SONG ACQUISITION AND CONTROL IN THE CHAFFINCH 'FRINGILLA COELEBS' : THE ORGANISATION OF A BEHAVIOURAL REPERTOIRE

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Song acquisition and control in the chaffinch *Fringilla coelebs*: the organisation of a behavioural repertoire

by

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Submitted in fulfilment of the requirements for
the degree of Doctor of Philosophy.
University of St. Andrews

February 1998

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Abstract

Bird song provides us with one of the best models with which to investigate learning, communication and the organisation of behavioural repertoires. This study describes temporal organisation and song pattern choice in the chaffinch in order to develop hypotheses for possible song control mechanisms. Influences of the song learning process and motivation on performance are tested in experiments. The role of nature and nurture in shaping females' song preferences is investigated by using operant tasks.

A first quantitative assessment of temporal organisation within songs is provided in Chapter 2. Chaffinches sing with eventual variety, each song type in a male's repertoire is repeated a few times before a switch to the next type occurs. Chapter 3 tests two hypotheses for mechanisms controlling song type switching: that a maximum number of repetitions or that a maximum duration (time window) sets the upper limit. Clear evidence for a time window as an upper constraint was found in wild birds as song type bouts with many repetitions were sung at fast rates only, whereas those with few repetitions could be sung at either fast or slow rates. However, the mean number of song type repetitions depended strongly both on the subject and the song type. No evidence could be found that number of repetitions per song type were influenced by the tutor's singing style in hand-reared chaffinches (Chapter 4). Playbacks of single songs to wild males revealed the motivation dependent flexibility of the system as the birds reacted with distinct increases in bout duration (Chapter 5) but showed a different response to playbacks of songs that were the same or different from that being performed by the subject.

Song was used as a positive reinforcer in an operant conditioning task with female chaffinches (Chapter 6). The influence of early exposure to song on later preferences and the relative importance of the trill and flourish sections of the song were tested this way. Females showed no preference for familiar over unfamiliar songs, but preferred songs with flourishes over those without.

Chapter 1

Introduction

General introduction

Bird song has been described as having two main communicative functions: territory defence and mate attraction (Kroodsma & Byers 1991, Catchpole & Slater 1995). The balance in the importance of those differs between species, as does the pattern of singing. Most strikingly repertoires can vary from one single song e.g. zebra finch *Taeniopygia guttata* (Sossinka & Böhner 1980) and many thousand e.g. brown thrasher *Toxostoma rufum* (Boughey & Thompson 1981). In some species different songs are used in different contexts (for species list see Nelson & Croner 1991), in many others all songs within an individual's repertoire seem to serve the same communicative functions. The great variability allows the sender to encode both its individual and species identity while marking a territory and advertising for potential mates.

The discovery that another acoustic communication system apart from human language depended crucially on learning (Thorpe 1958b) triggered a wealth of studies and it remains today one of the most exciting and truly interdisciplinary fields of research in ethology (for recent reviews see Slater 1983a, 1989, Marler 1991, Nottebohm 1991, Margoliash *et al.* 1994, 1996, Nelson 1997) and one of the few areas where an integrative approach including all of Tinbergen's (1963) four questions (causation, function, ontogeny and evolution) has truly been realised. The identification of the brain circuitry involved in bird song learning has made the field one of the most exciting with which to study the anatomical and physiological correlates of the interaction between memory formation and behavioural control in the vertebrate brain (Nottebohm 1984). Bird song recently provided the first documented example in which the correlating brain structures for a hierarchical motor program were identified in a vertebrate brain (Margoliash et al. 1994, Yu & Margoliash 1996) and long and short term storage of songs has been traced in relation to exposure frequency (Chew *et al.* 1996) to name two recent exciting findings. However, the study of bird song has also provided excellent models for the study of social learning and cultural evolution, communication, sexual selection, casual mechanisms of development and sequencing of behavioural patterns and motivational analysis. The following paragraphs will briefly introduce some of the major areas of bird song research followed by the questions under study in this thesis so that they can be seen in wider context both within bird song and behavioural research more generally. Special reference will be made throughout to the chaffinch, being the subject of this thesis. As will soon become apparent, it is an almost ubiquitous research animal and certainly played a major role in many important discoveries.

