)}{(1 - \text{prop}) \cdot (\max - \min)}}$$

$$[3] \quad \text{If } \min \leq x \leq \max \text{ then } P = \frac{\text{prop}}{\max - \min}$$

where,

min & max are the minimum and maximum limits of the plateau within the filters; prop is the proportion of songs in a given population expected to fall within the limits of the filter. In set (j) this was varied from 0.9 to 0.1.

The wide or narrow alleles change the values of 'min' and 'max' such that the wide allele has a larger range between the two. The midpoint of the two was kept constant. These conditions allowed us to examine overall widening or narrowing of the filter. Set (k) examined the relative value of the min-max range for narrow and wide alleles. The narrow : wide ratio for this value was varied between 0.9 and 0.2.

4. Cultural mutation. Variation in songs was introduced by including occasional random mutation following the learning process. The rate of cultural mutation was varied from 0.005 to 0.2 in set (i), in all others, it was 0.1 (Slater & Ince, 1981). Mutation altered the song score randomly, over a range of 0.2 of the min-max range of the genetic predisposition.

5. Mating. An unmated male territory holder could mate with the offspring of any neighbour, given that those neighbours had been mated the previous year. Set (c) examined increased female dispersal, as was done for male dispersal (set d). Each year, each male had one mating opportunity. Mating was affected by the allele possessed by the female - i.e. whether she recognised the song, using equations 1-3

as before. The probability of mating, even if a male's song had been recognised, was varied from 0.6 to 1.0, in set (m), and was kept at 0.7 elsewhere.

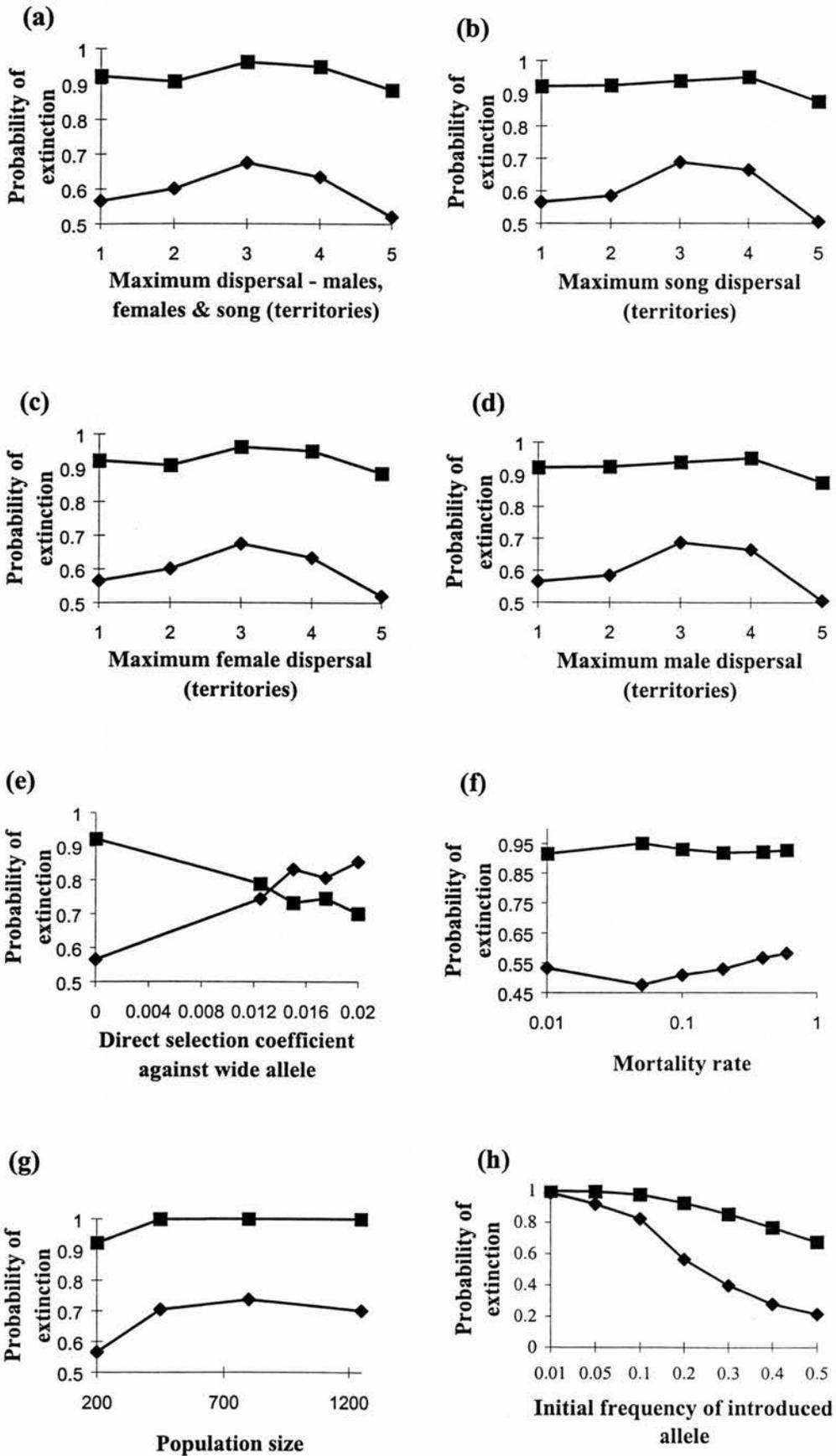
6. Inheritance. The inheritance of wide or narrow alleles by males and females followed a simple haploid scheme; i.e. the probability of inheriting the allele from each parent was 0.5.

7. Grid size. The size of the grid was 10 x 10 territories, except in set (g), where this was varied from 10 x 10 to 25 x 25 territories. In set (a), increased dispersal of males, females and songs together was examined. When dispersal was set to '5', all males, females and songs in the whole population were sampled. This made the model non-spatial.

8. A running in period of 500 years preceded the start of all simulations. This period was experimentally established to be long enough for a steady-state level of cultural diversity to be reached after random seeding. The simulation was started by the introduction into the population of 20 individuals (in two rows of 10), of the opposite type to the rest. In set (h), the initial frequency of 'mutants' was investigated. Here the initial frequency was varied from 0.05 to 0.5, corresponding to 0.5 to 5 rows of 10 territories. 2000 runs were carried out for each parameter setting: 1000 in which the wide allele was introduced into a population of narrow alleles, and 1000 with narrow alleles introduced into populations of wide alleles. Each run proceeded until one or other allele became extinct, or until 10000 years had passed. Fixation within this time-span occurred in all simulations, except when a very low mortality rate was set. This was clearly an artefact of the conditions rather than biological polymorphism. The results of the model were analysed simply by recording the number of instances of extinction of either allele in each condition.

2.6 Results

Fig. 2.2 summarises the results, and indicates that the wide allele was more successful than the narrow allele under nearly all conditions.



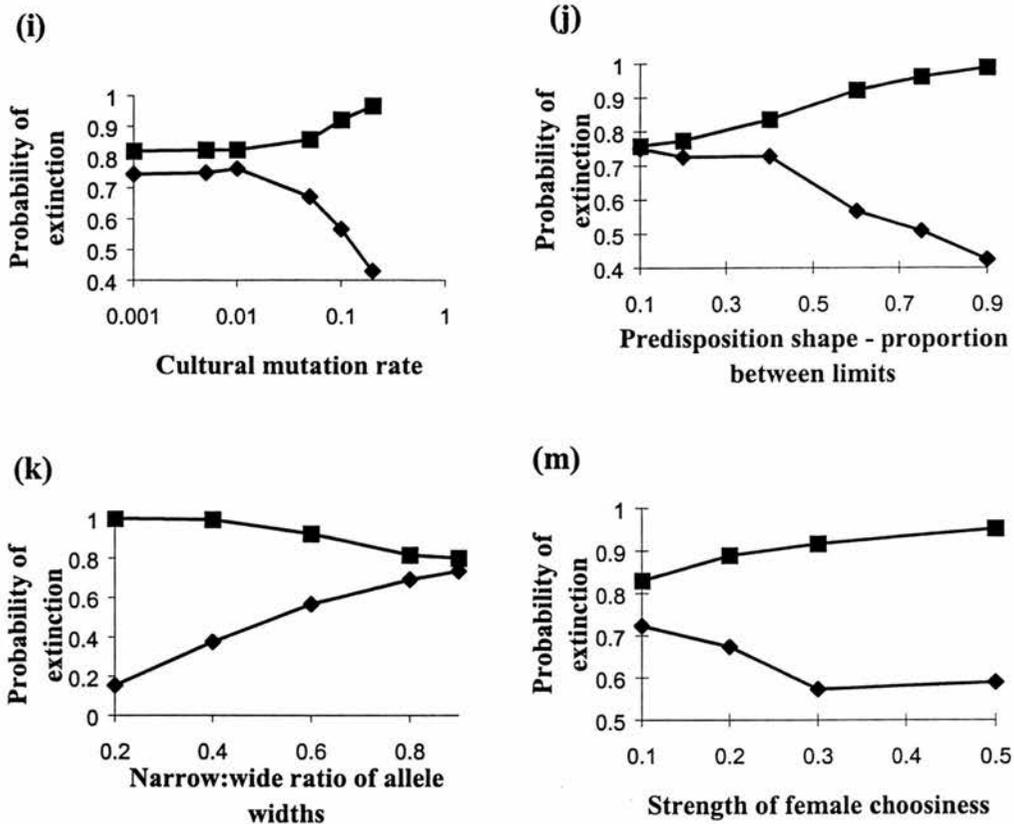


Fig. 2.2 The relative success of wide and narrow alleles under the various parameters tested. In all cases, the squares represent invasion by the narrow allele, and the diamonds invasion by the wide allele. The y-axis represents the probability that the invading allele will become extinct. See section 4 ('Description of the Model') for further details on the parameters.

over all ranges of dispersal - including the simple case (point '5') where the spatial element of the model was removed altogether (Fig. 2.2a). Dispersal of three territories produced the smallest difference between the two alleles. Figs. 2.2b-2.2d show a similar pattern when male, female, and song dispersal were considered independently. Again, dispersal of three territories produced the smallest difference between success of the alleles in all these graphs. Overall, variations in dispersal had only a small effect on the difference between the alleles.

A direct selection coefficient of around 0.013 was required to remove entirely the difference between the alleles (Fig. 2.2e). This strength of selection would be adequate for rapid evolutionary change, indicating that the effect of the cultural trap hypothesis is significant.

Varying mortality rate had only a small influence on the effect (Fig. 2.2f). Lower mortality rates tended to increase the difference between the alleles slightly - except for the lowest value, 0.01. This may have been because this was the only condition under which significant numbers of runs did not reach fixation within the allotted maximum time of 10000 years. Similarly, population size only had a small influence on the outcome (Fig. 2.2g). The success of the wide and narrow alleles slightly decreased at larger population sizes. However, it should also be borne in mind that the number of genetic mutations in the allele would also be expected to increase in larger populations. Therefore, one would expect wider predispositions in larger populations. Low initial starting frequency did clearly reduce the success of both alleles (Fig. 2.2h). However, even when the initial starting frequency was just 0.01 (i.e. 1 territory), the narrow allele succeeded in invading the population just once in the 1000 runs, whereas the wide allele succeeded in invading the population from this starting frequency 14 times in its 1000 runs.

Higher cultural mutation rates increased the difference in success between wide and narrow alleles (Fig. 2.2i). At values of 0.01 or less, only a small difference in the success of the two alleles was found. The graph probably did not converge further at the lowest values of mutation because there was not enough time from the random seeding of songs for a steady state rate of cultural variation to be established. The shape of the predisposition also had a marked effect on the outcome (Fig. 2.2j). For higher values of this score (which corresponded to nearly rectangular predisposition shapes), the success of the wide allele was greater. For low values of this score (which corresponded to nearly flat predisposition shapes), there was very little difference between the two. Given the low frequency of birds singing markedly unusual songs, a value near the high end of this range is to be expected. If Helb *et al's* (1985) estimate of the rate of heterospecific song learning (0.001) is accurate, then my default value of 0.6 may be considered conservative. The relative widths of the wide and narrow allele also affected the outcome markedly (Fig. 2.2k). The wider the relative width of the wide allele, the larger its relative success. However, it seems likely that the costs to the wide allele are likely to increase with its relative width, countering this to some extent.

Finally, female choosiness had a small influence on the outcome (Fig 2.2m). This value corresponded to the probability that a female would not mate with a male that she recognised, and therefore also indicated the relative importance of song recognition in mating. The choosier the females (i.e. the greater the role that song recognition played in mating), the greater the success of the wide allele. This makes sense, since female mate recognition drives the success of the wider alleles in my hypothesis.

2.7 Discussion

The arguments presented in this chapter run on two levels. I first presented a general framework under which song learning might be maintained. If wider genetic filters underlying song arise, cultural transmission can play an important part in shaping the song phenotype. In contrast, if the filters progressively narrow, the phenotype will eventually be determined entirely by the underlying genes, because no cultural variation could exist. Secondly, I described one hypothesis for how the wide allele could be more successful than the narrow. The cultural trap hypothesis proposed that the interaction between genes and culture alone might be sufficient to widen filters without learning leading to an increase in the average fitness in a population. The simulation model then examined some of the conditions under which the cultural trap hypothesis might exist. It found that an allele that widened the filter was more successful than a narrow allele over a broad range of conditions, therefore providing support for the hypothesis,

How might the assumptions and limitations of the hypothesis and simulation reflect on their applicability to the real world? Two key assumptions are the shared genetic basis of song recognition between the sexes, and an oblique mode of cultural transmission. Without the former, there would be no bias towards wider alleles in males. The necessity of oblique transmission is less clear-cut. A purely vertical transmission system would presumably remove the effect of the cultural trap hypothesis, because the distribution of songs sung by wide-filter males would not depend on the frequency of the wide filter in the population. The degree of vertical or possibly horizontal transmission required for the cultural trap to come into effect is unclear. Several aspects of the simulation also limit its realism. The haploid pattern

of genetic transmission would be unlikely to affect the results of the simulation unless dominance of one or other allele existed. Secondly, the preferences of males for alternative songs to copy may not be absolute, but in proportion to the genetic predisposition. As a result of this, wide males might copy more unusual songs than narrow males. However, a preliminary study suggested that this did not alter the results of the model, since the rule would apply both to narrow and wide filter males. Overall, while the limitations of this model require caution, it is possible that the cultural trap hypothesis may apply to a wide range of songbird species.

Previous models of the adaptiveness of culture have concluded that culture can out-compete genetic transmission only under extreme transmission rules (Cavalli-Sforza & Feldman 1983), or high environmental variability (Boyd & Richerson 1988), because of the higher fidelity of genetic transmission. By contrast, in my model, it is the low fidelity of cultural transmission that enables it to avoid replacement by genetic transmission. This difference occurs because any cultural trait is only selected against in certain contexts in my model, and because I assume the graded evolution of a genetic predisposition, as opposed to the direct replacement of a cultural trait with a genetic one.

Our results add to the debate as to whether 'maladaptive' cultural traits can survive in populations (Laland, 1996; Galef, 1996). The cultural trap hypothesis proposes that the evolution of a wider filter leads to no increase in average fitness. Moreover, since set (e) showed that the cultural trap effect can overcome significant levels of direct selection against the wide allele, the coevolved traits of unusual songs and wider filters must even be regarded as having the potential to be maladaptive.

Other hypotheses that suggest an adaptive benefit for song learning (Hansen, 1979; Nottebohm, 1972; Payne, 1982) are not excluded by the results. Indeed, it is probable that evolution has led to the exploitation of socially learned information. However, under the framework, it is not certain that any of these hypotheses would be sufficient to prevent song learning becoming increasingly constrained by genetic filters.

One goal of this research was to provide a testable hypothesis for the evolution of genetic filters. Our results indicate that variations in patterns of cultural evolution, especially cultural mutation rate, alter the success of wider predispositions. In general, factors that increased cultural diversity increased the success of the wide allele. The rate at which birds make mistakes in learning might be influenced by ecological variables such as population density, and degree of isolation, both of which would be likely to limit experience. If higher cultural mutation rates, or other factors that promote cultural diversity, do indeed lead to wider filters, then the hypothesis will be supported.

Chapter 3 Evolution of cultural communication systems: The coevolution of a cultural signal and a genetic filter.

3.1 Abstract

The coevolution of genetic filters that predispose individuals to recognise conspecific song, and culturally transmitted communication traits is analysed using deterministic population genetics models. Random cultural variation and mutation lead to selection of less restrictive filters, whereas selection of cultural conformity leads to selection of more restrictive filters. These results are discussed with reference to the origin and maintenance of song learning in birds, and the evolution of language. A further model examines the interaction of genes and culture in the vocal convergence of two species. Vocal convergence can only occur when the cost of mis-recognising heterospecifics as conspecifics is much lower than the cost of failing to recognise conspecifics.

3.2 Introduction

Cultural communication systems arise when signals are acquired by social learning between individuals. The most familiar examples of this are song learning by oscine birds (see Catchpole & Slater, 1995) and human language. There has been continued interest in the evolution of these types of communication (e.g. Pinker, 1994; Deacon, 1997; Nowicki *et al*, 1998). However, only a few studies (Aoki and Feldman, 1987, 1989, 1991; Aoki, 1989; Feldman & Aoki, 1992), have taken into account the evolutionary nature of culture.

The coevolutionary relationship of genetic and cultural transmission has been explored in a number of general models (Feldman & Zhivotovsky, 1992). These models have extended the techniques of theoretical population genetics to cultural transmission, drawing on the often noted analogies between the two forms of transmission. Both genes and culture are transferred between individuals. Differences between traits may have fitness consequences, which natural selection or cultural selection (arising from preference to learn one trait over another) can operate on. This evolutionary nature of cultural transmission has been highlighted in a number of anthropological studies

(Cavalli-Sforza *et al.*, 1982; Durham, 1991) and in some research on animal behaviour (Galef, 1988; Kawai, 1965; Laland & Plotkin, 1990; Laland *et al.* 1995, Lynch, 1996; Payne, 1996; Slater *et al.* 1980). Inclusion of cultural transmission in theories for the evolution of behavioural traits makes it clear that culture can play an active role in shaping genetic evolution (Feldman & Cavalli-Sforza, 1976; Boyd & Richerson, 1985). Gene-culture coevolution has been implicated in the evolution of various human genetic traits, including adult lactose tolerance (Aoki, 1986; Feldman & Cavalli-Sforza, 1989; Durham, 1991), and sickle cell anaemia (Durham, 1991).

While it is obvious that cultural innovation might give rise to completely new behaviours and skills, without the involvement of genes, some behaviours appear to have strong genetic bases in some animals, but have been regarded as having a strong cultural component in others. A behavioural ecological response to this is to ask why should genes surrender their control over the development of the phenotype to another evolving entity? There have been three hypotheses generated by those studying cultural evolution:

(1) Genes have not given up any of their dominion, and cultural variation is determined by genetically encoded filters (Lumsden & Wilson, 1981).

(2) Cultural transmission might be the form of information acquisition best tuned to a given set of conditions. Boyd & Richerson (1985, 1988) compared the 'adaptiveness' of transmission systems under different environmental conditions - in essence measuring the ability of the transmission systems to track environmental change. They found that culture did prove more adaptive at higher levels of environmental variability. On the other hand, Boyd & Richerson (1988) also showed that if the environment changes too rapidly, there is again no advantage to cultural transmission; what is learned, although beneficial at an earlier time, may be wrong for the environment next faced by the learner.

(3) There may be competition between cultural and genetic transmission. Cavalli-Sforza and Feldman (1983) considered the competition between genetic and cultural transmission of an adaptive skill. They found that under most modes of transmission, genetic transmission out-competed cultural transmission, because of the higher fidelity

of the former. However, the very rapid cultural transmission in such situations as ‘one-to-many’ transmission (Cavalli-Sforza and Feldman 1981), can enable culture to overcome genetic transmission.

Song learning by birds has long been recognised as a classic example of cultural transmission (see Catchpole & Slater, 1995; Kroodsma & Miller, 1996 for recent reviews). Songs are learned with remarkable accuracy, and song traditions can last for a number of generations (Payne, 1996; Harbison *et al*, 1999). The mode of transmission is most often oblique (see Catchpole & Slater, 1995). This means that birds learn their songs from a member of the parental generation other than the parent (Cavalli-Sforza, 1981). Moreover, social learning appears to be obligate in almost all species (but see Kroodsma *et al*, 1997, 1999); individuals that are deprived of conspecific song during development produce songs that differ markedly from normal (Kroodsma & Baylis, 1982).

Cultural evolution in bird song has been most successfully fitted to models analogous to genetic drift. Lynch (1996) found that song types are selectively neutral with respect to each other in a range of species, using a statistical analysis based on an “infinite alleles” model. Another feature of bird song appears to be random patterns of change, as shown by studies which have used patterns of cultural variation in both space and time to investigate the ‘mutation-rate’ (Slater *et al*, 1980) or turnover rate (Payne, 1996) of song types.

Genes have been recognised as playing an important role in the development of song learning. Genetic filters that predispose learning towards the songs of conspecifics (Marler & Sherman, 1985; Mundinger, 1995) have been demonstrated for several species. This is of interest, since the most obvious use of the socially learned information is for conspecific recognition (Becker, 1982), begging the question of why the filter does not provide all the information for song acquisition.

The communicative function of song has been the subject of much research, and the two functions, of repelling competing males and attracting mates, appear to apply to many species. However, it is not clear why learning is required to achieve these goals. Several hypotheses have been proposed: The matching hypothesis predicts that birds

benefit from sharing songs with neighbours through improved recognition and territory maintenance, and that this sharing can only be achieved through learning (Payne, 1982; Brown & Farabaugh, 1997). Alternatively, sexual selection for complexity, in the form of large repertoires, exists in some species (e.g. Buchanan & Catchpole, 1997). Constructing large repertoires may require learning. However, many species do not have large individual repertoires, and many do not match their neighbours. The great variation in song learning strategies would appear to preclude a single functional explanation, yet the ubiquity of song learning within the oscines (Kroodsma & Baylis, 1982) remains unexplained.

The arguments for the evolution of culture, based on general cultural evolution theory, are not adequate to explain the maintenance of song learning. If genes completely controlled song learning why should there be so many alternative traits? Moreover, heterospecific song learning should be non-existent, and the energetic and time costs associated with learning, combined with the lack of obvious adaptive benefits to it, is unexplained. Similarly, the hypothesis that song learning might follow environmental variation more efficiently (Hansen, 1979) is only occasionally supported by empirical data (Catchpole & Slater, 1995). Finally, the apparent selective neutrality of alternative song types means that it is unlikely that cultural evolution could outcompete genetic evolution in the acquisition of a skill (Cavalli-Sforza & Feldman, 1983).

While differing enormously in many respects, human language has several important features in common with bird song (Saiton & Maekawa, 1992; Marler, 1981). First, it is a culturally transmitted trait, although biological filters for language features appear to exist. The exact nature of these filters is not known, but there is evidence that at least some of them act in a similar way to those involved in bird song. A well-known example of this is in the categorical perception of phonemes by young infants. Here, pre-linguistic, neonatal infants exhibit the same tendency as adults to divide speech sounds (e.g. different consonants) that lie along acoustic continua into discrete categories, and recognise 'best' exemplars of these categories (Eimas *et al*, 1987). The fact that infants from different cultures do not vary in their perception, while adults do indicates a possible genetic bias to this behaviour. A second feature in common is that

bird song types or human languages both appear to be selectively relatively neutral with respect to alternative songs or languages, respectively.

This paper describes deterministic population genetics models of the interaction between genetic filters and culturally transmitted signals. As opposed to the models of Aoki & Feldman (Aoki, 1989; Aoki & Feldman, 1987; 1989; 1991; Feldman & Aoki, 1992), which examine the acquisition of inherently fitter ‘skills’, I assume that fitness differences between phenotypes only arise through the effect of their genetic filters on the outcome of interactions between individuals. My aim is to capture the apparent neutrality of alternative cultural communication traits within a system. These models are similar in some respect to the simulation studies in Chapter 2, but are more general in structure. The use of analytical models requires some simplification of the underlying processes described by the simulation models, but it permits generalisations to be made about the properties of the models over a wide range of parameter values. Moreover, while the simulation described in Chapter 2 was largely confined to territorial songbirds, a more general setting is important if the cultural trap hypothesis can be extended to other vocal learners, such as group living birds and mammals.

3.3 Model 1: inter-sexual interactions

This is the most literal deterministic transliteration of the simulations described in Chapter 2, investigating the ‘cultural trap’ hypothesis. Selection in the simulation model was created by females, whose mate choice was biased by their genetic filters. New song types, that might be discriminated against, arose at random by the process of cultural mutation, which corresponds to innovation or miscopying. The simulations indicated that populations with less restrictive filters – filters that allowed individuals to recognise and learn a wide range of songtypes – were unlikely to be invaded by birds with restrictive filters. It was suggested that the reason for this rather counterintuitive result was that there were costs to females with more restrictive filters (who would fail to recognise potential mates) and to males with less restrictive filters (who would not be recognised by some females, if they learned certain songs) when they were rare. Here, I generalise and mathematically explore this earlier model.

Consider a haploid population with two alleles, **A** and **a**, which affect the genetic filter to learn and recognise culturally transmitted traits. There are two cultural traits: **1** and **2**. These alternative cultural traits might correspond to two individual songs, or they might each correspond to a set of songs. For reasons of brevity, they shall be referred to as ‘songs’ in the remainder of this paper. Allele **A** allows learning of song **1** only, whereas allele **a** allows learning of either song **1** or song **2**, but any individual can only learn one song, and only males learn songs. In addition to influencing males’ song learning, the alleles also influence the mating preferences of females. Females with allele **A** prefer song **1**, whereas females with allele **a** do not have a preference for one song or the other. The strength of this preference is measured using a parameter s ; females with **A** discriminate against males singing **2** at the rate $(1-s)$. The transmission of songs is oblique. Males sample the whole population of their parents’ generation, and choose which song to learn using the frequency of songs in the parental generation, and their own genetic filter. Having learned a song, cultural mutation of song **1** into song **2** occurs with frequency μ_1 , and cultural mutation of song **2** into song **1** occurs with frequency μ_2 . The sex ratio at birth is even, and the alleles **A** and **a** are equally likely to be transmitted from an **A** \times **a** mating. Given this scenario, 6 phenogenotypes (allele-cultural trait combinations) can be defined: **A1** (male), **A2** (male), **a1** (male), **a2** (male), **A** (female), and **a** (female). The frequencies of these phenogenotypes are defined as x_1 , x_2 (which is by definition always 0), x_3 , x_4 , x_5 and x_6 respectively. Haploidy simplifies the analysis, but the results should be similar to those for diploids at least in the case of directional selection (this has been found for other gene-culture coevolutionary models of similar structure - e.g. Cavalli-Sforza & Feldman, 1983; and applies particularly in the absence of dominance).

The model was analysed by studying the change in phenogenotype frequencies from one generation to the next. These changes were expressed in a set of recursion equations which show the frequencies of phenogenotypes in one generation (denoted by ‘) as functions of the phenogenotype frequencies in the previous one, incorporating the assumptions described above. The recursion equations describing the changes in phenogenotype frequencies between generations for this system are:

$$D.x_1' = \frac{1}{4}(x_1.x_6 + 2.x_1.x_5 + x_3.x_5 + (1-s).x_4.x_5) \quad (1a)$$

$$D.(x_1 + x_3 + x_4).x_3' = \frac{1}{4}[(1-\mu_1)(x_1 + x_3) + \mu_2.x_4](x_1.x_6 + 2.x_3.x_6 + x_3.x_5 + 2.x_4.x_6 + (1-s).x_4.x_5) \quad (1b)$$

$$D.(x_1 + x_3 + x_4).x_4' = \frac{1}{4}[\mu_1(x_1 + x_3) + (1-\mu_2)x_4](x_1.x_6 + 2.x_3.x_6 + x_3.x_5 + 2.x_4.x_6 + (1-s).x_4.x_5) \quad (1c)$$

$$D.x_5' = \frac{1}{4}(x_1.x_6 + 2.x_1.x_5 + x_3.x_5 + (1-s).x_4.x_5) \quad (1d)$$

$$D.x_6' = \frac{1}{4}(x_1.x_6 + 2.x_3.x_6 + x_3.x_5 + 2.x_4.x_6 + (1-s).x_4.x_5) \quad (1e)$$

where,

$$D = x_1.x_5 + x_1.x_6 + x_3.x_5 + x_3.x_6 + x_4.x_6 + (1-s).x_4.x_5$$

In these recursions, the denominator, $4D$ is the sum of all possible matings, and is used to ensure that the allele frequencies still sum to 1 (after some matings are lost because of s). A similar convention is used in (1b) and (1c) where the sum of male allele frequencies is required, because the choice of which song to sing by male **a** birds is dependent on the frequencies of songs sung in the population.

Under this system, the sex ratio will remain constant at 1. As a result, the frequency of **A** will remain constant at $2.x_1$ and the frequency of **a** at $2.x_6$. Therefore, from (1a) and (1e),

$$|x_1' - x_6'| = \frac{|x_1 - x_6|}{4 \cdot D} \quad (2)$$

Since $4D < 1$ if $s > 0$, the frequencies of **a** and **A** will always diverge. As a result, there are no stable equilibria where both alleles occur.

The implications of equation (2) are that there is only one set of internal equilibria, occurring where the frequency of the two alleles a and A are equal. This was confirmed in a simulation of the recursion system (1). Here, a search of the feasible parameter space for equation system (1) revealed three equilibrium points, $a=1, A=0$; $a=A$; and $a=0, A=1$. Only the two trivial equilibria are stable.

The following phenogentype frequencies occur when $a=1$:

$$\begin{aligned}\hat{x}_1 &= 0 \\ \hat{x}_3 &= \frac{\mu_2}{2(\mu_1 + \mu_2)} \\ \hat{x}_4 &= \frac{\mu_1}{2(\mu_1 + \mu_2)} \\ \hat{x}_5 &= 0 \\ \hat{x}_6 &= \frac{1}{2}\end{aligned}\tag{3}$$

The stability of this equilibrium was tested by adding a small perturbation, ε_i , to each equilibrium phenogentype frequency, and calculating whether the recursion equations led to the phenogentype frequencies returning to the equilibrium values, and how quickly. I defined the perturbations as small enough to ignore products between them, creating a tractable linear system. The system of equations becomes:

$$\varepsilon_1' = \frac{1}{2} \left[\varepsilon_1 + \frac{\mu_2 + (1-s)\mu_1}{\mu_2 + \mu_1} \cdot \varepsilon_5 \right]\tag{4a}$$

$$\varepsilon_5' = \frac{1}{2} \left[\varepsilon_1 + \frac{\mu_2 + (1-s)\mu_1}{\mu_2 + \mu_1} \cdot \varepsilon_5 \right]\tag{4b}$$

The leading eigenvalue of (4) is :

$$1 - \frac{s\mu_1}{2(\mu_1 + \mu_2)} \quad (5)$$

Hence this equilibrium will be stable for all positive values of s , μ_1 , and μ_2 .

When $A=1$, the phenogenotype frequencies are:

$$\begin{aligned} \hat{x}_1 &= \frac{1}{2} \\ \hat{x}_3 &= 0 \\ \hat{x}_4 &= 0 \\ \hat{x}_5 &= \frac{1}{2} \\ \hat{x}_6 &= 0 \end{aligned}$$

Using the same technique to determine stability, the following linear system of equations resulted:

$$\varepsilon'_3 = \frac{1}{2}(1 - \mu_1) \cdot (\varepsilon_3 + (1 - s) \cdot \varepsilon_4 + \varepsilon_6) \quad (6a)$$

$$\varepsilon'_4 = \frac{1}{2}\mu_1 \cdot (\varepsilon_3 + (1 - s) \cdot \varepsilon_4 + \varepsilon_6) \quad (6b)$$

$$\varepsilon'_6 = \frac{1}{2}(\varepsilon_3 + (1 - s) \cdot \varepsilon_4 + \varepsilon_6) \quad (6c)$$

The leading eigenvalue of this system is:

$$1 - \frac{s\mu_1}{2} \quad (7)$$

Therefore this equilibrium will also always be stable. However, since $\mu_1 + \mu_2 < 1$, equilibrium 1 (a fixed) will be approached more rapidly than equilibrium 2 (A fixed) following a perturbation.

Simulations of this system indicated that the areas of global attraction for the two trivial equilibria are equal. However, it might be expected that repeated perturbations to either equilibrium might eventually lead to the system switching from one equilibrium to the other and that (because of the differences in eigenvalues for the two equilibria) this switch is more likely to occur from the equilibrium where a is fixed than the one where A is fixed.. This is compatible with the predictions of the cultural trap hypothesis. To determine whether such switching would actually occur, I carried out a further series of simulations.

The simulation modelled the recursion system (1). Initial starting conditions were the stable equilibrium positions. A small perturbation of 0.06 in allele frequency was added at the beginning of the simulation. The simulation then cycled through the recursions until fixation occurred. Further perturbations of 0.06 occurred at random intervals with a probability of 0.2 per generation. These perturbations altered the allele frequencies by the same amount, but were equally likely to add or take away from either allele. For the case of x_3 and x_4 , the effects of the perturbations were divided between the two in proportion to their frequencies. Parameter values of $\mu_1 = 0.05$, $\mu_2 = 0.05$, and $s = 0$ were used as default values, and these three parameters were varied independently. 10000 replicates of each parameter setting were carried out, starting from both stable equilibria. The proportion of simulations which resulted in fixation of the alternative allele was recorded.

Fig. 3.1 shows the results of the simulation. As predicted, the A equilibrium was more likely to switch to the a equilibrium than vice versa.. Increasing the cultural mutation rates, and the value of s both increased the difference in success between the two alleles.

Fig. 3.1a

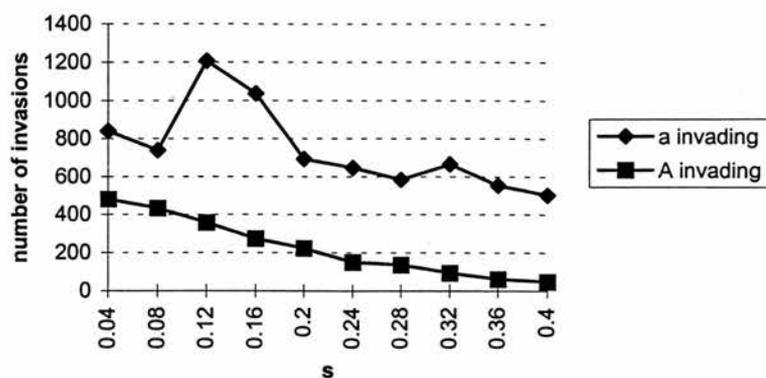


Fig. 3.1b

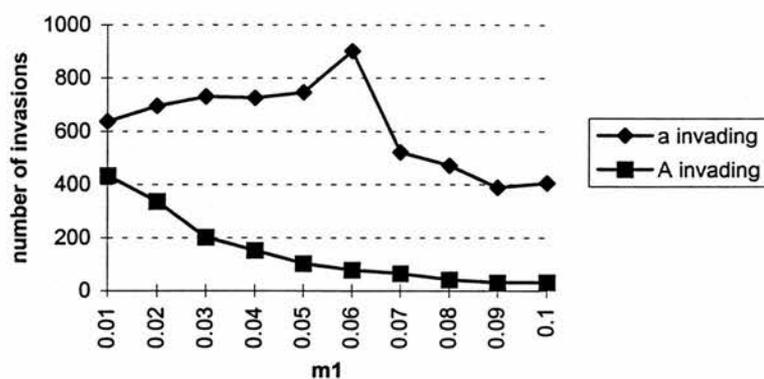


Fig. 3.1c

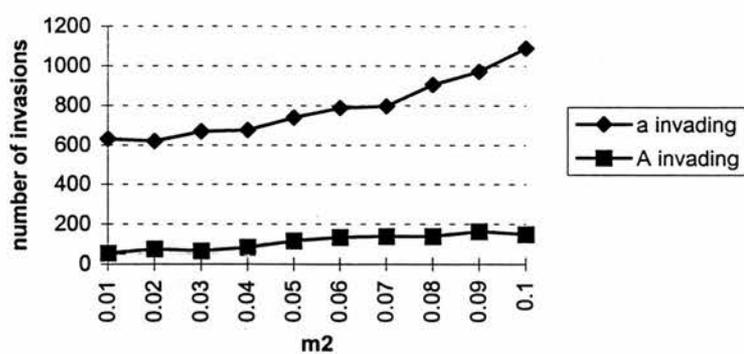


Fig. 3.1 Results of the random walk simulation of Model 1. The graphs show the number of times out of 10000 runs that the allele invaded a population. The three parameters of the model were varied independently (for 'm', read ' μ '). See text for more information.

This model demonstrates that the process described by the cultural trap hypothesis does favour filters that allow a wider variety of songs. Although the equilibria when both alleles are fixed are stable, random walks in allele frequencies will result in the system tended towards fixation at allele **a**. In the model, the only costs arise from the interaction between females with **A** (narrow filters) and males with **a2** (wide filters, and unusual songs). These are the two classes of individuals that mate at lower than expected frequencies, since they are mutually incompatible. The cost of this is greater for the rarer allele, hence the effect stems from the frequency of song type **2** within the **a** males. When **a** is rare, **2** can only arise as a result of cultural mutation, but when it is common, a higher frequency arises, and hence the number of incompatible pairings rises.

3.4 Model 2: intrasexual interactions

Model 2 generalises and extends model 1. Model 1 requires that only one sex signals, and that the other receives, and that signalling affects the probability of mating. Clearly, this is a rather limited circumstance, and both intrasexual vocal communication between (typically male) songbirds, and human language clearly do not fall within it. Therefore, in model 2, I examine a system, in which all individuals possess a cultural signal, and in which costs are applied that directly affect the probability of reproductive success.

One type of cost is applied when receivers do not recognise the signal (as in model 1) because of their filter. As an example of how this might act, consider two neighbouring male songbirds. Through singing, territorial boundaries are easily maintained. However, if one of the males did not recognise the other as a conspecific (because of possessing a narrower filter), then one might speculate that costly fights might break out more frequently. On average, these sort of fights would be expected to be equally costly to both individuals.

When both members of a communicating dyad possess a culturally transmitted trait, an alternative aspect of communication may arise. This occurs when two

individuals benefit because they share the same cultural trait. This phenomenon, cultural conformity (Boyd & Richerson, 1985), has often been proposed to exist in songbird vocal communication (e.g. Brown & Farabaugh, 1997). In some species, neighbouring males commonly share some or all of their repertoires, and attempt to match these songs during countersinging song bouts. It has been found that young male indigo buntings have greater breeding success if they share more songs with their neighbours (Payne 1982). A similar effect is clearly of importance in human communication where sharing of vocal cultural traits is a necessity of language communication, and cultural conformity has been shown to be important in sociolinguistic studies (Chambers, 1995).

As in model 1, there are two alleles: **a** and **A**, and two songs: **1** and **2**. Allele **A** does not recognise song **2**. Combinations of these give rise to three phenogenotypes: **A1**, **a1**, and **a2**, which have frequencies: x_1 , x_3 , and x_4 . Again, cultural transmission is oblique. Songs were copied at random from within the whole population, and cultural mutation between songs **1** and **2** was again determined by the rates μ_1 and μ_2 . Following transmission is a communication phase. Here, I introduce two fitness costs: **s** is a cost imposed (equally to both signaller and receiver) when two individuals do not possess the same song, **t** is a cost imposed (also equally to both signaller and receiver) when the receiver does not recognise the song at all. This occurs when an **A1** individual meets an **a2** individual, and is analogous to the cost **s** in Model 1. The recursion equations for this system are given in (8).

In the recursions, there are two stages. In the first stage, songs are acquired through the processes of cultural transmission and mutation. In the second stage, individuals communicate, interacting at frequencies proportional to their allele frequencies, and costs arising from failure to communicate arise. Here, the denominator w serves the same role as did **D** in model 1.

$$x_1' = x_1 \quad (8a)$$

$$x_3' = (x_3 + x_4) \cdot (x_3 + x_1) \cdot (1 - \mu_1) + (x_3 + x_4) \cdot x_4 \cdot \mu_2 \quad (8b) \text{ Transmission}$$

$$x_4' = (x_3 + x_4) \cdot (x_3 + x_1) \cdot \mu_1 + (x_3 + x_4) \cdot x_4 \cdot (1 - \mu_2) \quad (8c) \text{ Phase}$$

$$w \cdot x_1'' = x_1' \cdot (x_3' + x_1') + x_4' \cdot x_1' \cdot (1 - s - t) \quad (8d)$$

$$w \cdot x_3'' = x_3' \cdot (x_1' + x_3') + x_3' \cdot x_4' \cdot (1 - s) \quad (8e) \text{ Communication}$$

$$w \cdot x_4'' = x_4'^2 + x_3' \cdot x_4' \cdot (1 - s) + x_4' \cdot x_1' \cdot (1 - s - t) \quad (8f) \text{ Phase}$$

where

$$w = 1 - 2 \cdot s \cdot x_3' \cdot x_4' - 2 \cdot (s + t) \cdot x_4' \cdot x_1'$$

Using the same technique as in Model 1, I investigated the presence of internal equilibria. From equation (8):

$$|x_3'' + x_4'' - x_1''| = \left| \frac{x_3 + x_4 - x_1 - 2 \cdot s \cdot x_3' \cdot x_4'}{1 - 2 \cdot s \cdot x_3' \cdot x_4' - 2 \cdot (s + t) \cdot x_4' \cdot x_1'} \right| \quad (9)$$

There can be no stable internal equilibrium while

$$x_3'' + x_4'' - x_1'' > x_3 + x_4 - x_1 \quad (10)$$

Inequality (10) is always satisfied whenever $s = 0$ and $t > 0$ (i.e. analogous conditions to Model 1). However this is not the case when $s > 0$. To investigate this situation, I carried out a simulation of the recursion system (8). For each setting of the parameters (s , t , μ_1 and μ_2), I used 40 starting frequencies of x_1 , and divided the remainder between 40 further frequencies of x_3 and x_4 . These starting frequencies were

Fig. 3.2a

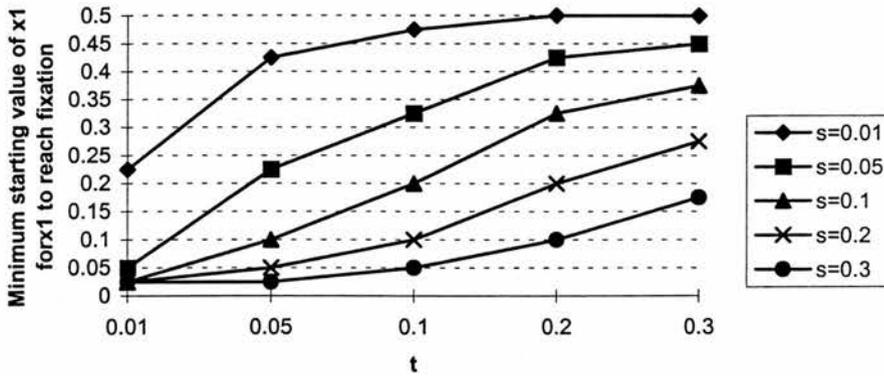


Fig. 3.2b

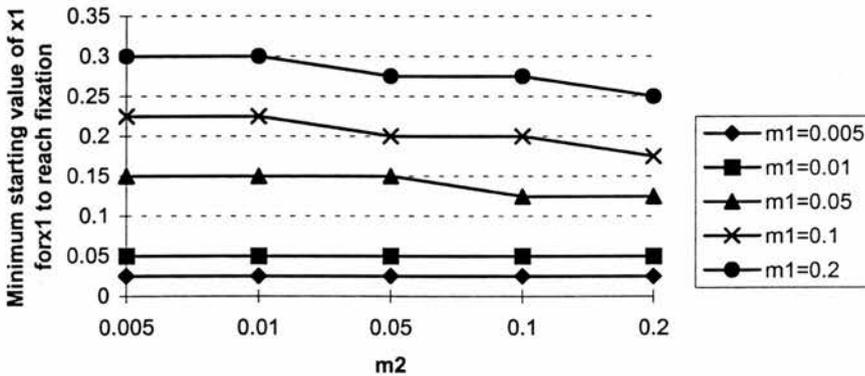


Fig. 3.2 Illustrates the global areas of attraction of a and A for certain parameter settings.