The role of bird song in the study of acoustic communication and vocal learning

Acoustic communication is widespread in the animal kingdom, in particular among vertebrate and insect taxa. However, apart from humans, there is little evidence for vocal learning and it remains the exception rather than the rule among mammals (Janik & Slater 1997). The contrast with the birds is striking. Vocal learning occurs in at least three avian groups. In the largest group, the *Oscines* or true songbirds (order Passeriformes), comprising at least 4000 of the 9000 or so living bird species, all of those studied to date show vocal learning in development (Kroodsma & Baylis 1982). Vocal learning has also been shown in parrots and their relatives (order Psitacciformes, e.g. Todt 1975b) and in hummingbirds (order Micropodiformes, Baptista & Schuchmann 1990). As the origin of vocal learning remains an evolutionary puzzle (Nottebohm 1972, 1991, 1996, Janik & Slater 1997), the fact that the ability to learn vocalisations has probably evolved three times independently in birds, as is most convincingly suggested by recent neuroanatomical and neurophysiological evidence (summarised in Brenowitz & Kroodsma 1996) and at least 4 times in mammals (Janik & Slater 1997) is remarkable. Birds with their great species diversity therefore constitute a complementary model for the study of ecological and social circumstances that might have caused vocal learning to arise as it provides ample opportunity for comparisons within and between taxa.

Suggestions that song is learned date as far back as 1720 when Graf von Pernau suggested learning in song birds (quoted in Thielcke 1988b). It was not until the 20th century that this question was taken up scientifically. Poulsen (1951) deduced from the impoverished song of his hand reared chaffinches that the lack of an adult model had caused the birds to sing aberrant song. Comparing these birds with autumn caught first year birds also made him suggest that phases for song learning might be limited to certain periods in a young bird's life. However, it was not until Thorpe (1954, 1958a, b) conducted a classic series of experiments on song learning that this was tested and confirmed in a systematic and controlled manner. These experiments can truly be considered to have started modern bird song research. Not only did Thorpe prove that the song was copied by young birds either from a live or tape tutor, he also showed that this was limited to a sensitive phase. And most important, his analysis was conducted with a sound spectrograph, the use of which he introduced and pioneered. Rather than conducting a crude comparison by ear or using a translation into musical scales, scientists now began to use spectrograms to compare them more objectively. These charts provide a translation of sounds into pictures of the signal's frequency and its intensity over time and thus allow one to measure the physical characteristics of animal vocalisations.

Further experiments on song learning confirmed and amplified Thorpe's initial findings that chaffinches learn during the first months after fledging and then again during their first breeding season while settling on territories and showed that they clearly did not learn songs in the periods in between or thereafter (Slater & Ince 1982, Thielcke 1988a, b, Thielcke & Krome 1989, 1991). After these initial experiments in the chaffinch, song learning research shifted to other species like the white-crowned sparrow *Zonotrichia leucophrys*, song sparrow *Melospiza melodia* and swamp sparrow *M. georgiana* (see Marler & Tamura 1964, Marler 1987) and the zebra finch (reviewed in Slater *et al.* 1988).

A series of physiological experiments revealed how the sensitive phase depended on the presence and absence of gonadal hormones and how manipulation of these could delay it into the second year (Nottebohm 1969). Subsequently, the investigation of the role hormones play in the development of neural mechanisms established itself as a new subdiscipline (Nottebohm 1980). Around the same time, Konishi (1965) and Nottebohm (1968) described the importance of auditory feedback for proper development of white-crowned sparrow and chaffinch song respectively. The question of whether or not auditory feedback was necessary for maintenance of adult song led Nottebohm to carry out denervation experiments which in turn led to the discovery of the lateralisation of song production (Nottebohm 1971).

The combined findings on behavioural and physiological aspects of song learning led to the 'sensorimotor model' for song learning (e.g. Konishi 1965, Marler 1976), which marked the beginning of one of the longest and most productive fusions of behavioural and brain research. Birds are proposed to hatch with a crude template of the species specific song characteristics. In a first (sensory) phase a bird memorises songs which refine this crude template into a template for a specific set of songs which the young bird tries to match during the motor learning phase.

This original model has been changed and updated in a number of ways. For example, Marler (1993, 1997) has introduced a further mechanism which he has termed 'action based learning'. This sees the overproduction during plastic song as giving a young bird a repertoire from which it chooses song types matching songs in its new settlement area (Nelson 1992, Nelson & Marler 1994). Interaction with singing conspecifics is argued to be the reinforcement which causes songs to be retained.

Social learning and cultural evolution

The development of species specific song needs exposure to a model. Bird song learning can be studied in the laboratory both with live conspecifics or with tape tutors (Slater 1989) which allow careful control of the acoustic input. Manipulating the presence, absence and timing of exposure to tutors allows one to assess the importance of social tutoring and the duration of the sensitive phase (for recent reviews see Snowdon & Hausberger 1997). Song memorisation during the early sensitive phase just after fledging in combination with small copy errors can establish local traditions or dialects (Thielcke 1969, 1973, Slater *et al.* 1984, Williams & Slater 1990). The chaffinch became perhaps the main model for cultural evolution in bird vocalisations both for song (for further review see e.g. Jenkins 1978, Slater & Ince 1979, Williams & Slater 1990, Metzmacher 1995, Lynch 1996) and for calls (e.g. Bergmann *et al.* 1988, Baptista 1990, Bergmann 1993, Riebel & Slater in press). This was partly due to its wide distribution all over Europe including various island populations like the canaries and the Azores (plus its introduction into New Zealand) but also because of its clear and stereotyped song. Observations like those made in the chaffinch, and also notably on the indigo bunting *Passerina cyanea* (Payne 1996), established a theoretical and comparative approach to studying bird song as a well documented case of cultural evolution providing sufficient data for a modelling approach (Goodfellow & Slater 1986, Lynch *et al.* 1989, Williams & Slater 1990, Lynch & Baker 1993, 1994). Appropriate for the species under study, these models assume that the likelihood for a particular pattern to be transmitted only depends on its frequency in the population. In some species, however this scenario does not apply. In the brood-parasitic brown headed cowbird *Moluthrus ater* for example (West & King 1988), females show occasional wing displays during males' performance of some songs. These songs are preferentially retained in a male's repertoire. These findings reinforce the importance of comparative work and stress how much the species richness within the Oscines demands a careful comparison of related species, habitats, social systems or other life history traits.

The study of mechanisms in behavioural development

Song learning has been most intensely studied in the zebra finch. Its short reproductive cycle, domesticated stocks, and social rather than territorial lifestyle, together with a variety of secondary sexual traits in morphology, have made it a good model both for song learning and imprinting and the possible interactions between the two processes (for review see ten Cate 1994, Clayton 1994). Zebra finches were originally described as having a clearly limited sensitive phase for song learning and not copying songs from a tape. Both findings have been overthrown recently, further confirming the amazing flexibility of the song learning system. The lack of a tutor can delay the end of the sensitive phase (Slater *et al.* 1993) and, although earlier thought to depend on interaction with the tutor for song learning, zebra finches are now known to copy from tapes (Houx & ten Cate, in prep.). This reveals an interesting parallel with imprinting, which was for long labelled as a special irreversible kind of learning with a strictly limited sensitive phase (Immelmann 1972), but has recently proven to be both reversible and delayable, thereby stressing the similarities of song learning and imprinting (ten Cate *et al.* 1993, ten Cate 1994). In combination with the strong neuroethological research in the field, this behavioural work will further our understanding on social learning and sensitive phases and their influence on behaviour in adults. Furthermore, the results emphasise the importance of integrating the study of the developmental mechanisms into those on functions of signalling behaviour.

Memorisation and recall

Song learning is subject to sensitive phases (Thorpe 1958b, Marler & Tamura 1964) and memorisation occurs before song production in most species (Slater 1989), so a unique opportunity arises to study memorisation and recall. The impact that learning might have on features other than song structure, like their timing and sequencing, has only recently been realised. Studies on the nightingale *Luscinia megarhynchos* (reviewed in Todt & Hultsch 1996) have revealed that context of memorisation, serial order effects and spaced versus massed presentation of songs all influence the way a young nightingale will later sequence its own song type repertoire. The blue-winged warbler *Vermivora pinus* sings two types of song, one preferentially at dawn and the other during the rest of the day. In a tape tutoring experiment with hand-reared subjects, Kroodsma (1988) reversed the context for the two songs, and this led to a reverse context use in these subjects. Both findings are intriguing and point to a whole new field of research. Even more so as some findings in the nightingale, for example the preferred chunking of song sequences in subunits of 3-7 songs (Hultsch & Todt 1989) or recency and primer effects (Hultsch & Todt 1996), show striking parallels to human serial learning (Miller 1956, Simon 1974, Crowder 1976) although the brain structures involved for song learning are not homologous to any structure in the mammal brain (Doupe 1993).