The graphs show the minimum starting frequency of x_1 that led to x_1 reaching fixation under the given parameter settings. s and t are the costs referred to in the text; m_1 and m_2 are the cultural mutation rates. The default conditions were $s = 0.2$, $t = 0.2$, $\mu_1 = 0.05$, and $\mu_2 = 0.05$.

spread evenly between 0 and 1. The simulation proceeded until it approached within 0.0001 of fixation for one of the alleles, or changed by a factor of less than 1.001 from one generation to the next.

The results of the simulation indicated first that there were no stable equilibria under any starting frequency or parameter setting in the model. The second finding was that the global sphere of attraction for **A** was always larger than that for **a** when $s > 0$. This is illustrated in Fig. 3.2, which shows the minimum starting frequency of x_1 that led to fixation of allele **a**.

There are equilibria in this model when either **a** or **A** is fixed. First, when **A** is fixed, there is a stable equilibrium since the principle eigenvalue of this system is:

$$\lambda = 1 - \mu_1 \cdot (s + t) \quad (12)$$

When **a** is fixed, the model becomes more complex. There are three possible equilibria along this edge, since the recursion equations resolve into a cubic equation:

$$x_3'' = a \cdot x_3^3 + b \cdot x_3^2 + c \cdot x_3 + d \quad (13)$$

where:

$$a = -2 \cdot s \cdot (1 - \mu_1 - \mu_2)^2$$

$$b = s \cdot \left((1 - \mu_1 - \mu_2)^2 + 2 \cdot (1 - \mu_1 - \mu_2) \cdot (1 - 2 \cdot \mu_2) \right)$$

$$c = -\mu_1 - \mu_2 - s \cdot \left[(1 - \mu_1 - \mu_2) \cdot (1 - 2 \cdot \mu_2) - 2 \cdot \mu_2 \cdot (1 - \mu_2) \right]$$

$$d = \mu_2 - s \cdot \mu_2 \cdot (1 - \mu_2)$$

Since the solutions to (9) are not simple, I take two special instances of this model:

(1) $s = 0$

This is a similar situation to that found in model 1, with no cost to non-matching. Equation (13) becomes much simplified, with a single equilibrium:

$$\hat{x}_3 = \frac{\mu_2}{\mu_1 + \mu_2} \quad (14)$$

This is obviously very similar to the first equilibrium obtained for model 1. Analysing the stability of this equation, in the same manner as for model 1, the principle eigenvalue is:

$$\lambda = 1 - t \cdot \frac{\mu_1}{\mu_1 + \mu_2} \quad (15)$$

Again, this is a very similar result to model 1, as might be expected. For $s = 0$, the comparison between the two stable equilibria yields the same result as for model 1 - the equilibrium where the wide allele is fixed is more stable while the sum of the mutation rates is less than 1.

(2) $\mu_1 = \mu_2 = \mu$

In this case, equation (13) can be solved, giving three equilibria:

$$\hat{x}_3 = \frac{1}{2}$$

$$\hat{x}_3 = \frac{1}{2} \pm \frac{\sqrt{s-4\cdot\mu}}{2\cdot(1-2\cdot\mu)\cdot\sqrt{s}}$$

The analysis of stability of the first of these - which is the only valid equilibrium when $s < 4\mu$ - to invasion by **A** has the principal eigenvalue:

$$\lambda = \frac{1 - \frac{1}{2} \cdot (s+t)}{1 - \frac{1}{2} \cdot s} \quad (16)$$

Thus while $t = 0$, $\lambda = 1$, and the equilibrium $x_1 = 1$ will be most stable. When $t > 0$, the equilibrium with **a** fixed will be more stable when:

$$t > s \cdot \left(\frac{\mu \cdot (2-s)}{1 - \mu \cdot (2-s)} \right) \quad (17)$$

For the other equilibria, the leading eigenvalue becomes:

$$\lambda = \frac{1 - \frac{1}{2} \cdot (s+t) \cdot \left(1 \mp \frac{\sqrt{s-4\cdot\mu}}{\sqrt{s}} \right)}{1 - 2\cdot\mu} \quad (18)$$

Comparing this to the eigenvalue obtained when **A** was fixed (equation 12), gives the following condition under which **a** at fixation is more stable than when **A** is fixed:

$$t > \frac{4 \cdot \mu \cdot \sqrt{s}}{\sqrt{s} \cdot (1 - 2 \cdot \mu + 4 \cdot \mu^2) \mp \sqrt{s - 4 \cdot \mu}} - s \quad (19)$$

The local stability analysis of this model suggest that there may be some situations in which the equilibrium where **a** is fixed is more stable than the equilibrium where **A** is fixed. The local stability analysis was in agreement with the simulation study of global attraction in that the cost **s** appears to favour (i.e. creates larger area of attraction, and makes it more stable at equilibrium) allele **A**, whereas cost **t** favours allele **a**. The balance between these two is not clear, however, from these analyses. To resolve this, I carried out another random walk simulation. The design of this was identical to that in Model 1, except with the inclusion of the recursion set (8), and the parameter **t**.

The results of the simulation (Fig. 4.3) confirmed the predictions of the model. Allele **a** was favoured only in the absence of **s** (the analogous situation to model 1), or at low values of **s**. Overall, **t** had to be considerably larger than **s** for allele **a** to be selected. Cultural mutation rate, in comparison, had a much lower effect on the relative success of the alleles than did **s** and **t**.

In summary, model 2 shows firstly that selection for wider filters, caused by a cost to not recognising another communicating individual, also occurs when communication is intrasexual, or independent of sex. It also suggests that one of the simplest forms of interaction of cultural signals - a benefit to cultural conformity - creates selection in the opposite direction, for more restrictive filters.

Fig. 3.3a

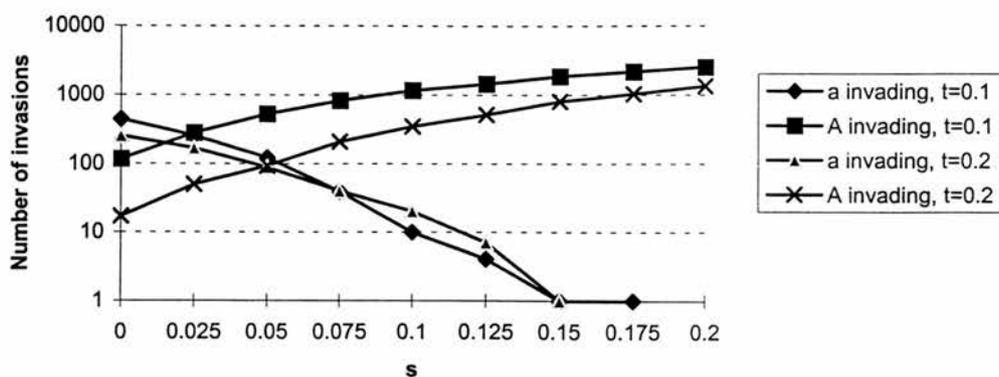


Fig. 3.3b

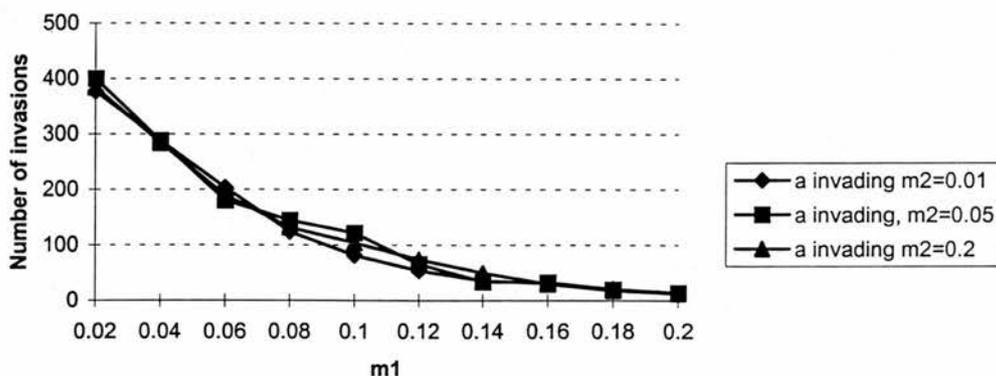


Fig.3.3 c

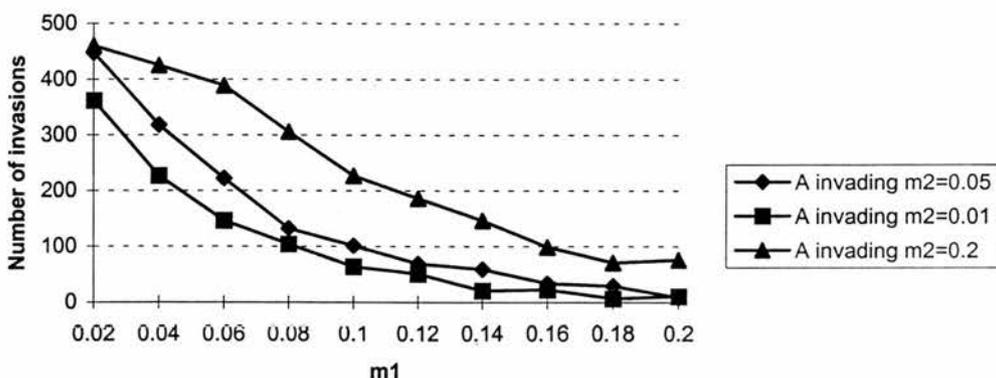


Fig. 3.3 Results of the random walk simulation of Model 2. The graphs show the probability that an allele will invade a population, starting at very low frequency, in terms of the number of simulations (out of 10000) in which invasion occurred. The three parameters of the model were varied independently (for 'm', read 'μ'). See text for more information.

3.5 Model 3.

It is well known that bird song provides species recognition cues (Becker, 1982). However, there are cases where this system breaks down. Cases of occasional interspecific learning are often reported (Helb *et al*, 1985), and in some species, such as for the short-toed and common treecreepers (Thielcke, 1986), interspecific copying can be common within populations. One of the questions that arises from this phenomenon is whether such learning will lead to selection for increased vocal convergence, or divergence. In some cases, such as the 'chink' call of chaffinches and great tits, the calls of two species are hard to distinguish (Reed, 1982). Clearly costs may arise from mis-identifying heterospecifics as conspecifics. But also, as examined in models 1 and 2 and in Chapter 2, costs arising from failing to identify a conspecific select for less restrictive genetic filters. Consequently, heterospecifically copied songs may cause selection for filters that lead to them being recognised as species-typical.

The cultural trap hypothesis predicts ever widening filters. One of the most likely sources of selection that would halt this process would be interspecific confusion. The question this model addresses is whether interspecific interaction and learning halts or accelerates the widening of genetic filters. The model is adapted from the general structure of Model 2. In this model, however, there exist two species, A and B. Two alleles exist for each species: **A** and **a**, and **B** and **b**. Between the two species, there exists two songs: **1** and **2**. **A** sings only **1**, **B** sings only **2**, whereas **a** and **b** both sing either **1** or **2**. Hence there are 6 phenogenotypes in this system, **A1** - **b2**. The frequencies of these phenogeneotypes are given as x_1 , x_3 , x_4 , x_5 , x_7 , and x_8 for phenogenotypes **A1**, **a1**, **a2**, **B2**, **b1**, and **b2**. Vocal convergence of the two species occurs when a situation where only **A** and **B** exist changes to a situation where only **a** and **b** exist. The model is adapted from model 2, with no cost to non-matching. There exist four cultural mutation rates: μ_1 (**1** to **2** for species A), μ_2 (**2** to **1** for species A), μ_3 (**1** to **2** for species B), and μ_4 (**2** to **1** for species B), and 2 costs: s is the cost of mis-recognising a heterospecific as a conspecific. Such a cost might arise from events as simple as wasting time communicating, or as profound as producing non-viable offspring resulting from a heterospecific mating. t is the cost of failing to recognise a conspecific, and is identical

to cost t in Model 2. I assume that both species remain at equal frequency relative to each other. The recursion equations of these systems are:

$$x_1' = x_1 \quad (20a)$$

$$x_3' = \frac{1}{2} \cdot (x_3 + x_4) \cdot (x_1 + x_3 + x_7) \cdot (1 - \mu_1) + \frac{1}{2} \cdot (x_3 + x_4) \cdot (x_4 + x_5 + x_8) \cdot \mu_2 \quad (20b)$$

$$x_4' = \frac{1}{2} \cdot (x_3 + x_4) \cdot (x_1 + x_3 + x_7) \cdot \mu_1 + \frac{1}{2} \cdot (x_3 + x_4) \cdot (x_4 + x_5 + x_8) \cdot (1 - \mu_2) \quad (20c)$$

$$x_5' = x_5 \quad (20d)$$

$$x_7' = \frac{1}{2} \cdot (x_7 + x_8) \cdot (x_1 + x_3 + x_7) \cdot (1 - \mu_3) + \frac{1}{2} \cdot (x_7 + x_8) \cdot (x_4 + x_5 + x_8) \cdot \mu_4 \quad (20e)$$

$$x_8' = \frac{1}{2} \cdot (x_7 + x_8) \cdot (x_1 + x_3 + x_7) \cdot \mu_3 + \frac{1}{2} \cdot (x_7 + x_8) \cdot (x_4 + x_5 + x_8) \cdot (1 - \mu_4) \quad (20f)$$

$$D_1 \cdot x_1'' = x_1' \cdot (1 - s \cdot x_7' - t \cdot x_4') \quad (20g)$$

$$D_1 \cdot x_3'' = x_3' \cdot (1 - s) \quad (20h)$$

$$D_1 \cdot x_4'' = x_4' \cdot (1 - s - t \cdot x_1') \quad (20i)$$

$$D_2 \cdot x_5'' = x_5' \cdot (1 - s \cdot x_4' - t \cdot x_7') \quad (20j)$$

$$D_2 \cdot x_7'' = x_7' \cdot (1 - s - t \cdot x_5') \quad (20k)$$

$$D_2 \cdot x_8'' = x_8' \cdot (1 - s) \quad (20l)$$

where

$$D_1 = 1 - s \cdot \left(1 - x_1' \cdot (1 - x_7')\right) - 2 \cdot t \cdot x_1' \cdot x_4'$$

$$D_2 = 1 - s \cdot \left(1 - x_5' \cdot (1 - x_4')\right) - 2 \cdot t \cdot x_5' \cdot x_7'$$

As with Models 1 and 2, I carried out a simulation to investigate the global areas of attraction. The simulation used here was directly adapted from these precursors. Starting frequencies of the two systems of equations were varied independently. I found no conditions in which a stable internal equilibrium existed for either system. Varying cultural mutation rate had very little effect on the outcome of the model, but varying the costs s and t did. As expected, high levels of t led to situations where alleles a and b were increasingly successful (Fig.3.4). However, in all circumstances measured, alleles A and B were more successful than a and b .

Fig. 3.4

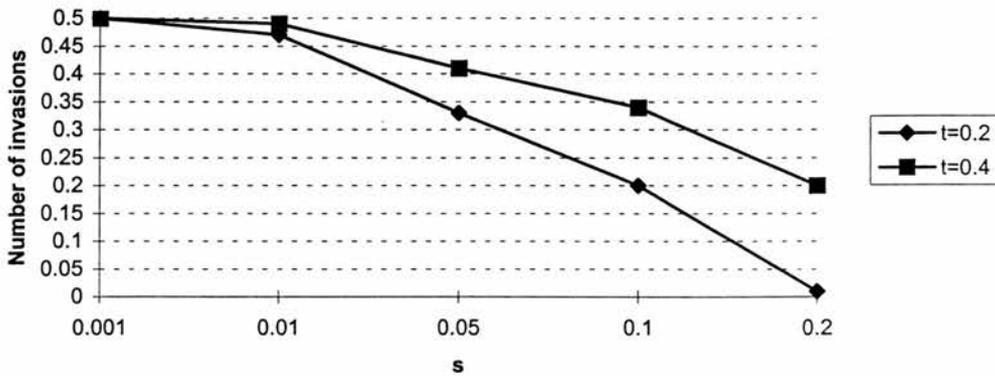
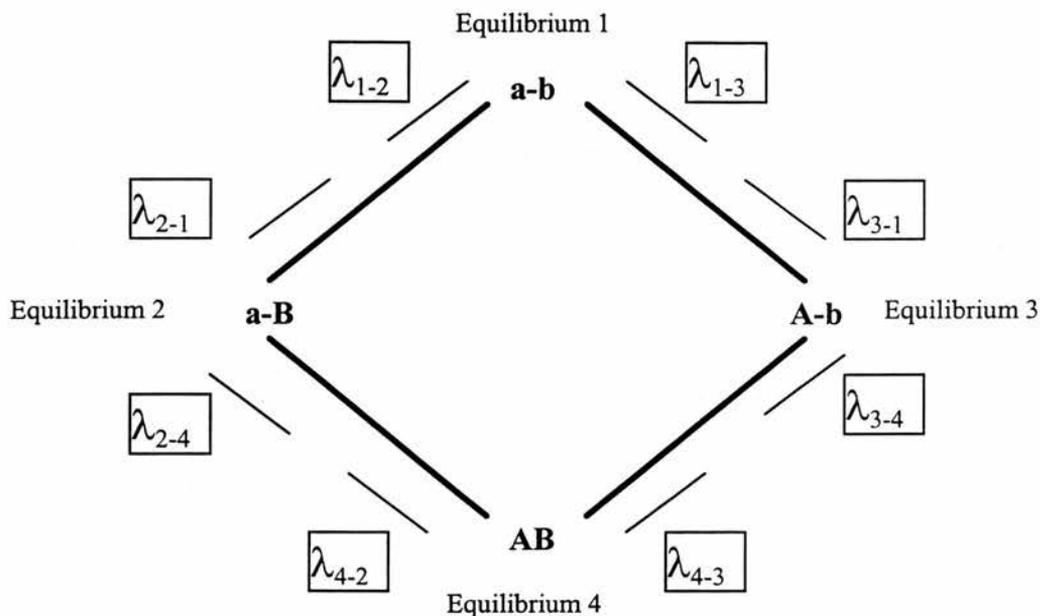


Fig. 3.4 Illustrates the global areas of attraction of a/b and A/B for certain parameter settings. The graphs show the minimum starting frequency of x_1 or x_5 that led to x_1 or x_5 reaching fixation under the given parameter settings. s and t are the costs referred to in the text; are the cultural mutation rates. The default conditions were, $\mu_1 = \mu_2 = \mu_3 = \mu_4 = 0.05$.

To analyse this system of equations, I examined the stabilities of four equilibria, and 8 eigenvalues, as shown in Figure 3.5.

Fig. 3.5 Diagram illustrating the four equilibria possible in Model 3. The apices of the graph represent point of fixation for the alleles, as indicated. The edges represent the fixation of one allele only.



The phenotype frequencies at the 4 equilibria are as follows:

Equilibrium 1: **a, b** fixed

$$\hat{x}_1 = \hat{x}_5 = 0$$

$$\hat{x}_3 = \frac{\mu_2(1 + \mu_3) + \mu_4(1 - \mu_1)}{\mu_1 + \mu_2 + \mu_3 + \mu_4}$$

$$\hat{x}_4 = 1 - \hat{x}_3$$

$$\hat{x}_7 = \frac{\mu_3(1 - \mu_2) + \mu_4(1 + \mu_1)}{\mu_1 + \mu_2 + \mu_3 + \mu_4}$$

$$\hat{x}_8 = 1 - \hat{x}_7$$

Equilibrium 2 - **a-B** fixed

$$x_1 = x_7 = x_8 = 0$$

$$x_3 = \frac{1 + \mu_1 - \mu_2}{1 + \mu_1 + \mu_2}$$

$$x_4 = \frac{2 \cdot \mu_2}{1 + \mu_1 + \mu_2}$$

$$x_5 = 1$$

Equilibrium 3 - **A-b** fixed

$$x_1 = 1$$

$$x_3 = x_4 = x_5 = 0$$

$$x_7 = \frac{2 \cdot \mu_3}{1 + \mu_3 + \mu_4}$$

$$x_8 = \frac{1 - \mu_3 + \mu_4}{1 + \mu_3 + \mu_4}$$

Equilibrium 4 - **A-B** fixed

$$x_1 = x_5 = 1$$

$$x_3 = x_4 = x_7 = x_8 = 0$$

As shown in Fig. 3.5, there are 8 principle eigenvalues that indicate the invasion of one allele into one of the 8 equilibria. This ignores the possibility of two alleles invading an equilibria simultaneously, as such a situation is considered unlikely. The values of the 8 eigenvalues are:

$$\lambda_{1-2} = 1 + \frac{s \cdot \hat{x}_8 - t \cdot \hat{x}_7}{1-s} \quad (21 \text{ a})$$

$$\lambda_{1-3} = 1 + \frac{s \cdot \hat{x}_8 - t \cdot \hat{x}_4}{1-s} \quad (21 \text{ b})$$

where the equilibria values refer to the values in Equilibrium 1.

$$\lambda_{2-1} = 1 + \frac{2 \cdot \mu_2 \cdot s - t \cdot ((1 + \mu_1) \cdot \mu_4 + (1 - \mu_3) \cdot \mu_2)}{1 + \mu_2 + \mu_1 - s \cdot (1 - \mu_2 + \mu_1)} \quad (22 \text{ a})$$

$$\lambda_{2-4} = \frac{1 - t \cdot \hat{x}_4}{1-s} \quad (22 \text{ b})$$

where equilibrium values refer to Equilibrium 2.

$$\lambda_{3-1} = 1 + \frac{2 \cdot \mu_3 \cdot s - t \cdot ((1 + \mu_4) \cdot \mu_1 + (1 - \mu_2) \cdot \mu_3)}{1 + \mu_3 + \mu_4 - s \cdot (1 - \mu_3 + \mu_4)} \quad (23 \text{ a})$$

$$\lambda_{3-4} = \frac{1 - t \cdot \hat{x}_7}{1-s} \quad (23 \text{ b})$$

where equilibrium values refer to Equilibrium 3.

$$\lambda_{4-2} = 1 - s + \frac{1}{2} \cdot t \cdot (1 + \mu_1 - \mu_2) \quad (24 \text{ a})$$

$$\lambda_{4-3} = 1 - s + \frac{1}{2} \cdot t \cdot (1 + \mu_4 - \mu_3) \quad (24 \text{ b})$$

Equilibria 2 and 3 are clearly symmetrical in their relationships with equilibria 1 and 4. The aim of the model was to examine whether **A** or **a** is the most stable. To do this, I compared the stability of the equilibrium 1 to invasion by **A** (equation 21 a) with the stability of equilibrium 2 to invasion by **a** (equation 22a), as shown in equation 25. I will also compare the stability of equilibrium 3 to invasion by **a** (equation 23 b) with the stability of equilibrium 4 to invasion by **A** (equation 24 b), as shown in equation 26.

$$t > s \cdot \left[1 + \frac{(1-s) \cdot L \cdot (\mu_1 + \mu_3 \cdot (1-2 \cdot s)) + (\mu_3 \cdot \mu_2 - \mu_4 \cdot \mu_1) \cdot [(1-s) \cdot (2 \cdot M + L) + 4 \cdot \mu_3 \cdot s]}{[\mu_1 \cdot (1 + \mu_4) + \mu_3 \cdot (1 - \mu_2)] \cdot [(1-s) \cdot M + 2 \cdot \mu_3 \cdot s]} \right]$$

$$\begin{aligned} \text{where } L &= \mu_1 + \mu_2 + \mu_3 + \mu_4 & (25) \\ M &= 1 - \mu_1 - \mu_2 \end{aligned}$$

$$t > s \cdot \left[\frac{2 \cdot (2-s) \cdot (1 + \mu_1 + \mu_2)}{(1 + \mu_1 - \mu_2) \cdot (2 + (1-s) \cdot (1 + \mu_1 + \mu_2))} \right] \quad (26)$$

To make inequalities (25) and (26) more comprehensible, I considered a situation where the cultural mutation rates between song types are equal within, but not between species, i.e.: $\mu_1 = \mu_2 = \mu_a$ and $\mu_3 = \mu_4 = \mu_b$. Here, (25) becomes:

$$t > s \cdot \left[1 + \frac{2 \cdot (1-s) \cdot (\mu_a + \mu_b \cdot (1-2 \cdot s))}{(1-s) \cdot (1-2 \cdot \mu_a) + 2 \cdot s \cdot \mu_b} \right] \quad (27)$$

And (26) becomes:

$$t > s \cdot \left[1 + \frac{4 \cdot \mu_a + (1-s) \cdot (1 + 2 \cdot \mu_a)}{2 + (1-s) \cdot (1 + 2 \cdot \mu_a)} \right] \quad (28)$$

In order to evaluate whether this system could lead to vocal convergence, I again carried out a random-walk simulation. In this version of the simulation, perturbations were initially made for both species A and B. A simple situation was chosen where $\mu_1 = \mu_2 = \mu_3 = \mu_4 = 0.1$, and $t = 0.05$. Perturbations occurred at frequency 0.2 (and occurred independently for each species), and were equally likely to act in either direction. The size of the perturbation was 0.1. These settings provided the conditions for a reasonable frequency of invasion, but it should be noted that the system was less prone to invasion than the other models. Three starting equilibria (**AB**, **aB**, **ab** fixed), and three transitions between them were investigated: **AB** → **ab**, **AB** → **aB**, and **aB** → **ab** (see Fig. 3.6). Because of the equal values of cultural mutation rate, one would expect that the behaviour of B would be the same as that of A, and therefore, these three transitions provided a complete picture of the system.

The results of these simulations (Fig. 3.6) indicate that only in very special conditions could convergence occur. Specifically, s had to be more than an order of magnitude lower than t for convergence to occur. In summary, this model suggested that

Fig. 3.6a

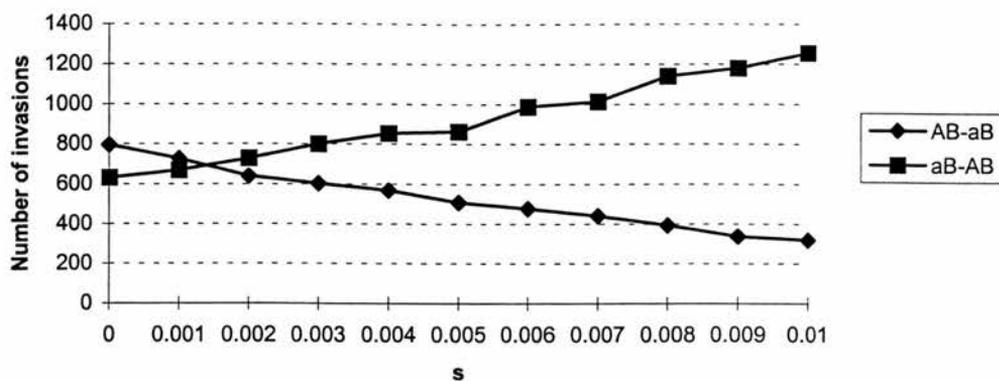


Fig. 3.6b

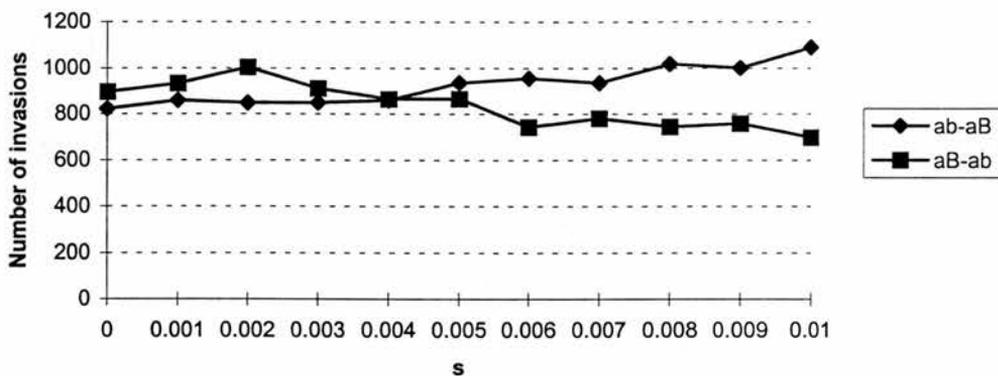


Fig. 3.6c

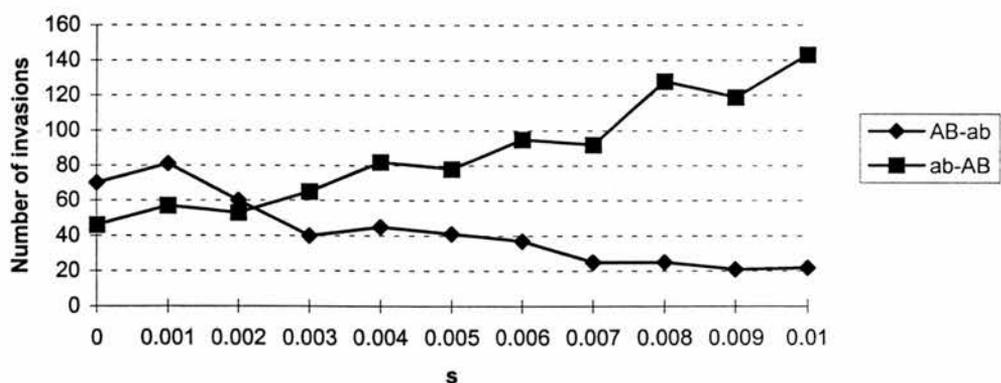


Fig. 3.4 Results of the random walk simulation of Model 3. The graphs show the probability that an allele will invade a population, starting at very low frequency, in terms of the number of simulations (out of 10000) in which invasion occurred. The legends represent the transition within the recursion system that was occurring. See text for more information.

a combination of selection pressures to ensure recognition of conspecifics, and to avoid falsely recognising heterospecifics did oppose each other, and that under some conditions, selection for vocal convergence could occur. However, these conditions were quite extreme, and it would appear more realistic for convergence to be selected against.

3.6 Discussion.

The results of these models show that: (1) wider genetic filters will be more successful, due to the interaction with culturally transmitted song, under general conditions, with either inter-sexual, or sex-independent communication. This supports the cultural trap hypothesis, and suggests that it might apply to a wide range of songbird species, and possibly elsewhere. (2) 'Cultural conformity' - fitness costs applied between individuals not sharing the same cultural trait - promotes more restrictive genetic filters to an extent that overcomes the selection for wider genetic filters in (1) under most conditions. (3) Vocal convergence can occur as a result of heterospecific song learning, but only if the cost of mistakenly recognising a heterospecific is much higher than the cost of failing to recognise a conspecific.

Although genetic filters have long been known to underlie many kinds of learning (e.g. Marler & Peters, 1977; Bolhuis, 1995), the evolutionary implications of this developmental mechanism have not been extensively examined. Cultural transmission provides an especially interesting case, since two separate evolutionary systems contribute to the phenotype. These models demonstrate that cultural evolution is likely to strongly influence the evolution of genetic filters that restrict learning. Different cultural processes influence this evolution in different ways. Cultural variation and mutation create selection for less restrictive filters. If cultural conformity is enforced, however, selection for more restrictive filters arises. In these models cultural conformity appeared to produce a much stronger effect than the cultural trap. However, the simplified formulation of the model may have resulted in this finding. In particular, the cultural traits each occupied a large segment of the genetic filter - for the narrow allele, one trait occupied the entire filter width. In reality, there are likely to be many different possible cultural traits for each filter, and cultural conformity may act at the level of each distinct song type rather than a range of song types. In the next chapter, I

investigate a more realistic spatial simulation of cultural conformity. The final result from this chapter indicated that interspecific interactions are indeed likely to provide an upper boundary to the continual widening of the genetic filter that would result from the cultural trap hypothesis. Only under very extreme circumstances did the filters of two species converge. This might partly explain why cases of frequent heterospecific song learning are rare.

These, of course, are only some of the processes involving cultural communication. They may, however, provide a reasonably accurate model for song learning by birds, since the biological existence of cultural mutation, drift, and matching have been established (Slater *et al*, 1980; Payne, 1982; Lynch, 1996; Payne, 1996). The significance of the evolution of wider or narrower genetic filters was in discussed Chapter 2. I argued that selection for wider filters is sufficient for the evolutionary maintenance of vocal learning. This is because learning could only disappear through the increasing constriction of the filter. The results of this chapter extend the finding that the cultural trap hypothesis might be responsible for the evolutionary maintenance of vocal learning. In these models, the cultural trap effect was found in much more general conditions, indicating that this effect may be found in non-territorial situations (without local song copying), and that it might occur in the interactions between males, as well as the interactions between males and females. Moreover, in an even more general interpretation of these models, I could regard **A** as a 'non-learning' allele and **a** as an allele supporting learning. In this situation the origin, as well as the maintenance, of learning might be explained.

A number of authors have argued that benefits resulting from song sharing between individuals, especially between neighbours, might provide an evolutionary explanation for song learning (Payne, 1982; Brown & Farabaugh, 1997). However, the results suggest that under very general conditions at least, this is not the case. Selection of cultural conformers leads to the evolution of narrower filters, and this progressive constraint on song learning would eventually lead to learning disappearing. Again, this perspective can be supported by viewing the cultural traits as either ranges of song-types, or as individual song types. In the latter scenario, learning is effectively removed by selection of conformers.

Finally, a gene-culture coevolutionary approach can lead to a more formal examination of the role of song learning in vocal convergence or divergence. The involvement of song learning in generating the apparently high number of oscine species (approximately 4000) has often been postulated (e.g. Martens, 1996 although Baptista & Trail, 1992 contest some of the empirical evidence for this). The results suggest that song might not serve as a particularly efficient interbreeding barrier to populations that may have diverged in allopatry under all conditions. However, a very low cost to interbreeding or interspecific communication would be required for the barrier to be removed.

Recently, biologists studying bird song have begun to investigate the interactions between ecology, function and developmental mechanism in increasing depth (Kroodsma, 1996). I would argue on the basis of the findings that any such research programme should consider the evolutionary nature of cultural transmission, and its interactions with genetic evolution. Not only does it serve as a useful way of creating testable hypotheses from evolutionary arguments, but it has also provided results that would seem counterintuitive without its perspective.

Processes such as I have described here leading to changes in filter width for song birds, may also occur in the evolution of human language. However, the increased structural and social complexity of human cultural communication means that I can be less certain about the applicability of the model. One of the most obvious examples of this is the concept of cultural mutation. In these models, mutation is a random event. This is unrealistic since innovation of novel communication forms is unlikely to be random in humans. The adoption of novel communication traits has been shown to be strongly biased by factors such as social dominance (Chambers, 1995). Nevertheless, I believe that these models may serve a useful purpose in illustrating some of the evolutionary interactions that may have occurred between the cultural and genetic transmission of language.

Chapter 4 Cultural conformity of vocalisations in birds and mammals: a gene-culture coevolutionary approach.

4.1 Abstract

Cultural conformity arises when individuals share the commonest cultural traits of an area. It has been proposed that it has played an important role in the evolutionary origin and maintenance of vocal learning. I examined this hypothesis, and suggest that cultural conformity could not explain the origin of vocal learning. A simulation model was used to explore the role of conformity in the maintenance of vocal learning and to show that conformity can create selection that would lead to learning disappearing.

I then examined why conformity itself may have arisen. Because of the lack of widespread evidence for an external benefit to vocal sharing, I developed a gene-culture co-evolutionary model of the evolution of cultural conformity. In this model, conformity enforcing behaviour can evolve if the probability of winning a territorial encounter is proportional to the number of territorial disputes entered into.

Finally, I extended the cultural trap hypothesis (Chapter 1), to an intra-sexual communication situation, and examined its interaction with cultural conformity.

4.2 Introduction

Cultural conformism occurs when there is a tendency for individuals to learn socially the commonest behaviour of a local area or social group, generating positive frequency dependent cultural transmission (Boyd & Richerson, 1985). In the case of song learning in birds, it has been regarded as a central aspect of the cultural communication system (Payne, 1996). In a wide range of species, the pattern of cultural transmission can be explained by geographical proximity, and the classical pattern of geographical variation in mosaic-like 'dialects' probably arises from a form of frequency dependent learning. As a result, many explanations of the function of vocal learning assume that there are benefits from learning local song or call variants. In this chapter, I aim to disentangle various issues concerned with cultural conformism in vocal

communication, its role in the origin and maintenance of vocal learning, and how it might have arisen itself.

Vocal learning is a phylogenetically restricted trait. It appears to have arisen on four occasions in mammals (Janik & Slater 1997), and three times in birds (Kroodsma and Baylis 1982). In the best studied clade - the songbirds -vocal learning appears to have had only one origin, and has never subsequently disappeared (Kroodsma and Baylis 1982). Despite this, vocally learned behaviours are enormously variable. Intraspecific variation in repertoire size, geographical variation, timing of development, and organisation have been documented in a number of species, especially among the songbirds. One of the only common features is that song learning normally involves cultural transmission. Individual learning of vocal traits, or innovation, has only been conclusively demonstrated for two species (Kroodsma *et al.* 1997, 1999). Cultural transmission has been shown in laboratory studies (e.g. Thorpe 1958), and through studies of song variation in populations in both space (e.g. Slater *et al.* 1980; Lynch 1996) and time (e.g. Payne 1996; Ince *et al.* 1980). The questions of the origin and maintenance of vocal learning have therefore been of considerable interest. Why has learning, which occurs in many different contexts, only evolved so infrequently?

A natural place to start with these questions is by examining how patterns of cultural transmission are used in vocal communication today. Cultural transmission patterns have been extensively studied in songbirds. Notably, vertical transmission appears to be rare, the only well documented exceptions being Darwin's Finches (Grant and Grant 1996) and greater horseshoe bats (Jones and Ransome 1993). In the absence of this factor, vocal learning seems to be almost entirely from individuals in close geographic or social proximity. However, while studies with songbirds have mostly demonstrated preferences to learn from neighbours (e.g. Payne, 1981), others have found birds avoiding learning from neighbours (e.g. Rich, 1981) or exhibit no preference at all (Slater & Ince, 1982). In the last two cases, however, the geographical distribution of song types still suggests birds are learning from individuals relatively nearby.

As a result of these patterns of transmission, song or call sharing between neighbouring individuals occurs at relatively high frequency in many species, and

several hypotheses on the functional significance of this have been put forward. The most direct evidence that song sharing between neighbours is of importance is the study by Payne (1982), who found that young male indigo buntings that shared more songs with neighbours had higher breeding success than young males that did not. He found that first year males were more than twice as likely to have a female on their territory, have a nest, and to fledge at least one nestling if they matched the song of their neighbours than those that performed different songs from their neighbours.

Matched countersinging (Catchpole & Slater, 1995) or call matching (Janik and Slater 1998) is a common behaviour associated with song or call sharing. Matching occurs when a pair of neighbouring individuals reply to each other with shared elements of their repertoires during a calling or singing bout. Similarly, many species living in non-territorial social groups seem to use learned group-specific calls for group recognition (e.g. budgerigars - Farabaugh *et al*, 1994; Australian magpies - Brown & Farabaugh, 1991; caciques - Feeke: 1982; and greater spear-nosed bats - Boughman 1997, 1998). Although matching appears to be a distinctive aspect of communication in some species, its precise function remains controversial. The most popular hypothesis is that matching allows familiar individuals to recognise one another based on shared repertoires. The adaptive consequences of neighbour recognition in birds are thought to include increased ability to prevent invasion by strangers (Ydenberg *et al* 1988). However, the role of song matching in neighbour recognition in birds is doubtful, and Payne (1983) himself has ruled out increased recognition as an explanation for his earlier results. Another hypothesis is that matching can be used to address a specific individual more effectively if many animals are vocalizing at the same time. This might hold within an aggressive interaction between a territory holder and an intruder or in the cohesion of a social group of animals.

Morton has argued that receivers might be more able to assess the attenuation of songs that they themselves have within their repertoire (Morton 1982; Morton and Young 1986), and that this might be valuable in territorial interactions. Again, while distance assessment is likely to be of adaptive value, the empirical evidence that such ranging is improved by song sharing in birds is equivocal (Naguib 1997).

Song also serves an intersexual communicative function, and cultural conformism could conceivably be imposed through the song preferences of females. There is some evidence that females also learn song (e.g. Balaban, 1988 b), and Nottebohm (1972) suggested that females might use this information to choose mates that are well adapted to themselves. Several studies (reviewed in Searcy and Yasukawa 1996) have demonstrated female preferences for familiar over alien dialects. Although females do not actually sing in most of the songbird species studied, the evolutionary consequences of their learned preferences may be somewhat similar to those of males discussed earlier. As with the intrasexual examples, two individuals (male and female this time) may benefit from possessing the same cultural trait. Experimental testing of this hypothesis on the white-crowned sparrow has again provided only equivocal support for the idea (Baker *et al.* 1984; Zink and Barrowclough 1984), although correlations between cultural and genetic variation has been found in swamp sparrows (Balaban 1988a, b) populations across North America. This agrees with the assortative mating hypothesis, but could also be explained by the independent differentiation of genes and culture between the two populations if the two populations had been separated until recently. Similarly, the early results suggesting mating preferences between dialects in the white-crowned sparrow probably reflect the fact that the populations compared were genetically distinct from one another.