Behavioural sequencing and the study of motivation

Most song bird species have repertoires of more than one song. Only a few species show context specific usage of their song types, whereas in the great majority all songs within a repertoire most likely serve the same communicative function. Hinde (1958) consequently termed them alternative motor patterns thereby stressing the parallels between singing and other behavioural processes (Dawkins 1976). The great advantages bird song has in contrast to many other behavioural processes, are its clearly defined on- and offsets, and its high stereotypy of patterns which are regularly spaced and easily transcribed or recorded. First descriptive studies quickly revealed that sequencing was not random, but not fixed either (Hinde 1958, Isaac & Marler 1963, Lemon 1968). However, they also revealed a great diversity in song organisation. In some species, the different song types in a repertoire are delivered discontinuously (i.e. clearly separated by silent intersong intervals) and in bouts. The chaffinch is a classic representative of this singing style which has been termed 'eventual variety'. This singing style is employed by many song birds that have a small repertoire of stereotyped song types and contrasts with two other major singing styles (reviewed in Krebs & Kroodsma 1980, Kroodsma 1982): birds with large song type repertoires switching after each rendition of a particular song type ('immediate variety', e.g. nightingale, Todt 1971) and those continuously rearranging the elements of their songs into new combinations ('continuous variety', e.g. sedge warbler *Acrocephalus schoenobaenus*, Catchpole 1976). Following the first descriptions of this great diversity were attempts at describing the underlying rules and mechanisms and ultimately their possible function in communication (Krebs & Kroodsma 1980). As a first step, the application of statistical models like Markov chains proved the interdependency of songs within sequences (Lemon & Chatfield 1971, 1973, Falls & Krebs 1975), but this approached stalled for two reasons. It did not explain what had caused the preferred sequencing and also, although it proved the sequencing non-random, it did not allow one to predict or model the singing styles of the species under study. Subsequently, a series of models were developed which were all based on Hinde's initial idea of alternative motor patterns. A linear model was suggested for versatile singing such as that of the blackbird *Turdus merula* by Todt (1975a, Todt & Wolffgramm 1975) with three main components affecting motivational levels for each song type independently. One component is self-inhibiting (triggered either by auditory or proprioceptive feedback mechanisms). A facilitating component is activated by external stimulation (i.e. conspecific song with matching song types). And last, a periodicity component increases eigenvalues for song types over time. Simulations resulted in an output achieving a good match with observed blackbird song sequencing (Todt & Wolffgramm 1975).

Competition between behaviour patterns has been suggested as a mechanism accounting for the observed singing style in the chaffinch (Slater 1983b) and the varied thrush (Whitney 1981). These models assume motivational levels for a song type to decrease with continuing performance thereby enabling one of the alternative patterns, which has increased their motivational levels with distance from last performance to take over. These were similar to more generalised behavioural models and resulted in working simulations (Slater 1975, 1978).

The rise of behavioural ecology as a new subdiscipline in the 1970s shifted interest a great deal towards the function of behaviour and, although studies on song control mechanisms continued in the area of song learning and neuroethology, studies of song organisation on the proximate level gave way to studies focussing on the function of song and its role in inter- and intrasexual selection. However, no research investigating possible functions of behaviour can afford to neglect the proximate level and the emphasis has now returned to integration between the two (Curio 1994, Krebs & Davies 1996b), a fact that becomes clear if the most recent edition of the book *Behavioural Ecology* (Krebs & Davies 1996a) is compared with its first edition (Krebs & Davies 1978).

Background and aims of the study

This study investigates details of temporal organisation and pattern choice in the chaffinch, a bird with singing style and repertoire organisation similar to that of many other species. This study stands in the tradition that sees bird song as a prime model for analysis of the organisation of behaviour and its underlying intrinsic rules in order to provide testable hypotheses and models for physiologists and neurobiologists in the long run. It also sees the study of behavioural mechanisms as an end in itself, but being part of an integrative approach in the Tinbergian sense as only understanding in detail of the "how" allows one to understand the "why". By focussing on temporal organisation and the song acquisition process, an attempt was made to identify proximate factors acting on song type choice and switching between song types in a series of experiments both in the field and laboratory. In taking advantage of the great progress that has been made in the techniques available for sound analysis it was possible to analyse temporal parameters with a finer resolution than was possible in the past. In the following paragraphs, each of the questions treated in this study will be introduced in turn.

The chaffinch is a common song bird throughout Europe, Western Asia and North Africa. Its behaviour and ecology are widely described and have been the subject of two monographs (Marler 1956, Bergmann 1993). Male chaffinches have one to six different song types, most commonly two or three. Each chaffinch song has two parts: a trill consisting of one to four phrases of rapid syllable repetitions followed by the so called terminal flourish, a sequence of more complex and non-repeated elements. Songs are separated by silent intersong intervals and each song type is repeated a few times before the bird switches to another type.

The same characteristics, i.e. small repertoire of easily recognisable song types, that have made the chaffinch such a good model for the study of cultural evolution also make it a good model in which to study song organisation, the rules underlying pattern choice and its temporal delivery (Hinde 1958, Hansen 1981, Slater 1983b).

Although many aspects of song have been studied in the chaffinch, many questions remain open or have emerged with advancing knowledge. In contrast with the species producing continuous variety the chaffinch's songs are highly stereotyped so that even small differences between songs are enough to establish them as two song types (Slater *et al.* 1980). However, although an individual delivers the syllables of its repertoire with great precision, the number of syllable repetitions within a trill phrase can vary substantially (Slater & Ince 1982). Further variation arises through the relatively common occurrence of incomplete songs, i.e. songs that are interrupted before all their elements have been sung (Heymann & Bergmann 1988, Nürnberger *et al.* 1989). Chapter 2 will describe the rules underlying temporal organisation within chaffinch song and will attempt to identify possible constraints on performance.

On the between song level the chaffinch like many other song birds (Lemon & Chatfield 1971, Todt 1971, Whitney 1985) has been found to deliver its song types not at random but to show preferred sequencing of types (Hinde 1958, Slater 1983b) and different number of repetitions for the different types (Slater 1981).

Nonetheless, the mechanisms underlying switches between song types are not clear. Revealing the mechanisms that underlie switches between such alternative motor patterns is not only interesting and relevant in terms of explaining bird song organisation, but is of general interest to ethologists. Many behaviours occur in bouts and, where alternative motor patterns are observed, detailed temporal analysis is one way to come to grips with motivational changes (Slater 1973, 1975). In Chapter 3 description of wild spontaneous song will focus on bout length. The data are used to test two hypotheses (timing or counting) as possible mechanisms triggering song type switches. This subject is taken further in Chapter 5 which reports the outcome of a playback experiment which was designed to test the flexibility of the song control mechanisms. Playbacks of single songs from a bird's own repertoire were employed to see whether they would facilitate changes in bout duration and alter the rates of song type switching.

As mentioned above, learning through exposure to conspecific song is crucial if a bird is to develop the species specific song structure. Does learning also influence other parameters of song delivery like timing and sequencing? Chapter 4 describes a song tutoring experiment which tests whether the number of song type repetitions in a bout and the song type sequencing are copied by young hand reared chaffinches from their tape tutor. At the same time the ability of young chaffinches to copy calls from a tape tutor is also tested. The important role chaffinch song played in developing models of cultural evolution has been mentioned already. These studies have also included investigation of regional differences in call structure (see Baptista 1990, Bergmann 1993, Lynch 1996). It has long been suggested that splitting bird vocalisations into song (learned, used only in the context of reproductive behaviour) and calls (relatively simpler, used all year round by both sexes) is too rigid and artificially establishes categories where there is in reality a continuum (e.g. Catchpole & Slater 1995). That some of the chaffinch's calls are learned seems likely because of the small regional scale with which they are observed to vary. As a first step, this long standing hypothesis is tested by playing back calls of different geographical origin as well as the song tutor sequence.

Much of the thesis will focus on the learning and use of song by male birds. This reflects the state of play in bird song research: Acquisition and usage of song in male song birds has been studied to a far greater extent simply because in most species only males sing. They are easier to study in the field and laboratory. The role song plays in intrasexual communication is therefore better understood than the role song plays in the communication between the sexes. This is a striking bias as females form half of the audience and mate attraction is one of the prime functions of bird song (Kroodsma & Byers 1991). Moreover, modern theories of sexual selection suggest that female preferences have an important role in the shaping of signals (Andersson 1994, Searcy & Yasukawa 1996). Chapter 6 reports on the development of a new technique to test female song preferences. It is used to examine the influence of song tutoring on female preferences and the relative importance of some song parts over others on them.