Although most research has focused on situations where sharing a learned vocalisation is beneficial in some way, there are also cases of animals exhibiting preferences for vocalisations that are different from their own. Along with species in which sharing between neighbours is avoided (Grant and Grant 1979; Bradley 1981), Hansen (1981) found that yellowhammers attempt not to match songs.

Cultural transmission has also recently been approached from a theoretical viewpoint (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland, *et al.* 1993) using modifying population genetic models to take advantage of the similarities between cultural and genetic transmission. The evolutionary nature of culture led to examinations of evolutionary interactions with genes, which has provided novel answers to some questions of human evolution (Feldman and Cavalli-Sforza 1976; Laland *et al.* 1995). These studies have made it clear that any hypothesis pertaining to the evolution

of a genetic trait linked to a cultural trait needs to take into account the evolutionary dynamics created by culture itself. Boyd & Richerson (1985) examined the evolution of conformity, when culture led to the acquisition of a skill. However, alternative bird song types cannot be regarded as alternate 'skills'. In fact empirical evidence suggests that they are mainly selectively neutral with respect to one another (Lynch, 1996).

In summary, a wide range of empirical studies have suggested that cultural conformity in vocal communication exists, and that conformity incurs some kind of benefit. However, the reasons why conformity is adaptive are still unclear, and its links to the evolution of learning itself even more so. In this chapter, I look at three principle evolutionary issues associated with cultural conformity: can conformity account for the evolutionary origin of vocal learning? Can it account for the evolutionary maintenance of vocal learning? And why did cultural conformity itself arise?

4.3 Cultural conformity and the origin of vocal learning

Several authors have hypothesised that matching could have played a major role in the evolutionary origin of vocal learning (e.g. Thorpe 1966; Brown and Farabaugh 1997). Matching can certainly be used in the contexts of addressing specific individuals and of group cohesion. However, is the apparently widespread use of vocal learning indicative of the context in which learning evolved? For matching to be involved in the origin of learning, we must assume that matching was adaptive, prior to the evolution of learning. However, vocal signals in species that do not learn their songs are characteristically stereotyped, and it is hard to see how preferences for matched calls could exist in these species.

There is one special situation that would favour the evolution of vocal learning to enhance conformity between individuals and this is vertical cultural transmission to facilitate mother-offspring recognition in a noisy environment. Greater horseshoe bats roost in large aggregations and mothers must find their offspring when they return from their feeding trips. Background noise in such roosts is high due to the large number of vocalizing conspecifics. This bat species does not develop specific recognition calls to facilitate mother-infant reunion (Matsumura 1979) but infants learn to match the echolocation click peak frequencies of their mothers (Jones and Ransome 1993). If

mothers recognize the echoes of their own echolocation clicks by locking on to their peak frequency, infants that call in reply with a matching peak frequency in their clicks would constitute a very dominant echo to the female. This could elicit an approach and facilitate mother-offspring recognition. Bats use olfactory cues once they are closer to each other and this would avoid deception by other infants. Thus, the system would be evolutionarily stable. However, this is a very specific and speculative case and only applies to echolocating animals.

4.4 Cultural conformity and the maintenance of vocal learning.

In Chapter 2 I developed a framework for assessing hypotheses for the evolutionary maintenance of vocal learning. In song bird learning, at least, learning appears to be constrained by genetic filters that ensure that species typical song is normally learned (Marler and Sherman 1985). I suggested that the evolution of this filter is likely to be central to the evolution of song learning. In this section, I shall attempt to examine the hypothesis that cultural conformity is sufficient to maintain song learning. I use a spatial simulation model to do this. In the model, the success of two alleles, which lead to wider or narrower filters, is compared. While simulation models may not always be appropriate for asking questions about events in the past (such as the origin of learning), because they require assumptions that can only be justified with present-day evidence, they do provide a way to examine and quantify the implications of hypotheses about complex evolutionary issues. They are therefore ideal for questions such as those concerning the maintenance of learning.

Two sets of simulations were carried out. In the first the effect of cultural conformity between neighbouring males on selection for wide or narrow filters was examined. Payne (1982) found that males that shared a high proportion of their songs with neighbours had enhanced breeding success. In this model, I instead imposed a mortality cost on pairs of individuals that did not share songs, a difference that would not be expected to qualitatively change the results. In a second set of simulations, I examined how female mate choice might impose conformity. In this case, females learned one song from their natal area and preferred to mate with males whose song was most similar to this.

Finally, I also examined the interaction between cultural conformity and the cultural trap effect (Chapter 2,3). The cultural trap effect favours wider genetic filters because of the way they interact with culturally transmitted song. It depends on females possessing a genetic filter which they use in the recognition of species-typical mates. Thus, females with narrow filter alleles are not completely compatible with males with alleles for a wide filter, since they may sing songs that are outside the range of the females' filter. However, the costs this incompatibility imposes on rare alleles are not equal. When the narrow allele is rare, the frequency of wide-allele males singing incompatible songs is higher than when the wide allele is rare. This increases the probability of the narrow allele becoming extinct.

I have extended the cultural trap hypothesis here by also examining intra-sexual interactions. Many playback studies have demonstrated that male birds respond more actively to conspecifics. I speculate that if an individual fails to recognise his neighbour, because the neighbour's song does not fall within the limits of his genetic filter, then a fitness cost will be incurred by both males, because the territorial interactions that are mediated through song will break down. This is analogous to the mating preference model discussed in Chapter 2.

4.4.1 Description of the model

The model is adapted from that used in Chapter 2, and more detailed justification of some of the more general aspects of the model can be found there. I designed the model as a spatial simulation. In other words, the model consisted of a grid, in which each cell represents a territory. 'Individuals' were assigned to each location, and the model cycled through the relevant aspects of the life cycle: birth, death, migration, song learning, matching, and mating. In the first set of models (labelled sets 1.x), I examined intrasexual cultural conformity, and therefore, all males were assigned to be mated; in the second set of models (labelled sets 2.x), I examined intersexual cultural conformity, and mating was dependent on aspects of matching. Integral to the model are a number of parameters whose effect on the outcome of the model I investigated. Table 4.1 outlines these parameters.

1) In the first phase of the model, a mortality rate caused a given proportion of individuals to die. The mortality rate was fixed at 0.4, except in set 1.1. In the intrasexual models, the mortality rate was also affected by the number of neighbours an individual shared his song with. If all neighbours shared its song, no extra mortality cost

Table 4.1 List of parameters varied in simulations

Set (1.x refers to intra-sexual model; 2.x to inter-sexual model)	Parameter varied	Range parameter values	Default parameter values
1.1	mortality rate	0.05-0.5	0.4
1.2	maximum mortality cost to non-sharing	0.05-0.4	0.2
1.3	male dispersal (territories)	1 - 4 -entire population	1
1.4	strength of adaptive matching	0 – 2	0
1.5	cultural mutation rate	0.001 - 0.2	0.1
1.6	cost of non-recognition (relative to non-sharing)	0 – 2	0
1.7	initial frequency of introduced allele	0.1 - 0.5	0.2
2.1	variance around female preference	0.08 - 0.64	0.16
2.2	female dispersal (territories)	1-4- entire population	1
2.3	variance of learned female preference	0.04 - 0.32	n/a

was imposed. For each non-sharing neighbour, a fitness cost was added to the mortality rate, up to a maximum of 0.2 if no neighbours shared the individual's song. The maximum of this additional cost was varied in set 1.2 from 0.05 to 0.4.

2) After the death of a male, empty territories were taken over by young males. Normally, these were the offspring from one of the neighbouring territories, but in set

1.3, male dispersal was increased to up to 4 territories, and then to over the entire population. Empty territories were always taken up, with the result that the population size was constant.

3) Young males learned a song in the first year of life after acquiring a territory. Learning was restricted to being from an immediate neighbour (including diagonals). The preference for song depended only upon the genetic filter of the learner. Songs were coded as a value along one dimension, and the genetic filter assigned a preference value for a given song value. The genetic filter was shaped such that there was no preference for one song type over another within certain limits, but that preference decreased exponentially outside those limits (as in Chapter 2). In set 1.4, individuals also possessed a frequency dependent bias - such that they preferred to copy the most common song. The strength of this bias was calculated as the power to which the number of neighbours with a given song type was raised (equation 4.1).

$$P = P_f \cdot n^a \quad \text{Equation 4.1}$$

where:

P = overall preference for learning a song

P_f = preference for learning song after comparison with genetic filter

n = number of neighbours sharing song

a = parameter varied to alter strength of frequency dependent learning. This was varied from 0.5 to 2 (default: 0).

During learning, cultural mutation occurred randomly in a given number of song learning events. This mutation rate was set as 0.1 except in set 1.5 where it was varied between 0.001 and 0.2. Cultural mutation altered the song value randomly within a fixed range (20% of the limits of wide filter) in either direction.

4) After song learning, pairing occurred. Except in the second group of simulations, all males were mated. In the second (intra-sexual) group of simulations (2.1-2.3), mating was affected by the song that she had learned from her natal area. For each unpaired male, a neighbouring unpaired female was chosen. Females learned songs in the same way as males. They learned a preference for one song type, and did this from their father, or from one of his neighbours. The preference was expressed as a distribution of

preferences for song values, such that the more similar a song was to the learned song, the more likely a female was to mate with the singer. This distribution was Gaussian, with a mean corresponding to the learned song type (see Equation 4.2), while the variance was varied in set 2.1. This preference value was multiplied by a random number, and if the resulting score was higher than the threshold value of 0.3 (chosen experimentally), pairing occurred.

$$P = e^{-v^2 \cdot (s_m - s_f)^2} \quad \text{Equation 4.2}$$

Where:

P is the preference to mate with a male

v is the variance around the learned song preference

s_m is the song value of the male's song

s_f is the song value of the female's learned preference

Again, females that males mated with were selected from the offspring of the neighbouring territories, except in set 2.2, where females dispersed from 1 to 4 territories, and in one condition, over the entire population.

5) I examined the interaction between conformity and the cultural trap hypothesis in sets 1.6 and 2.3. In the former, an additional mortality cost was incurred if the song of one individual was outside the genetic filter of any of his neighbours. The cost was applied to both individuals. The size of the cost was varied from 0.05 to 0.4. In set 2.3, mating preferences of females was also affected by both their own genetic filters, which were assumed to have the same basis as the males' filters (as was done in Chapter 2), and the song that they had learned. The variance around the learned preference was varied as for set 2.2 in this set.

6) The model was randomly seeded with random song types, the values of which were within the genetic filter, and allowed to cycle through these stages (each cycle corresponding to one 'year') for 100 cycles, to allow a more realistic cultural situation to occur. Then, the genetic filter of the individuals from a number of territories was changed from wide to narrow, or vice versa. In set 1.7 this number of territories was

varied from 80 to 20 individuals (out of 200); in other sets, it was kept constant at 40. The ratio of width of 'wide' to 'narrow' allele was 1.6, except in set 1.8 where this was varied from 1.0 to 2.0. Each run proceeded until one or other allele became extinct. The frequency with which either allele became extinct was recorded as the results of the simulation. 2000 runs were conducted for each parameter setting, 1000 with the wide allele being introduced, and 1000 with the narrow allele being introduced.

4.4.2 Results.

Under no circumstances did cultural conformity lead to wider filters being more successful (Figs 4.1 & 4.2). Instead, under most situations, the narrow allele was more successful. Increased levels of cultural mutation, and increased costs to non-matching both increased the relative success of the narrow allele (Figs 4.1.2 & 4.1.5). As cultural mutation rate leads to greater diversity in song types, these two results might seem to have similar roots - the greater the amount of non-sharing incompatibility, the more successful the narrow allele was. The initial frequencies of the invading allele (Fig. 4.1.7), male dispersal (Fig. 4.1.3), and overall mortality rate (Fig. 4.1.1) did not greatly affect the difference in success of the wide and narrow alleles. Even at initial frequencies of 0.01 (1 territory), the narrow allele invaded more frequently than the wide allele (18 versus 11 successful invasions in 1000 years).

Adaptive matching did tend to remove the difference between the two alleles (Fig 4.1.4). However, there was no indication that the wider allele could have become more successful than the narrow allele.

The results of female-imposed cultural conformity were qualitatively similar to those for male-imposed cultural conformity (Fig. 4.2). The more specific the female's preference for her learned song type, the stronger the selection for the narrow allele (Fig. 4.2.1). Female dispersal had little effect on the selection for the narrow allele (Fig. 4.2.2).

Finally, Figs. 4.1.6 and 4.2.3 show the interaction of cultural conformity and the cultural trap effect. Fig 4.1.6 illustrated that the cultural trap effect also occurs in

Fig. 4.1.1

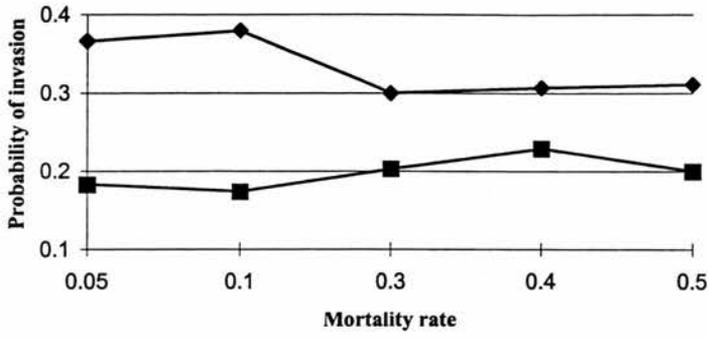


Fig. 4.1.2

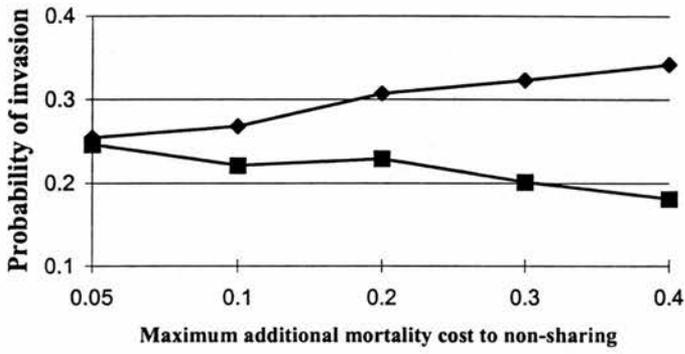


Fig. 4.1.3

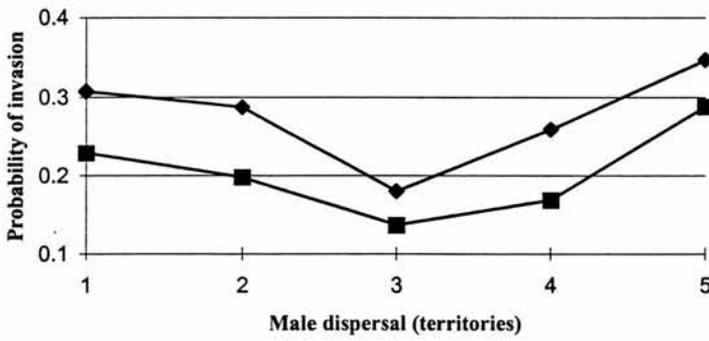


Fig. 4.1.4

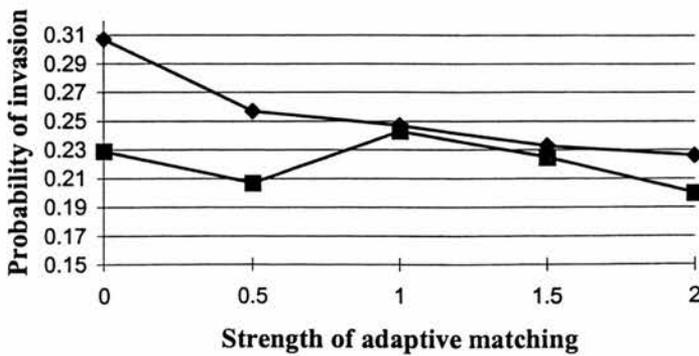


Fig. 4.1.5

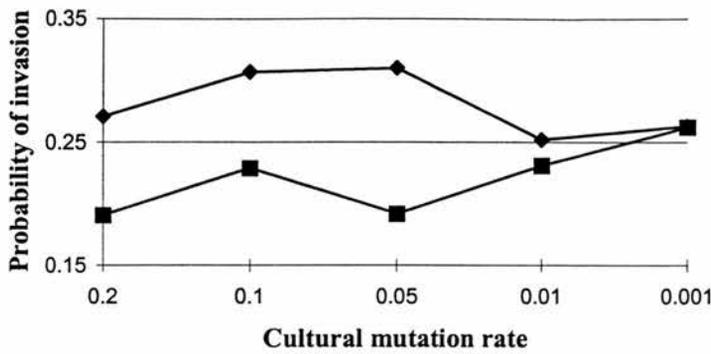


Fig. 4.1.6

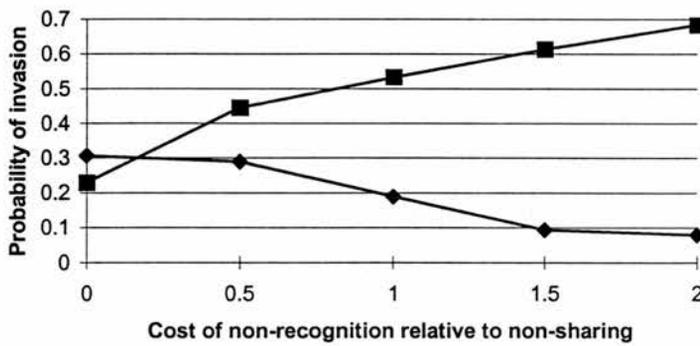


Fig. 4.1.7

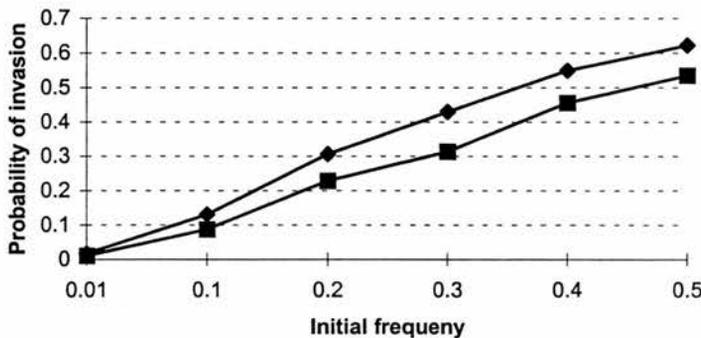


Figure 4.1. Intra-sexual cultural conformity and the evolutionary maintenance of vocal learning. Graphs show the probability of wide (diamonds) or narrow (squares) alleles invading when they were introduced into a population consisting of the other allele, over a number of parameters: 1.1: Mortality rate; 1.2: Mortality cost imposed for non-matching; 1.3: Male dispersal; 1.4: the strength of the preference of birds to copy the most common song; 1.5: Cultural mutation rate; 1.6: The interaction between conformity and the cultural trap effect. The x-axis denotes the relative strength of the cost imposed for failure to recognise a neighbour as a conspecific (i.e. the cultural trap effect) to the cost imposed for non-matching. 1.7: Initial frequency of the invading allele. Refer to the text for further details.

Fig. 4.2 Inter-sexual cultural conformity and the evolutionary maintenance of vocal learning. Graphs show the probability of wide (diamonds) or narrow (squares) alleles invading when they were introduced into a population consisting of the other allele, over a number of parameters: 2.1: variance in female learned preference. This is a parameter of how specific the females' preferences for a learned song were. The values refer to the variance of the preference distribution relative to the width of the genetic filter for species specific song. 2.2: Female dispersal; 2.3: The interaction of the cultural trap effect and inter-sexual cultural conformity. The x-axis again shows the variance in the learned preference distribution of the females.

Fig. 4.2.1

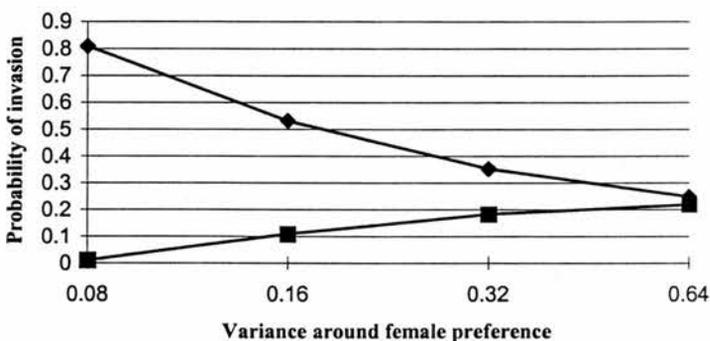


Fig. 4.2.2

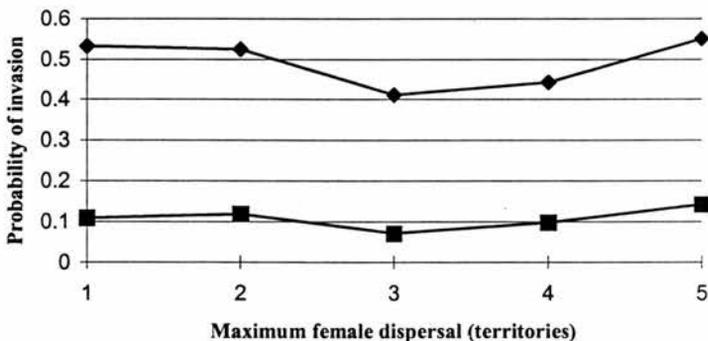
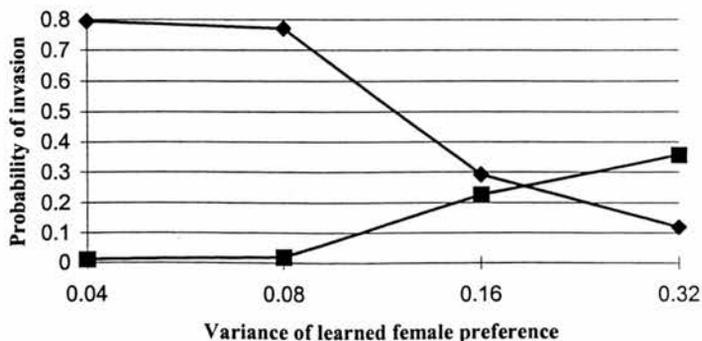


Fig. 4.2.3



intraspecific communication, as might be expected, and both graphs show that the evolutionary effects of conformity and the trap are opposed. Interestingly, in both cases, the cultural trap effect was strong enough to overcome the effects of cultural conformity in reasonably realistic conditions.

4.5 The Evolution of Cultural Conformity.

The first two sections of this chapter suggest that cultural conformity is more likely to have arisen after vocal learning has developed than the other way around. This provokes the question of what role the cultural evolution of song may have played in the evolution of conformity.

While the data from Payne's (1982) study show a clear benefit to conformity, and while behaviours linked to conformity, such as matched countersinging, are quite common, there have been no unequivocal answers to the question of why this should be so. However, several species seem to use conformity in group recognition. If this is one of the main applications for vocal learning in some species there may be a scenario in which it is evolutionarily stable.

At a more proximate level, several studies have indicated that song sharing increases the strength of response to a playback (McArthur, 1986; Stoddard *et al*, 1992). Why might receivers react in this way to shared songs?

One possibility is that a 'conformity-enforcing', or matching, behaviour is an evolutionarily stable strategy without conformity being of any external benefit. To examine this, I look at how individuals behave towards neighbours that do or do not match themselves. The model looks at agonistic territorial interactions between neighbours. 'Matchers' preferentially choose to attack neighbours that do not match themselves, whereas 'non-matchers' attack neighbours at random. In both cases, the choice of song tutor is random within a limited distance, although this does imply a level of positive frequency dependence. The key assumption of the model is that the probability of winning any given encounter is affected by the number of other fights that a male has been involved in. Specifically, the more fights he is fighting, the lower the probability of winning any of those fights. Although I am unaware of any empirical

evidence supporting this, it seems reasonable, if an individual's resources are limited, and must be divided between different encounters. It should be noted that these 'fights' refer to season-long territorial conflicts, rather than individual bouts, for which this assumption might seem less reasonable.

4.5.1 Description of the model.

The model was adapted directly from the intra-sexual model in the previous section. The model was changed in several ways:

- 1) Instead of varying the genetic filter width, the two alternative strategies (based on a single, haploid locus) were 'matchers' and 'non-matchers'.
- 2) Individuals learned only from one of their nearest neighbours (diagonals excluded).
- 3) Each individual was involved in a number of fights each year. Each individual chose to start one fight with one of its neighbour, and also had to fight any other neighbours that chose it to start a fight with. An mortality cost of 0.2 was incurred from losing each fight, and similarly, a benefit of the same amount accrued, from winning an encounter.
- 4) The decision of which individual to attack was the only difference between the two strategies. Non-matchers chose a neighbour to fight at random. In contrast, matchers selected individuals that did not share songs with themselves. If matchers were faced with more than one neighbour that did not match themselves, or if all neighbours matched their song, the choice of who to attack was made at random.
- 5) The probability of an individual winning a given encounter was inversely proportional to the number of fights that were fought by that individual in that year of the simulation (see Equation 4.3).

$$P = \frac{N_1}{N_1 + N_2}$$

Equation 4.3

P is the probability that individual 2 wins the fight between 1 and 2. N_1 and N_2 are the number of fights fought by the two individuals.

- 6) As in the previous model, the models were tested in sets of 1000 runs. For each parameter setting, the probability of matchers or non-matchers invading was estimated.

A running-in period of 100 years was included to allow a realistic cultural milieu to arise.

4.5.2 Results.

As Figs. 4.3.1 and 4.3.2 indicate, matchers were more successful than non-matchers over the conditions tested. Higher levels of cultural mutation rate increased this selection pressure (Fig. 4.3.1), as did lower levels of song dispersal. Both of these would tend to increase the frequency dependence of song learning. At low levels of cultural mutation, there would be so little variation in song that matchers too would be attacking neighbours mostly at random. The selection pressure was based on the fact that individuals could use non-matching as an indication of an unusual song, and that other individuals would also be attacking the same neighbour. The reliability of this would also be increased if individuals only learned song locally, which explains the results of Fig. 4.3.2. Overall, the results of this simulation suggest that conformity-enforcing behaviour would tend to be an evolutionarily stable strategy if the probability of winning a fight is inversely proportional to the number of fights an animal has.

Fig. 4.3. The evolution of conformity enforcing behaviour. Graphs show the probability of conformity-enforcing, and non-conformity-tolerant strategies invading when they were introduced into a population consisting of the other strategy, over a number of parameters: 3.1: The effect of cultural mutation rate, and 3.2: the effect of song dispersal distance (in terms of the number of territories a song can be learned from) on the selection for the matching allele.

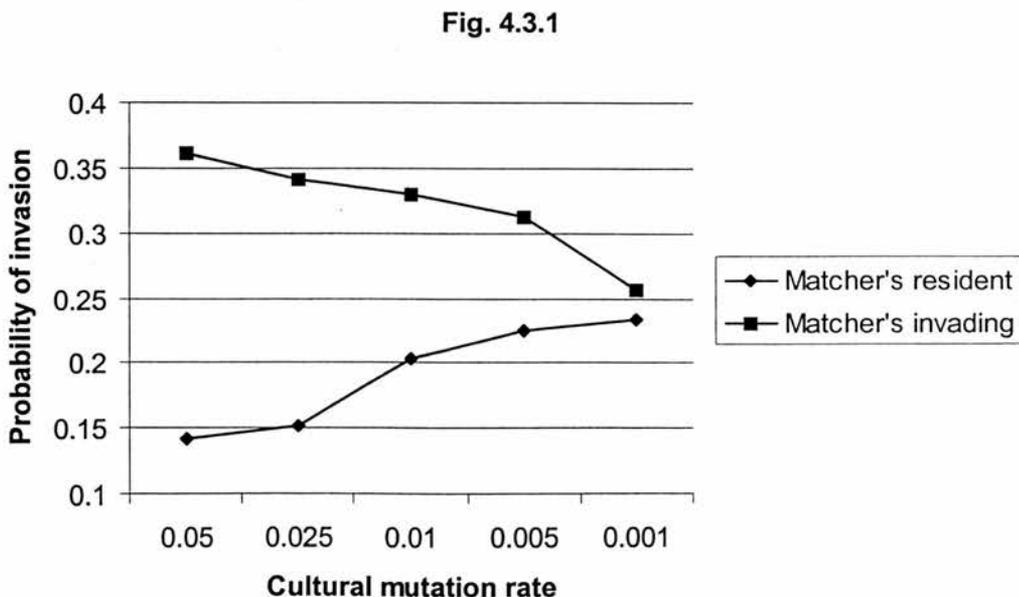
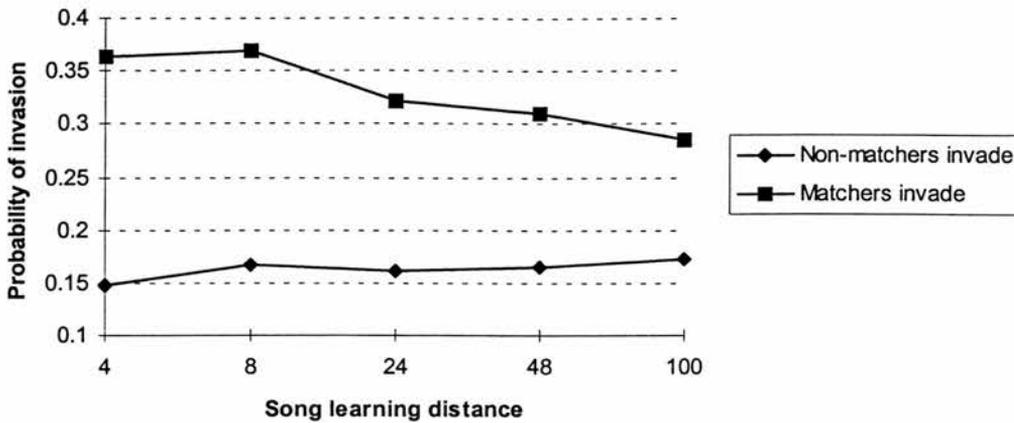


Fig. 4.3.2



4.6 Discussion.

Cultural conformity is a fundamental part of the cultural communication systems of many species (Kroodsma 1996), although it is certainly not found in every species (Catchpole & Slater, 1995). This chapter shows that cultural conformity (as imposed by social adaptation and assortative mating hypotheses) is unlikely to account for the evolutionary maintenance of vocal learning itself. With respect to the origins of learning I suggest that it possibly could have accounted for the initial evolution of learning if it was used in a deceptive context. However, this effect would most likely have only provided a transient advantage for learning, except perhaps for the rare case of the greater horseshoe bat.

The simulation models demonstrated clearly that conformity could not account for the maintenance of vocal learning under the conditions of the model. No condition could be found under which conformity led to selection for wider filters, which I consider crucial to the maintenance of learning. In fact, under many conditions, selection for narrower filters was found. For both intra- and inter-sexual models of communication, the cultural trap effect could overcome this selective force under realistic conditions.

Cultural conformity has been linked implicitly and explicitly with the evolution of vocal learning by a number of authors (e.g. Kroodsma, 1996, Catchpole & Slater, 1995, Brown and Farabaugh 1997). My analysis suggests that this hypothesis must be modified. However, this does not preclude any evolutionary interaction between vocal

learning and cultural conformity. Given that conformity cannot account for the evolution of learning, a natural question to ask is how conformity might have arisen. Curiously, while conformity is a well documented and distinctive behaviour in a wide range of species, and while a benefit arising from it has been found in a thorough field study (Payne 1982), there has been far less success in finding a general explanation for why it should be beneficial. The most generally supported finding linked with conformity in territorial songbirds is that matched countersinging is involved in aggressive territorial interactions. I therefore constructed a model for the evolution of conformity-enforcing behaviour: conformity-enforcers imposed costs to neighbours (and themselves) if they did not share their songs, whereas conformity-tolerant individuals did not. Under the condition that winning a fight is inversely proportional to the number of fights an individual is faced with, conformity-enforcing behaviour is the evolutionarily stable strategy. This hypothesis might account for the cases of conformity that occur when neighbour recognition does not appear to be enhanced by conformity.

The models I have presented in this chapter are gene-culture coevolutionary models (Feldman and Laland 1996). The patterns of song variation imposed by cultural transmission are central in creating the selection pressures for the alternative genetic traits. In vocal learning, one of the features of cultural transmission is that it creates relatively high levels of variation. This high amount of variation increases the selection pressure for narrower filters in our first models, because individuals with wider genetic filters have a wider choice of potential songs to learn, and subsequently are less likely to share songs with each other. This is illustrated by the effect of cultural mutation rate on the success of wide and narrow alleles. Similarly, in the second set of models, without substantial variation within a population, there could be no selection pressure leading to intolerance of non-conformity. Cultural conformity itself has been of interest to theoretical biologists investigating cultural evolution (Boyd & Richerson, 1985), because it could lead to situations in which group selection may occur. My second model provides a new explanation for how cultural conformity might arise.

Chapter 5 A new computer method for measuring the distance between vocal signals: MMPED.

5.1 Abstract

While the current strength of the field of bird song rests on the technological advancement of spectrography, analytical techniques to compare different spectrograms have been very limited. In this chapter I review the principles of sound comparison, and the strengths and weaknesses of current techniques. I then introduce a new sound comparison technique: MMPED. This technique aims to retain as much flexibility as possible, to help cope with inherent subjectivity in the task of comparison. It is based on measurements of Euclidean distance in the acoustic dimensions of a signal, at different time points. I measured the performance of the MMPED method using two samples of acoustic signals: dolphin signature whistles, and chaffinch song elements. I found that the MMPED comparison outperformed other computer methods, and closely matched human and biological categorisations.

5.2 Introduction

The classification of vocalisations into groups is one of the central methodological issues of bioacoustics (Janik, 1999; Nowicki & Nelson, 1990; Clark *et al.*, 1987); pattern recognition in general is of growing interest to scientists in fields such as perceptual psychology (Getty & Howard, 1981; Moore, 1995; Schwab & Nusbaum, 1986), and has generated a maturing mathematical and computing field of its own (Tou & Gonzalez, 1974). This wide-ranging interest reflects the fact that the challenges posed by pattern recognition are profound. Although sound recording and signal processing technology provide bioacousticians with an exceptionally detailed and mathematically tractable type of information compared to other aspects of animal behaviour, this final level of analysis is still in its technological infancy.

Most bioacoustical studies rely on visual inspection of spectrographic representations of vocalisations to establish categories. Although this may appear subjective, for most of these studies this is an appropriate technique (Janik, 1999,

Nelson & Nowicki, 1990). The human brain is by far the most sophisticated signal processing machine available, and with sensible design (i.e. 'blind' observations by several observers), this method can still provide important insights, that cannot always be matched by computer technology. However, it is widely recognised that using human classification has a number of limitations: First, humans are not perfectly consistent, both inter- and intra-individual variation may be considerable. Moreover, unless humans are unaware of what the underlying question in the study is, it is impossible to discount a directional bias based on their own predictions. Even in a completely blind study, it is hard to prevent observers developing their own hypotheses. Practically, for many bioacoustical studies, for which the analysis of a large number of spectrograms is required, it is impossible to adequately control for these variations. Secondly, even impartial humans make use of their own perceptual predispositions. These may differ in important regards from the perception of the study animals, as has been demonstrated for the categorisation of budgerigar and starling calls (Dooling *et al*, 1987 a, b, 1992). Whereas humans make use of the 'shape' of spectrograms - i.e. frequency change with time - these birds relied far more on absolute frequency. One important feature is that most human categorisations of acoustic signals are carried out in an entirely different modality, through the visual representation of vocalisations as spectrograms. It has been demonstrated that acoustic perception differs in important respects from visual perception in humans. For example, variation at the beginning of an artificial word-length sound is perceived far less precisely than variation at the end (Watson & Kelly, 1981). A final consideration is the precise task that is asked of human observers. While humans are adept at forming on the spot clusters, it is harder to turn these decisions into a precise measure of similarity or dissimilarity. In some cases, the reliability of making a certain decision has been used to estimate a distance between two signals (e.g. Deecke *et al*, 1999). However, it is unlikely that such a measure is metric in any sense, which limits its applicability.

Given these drawbacks, it has been realised for some time that a computer-based method for the comparison and classification of vocalisations would be of great use. Many issues in vocal communication involve analysing the amount of variation within an entire population, or require precise measurements of the similarity between vocalisations. For these cases, a more consistent method of comparison and classification is required.

5.3 Issues in the design of computer-based classification techniques.

The process of comparing vocalisations can be divided into three stages, which are common to all methods of classification (Tou & Gonzalez, 1974). In order to discuss the merits of existing techniques, and the design of new ones, I shall first these stages.

First of all, a numerical representation of the input data must be made. Ideally, such a representation should use all of the acoustic dimensions of the signal; each weighted in the same way as by the animal's perceptual system. These features might include: frequency, time, amplitude, timbre, or any rhythmical aspects to the signal, as well as any higher order combinations of these factors (frequency change with time being an especially likely example of this).

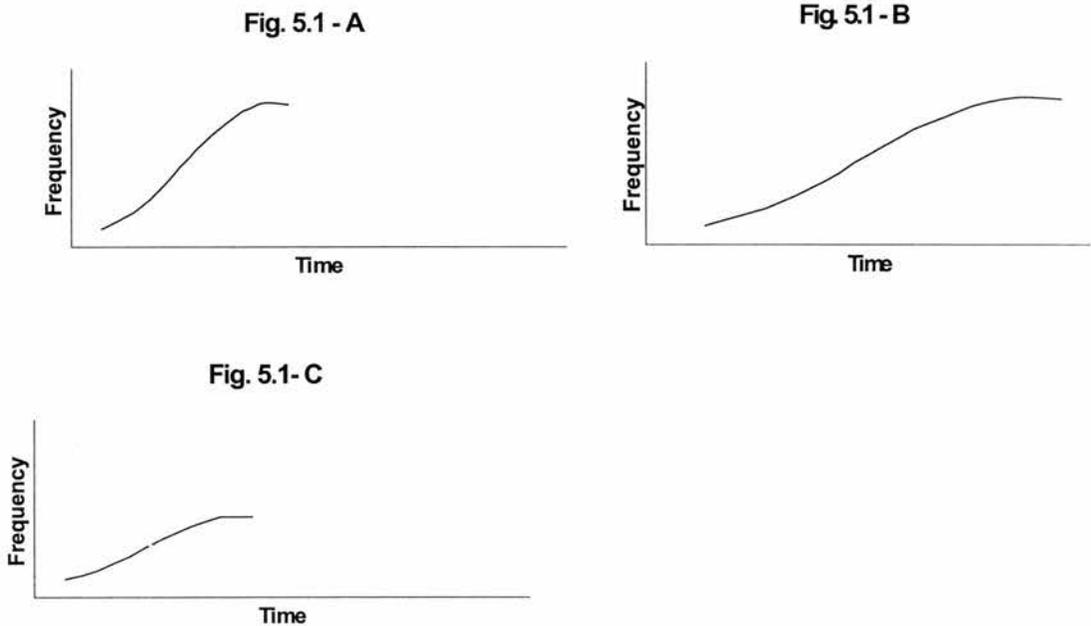
The second procedure is to extract from the representation of the data the characteristic features of the signal, and reduce its dimensionality. Again, this might be carried out in a number of ways, which ideally should reflect the way that animals process signals. At this stage the type of decisions that have to be made are illustrated by the following: which point in signal **b** will be compared with each point in signal **a**? How will overall shifts in timing or frequency be compensated for? Will all acoustic features be measured over the whole of the signal, or only in selected places? Will all parts of the signal be considered equally?

Finally, the process of classification must be carried out. How this is best carried out depends on the specific question addressed by the study, and there are again a multitude of techniques, and the statistical issues underlying each of these are quite complex. A general dichotomy is between processes which involve the assignment of cases to previously defined categories ('supervised' learning), and those in which the number of categories is determined by the classification method itself ('unsupervised' learning).

The most obvious point that arises from this description of the processes of comparison and classification is that a large number of decisions must be made. Making

these decisions is best based on a detailed knowledge of the perception and psychology of the study organism, since there is no other fundamental basis on which to make them. In fact, only a small proportion of these choices can be made on this basis at present for any species, and it is very likely that there will be considerable inter-species variation in perception and classification processes. The implication for the design of a system to classify vocalisations is that the ambiguities that result from this gap in our knowledge must be made as explicit as possible. The sensitivity of any result to the model's assumptions might then be investigated as thoroughly as possible.

The types of ambiguities that might arise in bird song recognition can be divided into several categories. The first category is the weighting of variation in any of the dimensions being measured. This is illustrated in Fig. 5.1. Is call **A** more similar to call **B** (same frequency sweep) or call **C** (same duration)?



A second type of ambiguity is whether absolute measures in any dimension should be used, or whether they should be relative to the variation within the signals being compared themselves. In Fig. 5.2, is call **A** more similar to another call of similar

overall dimensions, but different 'shape' (**B**), or a call with a very similar shape, but different scale (**C**)?

Related to this issue is another question of scale. Are two long signals (Fig. 5.3, **A**) more similar to each other than two short signals, with exactly the same relationship to each other, except that they are shorter (Fig. 5.3, **B**)?

Fig. 5.3 - A

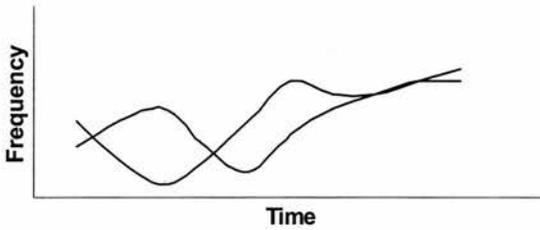
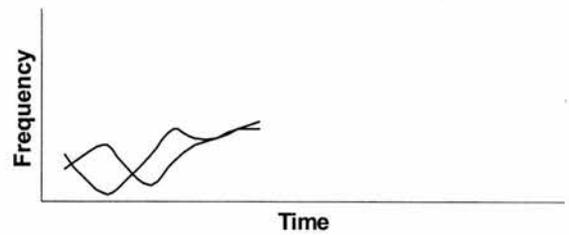


Fig 5.3 - B



Finally, consider a signal that overlaps perfectly with a segment of a second, larger signal (Fig. 5.4, **A** and **C**). Are these two signals more similar to one another than the larger signal is to one of roughly the same overall size and shape (Fig 5.4, **A** and **B**)? This ambiguity will be referred to as the difference between 'overlapping' and 'mapping'.