Chapter 2

Temporal organisation of chaffinch song - within song variability

2.1 Introduction

The variation between song types and the question of why birds have repertoires of functionally equivalent song types has been a subject of study for a long time and of many debates (reviewed in Catchpole & Slater 1995). On the one hand, the bird song literature amply describes between song variability, on the other, the within song temporal variability has had little attention to date and quantitative analyses have been few. This is partly for technical reasons: only now do the recent advances in digital sound analysis enable us to measure and analyse the temporal organisation of vocalisations in detail for large samples.

Measurements of timing are important towards understanding both the production of bird song, including species specific constraints (Nowicki *et al.* 1994, Podos *et al.* 1995, Podos 1996, 1997), and also song control mechanisms. This is because singing requires coordination between the neuronal circuitry in the brain controlling singing (Konishi 1994a, 1994b) and an extremely sophisticated sound apparatus (Brackenbury 1980) and breathing system (Allan & Suthers 1994, Suthers *et al.* 1994). It is also important to know which aspects of temporal organisation are relatively invariant as this determines whether they can be used for individual recognition (Weary 1990, Weary *et al.* 1990) or whether they are variable which means they can be used as a graded signal or as a motivation indicator (Slater 1975, Davis 1988, Weary *et al.* 1988). A detailed description of variable and invariant features is the basis with which to start to investigate the interactions between causes and consequences.

In the chaffinch, a typical song is composed of 2-3 phrases of repeated syllables and a terminal flourish (see Fig. 2). A repertoire consists of one to six different song types. The syntactical arrangement within songs is not subject to variation. In contrast, the number of syllable repetitions within phrases varies substantially which raises the question of how overall song duration is controlled. The phenomenon of within phrase variation has been documented in hand reared individuals (Thorpe 1954, Slater & Ince 1982), but no study has quantified it in wild birds. Hand reared birds showed a coefficient of variation of 8-20% for number of syllable repetitions within phrases, although they had been tutored with only one version of each song type (Slater & Ince 1980). It was suggested that variation of this feature is not learned in which case the range for wild songs should be similar.

By investigating variation both in phrase and song length it should be possible to test whether the observed variation in phrase duration is the cause or consequence of variation in song type duration within repertoires. In contrast, if song duration is a constraint in the chaffinch, variation within phrases should be interdependent within one song, so that the overall duration of a song remains relatively constant. In the great tit *Parus major,* one of the few species where within song variation has been studied in detail, increased number of syllable repetitions within a song and overall rate of singing are positively correlated, revealing yet another parameter that is subject to variation. Furthermore, long songs tend to slow down towards the end, a phenomenon which has been termed drift (reviewed in Lambrechts 1996). The chaffinch and the great tit are often quoted examples of discontinuous singers where the few song types in the repertoire are each repeated in bouts before a switch to another type occurs (eventual variety, reviewed in Kroodsma 1982). However, within this style species vary: e.g. the song sparrow *Melospiza melodia* has phonological variations within bouts (Podos *et al.* 1992) unlike the temporal variation in the great tit (Lambrechts & Dhondt 1987).

The aim of this study is therefore twofold. First, it aims to describe the temporal organisation within chaffinch songs in order to gain insight into its underlying control mechanisms. Second, the data will also be used to assess how similar or dissimilar is the organisation in species that are described to have the same singing style. The following questions will be investigated in detail:

- How is song duration controlled if phrases are so variable? Is the variation in duration for phrases similar to the variation in songs? Or do songs show less variation because they have a maximum duration which means that phrase durations should be negatively correlated with each other?
- How much variation in phrase duration is accounted for by the relationship between mean phrase and syllable duration?

2.2 Methods

Song output varies considerably between individual chaffinches. It is possible to find single males that perform long song bouts continuously with almost no neighbour interaction. During spring 1994 various recording sites in the surroundings of St. Andrews were visited during the period from 16 April to 19 July (Table 1). Individual males were recognised by their repertoires and singing post choice. Recordings were made between 0500 and 1100 BST with a Marantz CP430 cassette recorder and Sennheiser MD 400-k microphone (frequency response: 60-13500 Hz) mounted in an Atherstone parabolic reflector. The six males with the longest continuous recordings were chosen for further analysis. Two long continuous recordings from different days (mean 3.2 days between recordings, range 1-6) were selected for further analysis resulting in a mean of 522 songs (range 414-650) per individual and with a mean of 497 (range 396-622) songs measured (see Table 1). Three males had 3 song types and the other three had two types. The repertoires of the six males are illustrated in Fig.1 a-f). Note that there are shared song types between chaffinches C6 and C7 (types c6-2 and c7-2) and C4, C5 and C8 (types c5-1 and c8-1; c5-2, c4-2 and c8-2).