Fig. 5.4 - A

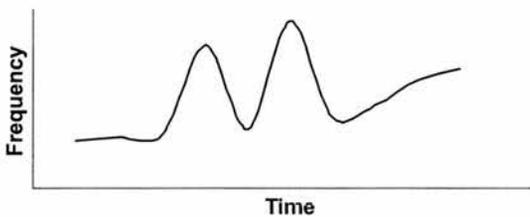


Fig. 5.4 - B

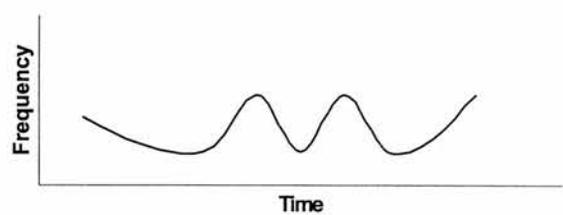
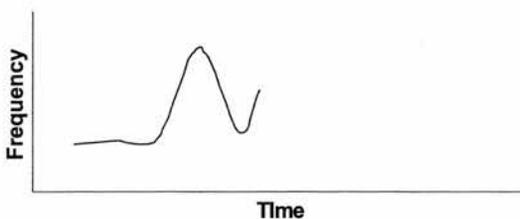


Fig. 5.4 - C



5.4 Existing computer classification techniques

There have been several attempts to apply computer technology to the problem of classifying vocalisations. Their designs can be compared in how they cope with the list of issues outlined above.

The first and most widely used computer-assisted vocalisation comparison system has been the multivariate analysis of many individual parameters of vocalisations (Sparling & Williams, 1978, Martindale, 1980). The development of multivariate statistics has allowed the investigator to confidently estimate and reduce the dimensionality of a set of vocalisations. However, to carry out such a study, it is essential to fully understand the perceptual psychology of the subject. If not, it is impossible to ensure that all the relevant measurements are made. For this reason, this technique has been generally criticised for failing to take into account the entire information in a signal (e.g. Clark *et al*, 1987). For many animal vocalisations, especially those that are complex and frequency modulated, there appears to be a preconception in the field that animals rely on a 'gestalt' comparison of the shape of the entire signal. The finding that, for example, dolphins tend to categorise signature whistles in the same way that humans classified the spectrograms of these whistles (Janik, 1999) reinforces this idea.

In summary, the multivariate statistics approach has tried to account for each pattern recognition ambiguity with a specific measure, in the hope that, with enough measures, an accurate overall measure will develop. However, without incorporating all of the data in a signal, it is hard to know whether this has been achieved. Current measurements do not, for example, include a reliable measurement of spectrographic 'shape'.

'Cross-correlation', or the 'sound comparative method' (Clark *et al*, 1987), is the second major computer-based technique. Its stated aim is that 'a full representation of a sound's frequency-time structure, rather than a few of its acoustic features, better serves the analytical process' (Clark *et al*, 1987, p.103). The technique relies on the three acoustic dimensions of time, frequency, and intensity, and is a development of simpler quantitative methods based on grids overlaid on spectrographic print-outs

(Bertram, 1970; Miller, 1979; Pickstock *et al*, 1980). Put most simply, cross correlation measures the two dimensional correlation, i.e. degree of overlap, in intensity of the spectrograms of two vocalisations if laid on top of one another. One obvious assumption is that any shift in either time or frequency has a large effect on the outcome. The solution to this problem has been to 'slide' one spectrogram past the other (theoretically in either frequency or time, although normally, only the latter is carried out), and record only the peak value of the correlation between the two spectrograms. Although this is a sensible way of dealing with an overall displacement, it still does not cope with signals being stretched, or condensed in either time or frequency. Fig. 5.5 shows the ramifications of this. **A** is compared with two others - one which is the same length and overall form, but is trilled (**B**), and one that is the same form, but has been contracted by a factor of 2 (**C**). This decision of which classifies most closely with **A** is clearly arbitrary, even if the whole signal is taken into account, without further knowledge of the perception of the organisms involved. However, since cross correlation only measures overlap, **A** would be classified with **B** not with **C**.

Fig. 5.5 - A

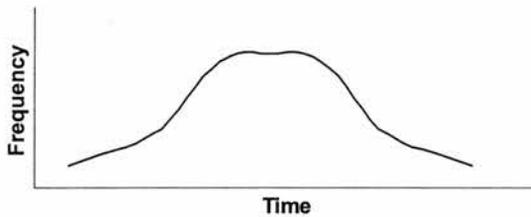


Fig. 5.5 - C

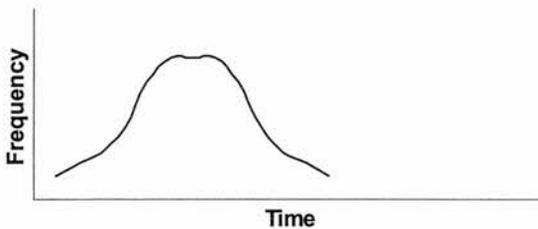
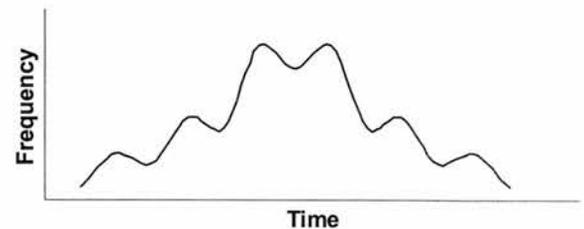


Fig. 5.5 - B



The other classes of ambiguities of classification are also dealt with rather inflexibly. In Fig. 5.3, the two shorter signals will always be measured as being more similar than the two longer signals. And for the issue of overlapping (Fig. 5.4), an arbitrary decision is made that all signals that differ in length by more than 25% are automatically given a very low correlation value.

Any comparison method such as cross correlation is best tested using known biological categories – categories that the study animals have made. In some of these, cross correlation has been successful. Clark *et al* (1987) found that cross correlation generated a useful classification of swamp sparrow note variation. However, in another case, it has clearly failed to identify a genuine biological category. Janik (1999) found that human observers recognised dolphin signature whistle categories (i.e. dolphin whistles that had been produced by known individuals in certain contingencies) far more precisely than cross correlation did. One of the differences between these two studies is that dolphin whistles are far more variable than swamp sparrow notes, and this would clearly accentuate the fundamental problems with the technique I have outlined above.

Overall, as has been pointed out in previous studies (Janik, 1999; Williams, 1991), the cross correlation technique fails in its goal of providing a technique for sound comparison that uses ‘a full representation of a sound’s frequency-time structure’ (Clark *et al*, 1987). The reason for this is that it does not take any account of the ambiguities involved in signal classification at all. The cross correlation technique can therefore be seen as occupying the opposite end of a spectrum to the multivariate statistics approach.

Finally, a third category of classification techniques makes use of simulation-type computer algorithms. This category includes dynamic programming (e.g. Williams, 1993), and neural network techniques (e.g. Deecke *et al*, 1999). Neural networks have been quite successful at identifying members of known categories (supervised learning), and measuring deviations from those categories. This is because the learning rules that such networks rely on cause them to consider only those parts of

the signal that give the net greater success in the training stage. However, when an unsupervised comparison is made, neural networks do not offer such an advantage. In this case, the network cannot develop for itself biases that allow it to distinguish members of input groups, because there is no way for it to validate those biases. Instead a measure of distance must be decided by the programmer, and this is no less problematic than for other methods. Furthermore, the decision rules underlying classification decisions are not made explicit, which, as with multivariate statistics, leads to a concern about whether all the relevant information has been considered.

The technique of dynamic programming measures the distance between two signals as the minimum number of discrete changes that need to be made to one signal to transform it into another (Williams, 1991). The changes involved include the substitution, insertion, and deletion of segments of the input data, each of which is assigned a 'cost'. The minimum number of changes required is found by computer simulation. In theory, this provides a method to include the subjective aspects of pattern recognition, through the weighting of the various costs – an advantage over cross correlation. However, these costs (insertion, deletion, substitution) are not conceptually similar to the likely perceptual dimensions (frequency, time, frequency change with time) that animals use. So, while this technique might prove effective at supervised learning tasks, its wider relevance is again limited.

In summary, a truly objective method of sound comparison is not a realistic goal, because pattern recognition is inherently subjective. Existing computer methods, however, have not been designed with this in mind, and are therefore inflexible when dealing with the inherent ambiguities associated with sound comparison. A second design feature is the extent to which the method uses all the information in the signal (cross correlation, neural networks), or just measures selected by observers as features that may be important (multidimensional analysis). While a more 'gestalt' method is more appealing, it should be borne in mind that incorporating all the information in the signal still requires arbitrary decisions to be made. Ideally, these decisions should be linked as closely as possible to the likely perceptual dimensions that are known for the relevant animal. In the next section, I describe a new computer classification method that attempts to take these aspects of design into account.

5.5 A new computer classification technique.

In general, previous computer techniques appear to suffer from a lack of flexibility, especially in taking into account the ambiguities of pattern classification. In order to describe more objectively the variation in a set of vocalisations, a new method is required which allows the experimenter to investigate the possible variations in classification decisions through sensitivity analysis.

The system I propose here is based on the frequency-time contours of vocalisations. For tonal, frequency modulated signals, such as the song of many songbirds, or cetacean calls, this method retains most of the information in the signal. Such data can be calculated from recordings by computer systems, such as SIGNAL or Avisoft, by measuring the frequency of maximum amplitude for each of a series of time bins, creating a data vector for each signal. One important result of doing this is that points are spaced equally only in the time dimension, not in any of the other dimensions in which the signal might vary. However, given that points in an acoustical signal are constrained to reach the observer equally spaced in time, this seems a reasonable assumption (although it should be noted as another way in which acoustic and visual classification of signals might vary).

The next design consideration is the dimensionality of each point in the frequency-time contour. In making this choice, a compromise must be made between clarity, which arises by considering only a few most basic dimensions of the signal, and the detail that is gathered by using every conceivable dimension, at the cost of being able to sensibly integrate them. I have tended towards the former, adding to frequency and time, change in frequency with time, as measured by the change in frequency from one time cell to the next. This latter measure is then transformed using the arctan function to give a value (in radians) of the slope. This would clearly differentiate, for example, between lines A and B in Fig. 5.5, and encompasses something of the 'shape' of the signal. Therefore, the data used in this analysis consist of a three-dimensional matrix, with the dimensions: frequency, time, and frequency-change with time.

The reduction of dimensionality for these dimensions is achieved through the use of distance measurements (as opposed to likelihood). Distance measurements are

appealing, since they are the most obvious way to compare two data vectors. The most widely used class of distance measurements is the Minkowski power metric:

$$d(x, y) = \left(\sum_{i=1}^n w_i \cdot |x_i - y_i|^r \right)^{1/r}, r \geq 1 \quad \text{Equation 5.1}$$

This family includes both the Euclidean ($r=2$) and City-Block ($r=1$) metrics. All members have the three properties of: (1) decomposability (the distance between two points is a function of the differences in the various dimensions); (2) intradimensional subtractivity (the contribution to distance in any dimension is the absolute difference between the points in that dimension); and (3) interdimensional additivity (interstimulus distance is a function of the sum of the dimensionwise contributions) (taken from Getty, *et al*, 1981). The Euclidean distance was picked as the most widely used measure of distance. The three dimensions can be independently weighted with the parameter w . This allows experimenters to carry out sensitivity analyses, or take into account knowledge of the perceptual systems of the study organisms.

Having picked a measure of distance for any two points on the frequency time contours, the next consideration is to decide which points are compared with each other. As illustrated by the cross correlation technique, only comparing matching points, when the time points are evenly spaced, does not accurately compare signals that are stretched with respect to each other. To overcome this problem, in this method the Euclidean distance between each pair of points in the two signals is calculated. For each point in the first signal, the closest point in the three-dimensional space of the other is found, and the distance between the two recorded. This process is iterated for each point in the first signal, and the mean of these minimum distances is taken as a measure of similarity.

For the Euclidean distance to be used, each of the dimensions used must be standardised with respect to one another. In this method, I standardised the data by dividing by the population ranges of frequency and time to do this. Similarly, I divided the value of the frequency change with time scores by 3, since the radian scale runs from approximately -1.5 to 1.5 .

If calls are not of the same length, the similarity of call **A** to call **B**, for example, may not be the same as the similarity of call **B** to call **A**. The similarity of the shorter call to the longer call corresponds to overlapping (i.e. how well a short call can fit over a segment of a longer call). The converse should correspond, therefore, to mapping (i.e. how well the points on a long call can be mapped onto a shorter call). For mapping, the relative lengths of the calls must be taken into account. As I have described it, however, the similarity of the longer call to the shorter call might simply be overlapping in the middle. To incorporate the relative position of points within a signal, the relative value of points within the range of the signal itself was calculated for each of the three dimensions, and these were used for the procedure of finding the closest point in the other signal. For the calculation of the actual mapping distance itself, the absolute measures were substituted back in. Both overlapping and mapping were carried out for each comparison. They were then divided by the average measure of overlapping or mapping for the entire set of call comparisons, and summed for each comparison to give a measure of similarity (Equation 5.2). Parameter ν provided a method of varying the relative importance of overlapping relative to that of mapping:

$$D = \nu \cdot D_{ov} + (1 - \nu) \cdot D_{map} \quad \text{Equation 5.2}$$

where D represents the overall distance between two signals, and the two subscripted D 's represent the overlapping and mapping distances.

A further problem is that, in a comparison between an irregular call and a regular call (such as between calls **A** and **B** in Fig.5.5), the similarity between the regular call and the irregular call will be higher than vice versa, because there might always be some local point in the irregular call which is close to the regular call, but not the other way around. To counteract this, two more comparisons were carried out between each pair of signals. One was the comparison of segments of the longer signal of the same size as the shorter signal with the shorter signal itself. This could be compared with the overlapping comparison described above, and the larger of the two was chosen as the measure of overlap. The second, correspondingly, is between the shorter signal and the larger signal as an alternative measure of mapping. Again, the larger of the two measures was selected.

The measurement of similarity is summarised in Equation 5.3.

D is the measure of distance – *ov* for overlap; *map* for mapping;

n is the number of points in the shorter signal;

m is the number of points in the longer signal;

t is the number of dimensions over which the distance is being calculated (*frequency, time, and frequency change per unit time*);

w is the weighting given to each dimension - a higher value increases the role of that dimension in determining the clusters;

r is the range of each dimension, over the whole set of signals, used to standardise the dimensions.

s is the range of each dimension, for each signal, used to standardise the dimensions.

X is the matrix of values in t dimensions for the shorter signal;

Y is the matrix of value in t dimensions for the longer signal.

$$D_1 = \frac{1}{n} \cdot \sum_{i=1}^n \text{Min}_{j=1}^m \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot Y_{jk}}{r_k} - \frac{w_k \cdot X_{ik}}{r_k} \right)^2} \right)$$

$$D_2 = \frac{1}{m} \cdot \sum_{i=1}^m \text{Min}_{j=1}^n \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot X_{jk}}{r_k} - \frac{w_k \cdot Y_{ik}}{r_k} \right)^2} \right)$$

Equation 5.3 - a

$$D_{ov} = \text{Max}_{i=1}^2 (D_i)$$

Over all i (1 to n),

$$L_i = \text{Vector of } Y \text{ giving } \underset{j=1}{\overset{m}{\text{Min}}} \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot Y_{jk}}{s_{jk}} - \frac{w_k \cdot X_{ik}}{s_{ik}} \right)^2} \right)$$

Over all j (1 to m),

$$P_j = \text{Vector of } X \text{ giving } \underset{i=1}{\overset{n}{\text{Min}}} \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot Y_{jk}}{s_{jk}} - \frac{w_k \cdot X_{ik}}{s_{ik}} \right)^2} \right)$$

Equation 5.3 - b

then

$$D_1 = \frac{1}{m} \cdot \sum_{j=1}^m \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot Y_{jk}}{r_k} - \frac{w_k \cdot P_{jk}}{r_k} \right)^2} \right)$$

$$D_2 = \frac{1}{n} \cdot \sum_{i=1}^n \left(\sqrt{\sum_{k=1}^t \left(\frac{w_k \cdot X_{jk}}{r_k} - \frac{w_k \cdot L_{ik}}{r_k} \right)^2} \right)$$

$$D_{map} = \underset{i=1}{\overset{2}{\text{Max}}} (D_i)$$

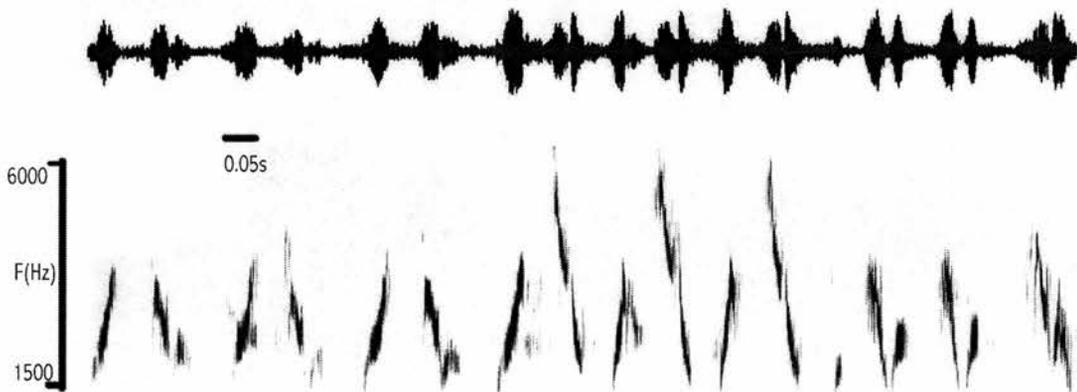
Finally, to take into account temporal non-alignment of the two signals, the shorter of the signals is slid past the larger signal, and the minimum value of distance obtained used.

To summarise the essential features of the method, it is named the Mean Minimum Point-wise Euclidean Distance (M.M.P.E.D.) measure.

5.6 Evaluating the M.M.P.E.D method of sound comparison.

In order to evaluate the ability of the MMPED method to compare vocalisations, I carried out three tests, using sample vocalisations from two species: 33 chaffinch (*Fringilla coelebs*) song elements from 5 birds on Gran Canaria; and 104 bottlenose dolphin (*Tursiops truncatus*) whistles recorded from 5 captive animals. The latter example extends work carried out on classification of these calls by Janik (1999). In each case, I compared the computer method with a different type of human classification and, in the dolphin example, I was also able to compare the performance of the MMPED method with the alternative computer techniques, and with an external biological validation of the calls' significance that were part of Janik's (1999) study.

Fig. 5.6 Oscillogram and spectrogram of chaffinch song from Gran Canaria.



5.6.1 Example 1: Canary Island chaffinch elements.

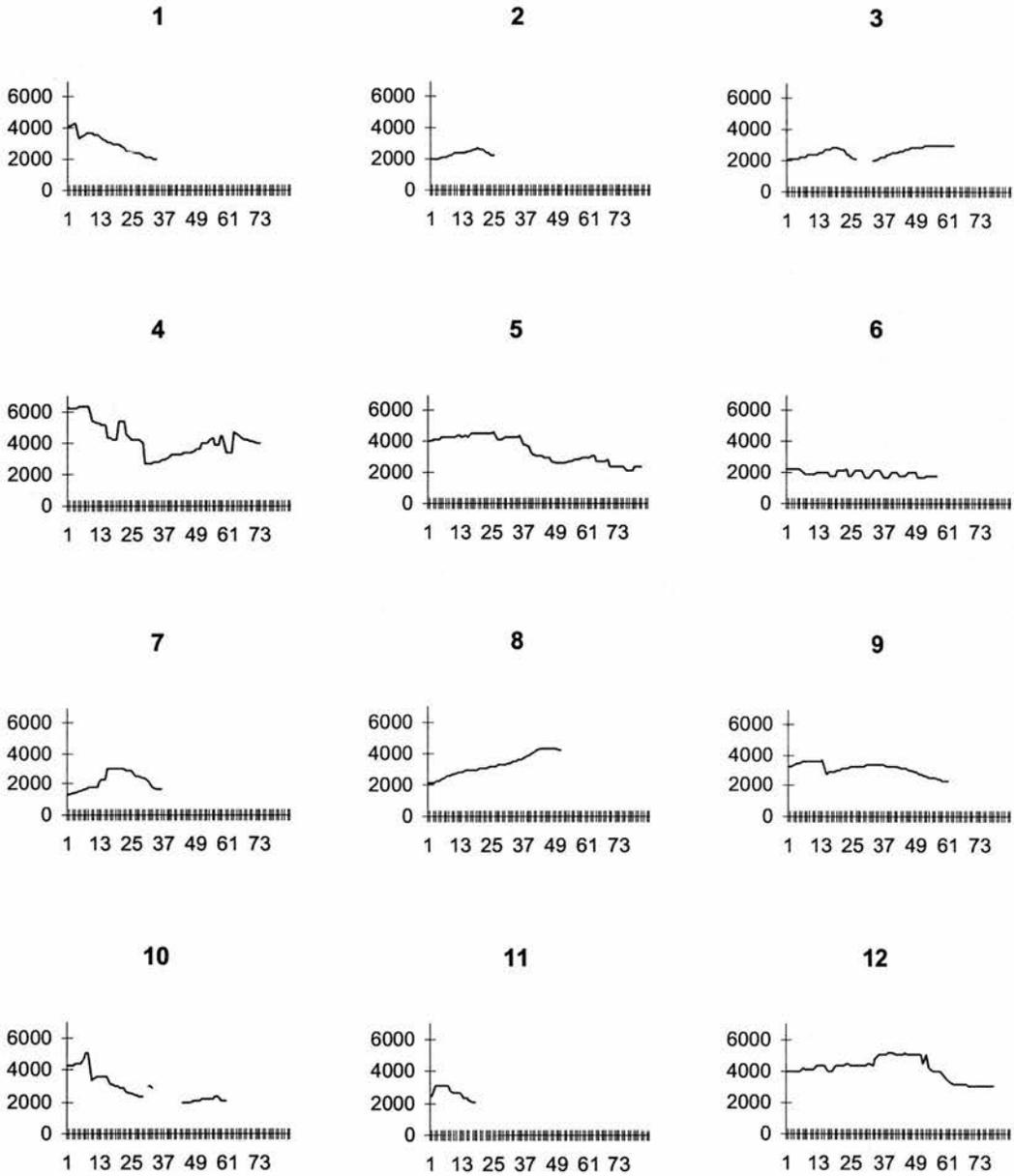
Chaffinches sing complex, frequency modulated songs (Fig. 5.6), that are hierarchically organised from elements (single uninterrupted units) into phrases (repeated groups of elements), into songs (e.g. Slater & Ince, 1979). A recent in-depth study by Lynch and Baker (1986,1994,1995) used population genetic techniques to describe processes of cultural differentiation and diversity in the chaffinch populations in the Atlantic islands of the Canaries, Madeira and the Azores, and in Africa and Europe. This study was based on the numbers of shared and un-shared song syllables

within and between populations. In order to do this, one of the authors compared and classified all the syllable types. The authors differentiate between syllable ‘variants’ and syllable ‘types’. Syllable types were taken as representing broad categories of syllable morphology, whereas variants were described as more superficial variation, including any variation at all. At a population level, variants and types showed very different patterns of variation, with much less sharing of variants between populations. But can such a distinction be made at all consistently?

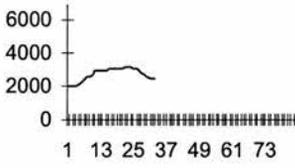
In order to investigate this, I took a sample of 33 song elements recorded from the songs of 5 individuals from Gran Canaria, in April, 1998 (a subset of the sample in Chapter 6). Two of these elements were identical as a control, and another two were equivalent elements from the same song-type as sung by two individuals. The other elements were selected randomly from different syllable types from the 5 individuals. Spectrograms of these elements were made using SIGNAL, (time resolution: 10.2ms, Fast Fourier Transform size: 256, interval between FFT steps: 0.400 ms, sampling rate: 25 KHz). Then the PEAK command was used to generate a spectral contour of maximal intensities (Fig. 5.7).

To assess human comparison and categorisation of the contours, I asked 6 volunteers to participate in a classification exercise. The volunteers were all experienced in the analysis and comparison of spectrograms - all have been authors of peer-reviewed papers in which they classified spectrograms, two of them involving chaffinches. Graphs were printed out of the 33 spectral contours with standardised time and frequency axes. The volunteers were asked to classify the graphs into 25, 20, 15, 10, and 5 categories sequentially. Their decisions were entered into a triangular distance matrix (example shown in Fig 5.8).

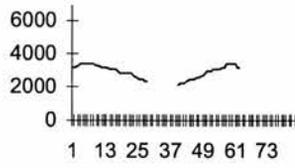
Fig. 5.7. Frequency contours of chaffinch elements used in human classification tasks.



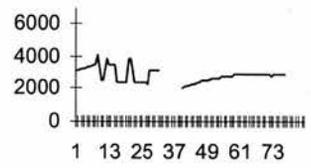
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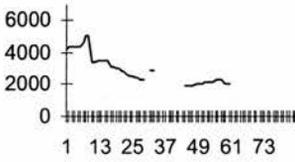
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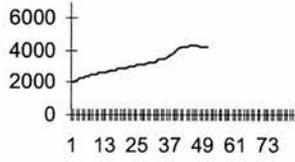
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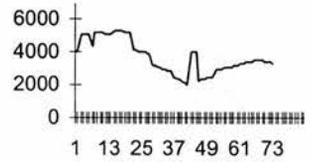
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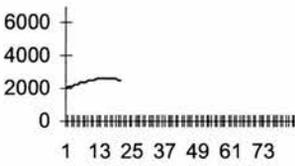
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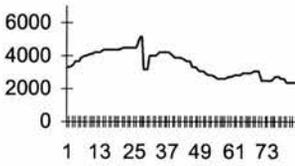
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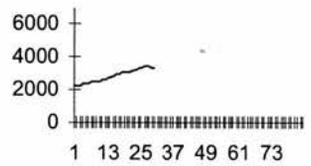
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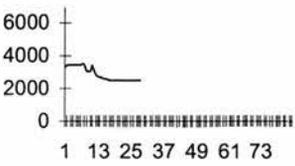
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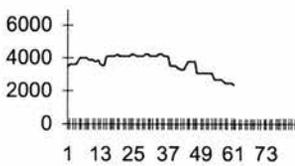
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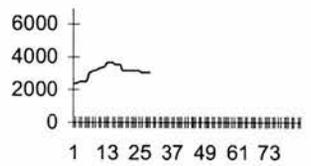
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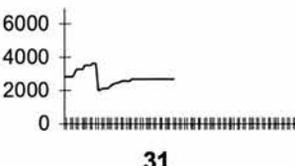
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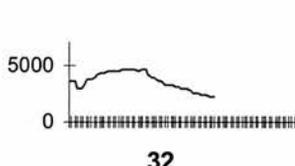
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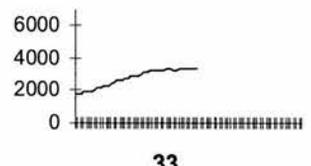
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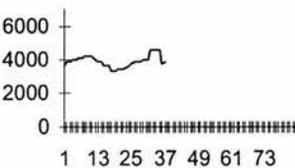
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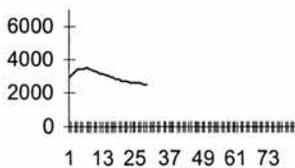
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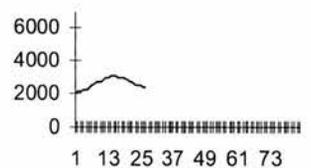


Fig. 5.9 - Average sharing of classification decisions between human observers at 5 different category levels.

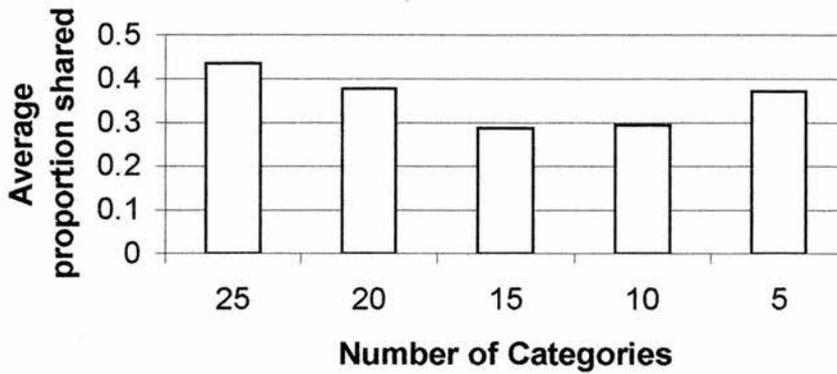


Fig. 5.9 shows the average sharing scores for all pairs of volunteers for the 5 classification levels. A distinctive trough in the middle levels of classification – especially at 15 – can be seen. However, even at the 25 categories level, which obtained the highest amount of sharing between volunteers, the sharing score does not reach 0.5.

The results of the individual comparisons are shown in Fig. 5.10. Again, the general trend is for a U-shape distribution (except for subject 4). However, there is substantial variation in the distributions of different individuals.

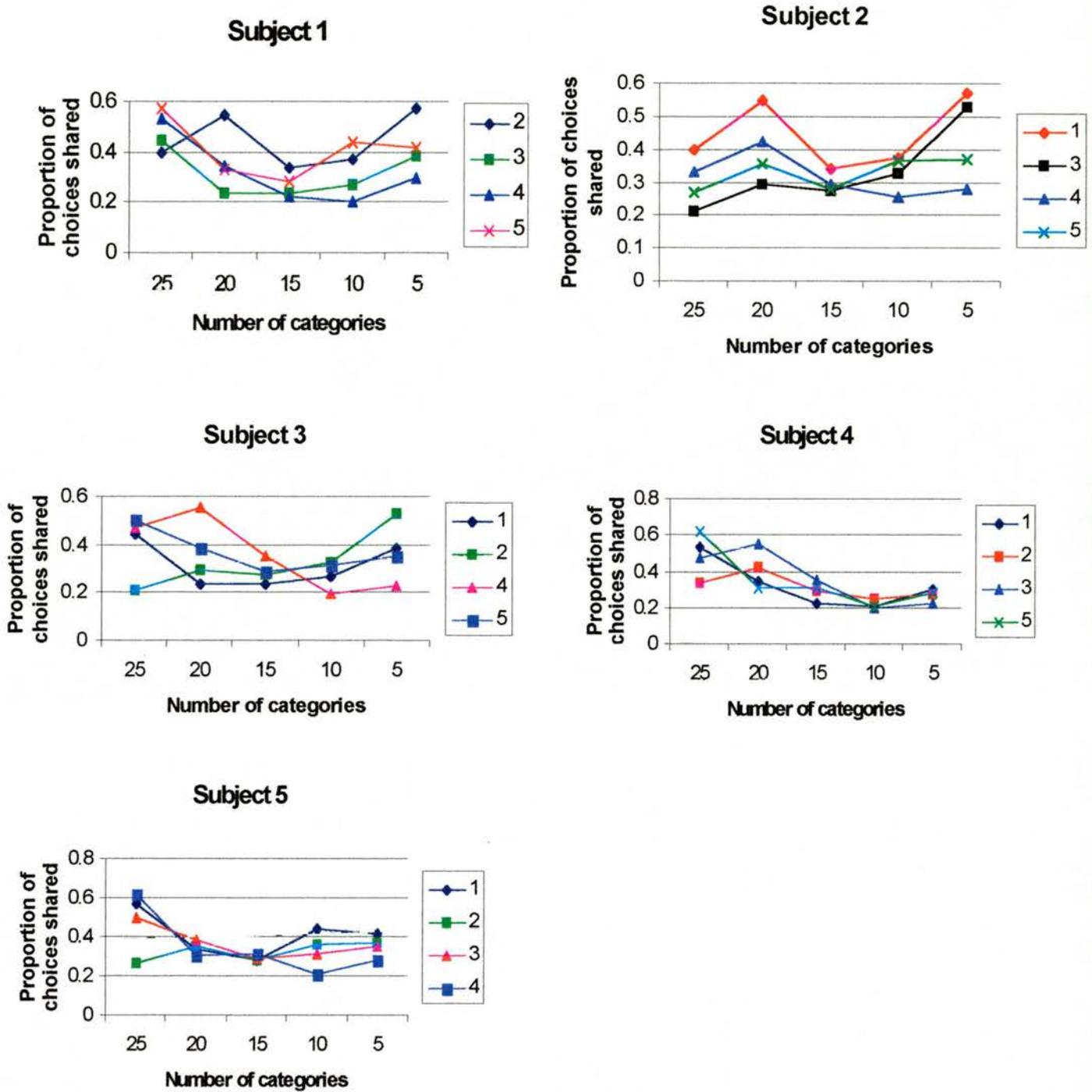
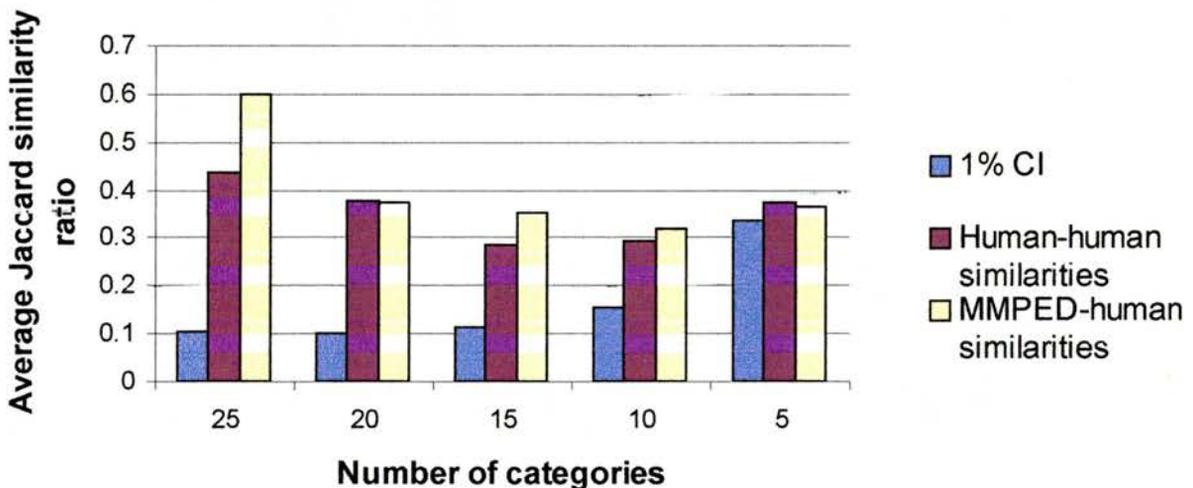


Fig. 5.10 The results of the comparisons for each individual in turn, as compared with the other four volunteers (labelled in the legends).

In order to assess the significance of these comparisons, a computer simulation was carried out. The simulation randomly generated two possible 'trees' consisting of 33 data points, and randomly assigning which element was most similar to which other element. The similarities of these trees could then be compared as had been done for the human comparisons. The largest similarity score at each level of categorisation, out of 1000 such random pairings at each categorisation level was taken as a measure of the 1% confidence limit. This procedure was replicated a further 100 times, and the mean of these values was used as the estimate of the 1% confidence limit. These values are given in Fig. 5.11. Clearly, at all levels except the 5 categories level, the proportion of sharing between individuals was highly significant. Even at the 5 categories level, only the comparisons involving subject 4 were not significant at this level. In summary, the broader the level of categorisation, the less consensus there was among the human subjects.

Fig. 5.11 Similarities within human classifications, and between human and MMPED classifications of chaffinch elements



The MMPED computer method was also applied to the data. The aspects of the measure that were varied were: frequency, time, frequency change per unit time, and overlap/mapping. The weightings of each of these four features were each set at 0.5, 1, and 2 in turn to observe their effects on the process of categorisation. The distance matrices produced by this procedure were entered into the 'Neighbour' UPGMA routine of the Phylip computer package (Felsenstein, 1995), and plotted on a dendrogram using

dendrogram using the Treedraw program. From this, a classification into the same category sizes as used by the human volunteers could be made. These data were also entered into the triangular distance matrix, and compared with the human results, using the same technique as described above. Fig. 5.11 shows the results of the settings that gave the highest similarity to the human comparisons. Here, absolute frequency was set to 0.5 as compared to the other dimensions. It demonstrates first, that the computer classifications were closer to the human classifications than would be expected by chance, since the values were higher than the random simulation confidence limit. Secondly, it shows that the computer classifications were at least as similar to the human classifications as the human classifications were to each other, since the values for the computer/human comparisons were higher in four of the five levels of categorisation.

5.6.2 Example 2: Bottlenose dolphin signature whistles.

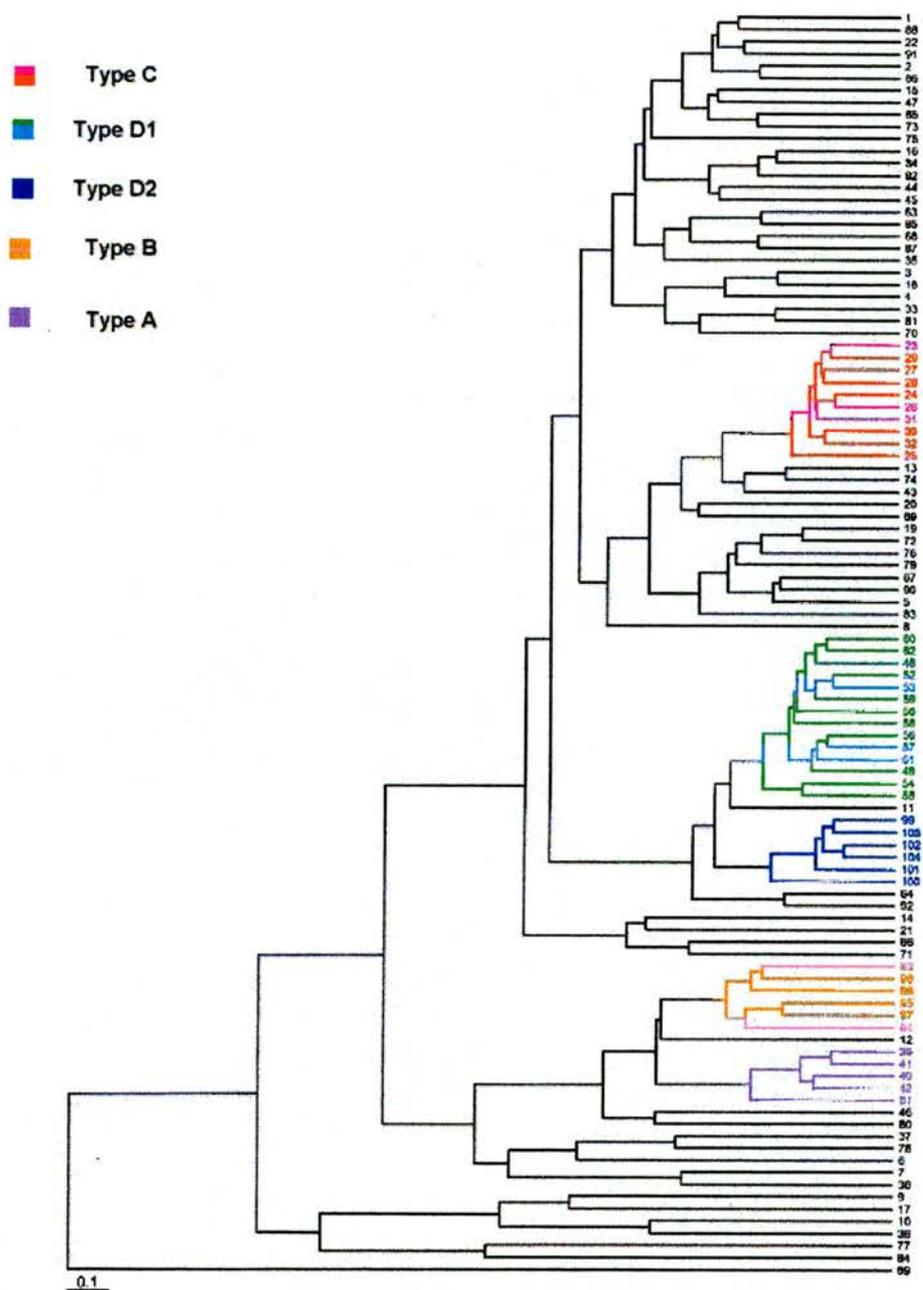
This example follows on from a study carried out by Janik (1999). Bottlenose dolphins produce apparently stereotyped whistles, and this appears to be biologically relevant because these calls are produced almost exclusively when the subject is isolated from the rest of its social group (Janik & Slater, 1998). Are these calls ‘signature whistles’? While they do appear stereotyped to the eye, previous attempts to show this with computer based techniques have all failed. Janik (1999) compared three computer techniques (cross correlation, and two multivariate statistics approaches) with the rankings of five observers. While all the observers reliably placed the signature whistles into separate classes, the computer methods could, at best, identify only one of the whistle types. Therefore, I applied the MMPED method to this data set to compare its performance with these other techniques.

The data set consisted of 104 frequency contours, extracted from spectrograms (sampling rate: 50 kHz; FFT size: 1024; time resolution: 20.5 ms; frequency resolution: 48.8Hz; weighting function: Hanning window), as described in Janik (1999). The data set consisted of five groups of signature whistles: Types A (5 contours, numbers 39-42, 51); B (6 contours, numbers 93-98); C (10 contours, numbers 23-32); D1 (15 contours, numbers 45, 48-50, 52-62); and D2 (6 contours, numbers 99-104). Each of these was recorded from one of the individuals of a social group when that individual was isolated

from the rest of the group. In addition, there were 62 contours that were not signature whistles – i.e., they were recorded from all members of the group, or when the group was together.

Fig. 5.12 shows the results of applying MMPED to this data set. In this example, all settings are equal. The tree was constructed in the same way as for the chaffinch data described above. The five signature whistle categories are highlighted on the graph. Only one error was made by the method – contour 45. It turns out that this whistle does in fact differ considerably from the other D1 calls in the frequency dimension. The frequency range of contour 45 is 6392 – 6873 Hz; for the rest of the contours of type D1, the range was 7478 – 9466 Hz. Within the correctly classified groups, the method also correctly identified the outlier of the group. For call A, contour number 51 is a clear outlier, since it is missing a brief ‘notch’ in the contour near the beginning, and it was only successfully classified by 3 of the 5 observers. For call B, contour 94 is a clear outlier, since it appears to be an abbreviated version of the other contours in this group. For call C, contour 25 is an outlier because it is considerably shorter than the rest of the calls. For call D1, contours 54 and 55 are also considerably shorter than the rest of the contours (and were only correctly assigned by 4 of the human observers). Finally, for call D2, contour 101 shows considerably more frequency modulation than the other calls. Again, it was only successfully classified by 4 of the 5 observers. In summary, the MMPED method matched very precisely the decisions of the human observers, and is externally validated by the knowledge of exactly which animal each call came from.

Fig. 5-12 UPGMA phenogram of dolphin whistles resulting from MMPED analysis, showing clustering of signature whistle types.



5.7 Discussion

Computer based classification techniques are a natural technological advance for bioacoustics that could greatly widen the scope of the field. However, current methods have been designed with a very narrow range of applications in mind. In particular, most methods appear to have neglected the problems posed by inherent subjective aspects of pattern recognition. In this chapter, I described a new method for sound comparison. By using Euclidean space in psychologically relevant dimensions, the method aims to eventually link perceptual knowledge of pattern classification with the design of the method of comparison itself.

To test this method, comparisons were made of human, computer, and animal classification results, from an avian and a cetacean species. The results suggested that the new method clearly outperformed existing computer techniques, that it was at least as accurate as human classifications, and that it matched the behaviour of dolphins precisely.

The method cannot yet be used to investigate all types of signals. In particular, gaps in signals are not dealt with. Similarly, signals with complex or harmonic structure have not yet been considered. However, I believe that the flexibility of the approach of the model will lend itself to a much wider range of signals.

Although the main aim of this chapter was to develop a new technique for sound comparative, rather than to consider specific biological problems, some of the biological results are worth commenting on. In the first example, I was interested in the human classification of chaffinch elements into different numbers of categories. While in most bioacoustical studies, human classification tasks have been restricted to confirming whether or not two signals are identical, in others it has been the aim to establish much broader categories of elements (e.g. Lynch & Baker, 1994, 1995; Marler & Sherman, 1985; Baker & Boylan, 1995). However, my comparison between human observers suggests, however, that the broader the level of categorisation, the more disagreement there was between the observers. By contrast, a random simulation found that there would be more agreement at broader categorisation levels, because the probability of any two elements being in the same category was higher when the

number of categories became lower. This would suggest that studies based on broad categorisations of elements might be those that would benefit most from computer based techniques, and that existing results based on the observations of a single observer should be treated with extreme caution. However, the design of this study means that it would be premature to suggest that the MMPED study performed better than humans at broad classification levels, only that it would be more repeatable.

My second empirical example was that of dolphin signature whistles. There has been considerable controversy over whether or not individually distinctive vocal signals exist in bottlenose dolphins (Janik, 1999; McCowan & Reiss, 1995). A previous computer technique, designed specifically for the task of examining these whistles, found no evidence that calls made in isolation were stereotyped in any way (McCowan & Reiss, 1995). However, Janik (1999) showed that human observers were able to reliably identify signature whistles from his sample, while the method of McCowan & Reiss, as well as other more standard bioacoustical techniques were not. By contrast with these earlier methods, the MMPED method developed here clearly identifies all the signature whistles in Janik's data set, and indicates that they are more stereotyped than other aspects of the dolphins' whistle repertoires. This provides unequivocal support for the signature whistle hypothesis.

Computer based classification techniques should be a realistic option in bioacoustical analysis, but this is not so of current techniques. The MMPED method may meet the requirements of a much wider range of investigations, and allow researchers to capitalise on the data provided in spectrograms.

Chapter 6 Variation in cultural transmission and song structure in the chaffinch populations of the Canary Islands.

6.1 Abstract

In earlier chapters, I described the cultural trap hypothesis, which linked the cultural evolution of song with the genetic predisposition to learn species specific song. One of the predictions of this theory was that factors that increased cultural diversity (population size, cultural mutation rate) increase the success of wider predispositions. In this chapter, I compared the cultural diversity of three genetically isolated populations of chaffinches from the Canary Islands, and found large differences between them, consistent with the populations' sizes. I then examined an aspect of song structure, and an aspect of song organisation, that were both broad enough to possibly reflect the genetic predisposition. Again, I found large differences between the populations that were consistent with the cultural trap hypothesis. Finally, I conducted an MMPED analysis of song element structure. The results of this analysis found differentiation in element structure between the populations; however the pattern of this differentiation was not consistent with the cultural trap hypothesis.

6.2 Introduction

Cultural transmission occurs when information is transferred between individuals by social learning. Social learning is learning that is biased by the actions or presence of another individual (Whiten & Ham, 1992). Although normally associated with humans, cultural transmission in other animal species has been demonstrated in laboratory and field experiments in contexts as diverse as predator avoidance (Curio *et al.*, 1978), foraging (e.g. Terkel, 1996), mate choice (Dugatkin, 1996), and communication (e.g. Thorpe, 1958). Because they both result in the transfer of information between individuals, analogies between cultural and genetic transmission have often been drawn (e.g. Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985), suggesting that cultural transmission

might lead to a form of non-genetic Darwinian evolution - cultural evolution. A considerable theoretical literature, based on population genetics, has developed this concept. These studies have focused on the dynamics of cultural evolution itself (Cavalli-Sforza & Feldman, 1981; Laland *et al*, 1996), as well as the interactions between cultural evolution and genetic evolution (Feldman & Cavalli-Sforza, 1976; Feldman & Laland, 1996).

Theories based on the spread of cultural and genetic traits through populations cannot be tested using the approach that typifies most experiments on cultural transmission. Such experiments are normally laboratory based, focus on pairs consisting of observers and tutors, and involve transmission of information that would be unnatural for the animal in its natural environment. While these approaches have been essential in elucidating the mechanisms of cultural transmission, in order to investigate evolutionary hypotheses at the level of the population, it is necessary to examine the evolution of cultural traits in natural populations, in a naturalistic setting.

For most cases of cultural transmission in animals, there have been no attempts to examine cultural transmission throughout a natural population. There is good reason for this, since most of these studies have focused on foraging behaviour. In many cases, cultural transmission of this information is ephemeral, and horizontal in mode (Laland *et al*, 1996). It may also vary dramatically depending on the local environment, since much foraging information is about that local environment itself (e.g. food locations). These factors make it very hard to dissociate social learning from individual learning, and given the heterogeneity of the behaviour patterns exhibited, it is hard to know whether foraging behaviour is socially learned in one area, but not in another. The most in-depth study of population-wide levels of cultural evolution is that of Whiten *et al* (1999) on chimpanzee foraging techniques across Africa. Here, 23 traits were suggested to be cultural in nature, based on patterns of variation rather than experimental data. Another recent series of studies (summarised in Terkel, 1996) involves the serendipitous discovery of rats making use of a novel ecological niche (pine forests in Israel), provided by humans. This has led to the cultural

transmission of a feeding technique for unravelling pine cones. Unusually, vertical cultural transmission appeared to be of considerable importance here.

The situation for biologists investigating animal cultural evolution is in complete contrast to the situation for studies of human cultural evolution. Here, the problem is that controlled experiments exploring the mechanism of transmission are obviously unfeasible for ethical reasons. But, because of the prevalence of cultural transmission in humans, and because of the apparently greater importance of vertical and oblique modes of transmission (Cavalli-Sforza *et al*, 1982), there have been a number of successful attempts to apply cultural evolutionary theory to population-level anthropological data (e.g. Boyd & Richerson, 1985; Durham, 1992; Laland *et al*, 1995).

There has been one other successful case in which cultural transmission between animals has been projected onto variation at the level of the population. This has been the study of song learning by oscine birds. This differs from many other examples of animal cultural transmission in a number of ways. First, bird song is normally transmitted obliquely – from adult neighbours to young males setting up their territories. Only in Darwin's finches has a strong degree of vertical transmission been demonstrated (Grant & Grant, 1996). Secondly, it is known that without cultural transmission, young songbirds are normally unable to acquire a species typical song (e.g. Thorpe, 1958); individual learning is uncommon and has only been demonstrated in two species (Kroodsma *et al*, 1997, 1999). Moreover, it appears that changes in song traditions may be caused by random miscopying, or 'cultural mutation' (Lemon, 1975; Slater *et al*, 1981). Finally, the development of acoustic analytical tools, especially the spectrograph, has allowed easy categorisation and comparison of sounds.

As a result of these advantages, patterns of cultural evolution of song have been studied quite intensively for around 40 years. Initially, interest focused on mapping patterns of geographical variation, especially so-called 'dialects', the mosaic pattern of song sharing that has been observed in several territorial species (e.g. Marler & Tamura, 1964; McGregor, 1980). However, more

analytical techniques have also been employed recently. One approach has been to examine the change in song along lineages, or in one area, over a period of time (Ince *et al*, 1980; Thielcke, 1987; Chilton & Lein, 1996; Payne, 1996; Harbison *et al*, 1999). Alternatively, inferences about parameters of cultural evolution can be drawn from measurements of the extent of song sharing in a population at one point in time (Lynch & Baker, 1993, Slater *et al*, 1981).

There have been few attempts to develop theories about bird song from a cultural evolutionary viewpoint. Perhaps the most intensively studied is the concept that patterns of geographical variations, such as dialects, are created and maintained only by the processes of cultural mutation and cultural drift (Andrew, 1962; Catchpole & Slater, 1995; Lynch, 1996) . One of the general, and successful, approaches of several studies has therefore been to fit patterns of variation in space or time to a 'neutral' model using models adapted from population genetics (Ince *et al*, 1980; Slater *et al*, 1981, Lynch, 1996; Payne, 1996) or by using spatial simulations (Goodfellow & Slater, 1986, Williams & Slater, 1990).

In previous chapters (2-4), I developed a theoretical model of gene-culture coevolution in bird song, the cultural trap hypothesis. This examined the interaction between a neutral model of cultural transmission and a genetic filter that predisposed birds to learn species typical songs. Simulation and mathematical versions of this model found less restrictive filters (i.e. filters under which a wider range of songs was accepted as species typical by males learning song and females choosing mates) were more successful. This result stemmed from the interaction between genes and culture under boundary conditions. A clear prediction of the models was that factors that increased cultural diversity increased the success of wider filters.

There have been several previous studies investigating differences in cultural diversity between songbird populations. The results of these studies can be split into two categories. The first general result is that isolated, island populations tend to show lower cultural diversity than larger populations (e.g.

M.C.Baker, 1996; Chapter 7 of this thesis). The second finding is that migratory populations have higher cultural diversity than non-migratory populations (e.g. Nelson *et al*, 1996, Hughes *et al*, 1998).

Measuring cultural diversity in song presents certain problems, because of its oblique, geographically based mode of transmission. Two approaches have been used to date. The first method is to measure the amount (i.e. average probability) of song sharing between neighbouring individuals. However, this approach under-represents population-wide diversity. Consider three populations, all of which consist of 100 individuals. In the first two populations 50 individuals have song type **A**, and 50 sing song type **B**. The first of these has two dialect areas, one of **A**'s, and one of **B**'s. In the second, the **A**'s and the **B**'s are randomly interspersed. Finally, the third population possesses 4 song types, all mixed up, as in the second population. In this scenario, measuring song sharing between neighbours would indicate that populations 2 and 3 have similar levels of diversity, much higher than population 1.

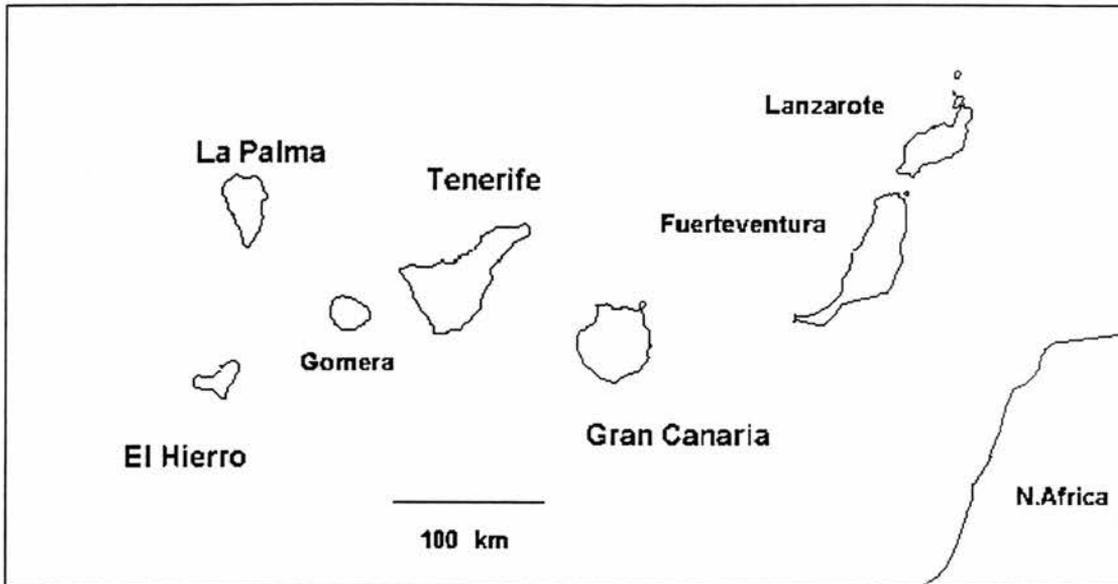
The second approach has been to count the total number of song types within a certain population, or sub-population, and use that, or some derivative of it, as the measure of cultural diversity. This would clearly place populations 1 and 2 together in the scenario described above. However, this approach has serious methodological difficulties. For a species like the chaffinch, it is normally not possible to record all the song types of a population because of the high level of cultural diversity. One solution is to estimate diversity from samples, using existing population genetics techniques (e.g. 'meme identity', Lynch & Baker, 1993). A requirement of such measurements is that a random sample is taken from the population. In a panmictic population, this is straightforward. However, where song sharing between nearby individuals is much higher than between individuals further apart from one another, this becomes much harder. In the case where population levels of variation has been estimated, this factor was not taken into account at all (Lynch & Baker, 1993, 1994). An alternative approach is to record all the songs from a sub-population, such as an individual wood (Slater *et*

al, 1981). However, no conclusions can subsequently be drawn about cultural diversity in the population as a whole.

Chaffinches (*Fringilla coelebs*) inhabit five of the seven Canary Islands, in laurel or pine forests. Molecular evidence from mitochondrial DNA and allozymes suggests that the islands were colonised from the mainland of Africa in one event (Baker *et al* 1990, 1999). Baker *et al* (1990) also found, from an analysis of allozyme variation, that the Canary Island populations have diverged considerably, both from the mainland and, more surprisingly, from each other.

The song of the chaffinch has been the subject of quite a considerable amount of research (Thorpe, 1958; Ince *et al*, 1980; Slater *et al*, 1981; Slater & Ince, 1982; Riebel & Slater, 1998, *in press*; Slater & Catchpole, 1987; Lynch & Baker, 1986, 1993, 1994; Baker & Jenkins, 1987). Recordings from the Canary Islands have indicated that the songs have a very different syntax from those from continental Europe or Britain, resembling the plastic songs of juvenile mainland males (Slater & Sellar, 1986; Lynch & Baker, 1993). This suggests that the developmental basis of singing has already been the subject of some evolution. In this chapter, I will focus on the evidence for cultural and genetic differentiation in song, between three of the islands: El Hierro, Tenerife, and Gran Canaria (Fig. 6.1).

Fig. 6.1 – Map of the Canary Islands



These islands vary considerably in size. Tenerife is the largest of the Canary islands, while Hierro is the smallest. In line with this, Tenerife has the largest area of habitat suitable for chaffinches, while Hierro has the smallest. While Gran Canaria is intermediate in size between the other two, it has a dryer climate, and more human interference, and subsequently a small area of habitat suitable for chaffinches.

A previous study suggested that there might be some variation in cultural diversity of phrases between the islands (Lynch & Baker, 1993). As might be expected under a neutral model, due to its larger size, Tenerife possessed greater cultural diversity than the other two islands. However, this study suffered from two methodological flaws. Firstly, as discussed in chapter 5, the repeatability of this study must be called into question, since it relied upon one observer to categorise chaffinch elements at a relatively broad level. The second problem is that Lynch & Baker adapted population genetics models (the infinite alleles model of Kimura & Crow (1964), combined with gene diversity and the effective number of alleles) that required either a panmictic population, or random

sampling. As discussed above, their pattern of sampling, as with many studies of song variation, was to take many recordings from a limited set of sampling sites. This would heavily bias their model.

In this chapter, I shall discuss an attempt to test the prediction of the cultural trap hypothesis using the chaffinch populations of these three Canary Islands. This study is based on a more thorough measurement of the cultural diversity on the islands. I have tried to incorporate local and population-wide levels of diversity by measuring song sharing between all birds in my samples, and then dividing the results into classes of geographic distance between the individuals compared.

The second aim of this study was to examine patterns of differentiation of some aspects of song at a broader level. Variation in such features might represent divergence in the genetic filters in the populations, and would thus provide a possible test for the cultural trap hypothesis.

6.3 Methods and Materials.

6.3.1 Recording locations and methods.

This study is based upon a set of recordings made in the Canary Islands between 14th March and 19th April, 1998. I recorded 1142 songs from 31 individuals on Tenerife; 1779 songs from 33 individuals on Gran Canaria; and 1336 songs from 30 individuals on Hierro, using a Telinga Pro 5 microphone to record cassette tape using a Sony WM-D6C Professional Walkman. To measure geographical variation in song sharing, I also noted the location of each of the birds I recorded, and later measured the geographic distance between each pair of individuals on a map (1:100,000 scale). It was possible to allocate each song to a specific individual, either because that individual did not have neighbours close to its territory, or through observations of territorial interactions between neighbours.

6.3.2 Analysis

The recordings were analysed using the real-time spectrograph function of the SIGNAL/RTS (Engineering design, 1996) computer system (set at: frequency resolution - 150Hz, sampling rate - 20 KHz).

Chaffinches sing with a hierarchical organisation. Continuous sound traces are known as elements (equivalent to 'notes'). Groups of several elements, known as syllables, are delimited by the fact that they are repeated. The repeated sequence of syllables is known as a phrase, and sequences of phrases make up a song type. Fig. 6.3 shows spectrograms of several chaffinch songs that demonstrate this organisation. Finally, each bird has a repertoire of one to several song types.

In this study, I considered the sharing of syllables, rather than songs or elements. This was because initial analysis of the pattern of sharing suggested that syllables rather than elements or song types were copied. Considerable

sharing of syllables was found between neighbours, compared to very little sharing of entire song types. All comparisons of syllable-sharing were carried out by the author. Only exact, or very close matches were recorded, as a study of human classification, summarised in Chapter 5, suggested that only the results of such comparisons were consistent between observers.

The repertoire of song types and phrase types was first established for each of the individuals. It might be expected that the repertoire measured for an individual might rise asymptotically as the number of songs recorded increased, as with a random (Poisson) distribution. To determine a threshold above which one could be fairly certain that all, or nearly all, of the repertoire had been recorded, I plotted the cumulative repertoire size of some of the individuals from whom I had the most recordings (Fig.6.2). This shows that both the song-type, and phrase-type, cumulative repertoires do indeed level off, as expected. I set the threshold at 40 songs, based on this graph, and to maximise the sample size of individuals available. Only data from individuals from which I had recorded at least 40 songs were used to estimate syllable diversity in the three populations. Three further males, that were probably juveniles, sang songs that were not fully developed, and that were not easy to categorise into discrete song and phrase

**Fig. 6.2 Cumulative repertoire sizes of
Canary Island chaffinches**

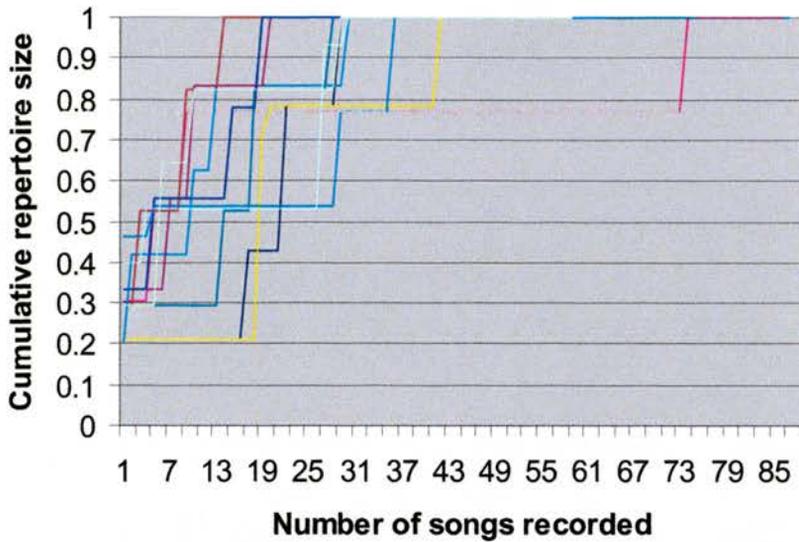


Fig. 6.2 shows the cumulative increase in repertoire size as more songs are produced, for a sample of 11 individuals from throughout the Canary islands, from which I had recorded at least 50 songs. The cumulative repertoire size is expressed as a proportion of the maximum recorded repertoire size for each individual, to improve the clarity of the graph.

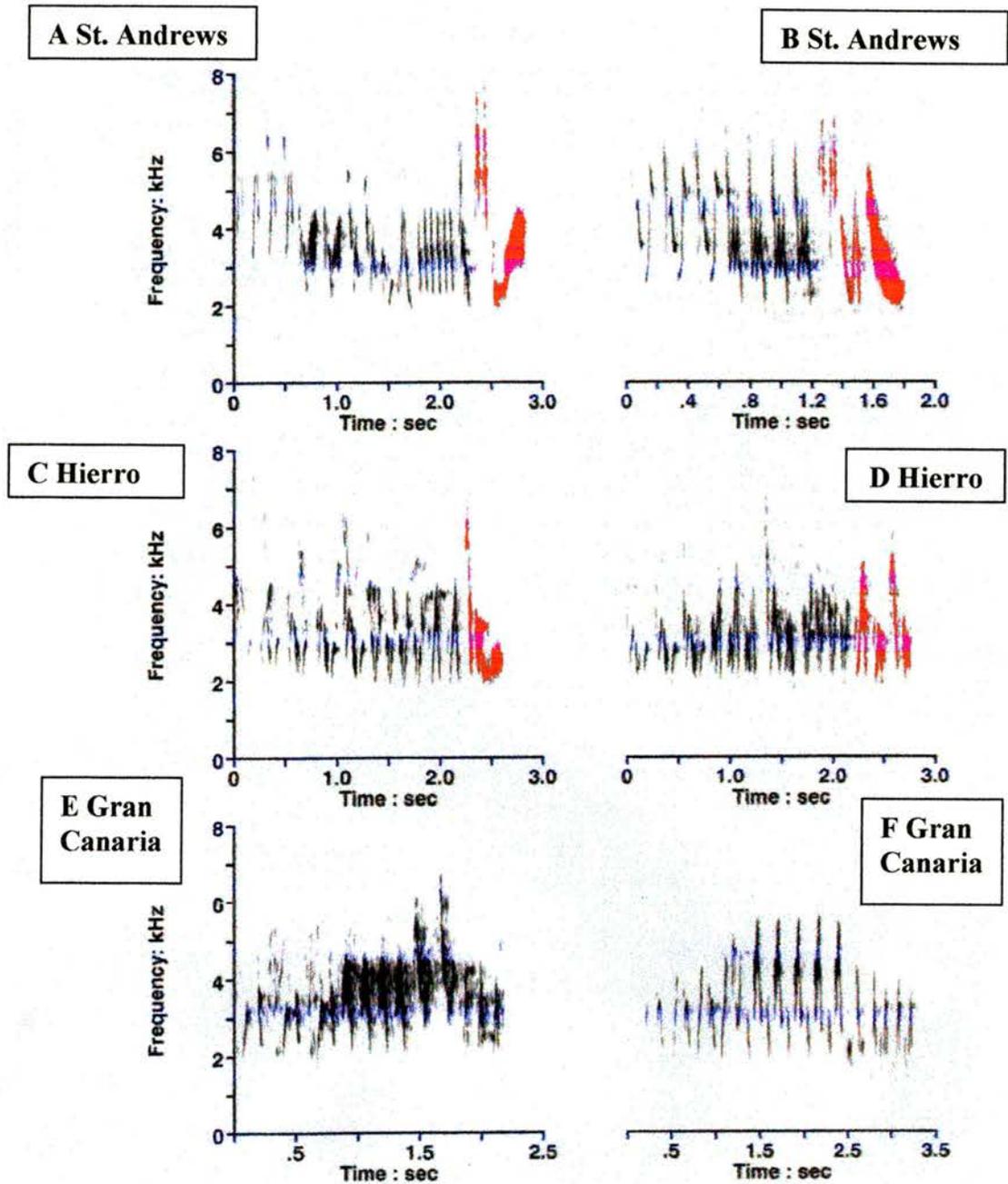
types. These too were discarded from the rest of the study. After this process, I was left with a sample size of 17 individuals from El Hierro, 17 individuals from Tenerife, and 20 individuals from Gran Canaria.

To measure syllable sharing, I first divided the pairs of individuals between geographic distance categories. I then used the Jaccard index of similarity (i.e. the number of shared phrases divided by the total number of different phrases) between the phrase repertoire of each pair of birds within a population. This index has been widely used for analogous studies in ecology, as well as in a previous study of cultural evolution in bird song (Williams & Slater, 1990). To establish confidence intervals, the Bootstrap procedure was modified and applied to the data (see Appendix 1 for details).

Chaffinch elements can be clearly divided into two categories. The first of these are tonal sounds, with a very narrow frequency range at any point in time. In contrast, the second category consists of elements that have a 'buzzy' quality. Spectrograms of these notes show that they consist of very rapid frequency modulation, which creates a broad band effect. The last elements of the spectrograms A-C in Fig. 6.3 are all buzz elements. While most elements in this study fell clearly into one or other of these categories, there does exist a continuum between the two. Since this is such a 'coarse-scale' classification of elements, there is a strong possibility that it represents part of the genetic filter for chaffinches. I therefore measured the proportion of these buzz and tonal elements in the three populations. I also subdivided the buzz elements into two distinct categories: buzz elements and 'wide buzz' elements. Wide buzz elements were similar to buzz elements, but there were distinct gaps between the different frequency modulations.

One of the main differences between European chaffinch song and song from the Canary Island populations is the frequent lack of a 'flourish' in the latter. The flourish differs from the rest of the song in that it consists of between 2 and 10 elements that are not repeated, and that often finish with a long element (Fig. 6.3 – A,B). Some Canary Island chaffinches sing songs with rudimentary flourishes (Fig. 6.3 – C,D), while others sing songs with no flourish whatsoever (Fig. 6.3 – E,F). For the next analysis, I measured the proportion of songs with flourishes between the three Canary Island populations, since such a fundamental and distinctive feature of (British) chaffinch song might also be likely to have a genetic basis. To do this, I counted the number of repetitions of each syllable, in each phrase for my entire sample of songs (excluding those from juvenile males). Songs that finished with a syllable that was not repeated were considered to possess a rudimentary flourish.

Fig. 6.3. Spectrograms of chaffinch song from Scotland and the Canary Islands. The highlighted areas represent flourishes



Finally, I took samples of elements which I used to carry out MMPED analyses of the variability of their shapes. A sample of 128 elements from Tenerife, 119 elements from Gran Canaria, and 100 elements from El Hierro were taken, avoiding sampling more than once from syllables that were shared between individuals. The elements were first isolated in the RTS program, and then exported to SIGNAL. Here, the frequency contour was extracted, by tracing over the spectrogram with the mouse, using the DRAW command. A standard SIGNAL set-up was used for all elements (time resolution: 10.2ms, Fast Fourier Transform size: 256, interval between FFT steps: 0.400 ms, sampling rate: 25 KHz).

An MMPED analysis, as described in Chapter 5, was then carried out, comparing the samples from the three populations. I carried out seven separate analyses. In the first of these, the three parameters of frequency, time, and change of frequency with time were set to be equal. In the subsequent tests, each of the parameters was varied, by setting it first to 0.5, and then to 2.0.

The aim of the MMPED analyses was to examine the data at a coarse scale, at a level that might reflect differences in genetic filters rather than in cultural transmission. I hypothesised that differences in genetic filters would result in areas in the multidimensional space that characterised the element structure that contained only elements from one population. Obviously much of the variation in these analyses reflected cultural variation. To assess differentiation in the element structure, I measured the reciprocal nearest neighbour MMPED distance between the populations. This means that, for each element in population 1, I found the element that was most similar in population 2, and recorded the MMPED distance between these two. I then repeated the procedure for each element in population 2 with the elements from population 1. If some element types were unique to just population 1, then the average nearest neighbour distance from population 1 to population 2 would be higher than the average nearest neighbour distance from population 2 to population 1.

Different patterns of cultural evolution may create a bias in this analysis if, for example many samples of very similar elements are taken from one population as a result. To overcome this problem, a threshold MMPED distance was set. Each new element to be analysed was then compared with each of the previous elements from that population, and discarded if it was within this threshold distance. In practice, a threshold value of 1.0 was found to produce reasonable samples from the data.

6.4 Results

6.4.1 Cultural diversity

Figs 6.4 and 6.5 show the relationship between song sharing and geographic distance for the three islands. It is immediately apparent that a large difference exists between the populations, with much lower rates of song sharing on Tenerife than the other islands. This was true both between nearby pairs of birds, and between pairs of birds much further apart. While the latter finding was expected, given Tenerife's much larger size, the lower level of sharing at lower inter-individual distances suggests that processes of cultural evolution are affected at all levels by the higher overall cultural diversity (see Chapter 7 for a similar investigation and result).

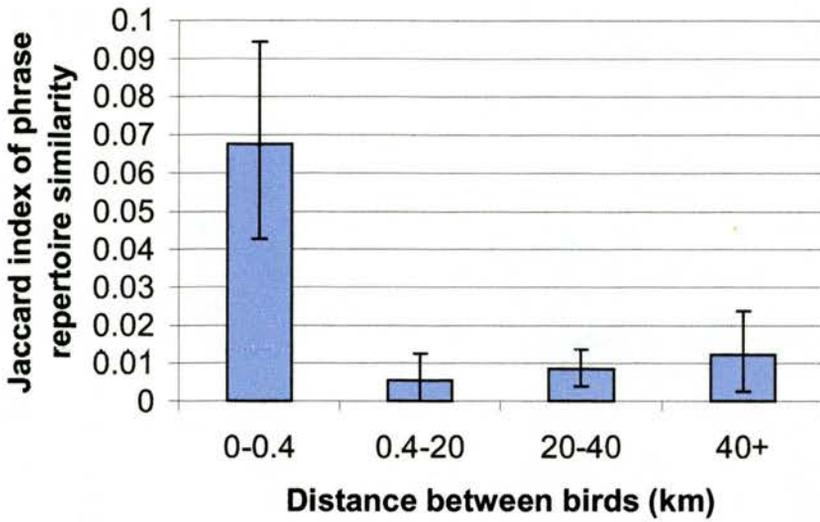


Fig. 6.4 shows the relationship between geographic distance and song sharing on the island of Tenerife. See methods for further information.

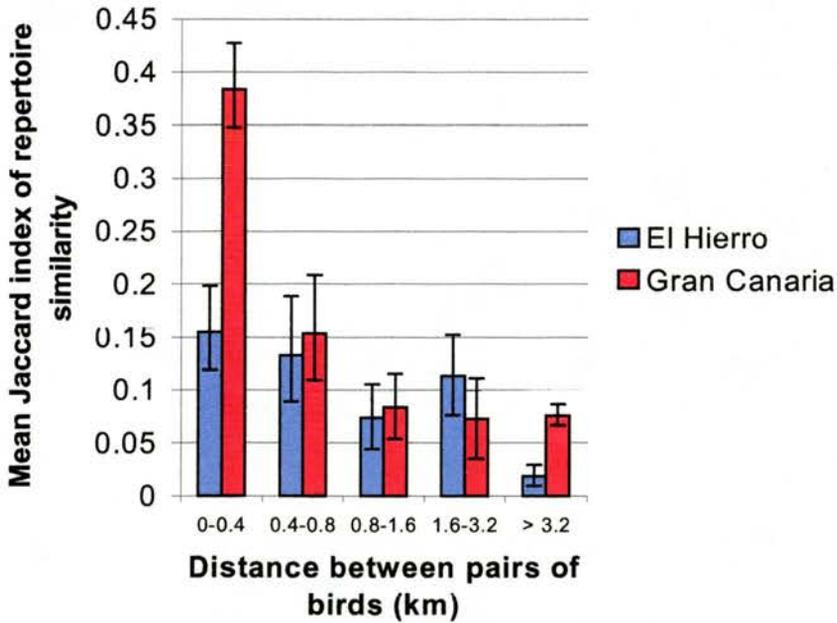
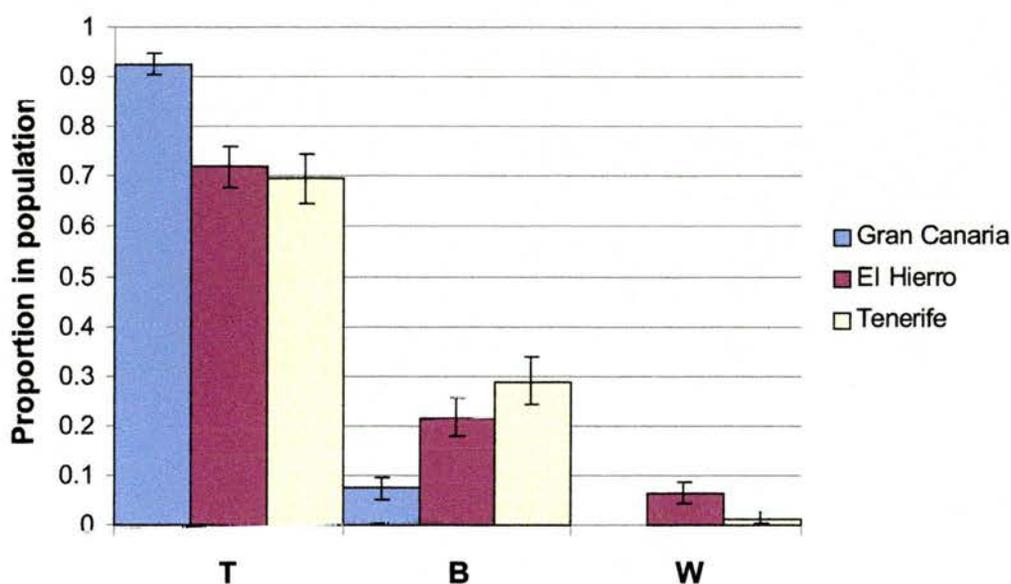


Fig. 6.5 shows the relationship between song sharing and geographic distance on the islands of Gran Canaria and El Hierro. See methods for further information.

6.4.2 Frequencies of buzz elements.

From the song recordings, I counted 424 elements from El Hierro; 539 elements from Gran Canaria; and 374 elements from Tenerife. As Fig. 6.6 shows, there were wide discrepancies in the proportion of buzz elements within these samples. While the proportion of buzz elements was nearly identical in Tenerife and El Hierro, it was only a quarter of this value in Gran Canaria.

Fig. 6.6 Frequencies of element types in Canary Island chaffinch populations



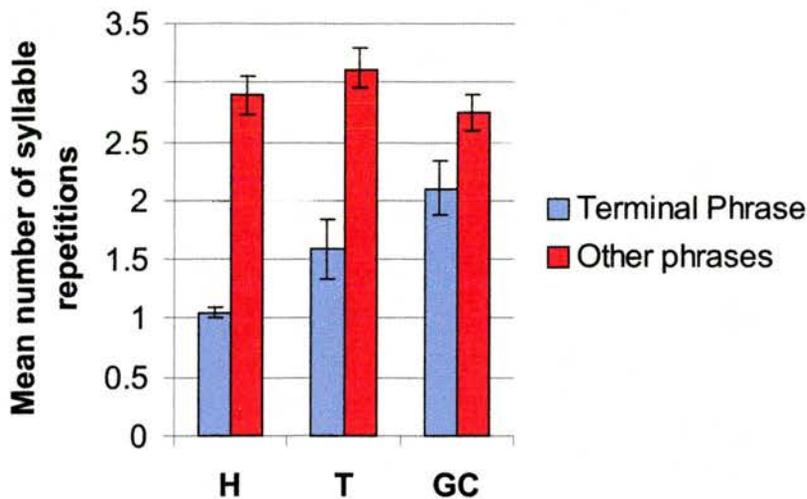
T: Tonal element; B: Buzz element; W: Wide buzz element

Moreover, while wide buzz elements were uncommon in both El Hierro and Tenerife, they were entirely absent in Gran Canaria. Overall, these results suggest a very marked difference between these populations. Because of the neutral transmission of song, the large ‘population’ size of elements, and the high cultural mutation rate, it seems unlikely that cultural evolution alone could have led to such a marked differentiation between the islands, considering that I sampled widely in all three populations, and given the sample sizes involved. The only exception to this would be if the differentiation reflected some variation in acoustic environment between the islands.

6.4.3 Frequencies of unrepeated terminal phrases.

From the recordings, I took a sample of 102 song types from El Hierro; 102 from Tenerife; and 130 from Gran Canaria. Fig. 6.7 shows the average number of repetitions of terminal and non-terminal phrases. Again, there was a clear difference between the three populations, with Gran Canaria having the highest and El Hierro the lowest number of repetitions of the terminal phrase. In this analysis, however, Tenerife occupied a position midway between these two extremes. These results suggest that El Hierro has rudimentary flourishes in nearly all of its song types; that Gran Canaria only rarely has such flourishes; and that Tenerife has a mixture of flourishes and non-flourishes.

Fig 6.7. Mean number of repetitions of syllables in the terminal and other phrases in Canary Island chaffinch populations



H: El Hierro; T: Tenerife; GC: Gran Canaria

6.4.4 MMPED analyses of element structure.

The MMPED analysis revealed consistent patterns of differentiation in element structure between the three populations. Figs 6.8 – 6.10 show the results of this investigation.

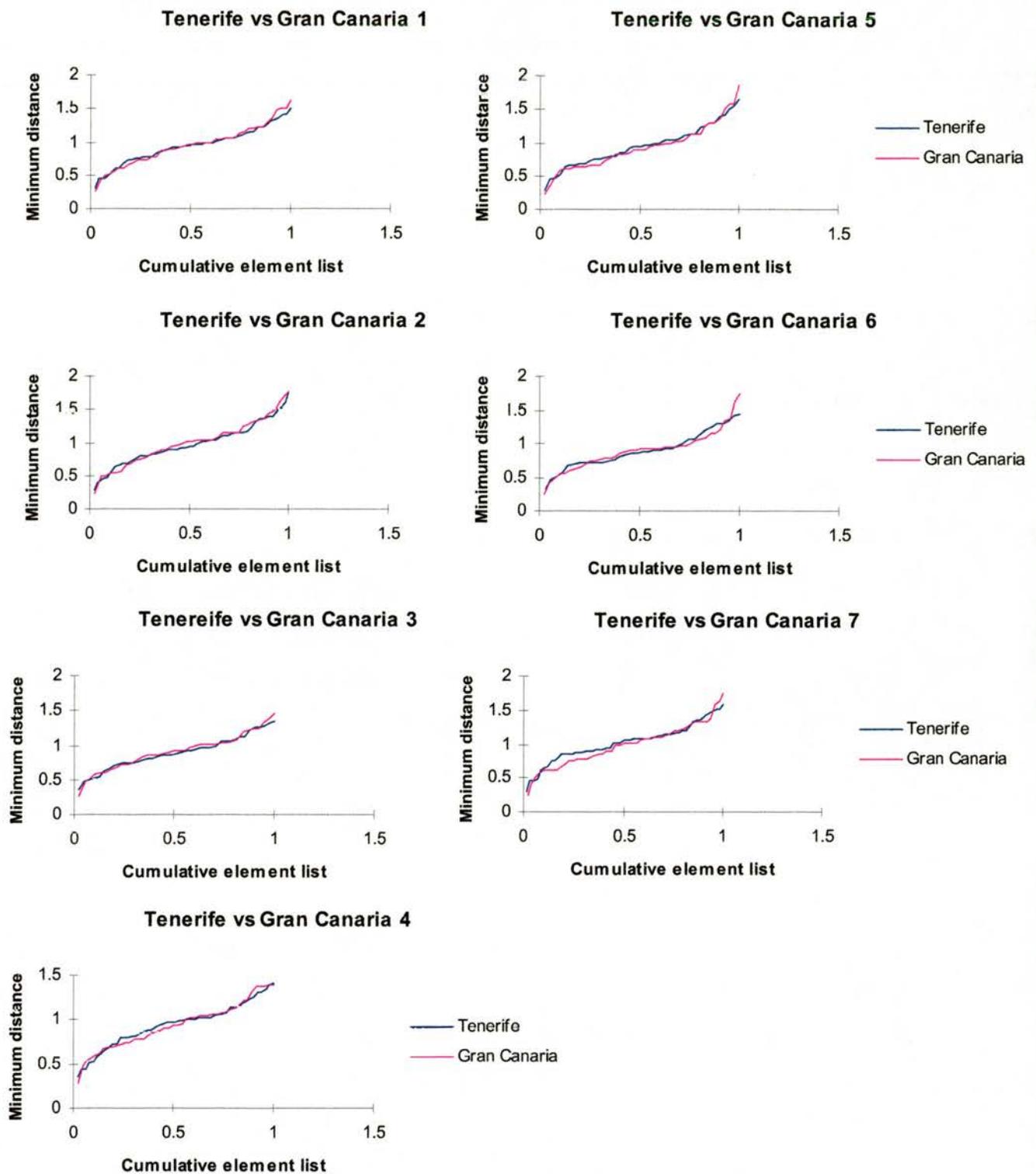


Fig. 6.8 MMPED comparison of elements from Gran Canaria and Tenerife. Y-axis refers to the minimum distance from one element type to the most similar element in the complement population. X-axis lists in order of score, the different element types, as a proportion of the total number of element types in that population. See above for explanation of different graphs. In these, graphs 1-7 refer to parameter settings: 1: All set at 1; 2: Frequency change set at 0.5; 3: Frequency change set at 2; 4: Frequency set at 0.5; 5: Frequency set at 2; 6: Time set at 0.5; 7: Time set at 2.

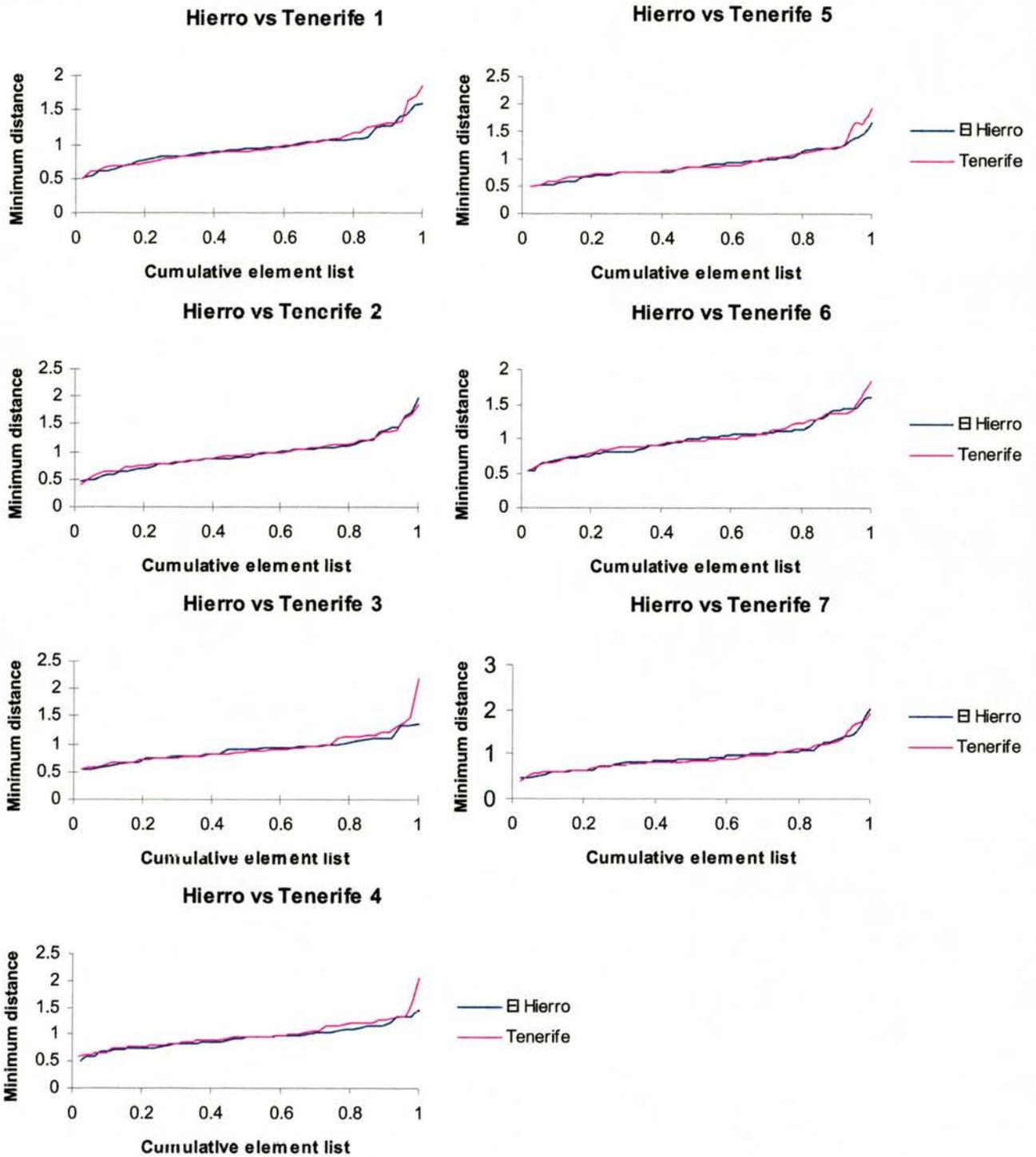


Fig. 6.9 MMPED comparison of elements from El Hierro and Tenerife. See fig. 6.8 for description of axes.

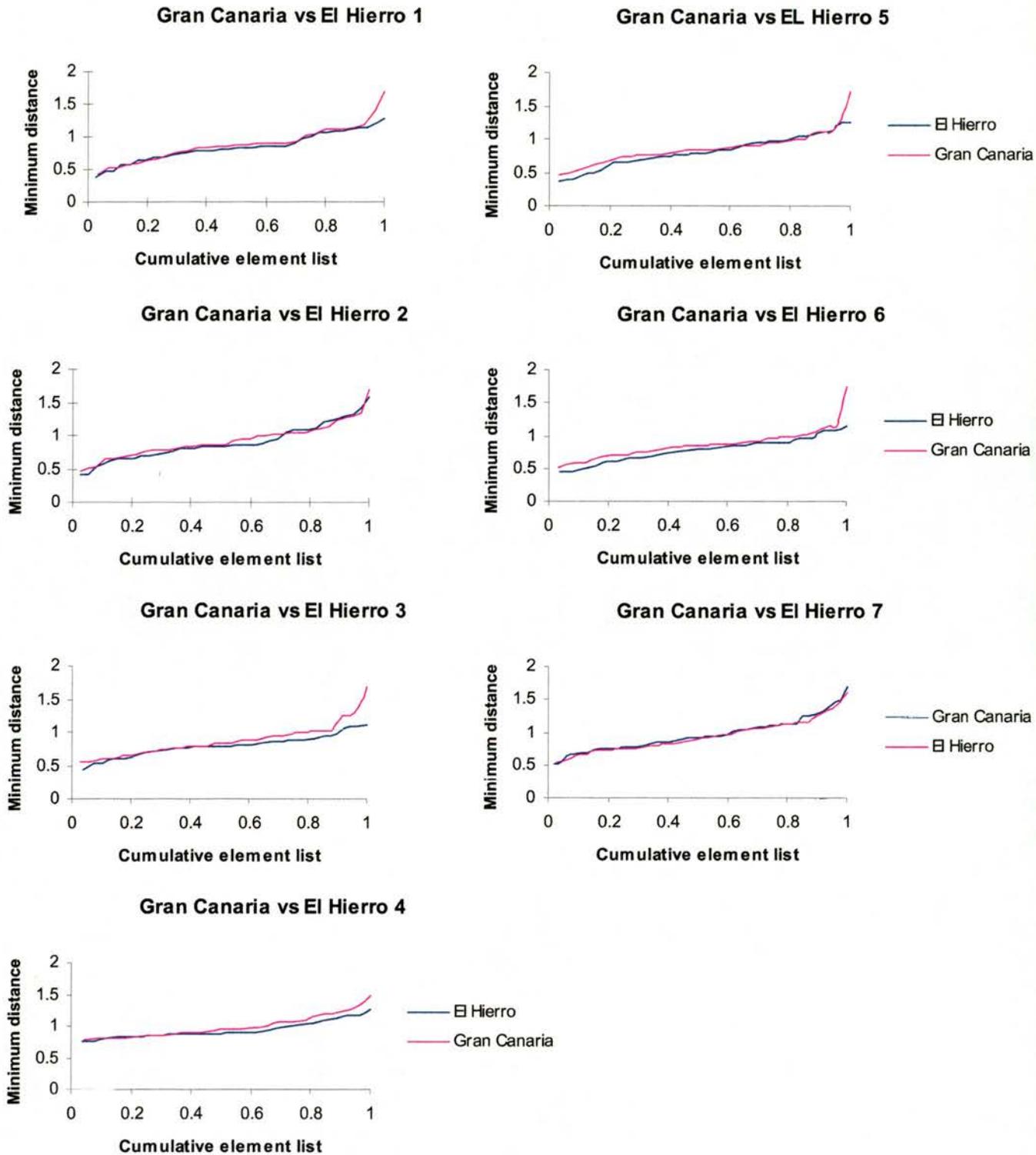


Fig. 6.10 MMPED comparison of elements from El Hierro and Gran Canaria. See fig. 6.8 for description of axes.

These graphs indicate that element types were found in all populations that were not found in the population they were compared to. Moreover, these element types were consistently identified under most of the MMPED settings (Fig. 6.11). Figs 6.12-6.14 illustrate the 5 most unique elements for each population, in each comparison.

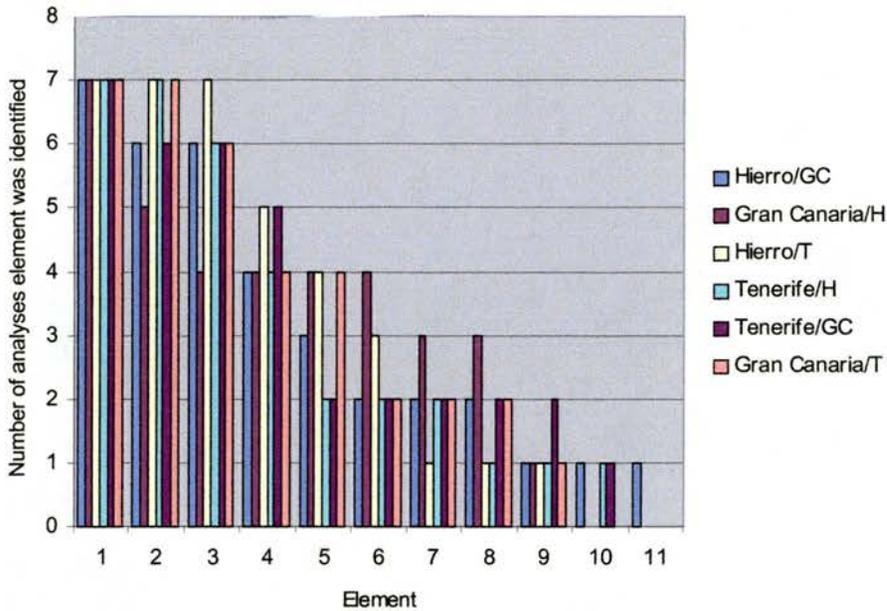
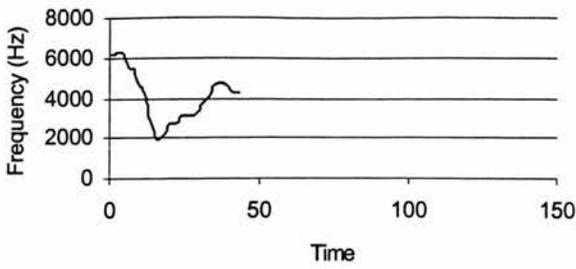
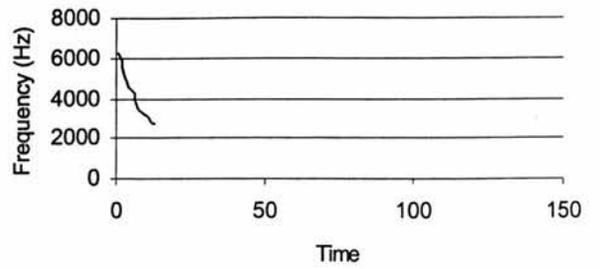


Fig. 6.11 The consistency of the MMPED analysis is shown in this graph. The y-axis represents the number of analyses (out of 7) that each element was identified as one of the five most unique elements. The x-axis represents the different elements identified in the analyses.

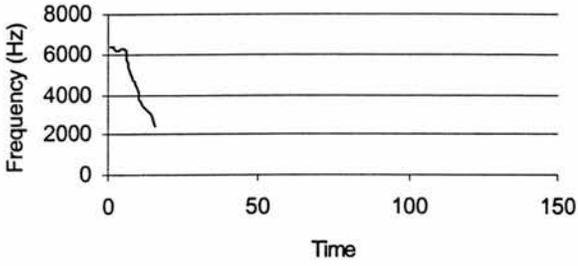
There was little evidence in this analysis that Tenerife possessed more unique element types than the other islands, except for a small trend in the comparison with El Hierro. The unique element types that were identified



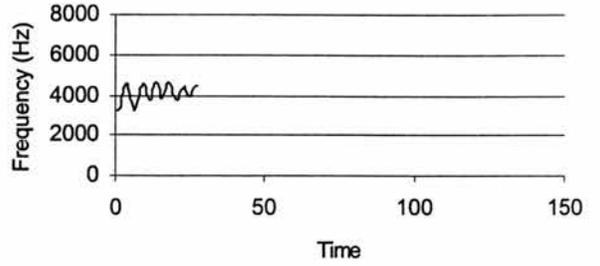
Gran Canaria 3



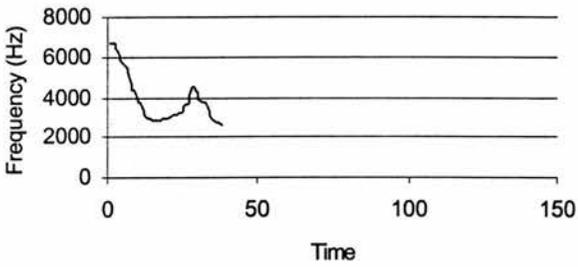
Gran Canaria 4



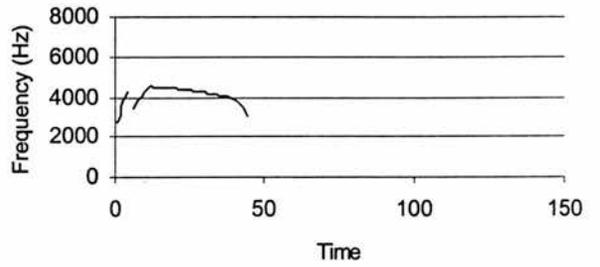
Gran Canaria 5



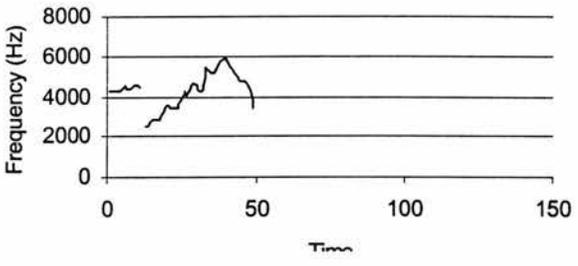
Tenerife 1



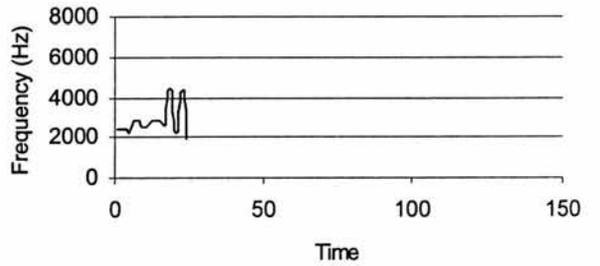
Tenerife 2



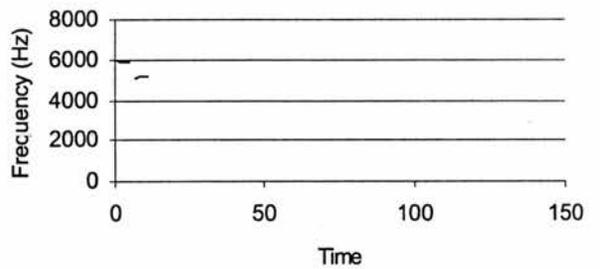
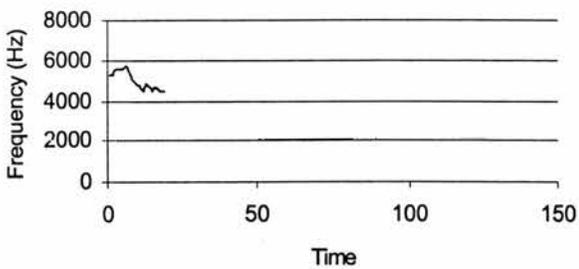
Tenerife 3



Tenerife 4



Tenerife 5



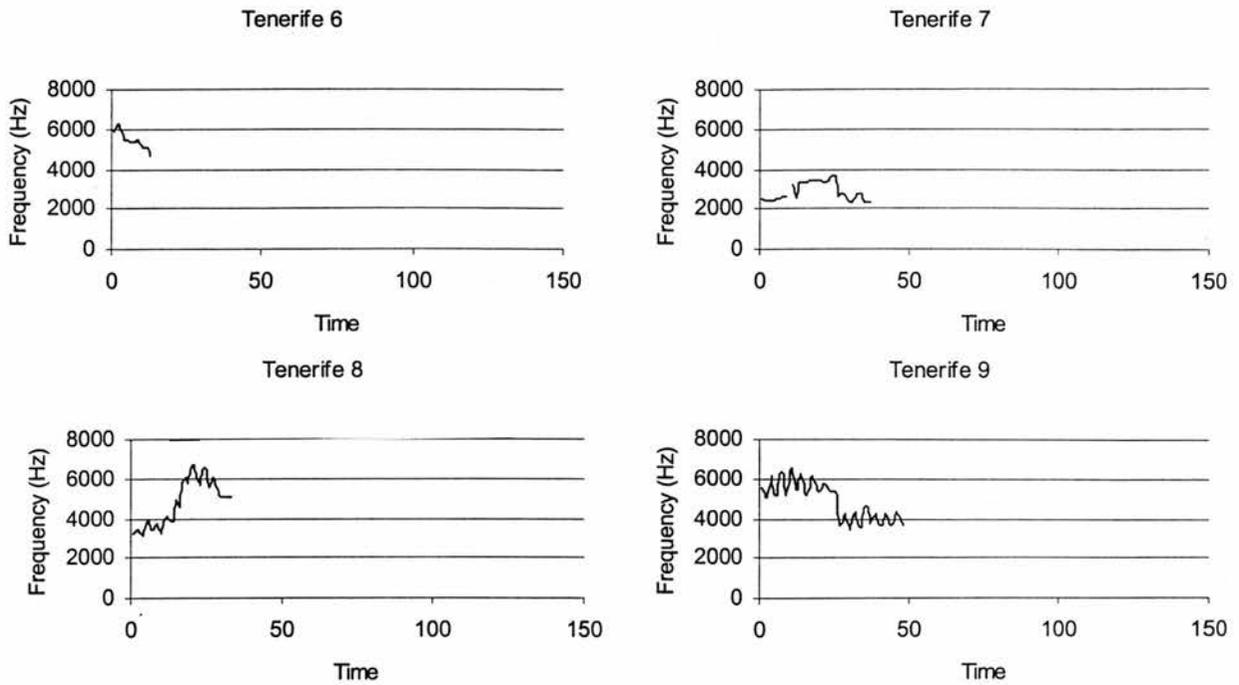
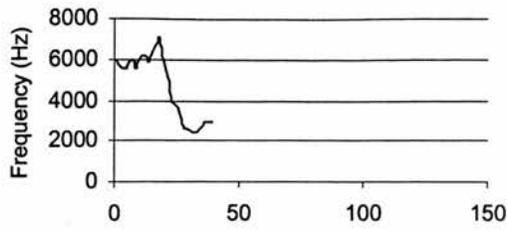


Fig. 6.12 Unique element types in the MMPED comparison of Gran Canaria and Tenerife. The graphs plots the frequency contours that were extracted from the spectrograms, and used in the analysis. 9 element types are shown for Tenerife, because numbers 1, 3, 4, 6, & 7 were tied in how often they were selected in the 7 MMPED analyses. Each unit on the time axis represents one unit in the analysis, and corresponds to 0.4 ms

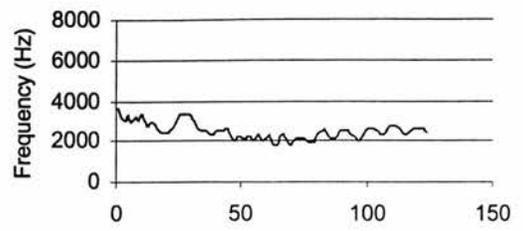
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Fig. 6.13 Unique elements in the MMPED comparison of El Hierro and Gran Canaria. The graphs plots the frequency contours that were extracted from the spectrograms, and used in the analysis. 6 element types are shown for Gran Canaria because numbers 1, 3, 4, & 5 were tied in how often they were selected in the 7 MMPED analyses. Each unit on the time axis represents one unit in the analysis, and corresponds to 0.4 ms.

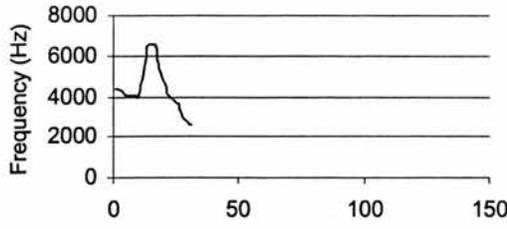
Hierro 1



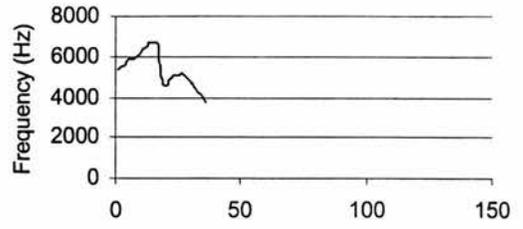
Hierro 2



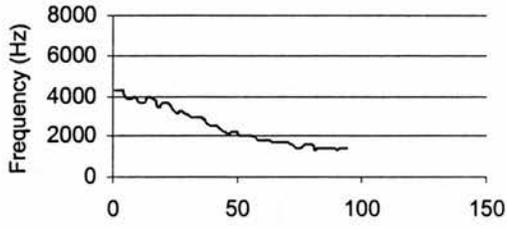
Hierro 3



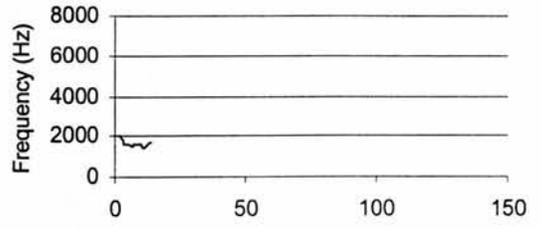
Hierro 4



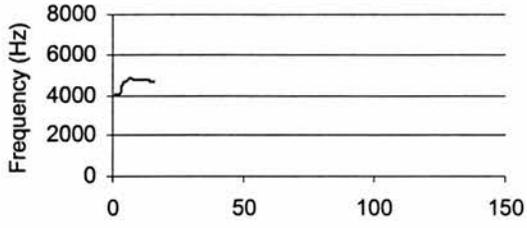
Hierro 5



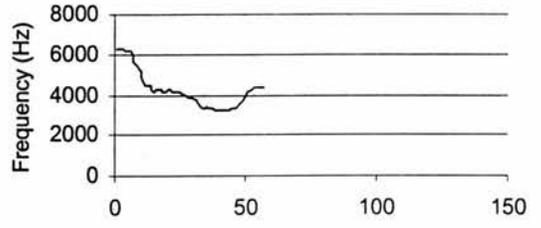
Gran Canaria 1



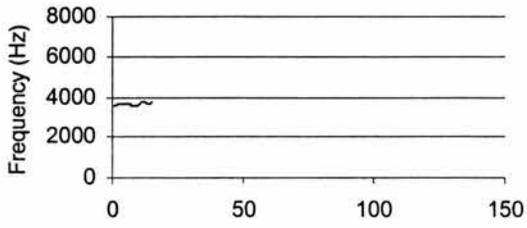
Gran Canaria 2



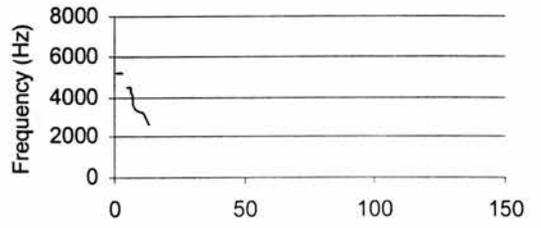
Gran Canaria 3



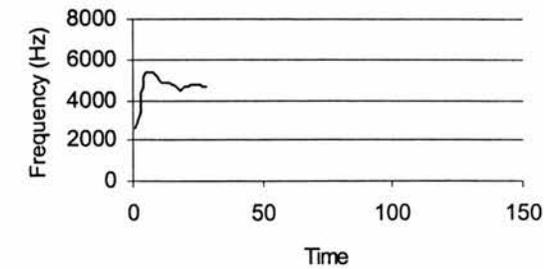
Gran Canaria 4



Gran Canaria 5



Gran Canaria 6



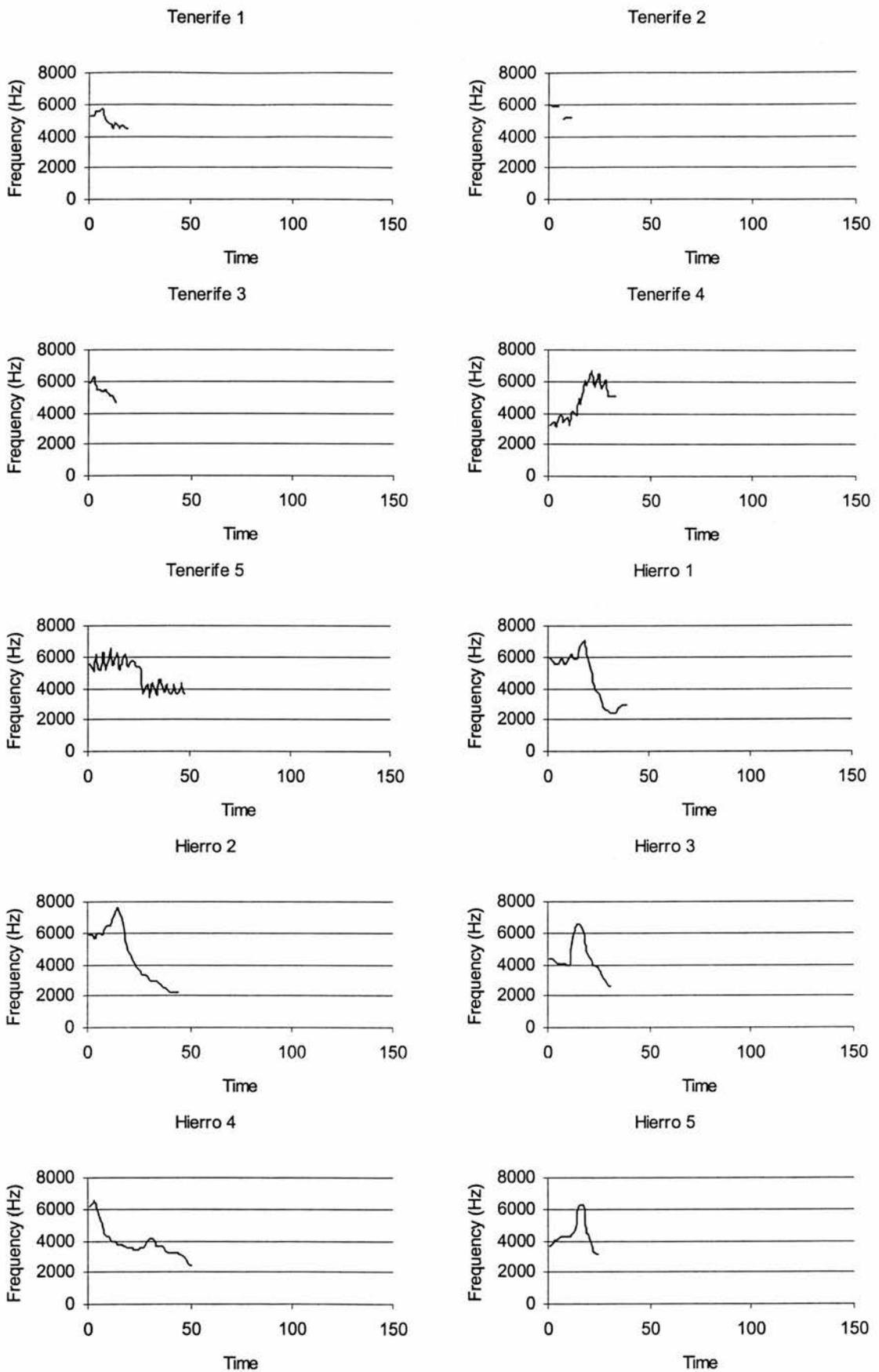


Fig. 6.14 Unique elements in the MMPED comparison of El Hierro and Tenerife. Each unit on the time axis represents one unit in the analysis, and corresponds to 0.4 ms. The graphs plots the frequency contours that were extracted from the spectrograms, and used in the analysis.

showed some similarity: for example, when compared to Gran Canaria, Tenerife possessed unusual buzz elements, mirroring the much higher proportion of this element category in the latter. However, in comparisons with both islands, it is apparent that Tenerife lacked tonal elements involving a steep down-sweep.

7.5 Discussion

The three populations I examined in this study can be viewed as one large island, Tenerife, with substantial areas of habitat, and two small islands, Gran Canaria and El Hierro, which both have much smaller areas of habitat. This division was reflected in the pattern of syllable sharing in the islands. There was far less song sharing between individuals in Tenerife than in the other populations. This was not merely a reflection of the larger size of the Tenerife population however, as even nearby individuals shared fewer syllables than on the other islands. This is consistent with a neutral model of cultural evolution in which patterns of song transmission vary with aspects of the population's ecology, a concept that is developed further in the next chapter. The effect of this variation on the environment of communication for these populations should be considered. In Tenerife, syllable sharing between neighbours is uncommon – many neighbours share no syllables at all. In the other islands, which are both well established, viable populations, some syllable sharing between neighbours is normal. The functional consequences of song sharing have been considered by many authors (see Chapter 4). In British chaffinches (*Fringilla coelebs gengleri*), playback of a matching song type has recently been shown to alter the pattern of singing (Riebel & Slater, in press). It is possible that the different pattern of song sharing is some sort of adaptation, but the presence of similar variations between genetically undifferentiated British populations (Chapter 7) suggests that this is not likely. This result is also similar to other studies which have compared song diversity in mainland and island populations, which have found higher diversity in the former (e.g. M.C.Baker, 1996).

Given that cultural evolution patterns have been shaped by their differing environments in the Canaries, how might this have affected the evolution of their

song? The cultural trap hypothesis would predict that the population with the highest level of diversity – Tenerife – should also have the widest genetic filter. Out of the three preliminary analyses I carried out to examine this, two supported this idea. The very low proportion of buzz elements on Gran Canaria was in great contrast to the other populations. It seems unlikely that this could be the result of cultural differentiation alone. The ‘population’ of song elements on the three islands is large, with approximately 30 elements per bird, and at least 500 pairs (an estimation from the amount of suitable habitat observed) in each population. Moreover, I sampled widely – recording across the entire range of chaffinches on each island. Another alternative is that element differentiation is the result of environmental differences between the islands that have changed the acoustic environment, and subsequently the transmission of the buzz and tonal elements. However, there is no obvious evidence of this. While buzz elements are often of relatively low frequency, they do not occur outside the frequency envelope of the tonal elements. And the habitat of chaffinches is restricted to laurel and pine forests on all three islands. On Gran Canaria, these habitats have been subject to greater human interference than the other two islands, although the area of the island which supports chaffinches is still rural. If anything the greater fragmentation of the habitat might have been expected to promote low frequency sounds, as these propagate furthest.

There was also considerable differentiation in song syntax between the three populations. Nearly all songs on Hierro possessed some form of flourish. This might be viewed as a ‘restrictive’ developmental pathway. Flourishes were almost completely absent on Gran Canaria. Even though there were some song types which ended in an unrepeated syllable, these syllables were typically very simple in structure, compared to the flourishes from El Hierro. This might also be viewed as a restrictive pattern of development. In comparison, the Tenerife sample included both fully developed flourishes, and song types without any flourish whatsoever. This evidence would suggest that Tenerife has the most variable song syntax of the three populations. It is also very likely that there is a strong genetic element in the existence of flourishes. Flourishes are ubiquitous in European chaffinches – being present in all of the approximately 350 song types

recorded in Scotland for the study recorded in Chapter 7, and are one of the most distinctive features of the song.

In the final analysis, I found no strong evidence of different patterns of differentiation in element structure in an MMPED analysis. Although some of the buzz elements on Tenerife did not have similar counterparts on Gran Canaria, there were other forms of element that were present only on the latter. In particular, down sweeps seemed equally distinctive of the Gran Canaria population. However, it is hard to assess the validity of such a comparison at this stage. For example, while down-sweeps were rare on Tenerife, many elements had an 'inverted V' structure, which included a large down-sweep. Does this reduce the importance of the uniqueness of the down-sweeps on Gran Canaria?

Clearly an experimental study of the song preferences of these populations is required before any firm conclusions can be drawn about the genetic basis of song differentiation between them. However, there is now some hint that genetic differentiation has occurred. Perhaps this should not be surprising. Nearly all songbird species sing highly species-typical songs, that are often the most reliable form of identification. The process of speciation must therefore involve considerable evolution in the genetic basis of song. Although the three populations studied in this chapter are all within eyesight of one another, considerable genetic differentiation has occurred between them, and this might be expected to include some differentiation of song. The populations therefore remain an exciting possible test for the cultural trap hypothesis.

Chapter 7 – Variation in the cultural evolution of song in British chaffinch populations by inference from patterns of geographical variation.

7.1 Abstract

Geographic variation in song is a common feature of temperate territorial songbird populations. However, there is controversy over the function of this variation. Is it an adaptation of the communication system, or a by-product of the process of cultural transmission? Moreover, even in well studied species, accurate estimates of the parameters underlying this variation, notably the rate at which new song types are generated, have not been made. In this chapter, I compare the geographical variation of chaffinch (*Fringilla coelebs*) song from 5 locations in Scotland. Considerable variation in cultural diversity was found, and this appeared to be linked to their habitat. This result supports the view that geographical variation in song is determined by the interaction of cultural transmission and the environment. By designing realistic spatially explicit simulation models of song learning, I was also able to estimate the rate of cultural mutation from the data I recorded in Scotland. The value of this lay between 0.001 and 0.04. Finally, these data also suggested that chaffinches choose a song tutor randomly within a range of approximately 3 territories. I discuss the implications of these findings on the process and function of cultural transmission of song in the chaffinch.

7.2 Introduction

The cultural transmission of bird song has been intensively studied for around 40 years (Catchpole & Slater, 1995). Much of this research effort has been applied to recording and analysing what is often the clearest manifestation of cultural transmission of bird song, the existence of patterns of geographical variation. The most spectacular example of geographical variation in song is when mosaic patterns of variation (often referred to as dialects) arise, with well-defined, and stable, boundaries between areas of the same song type occurring independently of any obvious geographical discontinuity, as has been reported, for example, in the corn bunting (McGregor, 1980). This pattern of

variation is only one extreme, and studies on a wide variety of species have demonstrated a diversity of patterns of geographic variation (Mundinger, 1982; Slater, 1989; Catchpole & Slater, 1995; Kroodsma, 1996). However, despite the wealth of information collected about the diversity of geographical variation, as Kroodsma (1996) bemoaned, there have been few successful attempts to relate this diversity to an underlying cause. One reason for this is that, because of its spatial component, it is not simple to reliably link the distribution of song types in an area to underlying features of cultural transmission, such as who birds copy their songs from, or how often new song types arrive.

An alternative, but related concept to geographical variation is that of cultural diversity. Cultural diversity reflects a population-wide estimation of the number of song types present. This concept was usefully adopted from population genetics and applied to the cultural transmission of bird song by Lynch & Baker (1993), although problems with their approach were discussed in Chapter 6. Although high levels of cultural diversity generally correspond to low levels of sharing between neighbours (a common measure of geographical variation), it is possible for low levels of cultural diversity to still lead to high levels of song sharing between neighbours, or vice versa.

While some geographical variation in song appears to be almost ubiquitous in the many temperate songbird species that have been investigated, there is very little understanding of how it is generated, maintained, and to what use birds put it. Views on these issues have tended to fall into two mutually exclusive camps.

The general principle of the first approach (henceforward the *functional* hypothesis) was first inspired by the striking 'dialect' patterns of song variation in some species, and was described by Kroodsma (1996): 'The variation of vocal signals over geographic space is undoubtedly determined by the audience the signal is used to "manage"... I envision selection for a style of vocal development that maximises the "management potential" of a signal over some "best" geographical area'. In other words, geographical variation is determined by the birds themselves. Differences in patterns of geographical variation consequently reflect adaptations to different styles of communication and life histories, and are likely to have a genetic basis.

The alternative idea (henceforward the *by-product* hypothesis) was first proposed by Andrew (1962). He suggested that geographical variation may be a meaningless, or epiphenomenal, by-product of the process of cultural transmission of bird song. Since birds are constrained to copy songs that they can hear, and since dispersal is often limited, songs from nearby are more likely to be copied than those from further away, automatically creating some form of geographical variation. Varying patterns of dispersal, density, song development, or sound transmission could generate the diversity in geographical variation, without it being adaptive. The important difference between these two hypotheses is therefore not about the use to which birds put patterns of geographical variation. As discussed in Chapter 4, song sharing can potentially be used in a variety of ways by neighbouring individuals. Instead, the principle issue is how geographical variation is generated and maintained. However, if there are large variations in patterns of song sharing between different areas, it is hard to see how birds can use song sharing information in the same way across these locations.

There is a degree of empirical support for both ideas. Kroodsma and co-workers have conducted a series of comparative experiments on *Cistothorus* wrens that may support the functional hypothesis (Kroodsma, 1996; Kroodsma *et al*, 1999). The sedentary marsh wren, and sedentary populations of sedge wrens, show high levels of song sharing between neighbours, whereas migratory North American populations of sedge wrens instead show very little if any song sharing. Hand rearing experiments suggest that this variation was due to some genetic difference in the ontogeny of song between these species, since hand reared marsh wrens copied extensively from a tape, whereas North American sedge wrens did not, yet still developed a normal repertoire. Similarly, differences in patterns of song sharing between neighbours have been documented between other migratory and non-migratory populations of several North American species (Hughes *et al*, 1998, Ewert & Kroodsma, 1996, Nelson *et al*, 1996), all of which have found less song sharing between neighbours in migratory populations. For the White-Crowned Sparrow, hand-rearing experiments have again suggested a genetic basis in song ontogeny to lie at the root of this difference (Nelson *et al*, 1996). However, those who have made these findings have not gone on to suggest why less song sharing is adaptive for migratory populations, but not for resident ones. Migratory birds presumably have a shorter period of time to learn their songs during the breeding season, and are likely to have adapted their song development to learn rapidly. It might

be expected, therefore, that mistakes in learning would occur more frequently in these populations, and that song sharing between neighbours would be reduced, as is observed. If this is the case, song learning adaptations have occurred as a result of a change of behaviour (migration), but not necessarily because they lead to an adaptive pattern of geographical variation. It is also hard for the functional hypothesis to take into account examples where there is no preference to learn from nearby neighbours, or from individuals further away. Slater & Ince (1982) demonstrated such a pattern of song learning in the chaffinch (*Fringilla coelebs*).

There have been a number of other studies demonstrating variations in the pattern of cultural diversity between populations. Some of these studies linked cultural diversity to specific ecological factors: for example island populations tend to have lower levels of cultural diversity (M.C.Baker, 1996; A.J.Baker & Jenkins, 1987; Naugler & Smith, 1991; and Chapter 6 of this thesis showed similar patterns of variation linked to the size of the island). In another case, cultural diversity was not linked specifically to any ecological factor, but considerable variation was found in cultural diversity in Atlantic Island and continental populations of chaffinches (Lynch & Baker, 1993). Finally, Harbison *et al* (1999) document differences in the temporal variation between song in local populations of montane white-crowned sparrows. Apart from the Atlantic Island chaffinch studies, these studies compared populations that were probably not genetically isolated from one another, and the variations in cultural diversity therefore support the by-product hypothesis.

The by-product hypothesis, in contrast to the functional hypothesis, would predict as much variation between local populations that were not genetically isolated as between more distant populations that were. This is because one of the key predictions of the by-product hypothesis is that geographical variation in song is dependent on patterns of cultural transmission, and that patterns of cultural transmission are likely to be affected by the ecology of the population. This idea has been developed in theoretical simulations of bird song cultural transmission (Goodfellow & Slater, 1986; Williams & Slater, 1991). In these studies, for example, cultural mutation rate played a key role in determining cultural diversity. Cultural mutation rate, which is the probability of birds making a mistake during learning, might well be altered by a number of ecological factors that might affect how well a tutor's song is heard, for example ambient noise

levels, or population density. We might predict that other ecological factors might interact with patterns of cultural diversity in different ways. For example, population density might affect the number of individuals a young male can hear during the song learning period, and subsequently cause him to learn from neighbours rather than from individuals further away. Population size might also have important effects on cultural diversity. As in population genetics and ecology it seems reasonable that diversity would be reduced in smaller populations.

This chapter reports a study of patterns of geographic variation in the song of 5 populations of chaffinches (*Fringilla coelebs gengleri*) in Scotland. The primary aim of this was to investigate whether these populations, which are not likely to be genetically isolated from one another, exhibit variations in patterns of cultural diversity that might reflect their ecology.

Analysis of patterns of geographical variation has also been used to infer in more detail the process of cultural transmission of bird song. While the literature on cultural transmission of bird song is large, some basic issues remain unresolved. For example, the origin of cultural diversity is poorly understood. There is some evidence that changes in song often arise from the accumulation of small changes, or cultural mutations, that perhaps occur as a result of mistakes during learning (Lemon, 1975; Slater *et al*, 1981). However, even with this simple model, the rate at which such mistakes occur has not been accurately measured. Similarly, questions about what is copied are poorly understood. Do individuals copy nearby individuals, or those further away? Do they tend to copy the most common song, or at random?

In order to determine specific features of cultural transmission from empirical data of geographical variation, it is necessary to develop some sort of cultural evolutionary model. Even if, for example, a study demonstrates considerable song sharing between neighbours, it still might be possible that individuals learned those songs from other tutors, further away. How can one state that birds in this population tend to copy their neighbours? The spatial nature of bird song cultural transmission makes the development of realistic deterministic models mathematically challenging. Alternatively, using current computer technology, realistic spatial simulations of cultural transmission of song can easily be developed and rapidly tested (see Chapter 2). However, previous

attempts to integrate empirical data into a theoretical model have either tended to use a drastically simplified model (Slater *et al*, 1981; Lynch and Baker, 1993), or have only used a few, coarse empirical parameters to integrate with a more realistic model (Goodfellow & Slater, 1986; Williams & Slater, 1990). Neither of these two approaches would be able to resolve the hypothetical dilemma described above.

The second aim of this chapter is therefore to fit the data collected from the five Scottish chaffinch populations to a realistic simulation model in order to understand more fully the underlying processes of bird song cultural transmission.

7.3. Patterns of song variation in Scottish chaffinch populations.

7.3.1 Introduction

Chaffinches (*Fringilla coelebs*) have been used as a subject in several previous studies of cultural transmission of bird song, starting with the pioneering work of Marler (1952), who first noticed geographical variation in song structure, and Thorpe (e.g 1958). Thorpe, using the sound spectrograph for the first time, found that hand-reared chaffinches required exposure to conspecific song to develop normal song themselves. There have also been more recent studies of population-level variation of song, using spectrographic technology. The cultural diversity of Stanmer wood in the south of England was measured from a sample collected during one year, and also by comparing the turnover of songs over a 17 year period (Ince *et al*, 1980; Slater *et al*, 1981). A third study (Slater & Ince, 1979) investigated an isolated island population from Orkney, which lies off the north coast of Scotland (which is also one of the sites in this study). These studies found that there appeared to be rapid turnover in songs, and their results also suggested that the cultural diversity in the south of England was higher than that of Orkney, although this was not formally analysed. Slater & Ince (1982) also recorded that song sharing was as common between neighbouring individuals as it was between individuals further apart, within Stanmer wood. In this study, I have added recordings from four further areas, and have used quantitative analysis of cultural diversity to gain a more detailed picture of patterns of geographical variation in the song of this species.

7.3.2 Recording Sites

Recordings were taken from 5 areas in Scotland. Two of these areas were on islands, or archipelagoes, off the North and West coasts of Scotland: Orkney and Lewis. The population sizes from these areas were very small. In the course of taking my recordings, I estimated the population of the Orkney population to consist of approximately 40 territories (32 were confirmed), and the population of Lewis to consist of about 50 territories (43 were confirmed). A large-scale survey (Gibbons *et al*, 1993), estimated the abundance of chaffinches in these populations at less than 0.4 pairs per tetrad (0.25 km²). In both areas, it is known that the populations were established, or at least greatly expanded, some time in the last century. Before this time, both areas were devoid of sufficient trees to support a reasonable population. In both areas, small woods were established during the last century. On Lewis, this consisted of one relatively large (approximately 2 km²) wood around the grounds of Lewis Castle (OS Grid reference: NB 420 330). More recently, in the last 20 years, commercial conifer plantations in Lewis and Harris have expanded the potential population size of chaffinches again. However, during this study (1998), these plantations had been affected by disease, and the trees were largely dead. Correspondingly, only a very few chaffinches were found in this area (OS grid reference: NB 260 320). In Orkney, the situation was rather different. The chaffinch population here was divided between several much smaller woods, as described by Slater & Ince (1979), on four separate islands. In this study, I recorded individuals from Binscarth Wood (OS Grid reference: HY 350 140), Vinden Farm (OS Grid reference: HY 366 158), and Woodwick House (OS Grid reference: HY 392 241) on the Mainland, the grounds of Balfour Castle (OS Grid reference: HY 475 165) on Shapinsay, and Trumland House (OS Grid reference: 428 278) on Rousay.

The other three recording areas were in North-East Fife, on the eastern coast of Scotland. In this area, trees and woods are much more abundant than in the previous populations. Also the area is not isolated from the rest of mainland Britain by any sizeable gap in woodland or trees. In consequence, chaffinches are also far more abundant here than in Orkney or Lewis, with at least 0.98 pairs (probably considerably more) per tetrad (Gibbons *et al*, 1993). The three different areas I recorded from comprised three different habitats. Magus Muir wood (OS grid reference: NO 460 150)

is mainly deciduous and mixed woodland; Tentsmuir Forest (OS grid reference:NO 490 250) is a mature coniferous plantation; and the St. Andrews area (OS grid reference: NO 510 160) which consists of parks and town gardens.

7.3.3 Recording Methods

Recordings were made between March, 1997 and May, 1998, using a Telinga Pro 5 microphone, recording onto cassette tape using a Sony WM-D6C Professional Walkman, and a Marantz CP430 Cassette Recorder. Although individuals were not marked, it was possible to unambiguously identify each singing individual. This is because chaffinches sing from preferred singing locations within their territories. Therefore, through observation, it was possible to estimate the extent of any individual's territory. Moreover, the tendency of chaffinches to countersing with neighbours helped avoid any confusion between nearby individuals. Chaffinches sing between 1 and 6 different song types (e.g. Slater & Ince, 1982), but do not always regularly cycle through their repertoires so that it is therefore impossible to be absolutely certain that any recording contains the entire repertoire of an individual. In this study, I used a cut-off point of 40 songs per individual, a sample which enabled me to be fairly certain that the repertoire had been accurately measured. As well as recording the songs of an individual, its Grid Reference noted from either 1:50,000 (Orkney & Lewis), or 1:25,000 (Fife) Ordnance Survey maps. I estimate that the precision of this process was within 100m, which is well within the accuracy required for the subsequent analysis (see below).

7.3.4 Analysis.

The recordings were analysed using the RTS (Real-Time Spectrogram) component of the SIGNAL computer system (Engineering Design, 1996). First, the repertoires of individual birds were established. As each bird has only a small repertoire, sings with eventual variation (AAAABBBBCCCCAAAAA etc. rather than immediate variation: ABCBACBAC), and since the alternative songs are usually highly distinctive, this was easily carried out through observation by the author. Second, the spectrograms of the song from the repertoires of different individuals were compared to establish the list of songs sung within a recording area. Some sample spectrograms of the songs of the 5 areas sampled here are shown in Fig. 7.1. Again, because of the high level of precision

of song production, and the distinctiveness of song types, it was straightforward for me to carry this out simply through observation, as had been found in other studies on the chaffinch (e.g. Slater *et al.*, 1981). In Chapter 5, I showed that inter-observer agreement was very high for very similar element types. The task of identifying individual song types was even easier, since songs consist of around a dozen different elements, produced in a more or less fixed sequence. These features make the different song types very distinctive.

Using these data, it was possible to construct two triangular matrices for each recording area: one for the geographic distance between each possible pair of individual males within the area, and one for the similarity of their repertoires. The geographic distance between two males was calculated from their grid references, by calculating the Euclidean distance using a simple computer program. The Jaccard index, which is widely used in ecology, was used as an index of similarity. This index is calculated as the number of song types shared between two birds divided by the combined repertoire of unique song types of the two birds (i.e. the sum of the two individual repertoires, minus the number of shared song types). Again, this was calculated using a computer program. These data were divided between 6 distance categories, and the average measure of similarity calculated for each category. In order to establish confidence intervals for these data sets, in the light of the severe lack of independence of the data points (i.e. pairs of individuals), the Bootstrapping procedure was adapted. The resample was calculated from the triangular matrix of song similarities between each pair of individuals. This was found to accurately estimate confidence intervals and standard errors in a simulation test of the technique.

In addition to this main analysis, I also compared the relative frequencies of the different song types, and also the repertoire sizes of each population.

Fig. 7.1 a Spectrograms of chaffinch song from British populations

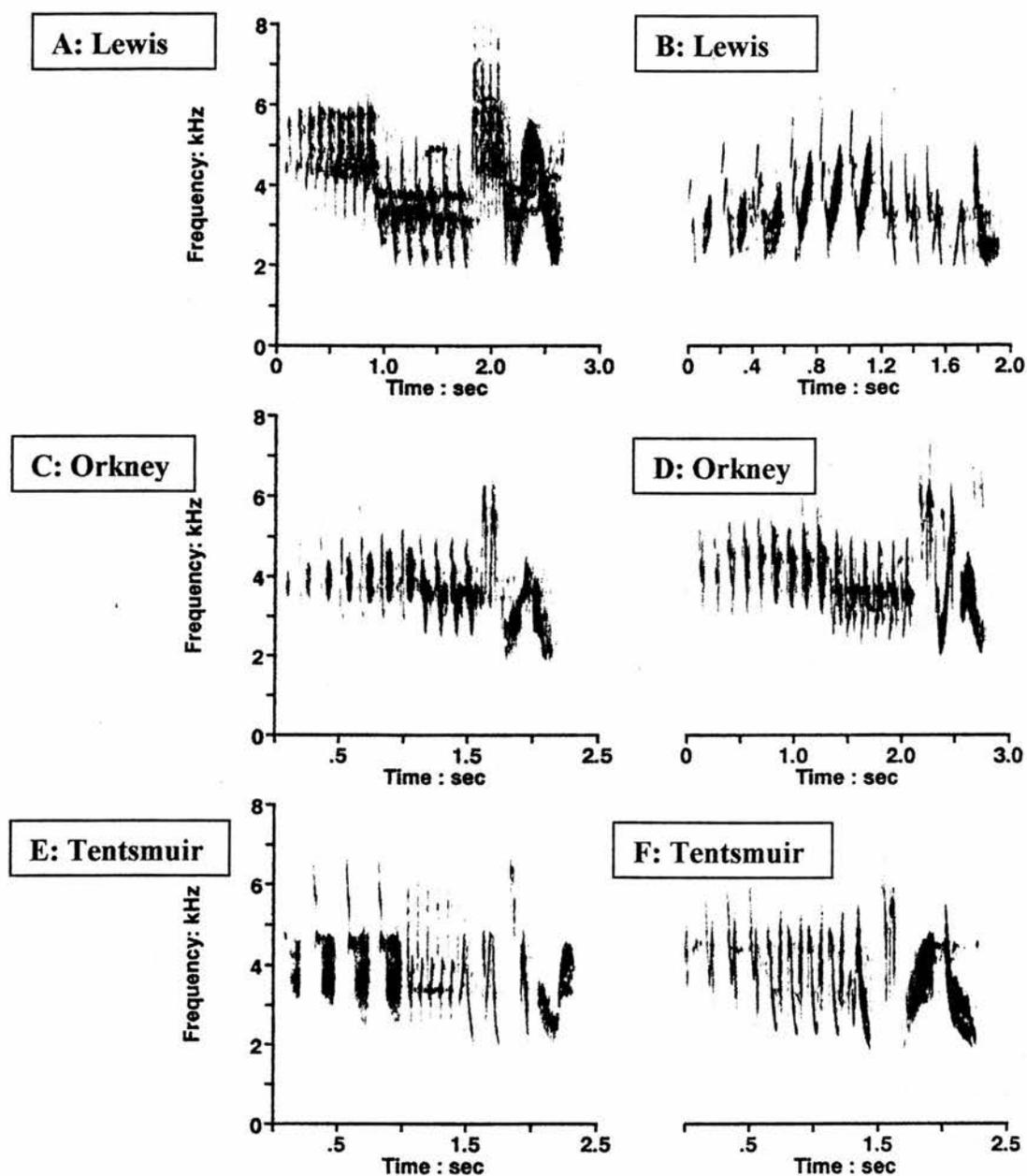
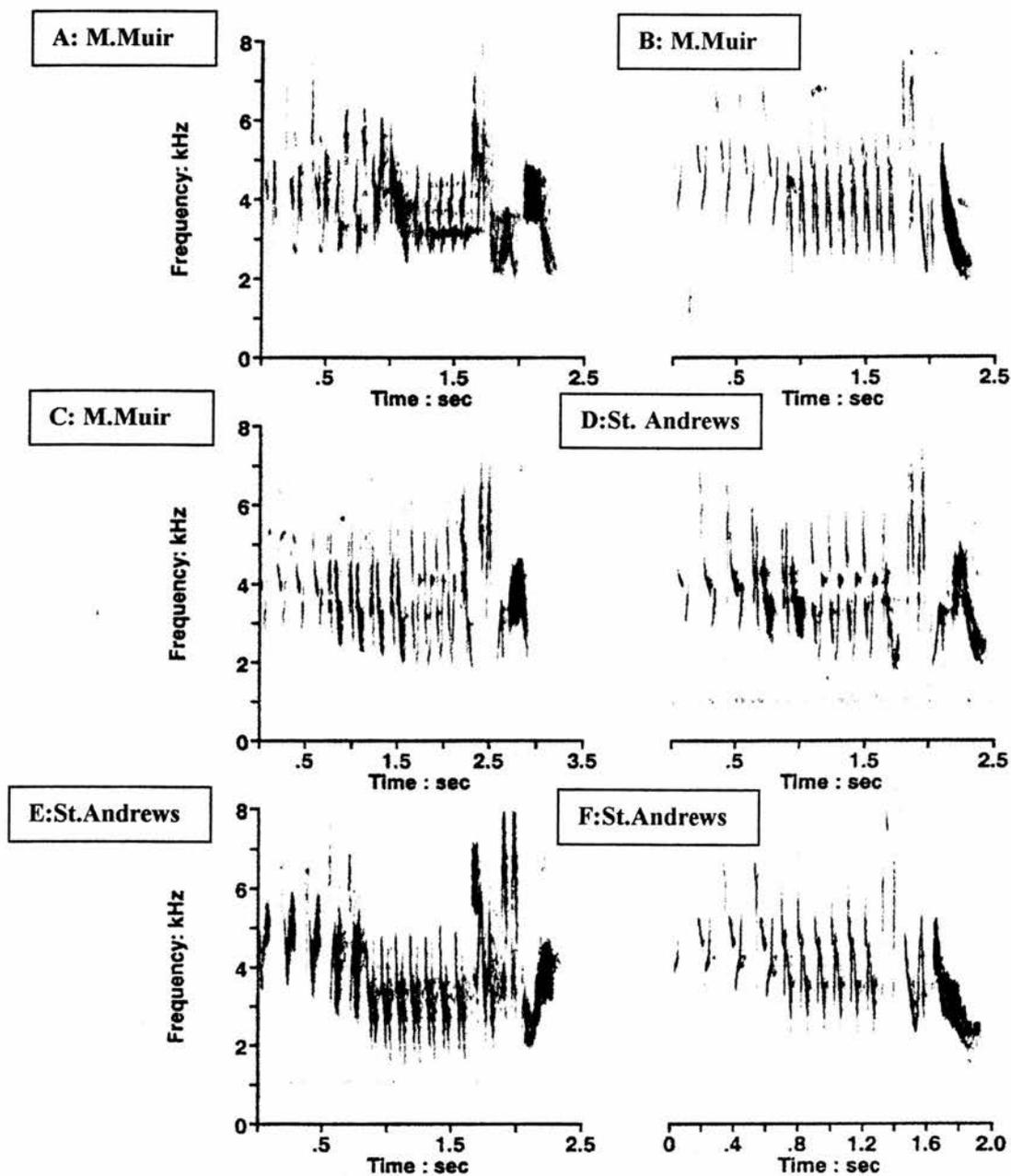


Fig. 7.1 b Spectrograms from British chaffinch populations. Note that (B) and (F) are the same song type, as are (C) and (D), despite (B) and (C) coming from different areas to (D) and (F).



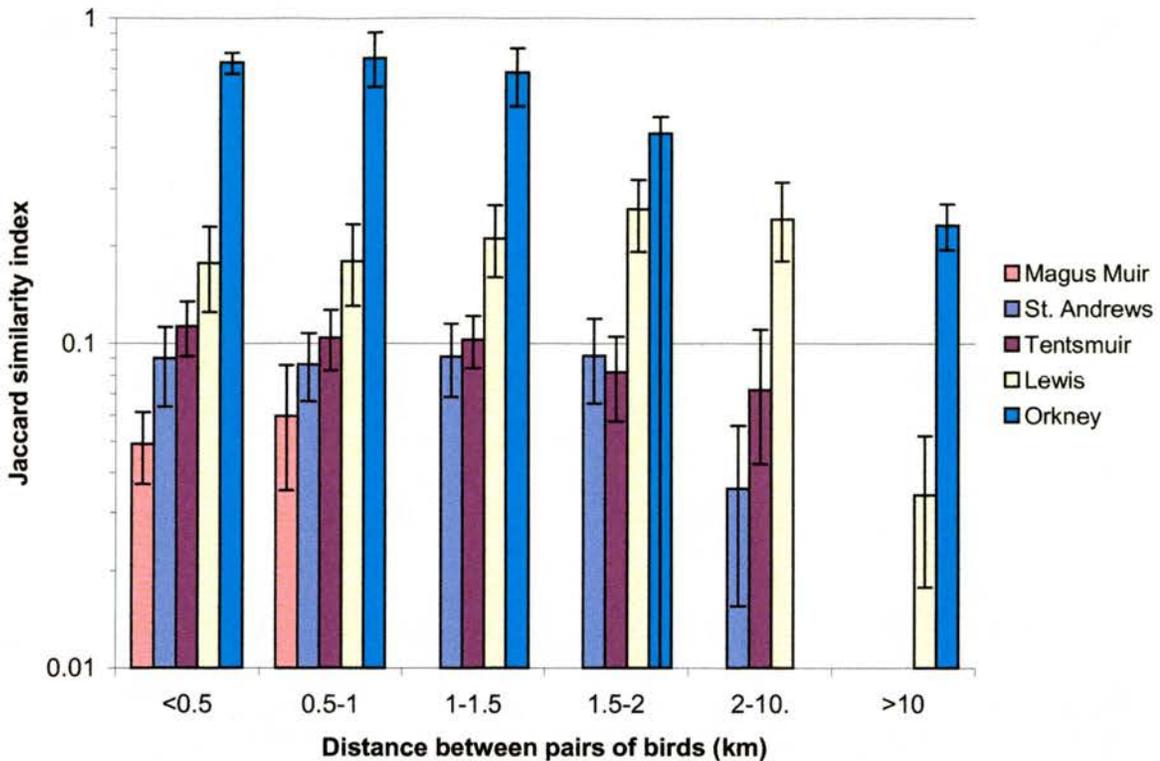


Figure 7.2 Mean levels of song sharing over different ranges of distance in Scottish chaffinch populations. The graph plots the average Jaccard similarity index, calculated for every combination of pairs of individual, divided between 6 geographic distance categories. The graph compares the 5 recording locations within Scotland. The error bars represent 95% confidence intervals (two-tailed), estimated through a Bootstrap procedure.

7.3.5 Results

Figs 7.2 shows the interaction between distance and level of song sharing. There appeared to be only a very weak relationship between the distance between two birds and the probability that they shared a song type. In fact, any correlational trend between these two factors was as likely to be positive as negative, when comparing small and intermediate distance classes. The dramatic effects of distance on song sharing exhibited at higher distances in the Orkney and Lewis samples reflected the fact that different islands in the former, and woods in the latter were being compared in this category. This effect was therefore likely to be due to the fact that pairs of birds in this category lived in

areas that were culturally isolated due to discontinuities in habitat.

Wide variations in the overall level of song sharing were observed between the different areas. As predicted by their isolation and small population sizes, Orkney and Lewis exhibited significantly higher levels of song sharing than the populations from Fife. Orkney, which was a smaller and more fragmented population than Lewis, had the highest levels of song sharing of all. However, there was also considerable, and significant variation between the three areas recorded in Fife. If the results of comparisons of birds less than 2km apart were pooled (this corresponds to the section of the graph where distance does not appear to play a role in affecting song sharing), then the 95% confidence limits for Magus Muir becomes: 0.042 – 0.63 with mean 0.052 ; for St. Andrews: 0.077– 0.10 with mean 0.089; and for Tentsmuir: 0.091 – 0.11 with mean 0.010. Therefore, Tentsmuir possessed the highest levels of song sharing, and Magus Muir the lowest. This pattern is in inverse relation to the probable population sizes of these locations. Tentsmuir forest is considerably larger than Magus Muir and St. Andrews put together, and, similarly, Magus Muir is much smaller than St. Andrews. Interestingly, the order of song sharing levels between these areas also corresponded with general levels of abundance between these habitat types. Coniferous forests tend to have lower levels of abundance than deciduous forest , while suburban, or garden areas lie somewhere in between the two (Newton, 1972).

I also measured the amount of song sharing between the three Fife populations. 8 song types were shared between Magus Muir and St. Andrews. These locations are only 2.6 km apart at their closest points, and moreover, a corridor of woodland links the two. After combining these two data sets, and re-analysing them, the mean Jaccard similarity index score of comparisons between the two areas was 0.024. There were no song types in common between Tentsmuir Forest and either St. Andrews (which is 7km distant) or Magus Muir (10km distant).

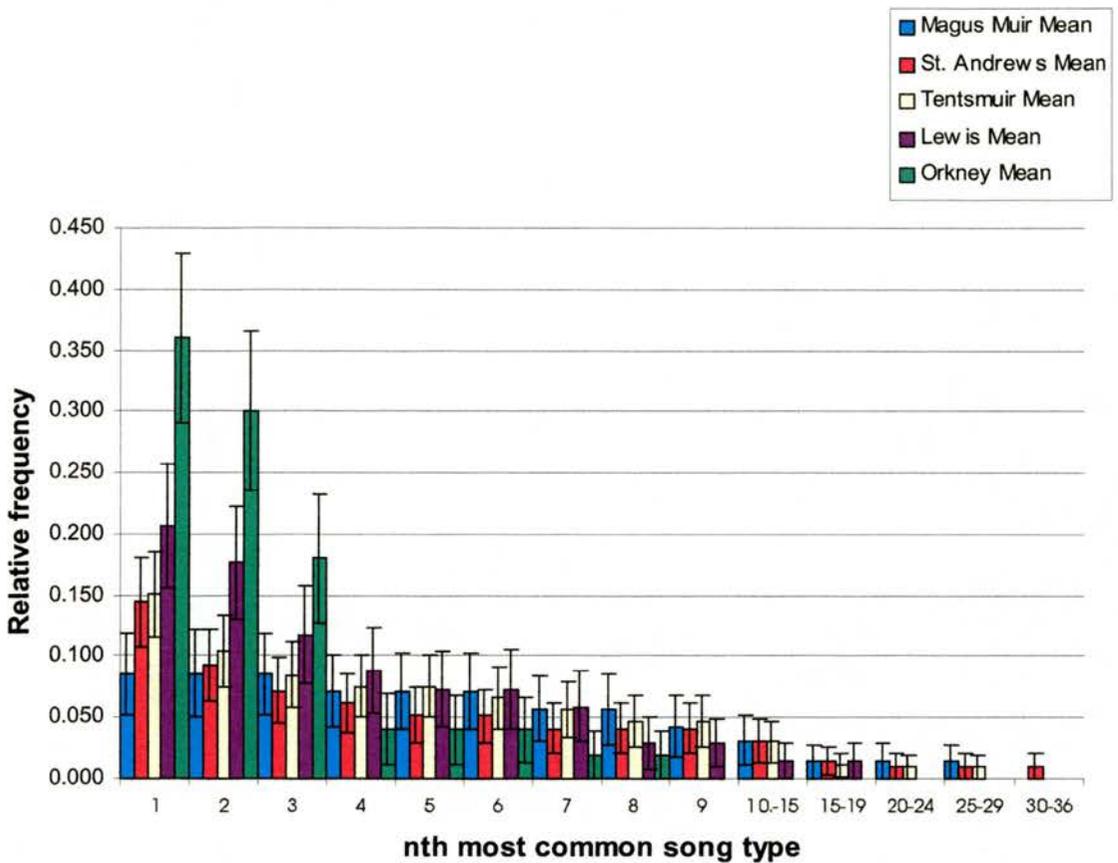


Fig. 7.3 shows the relative frequencies (and standard error) of the different song types in the 5 recording locations in Scotland. For the less common song types, graph shows mean value over range indicated.

There was variation in the relative frequencies of the different song types (Fig. 7.3) that corresponded to the variation in song sharing. The populations with the lower levels of song sharing also had more song types, and a more even distribution of the frequencies of the different song types.

There was also some variation in the average repertoire size of the recording locations (Fig. 7.4). In particular, St. Andrews had a higher mean repertoire size than the island populations, but curiously, Magus Muir had a smaller mean repertoire size than either of the other locations within Fife. Four individuals from the Lewis populations were recorded from the suburban environment of Stornoway. The mean repertoire size of these four individuals was 3.5.

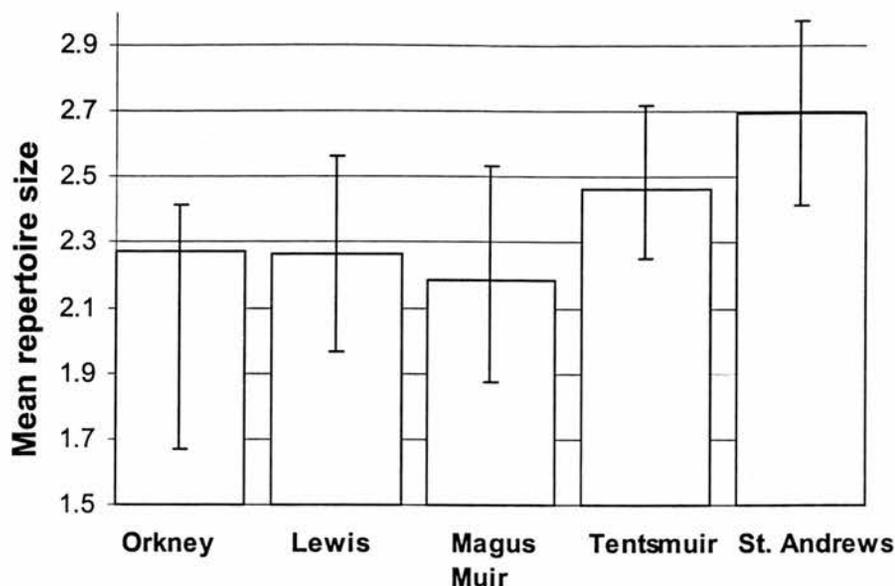


Fig. 7.4 shows the mean repertoire sizes of the five recording locations used in this study. The error bars represent 95% Bootstrapped confidence intervals.

7.4 Modelling cultural transmission of song using spatial simulations.

7.4.1 Introduction

Spatial simulations of the cultural transmission of song have been developed several times (Goodfellow & Slater, 1986; Williams & Slater, 1990; Chapters 2 & 4 of this thesis). The model described below was similar in structure to the spatial simulation described in Chapters 2 and 4. However, as the aim of this model was to accurately estimate parameters and features of cultural transmission using the empirical data collected from the Scottish chaffinch populations, some aspects of the design were modified to provide greater realism.

7.4.2 Description of the model.

The model consisted of a population of up to 400 males arranged in a grid. The population was constructed as a torus (i.e. if an individual moved off one edge, it would re-appear on the opposite edge). I considered this commonly used modelling abstraction more realistic than imposing arbitrarily shaped boundaries onto the population. Each

individual had 4 neighbours (this was achieved by deleting half of the grid locations, leaving a 'checkerboard' pattern). This was considered more realistic than the 8 neighbours used in the previous simulation. During any year, all the territories were possessed by a male (i.e there was a fixed population size). Individuals died at a set mortality rate of 0.4 (based on BTO census data), and each was immediately replaced by a young male.

Each individual possessed a repertoire of between 1 and 6 song types, which was learned in the first year of life. The song types were represented by a value between 0 and 1. The probability of possessing a repertoire of a particular size, p_n , could be varied. In practice, it was matched to a measurement of the frequencies of different sized repertoires taken from each of the Scottish populations that I was attempting to simulate. During song learning, individuals were first assigned a repertoire size at random, based on p_n . They then learned their songs, but could not learn the same song type twice within this repertoire. Although copying the same song type more than once account for variations in repertoire size in chaffinches (Slater, 1983), the aim of the simulation was to match the pattern of song distributions that I had recorded. The probability of an individual learning a song from a given distance (number of territories away) could also be varied. Aside from these factors, the choice of which song to learn was made at random. To compare the simulated data to the empirical results, I estimated 3 territories were equivalent to 0.5 km (based on the distribution of birds along a trasect through Tentsmuir Forest). New song types were generated through a process of cultural mutation. This occurred at a set rate, and altered the value of a given song type randomly within a range of 0.1 either side of the original song value. Because songs values were given on a scale that had 6 decimal places, the probability of cultural mutation generating a song type that was already present in the population was very low. There was no genetic predisposition as such, except that song values were bounded within limits for convenience.

In each run, the simulated population was randomly seeded with repertoires and song types. The simulation then proceeded for 500 years, which was found to be adequate for a 'steady state' level of variation to arise. At this point, various aspects of cultural diversity were measured from the population. The Jaccard index of similarity

between every possible pair of individuals was calculated. As with the Scottish data, these data were divided between classes of inter-individual distance. From the positions of birds singing in the data sample, I estimated that there were approximately 6 birds per km in the different populations. I therefore adjusted the distance classes in the simulation such that they matched those in the real-life data set. I also recorded the relative frequencies of the different song types, as for the Scottish data set.

I repeated this procedure for 1000 runs for each parameter setting. I independently varied the mortality rate, population size, pattern of song learning, and cultural mutation rate.

7.4.3 Analysis.

I varied three parameters in the model: population size, dispersal pattern, and cultural mutation rate. I examined how closely the results of the simulation matched the empirical data collected from two of the five locations. I did not attempt to match the pattern of variation in Orkney, because the high degree of fragmentation of this population could not be easily replicated in the simulation without making many more assumptions about the patterns of dispersal between the islands. Similarly, the St. Andrews and Magus Muir locations were partly interconnected, and rather patchily distributed. In comparison, Lewis, and in particular Tentsmuir Forest, consisted of largely homogenous habitat for chaffinches. To simulate Tentsmuir Forest, I set the population size to 400 (20 x 20 territories – equivalent to a large, homogenous population), and then varied cultural mutation rate and patterns of song dispersal. Fig. 7.5 illustrates the different song dispersal patterns. I repeated this procedure for Lewis, but with a population size varied between 40 and 60. Instead, for Lewis, I kept an even probability of learning from any distance, since the empirical results suggested no negative relationship between distance and song learning, and the slight positive relationship was likely to have been an artefact.

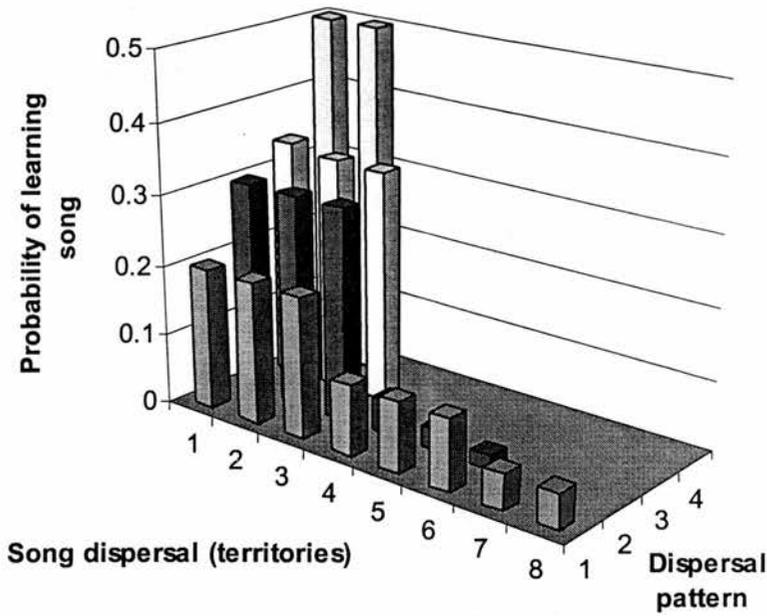


Fig. 7.5 shows the different Dispersal patterns, in terms of the probability of learning a song from a territory a given distance (no. of territories) away.

7.4.4 Results.

Fig 7.6 shows two of the most accurate simulations of the Tentsmuir and Lewis populations, together with the empirical data itself.

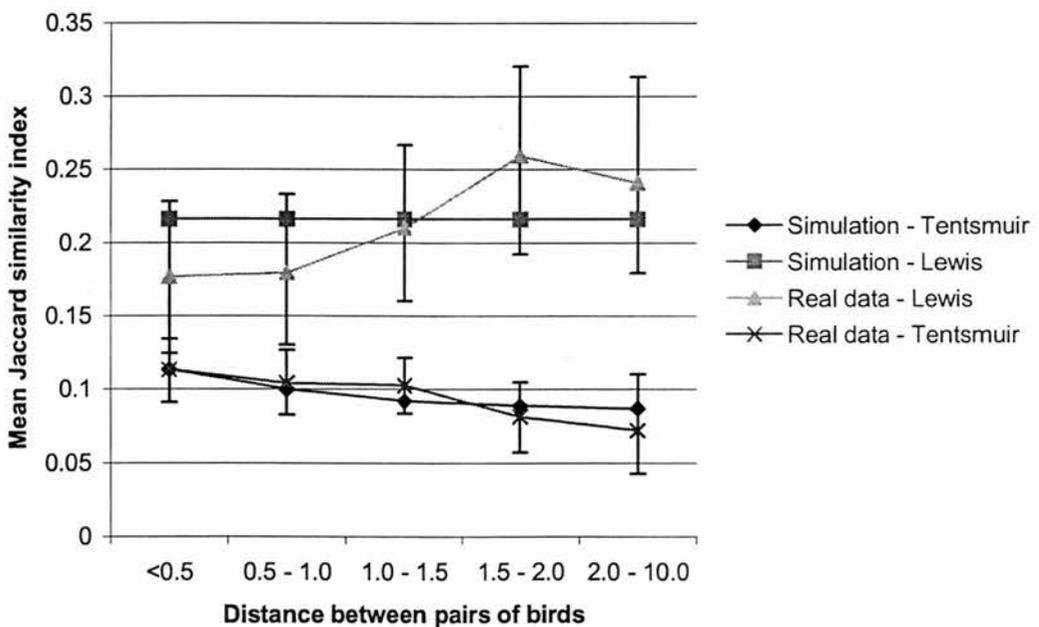


Fig. 7.6 demonstrates how closely the best simulations matched the empirical data. The error bars represent 95% confidence intervals established by bootstrapping around the real data. The Tentsmuir simulation had a mutation rate of 0.002; a population size of 400; and a pattern of dispersal 2. The Lewis simulation had a mutation rate of 0.02; a population size of 49; and the probability of song learning from any territory was even.

Fig. 7.8 shows the effect of altering the parameters on the pattern of song sharing. In order to investigate the sensitivity of the simulation to the parameters, the sum of squared deviations for each distance class was also calculated for each parameter setting. Fig. 7.7 shows the results of this. These figures indicate that variations in the parameters did indeed have a strong effect on the pattern of song sharing, and consequently how closely the simulation matched the empirical data. This suggests that the 'best fit' parameter values are a relatively precise estimate of the cultural mutation rate and pattern of dispersal. In general, it appears that cultural mutation rate and population size decrease song sharing. The song dispersal pattern was mirrored in the amount of song sharing. However, even if song was only copied from very near neighbours, there was still considerable song sharing with individuals further away.

Fig. 7.7a

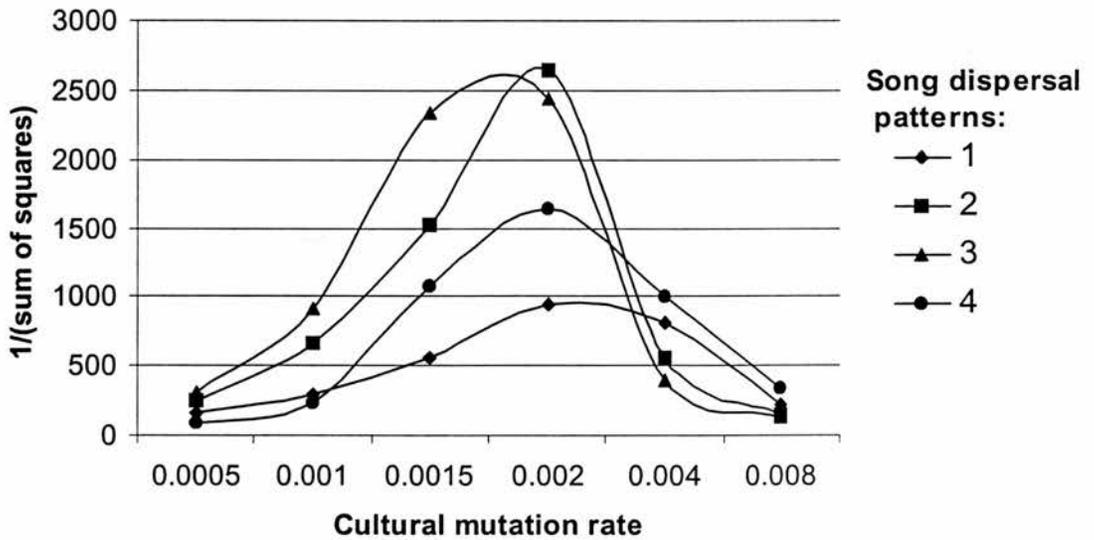


Fig. 7.7b

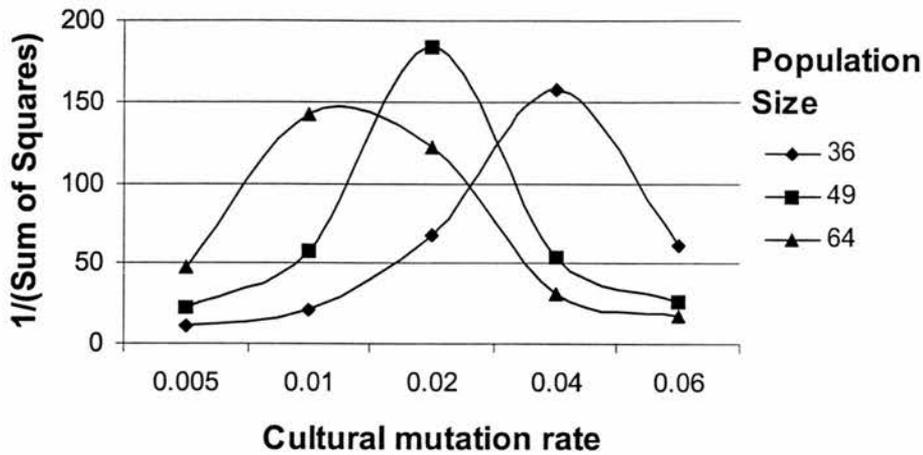


Fig. 7.7 Sum of squared deviations between simulated and empirical data for a variety of parameter settings. Fig. 7.7a shows the effect of cultural mutation rate and song dispersal on the similarity between the Tentsmuir simulation and the Tentsmuir data. Fig. 7.7b shows the effect of cultural mutation rate and population size on the similarity between the Lewis simulation and the Lewis data.

Fig. 7.8a

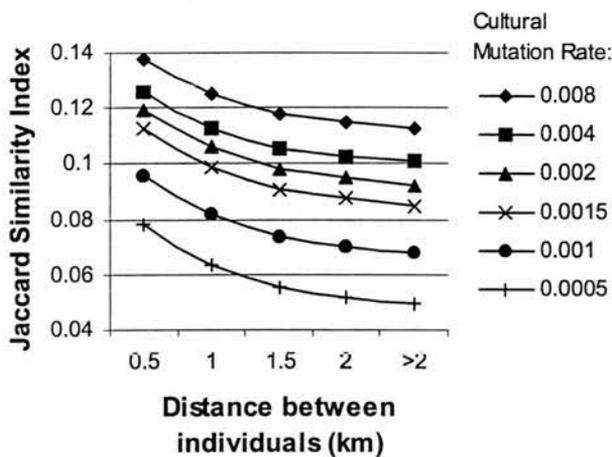


Fig. 7.8b

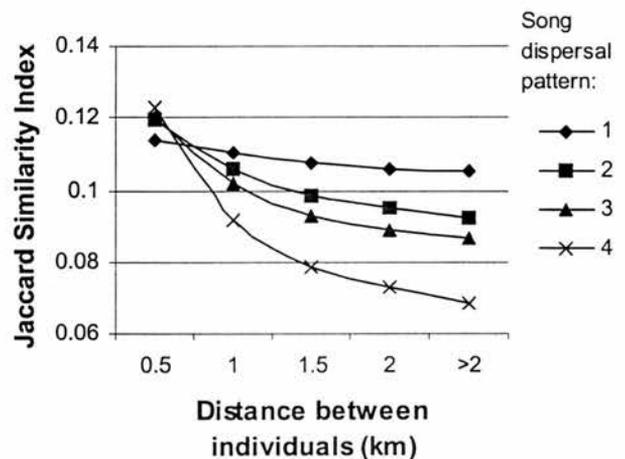


Fig 7.8c

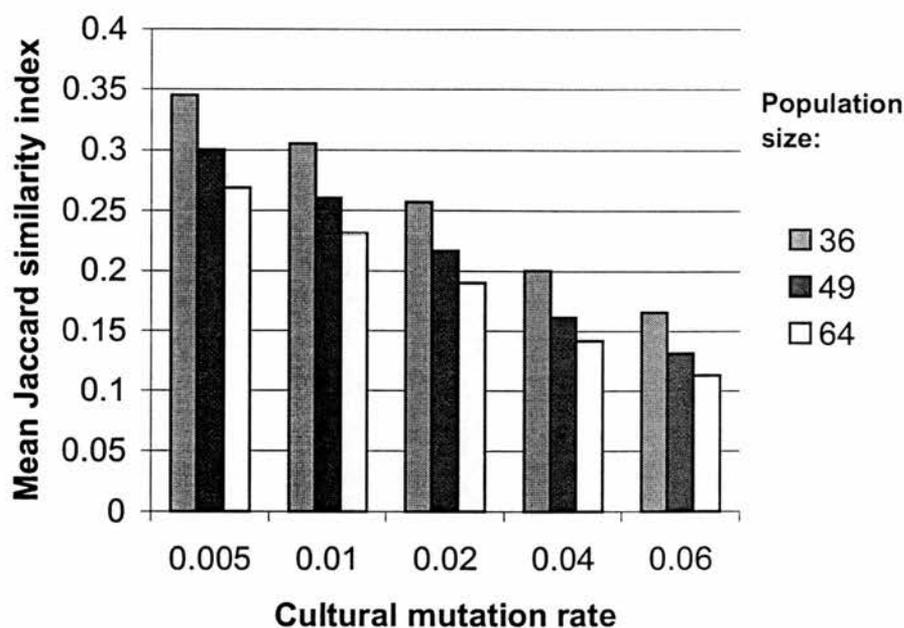


Fig. 7.8 illustrates how varying the model's parameters affected the pattern of song sharing. Fig. 7.8 a and b shows the effect of song dispersal and cultural mutation rate in the Tentsmuir simulation. In Fig. 7.8a, song dispersal pattern '2' was used; in Fig. 7.8b, cultural mutation rate of 0.002 was used. Fig. 7.8c shows the effect of cultural mutation rate and population size in the Lewis simulation

Taking into account the confidence interval around the empirical samples, a range of possible cultural mutation rates, m , could be provided. For Tentsmuir: $0.001 < m < 0.004$, with the best estimate provided by 0.002. For Lewis, the result depended on the estimated total population size (Fig. 7.6). At the most likely population size (around 50), $0.01 < m < 0.04$, with the best estimate provided by $m = 0.02$. Overall, the estimated cultural mutation rate was thus around a factor of 10 higher using the Lewis data than using the Tentsmuir data. Although the Lewis sample was largely contiguous, there were a small number of peripheral birds, that tended to sing unique song types, and that were not very near many other individuals. Moreover, it is likely that the Lewis population had recently undergone a reduction in population size due to the death of the coniferous plantations. Both of these may have been a factor in generating the difference between the two data sets.

I also examined how the relationship between geographic distance and song sharing might arise, using the Tentsmuir data as a reference. I did this by altering the probabilities of learning from a given number of territories away. It is conceivable, for example, that chaffinches do in fact copy their songs only from their neighbours, but that the high rate of turnover creates a dynamic pattern of cultural evolution. This might weaken the correlation between distance and song sharing, and create the pattern I recorded. Fig. 7.7a shows that this is not the case. The best results were provided when most song learning occurred from territories up to 3 territories distant, and at lower frequencies from further away. Although the relationship between song learning and song sharing does not necessarily reflect exactly the probability of learning from a certain distance away, the two are strongly linked.

7.5 Discussion.

The principle finding of this study was that there were considerable differences in the pattern of geographical variation, and therefore in cultural diversity, between various recording locations in Scotland. All British chaffinches are classified together as one subspecies (*F. c. gengleri*), and all are year round residents. It is extremely unlikely that there is any genetic differentiation between the populations. Even the island populations were founded at most two hundred years ago. Moreover, none of the islands are out of eyesight of the Scottish mainland.

In comparison, the differences in cultural diversity were consistent with the ecology of the populations. For example, the isolated island populations possessed less diversity than the mainland ones. It has been argued (M.C.Baker, 1996) that such reductions in cultural diversity in island populations might result from a founder effect, in direct analogy with the founder effect described in genetics (e.g. Carson & Templeton, 1984).

One important difference between genetic and cultural diversity, however, is the mutation rate. Genetic mutation rates are estimated at the order of 10^{-6} . Estimating mutation rates is not entirely straightforward in free-living populations, since it is often hard to differentiate between mutation and dispersal. Previous attempts to measure mutation rate have provided an estimate, or index of 'mutation plus dispersal' (Slater *et al*, 1981; Lynch & Baker, 1993). However, in this study, I have tried to partially overcome this problem on two fronts. By studying small, isolated island populations, I have been able to consider a population in which dispersal is necessarily very limited. Secondly, by developing a spatially explicit simulation model, I have also been able to take into account dispersal, and estimate cultural mutation rate within a large homogenous population. In both cases, however, these methods only partially overcome the problem. Presumably dispersal of songs occasionally might occur between the Scottish Mainland, and Orkney and Lewis. Similarly, while the simulation takes into account song dispersal over short distances, occasional song dispersal over larger distances would appear very similar to cultural mutation in the model. While it is known that young chaffinches normally learn their songs once they have established a territory, and that dispersal is normally limited to within a few kilometers, it is also known that young males can learn their song before natal dispersal, and that dispersal is occasionally much further than a few kilometers. Circumstantial evidence, however, suggests that such a process of long-distance song dispersal plays a minor part in generating song diversity. There was very little sharing of complete song types between the three locations in Fife – and none at all between Tentsmuir and the other locations. At the very least, the data provide a new maximum level of cultural mutation, of between 0.001 and 0.04. This estimate is at least around a factor of 4 lower than a previous estimate of cultural diversity in UK chaffinch populations. Slater *et al* (1980; Ince *et al*, 1981) estimated 'cultural mutation rate plus dispersal' at 0.15, although this estimate was developed from very simple models that were not spatially explicit.

Given that the cultural mutation rate in chaffinches is likely to be greater than 0.001, this is still 3 orders of magnitude greater than that found in genetic transmission. The implications of this are that the role of a founder effect in reducing island cultural diversity is likely to be very limited. Indeed, in the simulation models, which were randomly seeded with different song-types at a full population size, and had reached a steady state when measurements were taken, the estimate of mutation rate from the small

populations was very similar to that from the larger populations. This suggests that the lower levels of cultural diversity are more likely to be a result of the smaller population size than any founder effect.

The wide variety in song diversity between the five different populations suggests that song diversity is largely determined by the ecology of the population. Even between three nearby locations, each with relatively high levels of abundance, there was considerable variation in levels of song sharing. It seems very unlikely, therefore, that geographic variation in the song of the chaffinch serves any function in itself.

This conclusion is supported by the confirmation in this study of the finding that there is only a very weak relationship between distance and song sharing. The spatial simulations confirmed that such a relationship could only occur if songs were commonly learned from individuals that were not neighbours, as was suggested by Slater *et al* (1981), including the possibility of learning before dispersing from the natal territory. Clearly, the most parsimonious explanation of these results is that young chaffinches choose a song tutor randomly from the general area around its territory. However, if learning from around the natal territory, then it may be possible that there is significant levels of vertical transmission (Cavalli-Sforza *et al*, 1981) of song.

Over the last 40 years, a set of data of the geographic variation in bird songs has emerged that is unprecedented in animal behaviour. However, a detailed understanding of the processes that generate these patterns, and the functional reasons for them, is still lacking. In this chapter, my aim has been to analyse patterns of variation of chaffinch song in greater depth, and to try and clarify some of these details.

Chapter 8 General Discussion

This thesis focused on a relatively narrow range of topics. However, the methods I used to approach these issues were quite diverse, and I would like to first discuss how the results of these investigation may be integrated.

Chapters 2 - 4 were all concerned with the theoretical issues surrounding the coevolution of genetic filters (a form of direct bias), and culturally transmitted song. In Chapter 3, I developed mathematical models of this interaction. This form of modelling provides the greatest depth of insight into the questions being studied, and this was the case here. I found an overall selection pressure for filters that allowed birds to sing an extra range of song types. This occurred only because cultural transmission altered the frequency of the different song types for one key group of individuals - those with less restrictive filters - when that group was common or rare. Even though there was no directional external selection on song, the processes of cultural drift created a substantial selection pressure for the genes that underlie this behaviour. One of the interesting things about this result is the lack of an adaptive function for culture. The progressions from a narrow to a wide filter involves no increase in absolute fitness whatsoever. Indeed, as I discussed in Chapter 2, it is quite likely that considerable costs might be associated with possessing a wider filter, including confusion with other species (which Helb *et al*, 1985 document as a relatively regular occurrence), or the energetic costs of possessing the perceptual mechanisms to recognise the extra song types. In chapter 2, I examined a model which showed that this selection pressure can even act to converge the genetic filters of two species. There has been much interest in the popular literature about the evolutionary capabilities of culture. However, there have been few descriptions of cases where culture can out-compete genes, acting in its own interests. The concept of culture as a 'mind virus' might actually apply to the case of bird song learning.

In contrast, I found that the principle hypothesis that has arisen from the empirical literature for the evolutionary maintenance of bird song - cultural conformity - actually generated selection pressure for narrower genetic filters. I predict that any

hypothesis based on learning leading to individuals sounding more similar to one another will also generate the same sort of selection in these models. Presumably, selection for narrower filters will eventually lead to the genetic filter becoming so narrow that no variation in song is possible. It seems unlikely that conformity can support learning. Instead, I found (in Chapter 4) that conformity can evolve as a consequence of learning, to exploit the information that is available due to patterns of cultural transmission. In this model, possessing a rare song type provides your neighbours with the necessary information to 'gang up' on you. Here culture allows complex behaviour of co-operation to evolve very simply.

Chapters 1 and 3 were spatial simulation models. The advantage of this approach is that it provides greater realism, and produces more testable hypotheses. For example, hypothetically, the 'cultural trap' may have not existed in a spatial situation, while conformity may have started to generate selection for wider filters, and due to the complexity of spatial relations, it hard to dismiss this possibility without testing it explicitly. In these chapters, in fact, the results of Chapter 3 were strongly supported. I was also able to produce some testable predictions based on the cultural trap hypothesis. Generally, ecological and behavioural factors that increase cultural diversity should increase the selection pressure for wider filters.

As a result of this, I have begun an investigation to compare the cultural and genetic bases of song in island populations. Chapter 6 describes my initial results from this study. Patterns of cultural evolution do indeed vary between islands, and there is some evidence that more fundamental features of song, that might reflect genetic factors, vary as the cultural trap hypothesis would predict. However, a more sophisticated approach, based on the sound comparison technique I developed in Chapter 5 failed to find any such patterns of differentiation. Finally, I attempted to measure one of the less understood parameters of cultural transmission of song, that was particularly salient for my models, cultural mutation rate. Studies on a fairly large sample of birds from Scotland again showed considerable variation in the pattern of geographical variation, supporting a neutral pattern of transmission. I was able to estimate the cultural mutation rate at around 0.01. At this level, the cultural trap hypothesis would produce a significant selection pressure for wider filters.

In summary, biologists interested in gene-culture coevolution are fortunate to possess in bird song, a trait that is thoroughly understood, but also that is increasingly tractable for experimental study. It is surprising that either of the academic communities involved have not exploited this potential. Given that this thesis represents a very preliminary effort at doing this, what further studies are needed?

First and foremost, an empirical test of gene-culture coevolution is required. For the cultural trap hypothesis, this is now possible, if it can be shown that the genetic filters of bird populations have diverged as the theory predicts. The experimental techniques required are already available. Hand rearing experiments, which deprive subjects of auditory contact with conspecifics, in combination with song preference tests, provide a neat way of exploring genetic preferences for song. These already shown genetic differentiation between Canary breeds, for example (Mundinger, 1995), but have not yet always been linked to evolutionary hypotheses. For the Canary Island chaffinches, pilot data already suggest differential response to playback by adults in the wild. However, there are other suitable species to investigate. For example, it is becoming apparent that migratory populations of songbirds often have greater cultural diversity than sedentary ones. It is also not necessary to stick to the cultural trap hypothesis, or even the evolution of song learning itself. I have also found in simulation models that learning might promote allopatric speciation, as many ornithologists have postulated.

If studies are carried out on gene-culture coevolution in bird song, they would be of benefit not only to the study of song, but to the study of culture. Cultural evolutionists are hampered because on the one hand, it is not possible or desirable to carry out experiments on the most cultural species, man, yet other species tend to possess such ephemeral patterns of cultural evolution that coevolution is not very likely. Bird song may be unique in its ability to bridge the two demands, and serve as a model empirical system.

References

- Alexander, R. D. (1990). "Epigenetic Rules and Darwinian Algorithms. The Adaptive Study of Learning and Development." *Ethology & Sociobiology* **11**: 241-303.
- Andrew, R. J. (1962). "Evolution of intelligence and vocal mimicking." *Science* **137**: 585-589.
- Aoki, K. (1986). "A stochastic model of gene-culture coevolution suggested by the "culture historical hypothesis" for the evolution of adult lactose absorption in humans." *Proceedings of the National Academy of Science USA* **83**: 2929-2933.
- Aoki, K. (1989). "A sexual-selection model for the evolution of imitative learning of song in polygynous birds." *American Naturalist* **134**: 599-612.
- Aoki, K. and M. W. Feldman (1987). "Toward a theory for the evolution of cultural communication: Coevolution of signal transmission and reception." *Proceedings of the National Academy of Science USA* **84**: 7164-7168.
- Aoki, K. and M. W. Feldman (1989). "Pleiotropy and preadaptation in the evolution of human language capacity." *Theoretical Population Biology* **35**(2): 181-194.
- Aoki, K. and M. W. Feldman (1991). "Recessive hereditary deafness, assortative mating, and persistence of sign language." *Theoretical Population Biology* **39**: 358-372.
- Baker, A. J., M. D. Dennison, *et al.* (1990). "Genetic divergence in peripherally isolated populations of chaffinches in the Atlantic islands." *Evolution* **44**(4): 981-999.
- Baker, A. J. and P. F. Jenkins (1987). "Founder effect and cultural evolution of songs in an isolated population of chaffinches, *Fringilla coelebs*, in the Chatham islands." *Animal Behaviour* **35**: 1793-1803.
- Baker, M. C. (1996). "Depauperate meme pool of vocal signals in an island population of singing honeyeaters." *Animal Behaviour* **51**: 853-858.
- Baker, M. C. and J. T. Boylan (1995). "A catalog of song syllables of indigo and lazuli buntings." *Condor* **97**: 1028-1040.
- Baker, M. C. and M. A. Cunningham (1985). "The biology of bird-song dialects." *Behavioral & Brain Sciences* **8**: 85-133.
- Baker, M. C. and D. B. Thompson (1985). "Song dialects of white-crowned sparrows: Historical processes inferred from patterns of geographic variation." *Condor* **87**: 127-141.
- Baker, M. C., D. F. Tomback, *et al.* (1984). "Behavioral consequences of song learning: Discrimination of song types by male white-crowned sparrows." *Learning & Motivation* **15**: 428-440.
- Balaban, E. (1988). "Cultural and genetic variation in swamp sparrows (*Melospiza georgiana*) I. Song variation, genetic variation, and their relationship." *Behaviour* **105**: 250-291.
- Balaban, E. (1988). "Cultural and genetic variation in swamp sparrows (*Melospiza georgiana*) II. Behavioural salience of geographic song variants." *Behaviour* **105**: 292-322.
- Baptista, L. F. and M. L. Morton (1988). "Song learning in montane white-crowned sparrows: from whom and when?" *Animal Behaviour* **36**: 1753-1764.
- Baptista, L. F. and P. W. Trail (1992). "The role of song in the evolution of passerine diversity." *Systematic Biology* **41**: 242-247.
- Becker, P. H. (1982). "The coding of species-specific characteristics in bird sounds." IN *Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. New York, Academic Press. **1**: 213-252.

- Bertram, B. (1970). "The vocal behaviour of the Indian hill mynah." *Animal Behaviour Monographs*: 81-192.
- Bolhuis, J. J. (1996). "Development of perceptual mechanisms in birds: Predispositions and imprinting." IN *Neuroethological studies of cognitive and perceptual processes*. eds C. F. Moss and S. J. Shettleworth. Boulder Colorado, Westview Press: 158-184.
- Boughman, J. W. (1997). "Greater spear-nosed bats give group-distinctive calls." *Behavioural Ecology and Sociobiology* **40**: 61-70.
- Boughman, J. W. (1998). "Vocal learning by greater spear-nosed bats." *Proceedings of the Royal Society of London Series B* **265**: 227-233.
- Boyd, R. and P. J. Richerson (1983). "Why is Culture Adaptive?" *Quarterly Review of Biology* **58**: 209-214.
- Boyd, R. and P. J. Richerson (1985). *Culture and the Evolutionary Process*. Chicago, Chicago University Press.
- Boyd, R. and P. J. Richerson (1988). "An evolutionary model of social learning. The effects of spatial and temporal variation." IN *Social Learning: Psychological and Biological Perspectives*. eds T. R. Zentall and B. G. J. Galef. Hillsdale, New Jersey, Erlbaum.
- Bradley, R. A. (1981). "Song variation in a population of white-eyed vireos (*Vireo griseus*)." *Auk* **98**: 80-87.
- Bremond, J.-C. (1976). "Specific recognition in the song of Bonelli's warbler (*Phylloscopus bonelli*)." *Behaviour* **58**: 99-116.
- Brenowitz, E. A. (1991). "Altered perception of species-specific song by birds after lesions of a forebrain nucleus." *Science* **251**: 303-305.
- Brown, E. D. and S. M. Farabaugh (1991). "Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs." *Behaviour* **118**: 244-274.
- Brown, E. D. and S. M. Farabaugh (1997). "Vocal sharing in avian groups." IN *Social influences on vocal development*. eds C.T. Snowdon and M. Hausberger. Cambridge, Cambridge University Press.
- Buchanan, K. L. and C. K. Catchpole (1997). "Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality." *Proceedings of the Royal Society of London Series B* **264**: 521-526.
- Burnet, F. M. (1959). *The clonal selection theory of acquired immunity*. London, Cambridge University Press.
- Carson, H. L. and A. R. Templeton (1984). "Genetic revolutions in relation to speciation phenomena: the founding of new populations." *Annual Review of Ecology and Systematics* **15**: 97-131.
- Catchpole, C. K. and P. J. B. Slater (1995). *Bird Song. Biological themes and variations*. Cambridge, Cambridge University Press.
- Cavalli-Sforza, L. L. and M. W. Feldman (1981). *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton, Princeton University Press.
- Cavalli-Sforza, L. L. and M. W. Feldman (1983). "Cultural versus genetic adaptation." *Proceedings of the National Academy of Sciences, USA* **80**(August): 4993-4996.
- Cavalli-Sforza, L. L., M. W. Feldman, *et al.* (1982). "Theory and observation in cultural transmission." *Science* **218**: 19-27.
- Cavalli-Sforza, L. L., P. Menozzi, *et al.* (1993). "Demic Expansion and Human Evolution." *Science* **259**: 639-646.
- Chambers, J. K. (1995). *Sociolinguistic theory*. Oxford, U.K., Blackwell.
- Chilton, G. and M. R. Lein (1996). "Long-term changes in songs and song dialect boundaries of Puget sound white-crowned sparrows." *Condor* **98**: 567-580.

- Clark, C. W., P. Marler, *et al.* (1987). "Quantitative analysis of animal vocal phonology: An application to swamp sparrow song." *Ethology* **76**: 101-115.
- Clayton, N. S. (1990). "Subspecies recognition and song learning in zebra finches." *Animal Behaviour* **40**: 1009-1017.
- Coussi-Korbel, S. and D. M. Fragaszy (1995). "On the relation between social dynamics and social learning." *Animal Behaviour* **50**: 1441-1453.
- Curio, E., U. Ernst, *et al.* (1978). "The adaptive significance of avian mobbing II." *Zeitschrift fur Tierpsychologie* **48**: 184-202.
- Dawkins, R. (1976). *The Selfish Gene*. Oxford, Oxford University Press.
- Deacon, T. W. (1997). *The Symbolic Species*. New York, W.W.Norton.
- Deecke, V. B., J. K. B. Ford, *et al.* (1999). "Quantifying complex patterns of acoustic variation: use of a neural network to compare killer whale (*Orcinus orca*) dialects." *Journal of the Acoustical Society of America* **105**: 2499-2507.
- Dooling, R. J., S. D. Brown, *et al.* (1992). "Auditory perception of conspecific and heterospecific vocalizations in birds: evidence for special processes." *Journal of Comparative Psychology* **106**(1): 20-28.
- Dooling, R. J., S. D. Brown, *et al.* (1987). "Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Pure tones." *Journal of Comparative Psychology* **101**(2): 139-149.
- Dooling, R. J., T. J. Park, *et al.* (1987). "Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): II. Vocal signals." *Journal of Comparative Psychology* **101**: 367-381.
- Dugatkin, L. A. (1996). "Copying and mate choice." IN *Social learning in animals. The roots of culture*. eds C. M. Heyes and B. G. J. Galef. London, Academic Press: 85-107.
- Dugatkin, L. A. and J. G. J. Godin (1992). "Reversal of mate choice by copying in the guppy (*Poecilia reticulata*)." *Proceedings of the Royal Society of London Series B*. **249**: 179-184.
- Dugatkin, L. A. and J. G. J. Godin (1993). "Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects." *Behavioural Ecology* **4**(4): 289-292.
- Durham, W. H. (1991). *Coevolution*. Stanford, Stanford University Press.
- Eens, M. (1997). "Understanding the complex song of the European starling: an integrated ethological approach." *Advances in the Study of Behaviour* **26**: 355-413.
- Eimas, P. D., J. L. Miller, *et al.* (1987). "On infant perception and the acquisition of language." IN *Categorical perception. The groundwork of cognition*. eds S. Harnad. Cambridge, Cambridge University Press: 161-195.
- Emlen, S. (1972). "An experimental analysis of the parameters of bird song eliciting species recognition." *Behaviour* **41**: 130-171.
- Ewart, D. N. and D. E. Kroodsma (1994). "Song sharing and repertoires among migratory and resident rufous-sided towhees." *Condor* **96**: 190-196.
- Farabaugh, S. M., A. Linzenbold, *et al.* (1994). "Vocal plasticity in budgerigars (*Melopsittacus undulatus*): evidence for social factors in the learning of contact calls." *Journal of Comparative Psychology* **108**: 81-92.
- Feekes, F. (1977). "Colony specific song in *Cacicus cela* (Icteridae, Aves): The password hypothesis." *Ardea* **65**: 197-202.
- Feldman, M. W. and K. Aoki (1992). "Assortative mating and grandparental transmission facilitate the persistence of a sign language." *Theoretical Population Biology* **42**(2): 107-116.
- Feldman, M. W. and L. L. Cavalli-Sforza (1976). "Cultural and biological processes. Selection for a trait under complex transmission." *Theoretical Population Biology* **9**(2): 238-259.

- Feldman, M. W. and L. L. Cavalli-Sforza (1984). "Cultural and biological evolutionary processes: Gene-culture disequilibrium." *Proceedings of the National Academy of Sciences USA* **81**: 1604-1607.
- Feldman, M. W. and L. L. Cavalli-Sforza (1989). "On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem." IN *Mathematical Evolutionary Theory*. eds M. W. Feldman. Princeton, Princeton University Press.
- Feldman, M. W. and K. N. Laland (1996). "Gene-culture coevolutionary theory." *Trends in Ecology and Evolution* **11**(11): 453-457.
- Feldman, M. W. and L. A. Zhivotovsky (1992). "Gene-culture coevolution: Towards a general theory of vertical transmission." *Proceedings of the National Academy of Sciences USA* **89**: 11935-11938.
- Felsenstein, J. (1995). Phylip: phylogenetic inference package v. 3.57c. Seattle, Department of Genetics, University of Washington.
- Fisher, J. and R. A. Hinde (1949). "The opening of milk bottles by birds." *British Birds* **42**: 347-357.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford, Clarendon Press.
- Galef, B. G. J. (1988). "Communication of information concerning diets in a social, central-place foraging species: *Rattus norvegicus*." IN *Social Learning: Psychological and Biological Perspectives*. eds T. R. Zentall and B. G. J. Galef. Hillsdale, New Jersey., Lawrence Erlbaum: 119-139.
- Galef, B. G. J. (1996). "The adaptive value of social learning: a reply to Laland." *Animal Behaviour* **52**(3): 641-644.
- Gaunt, S. L. L., L. F. Baptista, *et al.* (1994). "Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*)." *Auk* **111**: 87-103.
- Getty, D. J. and J. H. J. Howard, Eds. (1981). *Auditory and visual pattern recognition*. Hillsdale, New Jersey Erlbaum.
- Getty, D. J., J. A. Swets, *et al.* (1981). "Multidimensional perception spaces: similarity judgment and identification." IN *Auditory and Visual Pattern Recognition*. eds D. J. Getty and J. H. J. Howard. Hillsdale, New Jersey Erlbaum: 161-181.
- Gibbons, D. W., J. B. Reid, *et al.* (1993). *The new atlas of breeding birds in Britain and Ireland: 1988-1991*. London, T & A.D.Poyser.
- Giraldeau, L. A. and L. Lefebvre (1987). "Scrounging prevents cultural transmission of food-finding behaviour in pigeons." *Animal Behaviour* **35**: 387-394.
- Giraldeau, L.-A. and L. Lefebvre (1986). "Exchangeable producer scrounger roles in a captive flock of feral pigeons." *Animal Behaviour* **34**: 797-803.
- Goodfellow, D. J. and P. J. B. Slater (1986). "A model of bird song dialects." *Animal Behaviour* **34**: 1579-1580.
- Grant, B. R. and P. R. Grant (1979). "Darwin's finches: population variation and sympatric speciation *Proceedings of the National Academy of Sciences USA* **76**: 2359-2363.
- Grant, B. R. and P. R. Grant (1996). "Cultural inheritance of song and its role in the evolution of Darwin's finches." *Evolution* **50**(6): 2471-2487.
- Hansen, P. (1979). "Vocal learning: its role in adapting sound structures to long-distance propagation and a hypothesis on its evolution." *Animal Behaviour* **27**: 1270-1271.
- Hansen, P. (1981). "Coordinated singing in neighbouring yellowhammers (*Emberiza citrinella*)." *Natura Jutlandica* **19**: 121-138.

- Harbison, H., D. A. Nelson, *et al.* (1999). "Long-term persistence of song dialects in the mountain white-crowned sparrow." *The Condor* **101**: 133-148.
- Helb, H.-W., F. Dowsett-Lemaire, *et al.* (1985). "Mixed singing in European songbirds - a review." *Zeitschrift fur Tierpsychologie* **69**: 27-41.
- Heyes, C. M. (1994). "Social Learning in animals: Categories and mechanisms." *Biological Reviews* **69**: 207-231.
- Heyes, C. M. and B. G. J. Galef, Eds. (1996). *Social learning in animals. The roots of culture*. London, Academic Press.
- Huffman, M. A. (1996). "Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques." IN *Social learning in animals. The roots of culture*. eds C. M. Heyes and B. G. J. Galef. London, Academic Press: 267-291.
- Hughes, M., S. Nowicki, *et al.* (1998). "Song-type sharing in song sparrows: implications for repertoire function and song learning." *Behavioural Ecology and Sociobiology* **42**: 437-446.
- Ince, S. A., P. J. B. Slater, *et al.* (1980). "Changes with time in the songs of a population of chaffinches." *Condor* **82**: 285-290.
- Janik, V. M. (1999). "Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods." *Animal Behaviour* **57**(1): 133-143.
- Janik, V. M. and P. J. B. Slater (1997). "Vocal learning in mammals." *Advances in the Study of Behaviour* **26**: 59-99.
- Janik, V. M. and P. J. B. Slater (1998). "Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls." *Animal Behaviour* **56**: 829-838.
- Jerne, N. K. (1985). "The generative grammar of the immune system." *Science* **229**: 1057-9.
- Jones, G. and R. D. Ransome (1993). "Echolocation calls of bats are influenced by maternal effects and change over a lifetime." *Proceedings of the Royal Society of London, Series B* **252**: 125-128.
- Kawai, M. (1965). "Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet." *Primates* **6**: 1-30.
- Kirkpatrick, M. and L. A. Dugatkin (1994). "Sexual selection and the evolutionary effects of copying mate choice." *Behavioural Ecology and Sociobiology* **34**: 443-449.
- Kroodsma, D. E. (1984). "Songs of the alder flycatcher (*Empidonax alnorum*) and willow flycatcher (*Empidonax traillii*) are innate." *Auk* **101**: 13-24.
- Kroodsma, D. E. (1996). "Ecology of passerine song development." IN *Ecology and Evolution of Acoustic Communication in birds*. eds D. E. Kroodsma and E. H. Miller. Ithaca and London, Comstock Publishing Associates: 3-19.
- Kroodsma, D. E. and J. R. Baylis (1982). "A world survey of evidence for vocal learning in birds." *Acoustic Communication in Birds*. D. E. Kroodsma and E. H. Miller. New York., Academic Press. **2**: 311-337.
- Kroodsma, D. E. and B. E. Byers (1991). "The function(s) of bird song." *American Zoologist* **31**: 318-328.
- Kroodsma, D. E., P. W. Houlihan, *et al.* (1997). "Song development by grey catbirds." *Animal Behaviour* **54**(2): 457-464.
- Kroodsma, D. E., W.-C. Liu, *et al.* (1999). "The ecology of song improvisation as illustrated by North American sedge wrens." *The Auk* **116**(2): 373-387.
- Kroodsma, D. E. and E. H. Miller Eds(1996). *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca and London, Comstock Publishing Association.
- Laland, K. N. (1992). "A Theoretical Investigation of the Role of Social Transmission in Evolution." *Ethology & Sociobiology* **13**: 87-113.

- Laland, K. N. (1994). "Sexual selection with a Culturally Transmitted Mating Preference." *Theoretical Population Biology* **45**(1): 1-15.
- Laland, K. N. (1996). "Is social learning always locally adaptive?" *Animal Behaviour* **52**(3): 637-641.
- Laland, K. N., J. Kumm, *et al.* (1995). "Gene-Culture Coevolutionary Theory." *Current Anthropology* **36**(1): 131-156.
- Laland, K. N. and H. C. Plotkin (1990). "Social learning and social transmission of digging for buried food in Norway rats." *Animal Learning and Behaviour* **18**(3): 246-251.
- Laland, K. N., P. J. Richerson, *et al.* (1993). "Animal social learning: towards a new theoretical approach." *Perspectives in Ethology* **10**.
- Laland, K. N., P. J. Richerson, *et al.* (1996). "Developing a theory of animal social learning." *Social learning in animals. The roots of culture*. C. M. Heyes and B. G. J. Galef. London, Academic Press: 129-155.
- Laland, K. N. and K. Williams (1997). "Schooling generates social learning of foraging information in Guppies." *Animal Behaviour* **52**: 1161-1169.
- Lefebvre, L. (1995). "The opening of milk bottles by birds: evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission." *Behavioural Processes* **34**: 43-54.
- Lefebvre, L. and B. Palameta (1988). "Mechanisms, ecology, and population diffusion of socially learned, food-finding behavior in feral pigeons." IN *Social Learning: Psychological and Biological Perspectives*. eds T. Zentall and B. G. J. Galef. Hillsdale, New Jersey, Erlbaum.
- Lemon, R. E. (1975). "How birds develop song dialects." *Condor* **77**: 385-406.
- Lumsden, C. J. and E. O. Wilson (1981). *Genes, Mind, and Culture*. Cambridge, Massachusetts, Harvard University Press.
- Lynch, A. (1996). "The population memetics of birdsong." IN *Ecology and Evolution of Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. Ithaca and London, Comstock Publishing Associates: 181-197.
- Lynch, A. and A. J. Baker (1986). "Congruence of morphometric and cultural evolution in Atlantic island chaffinch populations." *Canadian Journal of Zoology* **64**: 1576-1580.
- Lynch, A. and A. J. Baker (1991). "Increased vocal discrimination by learning in sympatry in two species of chaffinches." *Behaviour* **116**: 109-126.
- Lynch, A. and A. J. Baker (1993). "A population memetics approach to cultural evolution in chaffinch song: meme diversity within populations." *American Naturalist* **141**: 597-620.
- Lynch, A. and A. J. Baker (1994). "A population memetics approach to cultural evolution in chaffinch song: differentiation among populations." *Evolution* **48**: 351-359.
- Lynch, A., G. M. Plunkett, *et al.* (1989). "A model of cultural evolution of chaffinch song derived with the meme concept." *American Naturalist* **133**: 634-653.
- Marler, P. (1960). "Bird songs and mate selection." IN *Animal Sounds and Communication*. eds W. E. Lanyon and W. N. Tavolga. Washington, Amer. Inst. Biol. Sci.: 348-367.
- Marler, P. and D. Nelson (1992). "Neuroselection and song learning in birds: species universals in culturally transmitted behavior." *Seminars in the Neurosciences* **4**: 415-423.
- Marler, P. and S. Peters (1977). "Selective vocal learning in a sparrow." *Science* **198**: 519-521.

- Marler, P. and S. Peters (1981). "Birdsong and speech: evidence for special processing." IN *Perspectives in the Study of Speech*. eds P. D. Eimas and J. L. Miller. Hillsdale, New Jersey, Erlbaum. **75**: 112.
- Marler, P. and V. Sherman (1985). "Innate differences in singing behaviour in sparrows reared in isolation from adult conspecific song." *Animal Behaviour* **33**: 57-71.
- Marler, P. and M. Tamura (1964). "Song 'dialects' in three populations of white-crowned sparrows." *Science* **146**: 1483-1486.
- Marshall, H. D. and A. J. Baker (1999). "Colonization history of Atlantic Island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA." *Molecular Phylogenetics and Evolution* **11**(2): 201-212.
- Martens, J. (1996). "Vocalizations and speciation in Palearctic birds." IN *Ecology and Evolution of Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. Ithaca and London, Comstock Publishing Associates: 221-240.
- Martindale, S. (1980). Numerical approach to the analysis of solitary vireo songs. *Condor* **82**: 199-210
- Mathis, A., D. P. Chivers, *et al.* (1995). "Cultural transmission of predator recognition in fishes, intraspecific and interspecific learning." *Animal Behaviour* **51**(1): 185-201.
- Matsumura, S. (1979). "Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumquinum nippon*): development of vocalizations." *Journal of Mammalogy* **60**: 76-84.
- Maynard-Smith, J. and N. Warren (1982). "Models of cultural and genetic change." *Evolution* **36**: 620-627.
- McArthur, P. D. (1986). "Similarity of playback songs to self song as a determinant of response strength in song sparrows (*Melospiza melodia*)." *Animal Behaviour* **34**: 199-207.
- McCowan, B. and D. Reiss (1995). "Quantitative comparison of whistle repertoires from captive bottlenose dolphins (*Delphinidae*, *Tursiops truncatus*): a re-evaluation of the signature whistle hypothesis." *Ethology* **100**: 194-209.
- McGregor, P. K. (1980). "Song dialects in the corn bunting (*Emberiza calandra*)." *Zeitschrift fur Tierpsychologie* **54**: 285-297.
- Miller, E. H. (1979). "An approach to the analysis of graded vocalizations of birds." *Behavioural and Neural Biology* **27**: 25-38.
- Moore, B. C. J. (1989). *An introduction to the psychology of hearing*. London, Academic Press.
- Morton, E. S. (1982). "Grading, discreteness, redundancy and motivation-structural rules." IN *Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. New York, Academic Press: 183-212.
- Morton, E. S. (1986). "Predictions from the ranging hypothesis for the evolution of long distance signals in birds." *Behaviour* **99**: 65-86.
- Mundinger, P. C. (1982). "Microgeographic and macrogeographic variation in the acquired vocalizations of birds." IN *Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. New York, Academic Press. **2**: 147-208.
- Mundinger, P. C. (1995). "Behaviour-genetic analysis of canary song: inter-strain differences in sensory learning, and epigenetic rules." *Animal Behaviour* **50**: 1491-1511.
- Naguib, M. (1997). "Ranging of songs in Carolina wrens: effects on familiarity with the song type on use of different cues." *Behavioural Ecology and Sociobiology* **40**: 385-393.
- Naugler, C. T. and P. C. Smith (1991). "Song similarity in an isolated population of fox sparrows (*Passerella iliaca*)." *Condor* **93**: 1001-1003.

- Nelson, D. A. (1989). "The importance of invariant and distinctive features in species recognition of bird song." *Condor* **91**: 120-130.
- Nelson, D. A., C. Whaling, *et al.* (1996). "The capacity for song memorization varies in populations of the same species." *Animal Behaviour* **52**: 379-387.
- Newton, I. (1972). *Finches*. London, Collins.
- Nottebohm, F. (1968). "Auditory experience and song development in the chaffinch *Fringilla coelebs*." *Ibis* **110**: 549-568.
- Nottebohm, F. (1972). "The origins of vocal learning." *American Naturalist* **106**: 116-140.
- Nottebohm, F. and M. E. Nottebohm (1971). "Vocalizations and breeding behaviour of surgically deafened ring doves." *Animal Behaviour* **19**: 313-327.
- Nowicki, S. and D. A. Nelson (1990). "Defining natural categories in acoustic signals: comparison of three methods applied to 'chick-a-dee' call notes." *Ethology* **86**: 89-101.
- Nowicki, S., S. Peters, *et al.* (1998). "Song learning early nutrition and sexual selection in songbirds." *American Zoologist* **38**(1): 179-190.
- Papaj, D. R. and R. J. Prokopy (1989). "Ecological and evolutionary aspects of learning in phytophagous insects." *Annual Review of Entomology* **34**: 315-50.
- Payne, R. B. (1981). "Song learning and social interaction in indigo buntings." *Animal Behaviour* **29**: 688-697.
- Payne, R. B. (1982). "Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings." *Ecology* **63**: 401-411.
- Payne, R. B. (1983). "The social context of song mimicry: song-matching dialects in indigo buntings (*Passerina cyanea*)." *Animal Behaviour* **31**: 788-805.
- Payne, R. B. (1996). "Song traditions in indigo buntings: origin improvisation, dispersal, and extinction in cultural evolution." IN *Ecology and Evolution of Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. Ithaca and London, Comstock Publishing Associates: 198-220.
- Payne, R. B. and L. L. Payne (1993). "Song copying and cultural transmission in indigo buntings." *Animal Behaviour* **46**: 1045-1065.
- Payne, R. B., L. L. Payne, *et al.* (1988). "Biological and cultural success of song memes in indigo buntings." *Ecology* **69**: 104-117.
- Piazza, A., S. Rendine, *et al.* (1995). "Genetics and the origin of European languages." *Proceedings of the National Academy of Sciences USA* **92**(13): 5836-5840.
- Pickstock, J. C., J. R. Krebs, *et al.* (1980). "Quantitative comparison of sonagrams using an automatic image analyser: application to song dialects of chaffinches *Fringilla coelebs*." *Ibis* **122**: 103-109.
- Pinker, S. (1994). *The Language Instinct*, Boston, William Morrow & Co.
- Plotkin, H. C. (1993). *Darwin Machines and the Nature of Knowledge*. London, Penguin.
- Podos, J., S. Peters, *et al.* (1992). "The organisation of song repertoires in song sparrows: themes and variations." *Ethology* **90**: 89-106.
- Pulliam, H. R. and C. Dunsford (1980). *Programmed to learn: An essay on the evolution of culture*. New York, Columbia University Press.
- Reed, T. M. (1982). "Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: playback and removal experiments." *Animal Behaviour* **30**: 171-181.
- Rich, T. (1981). "Microgeographic variation in the song of the sage sparrow." *Condor* **83**: 113-119.
- Riebel, K. and P. J. B. Slater (1998). "Testing female chaffinch song preferences by operant conditioning." *Animal Behaviour* **56**(6): 1443-1453.

- Saito, N. and M. Maekawa (1993). "Birdsong: the interface with human language." *Brain & Development* **15**: 31-40.
- Searcy, W. A. (1992). "Song repertoire and mate choice in birds." *American Zoologist* **32**: 71-80.
- Searcy, W. A. and K. Yasukawa (1996). "Song and female choice." IN *Ecology and Evolution of Acoustic Communication in Birds*. eds D. E. Kroodsma and E. H. Miller. Ithaca and London, Comstock Publishing Associates: 454-473.
- Sibley, C. G. and J. E. Ahlquist (1990). *Phylogeny and classification of birds*. New Haven, Yale University Press.
- Slater, P. J. B. (1989). "Bird song learning: causes and consequences." *Ethology Ecology & Evolution* **1**: 19-46.
- Slater, P. J. B., L. A. Eales, *et al.* (1988). "Song learning in zebra finches: progress and prospects." *Advances in the Study of Behaviour* **18**: 1-34.
- Slater, P. J. B. and S. A. Ince (1979). "Cultural evolution in chaffinch song." *Behaviour* **71**: 146-166.
- Slater, P. J. B. and S. A. Ince (1982). "Song development in chaffinches: what is learnt and when?" *Ibis* **124**: 21-26.
- Slater, P. J. B., S. A. Ince, *et al.* (1980). "Chaffinch song types: their frequencies in the population and distribution between the repertoires of different individuals." *Behaviour* **75**: 207-218.
- Slater, P. J. B. and P. J. Sellar (1986). "Contrasts in the songs of two sympatric chaffinch species." *Behaviour* **99**: 46-64.
- Sparling, D. W. and J. D. Williams (1978). "Multivariate analysis of avian vocalizations." *Journal of Theoretical Biology* **74**: 83-107.
- Stoddard, P. K., M. D. Beecher, *et al.* (1992). "Song-type matching in the song sparrow." *Canadian Journal of Zoology* **70**: 1440-1444.
- Terkel, J. (1996). "Cultural transmission of feeding behavior in the black rat (*Rattus rattus*)." *Social learning in animals. The roots of culture*. C. M. Heyes and B. G. J. Galef. London, Academic Press: 17-49.
- Thielcke, G. (1986). "Constant proportions of mixed singers in treecreeper populations (*Certhia familiaris*)." *Zeitschrift fur Tierpsychologie* **72**: 154-164.
- Thielcke, G. (1987). "Langjährige Dialektronstanz beim Gartenbaumläufer (*Certhia brachydactyla*)." *Journal of Ornithology* **128**: 171-180.
- Thorpe, W. H. (1939). "Further experiments on pre-imaginal conditioning in insects." *Proceedings of the Royal Society of London Series B*. **127**: 424-433.
- Thorpe, W. H. (1961). *Bird Song*. Cambridge, Cambridge University Press.
- Tou, J. T. and R. C. Gonzalez (1974). *Pattern recognition principles*. Reading, Addison-Wesley.
- Watson, C. S. and W. J. Kelly (1981). "The role of stimulus uncertainty in the discrimination of auditory patterns." IN *Auditory and Visual Pattern Recognition*. eds D. J. Getty and J. H. J. Howard. Hillsdale, New Jersey Erlbaum: 37-61.
- West, M. J. and A. P. King (1986). "Song repertoire development in male cowbirds (*Molothrus ater*): its relation to female assessment of song potency." *Journal of Comparative Psychology* **100**: 296-303.
- West, M. J. and A. P. King (1988). "Female visual displays affect the development of male song in the cowbird." *Nature* **334**: 244-246.
- Whiten, A., J. Goodall, *et al.* (1999). "Culture in chimpanzees." *Nature* **399**(6737): 682-685.
- Whiten, A. and R. Ham (1992). "On the nature of imitation in the animal kingdom: reappraisal of a century of research." *Advances in the Study of Behaviour* **21**: 239-283.

- Williams, J. M. (1993). "Objective comparisons of song syllables: a dynamic programming approach." *Journal of Theoretical Biology* **161**: 317-328.
- Williams, J. M. and P. J. B. Slater (1990). "Modelling bird song dialects: the influence of repertoire size and numbers of neighbours." *Journal of Theoretical Biology* **145**: 487-496.
- Williams, J. M. and P. J. B. Slater (1991). "Simulation studies of song learning in birds." IN *Simulation of Adaptive Behavior*. eds J.-A. Meyer and S. Wilson, M.I.T.Press: 281-287.
- Ydenberg, R. C., L. A. Giraldeau, *et al.* (1988). "Neighbours, strangers and the asymmetric war of attrition." *Animal Behaviour* **36**: 343-347.
- Zann, R. (1990). "Song and call learning in wild zebra finches in south-east Australia." *Animal Behaviour* **40**: 811-828.
- Zink, R. M. and G. F. Barrowclough (1984). "Allozymes and song dialects: a reassessment." *Evolution* **38**: 444-448.