Table 1: Subjects and recording sites

Chaf-finch	Reper-toire Size	Total songs recorded day 1+2	Total songs measured[1]	Recording site	Recording Dates
C4	3	574	550	Kemback Wood	May 2nd and 8th 1994
C5	2	429	413	- " -	May 4th and 20th 1994
C6	2	650	622	Magus Muir	May 9th and 10th 1994
C7	3	550	517	- " -	May 14th and 16th 1994
C8	2	414	396	Kemback Wood	May 24th and 31st 1994
C11	3	517	483	Waterless Wood	June 15th and 19th 1994

[1] Only songs in complete bouts were used for analysis, for definition and details see Chapter 3.

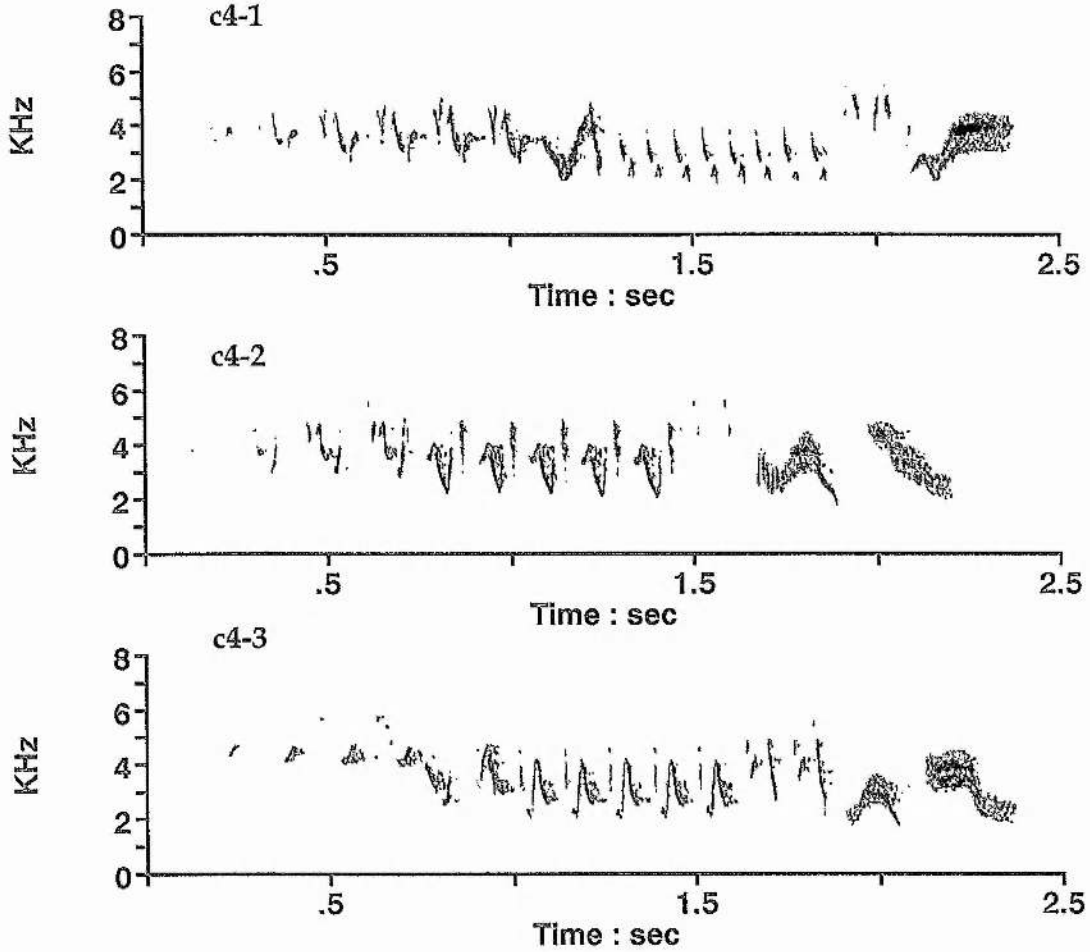


Fig. 1a): Song type repertoire of chaffinch 4.

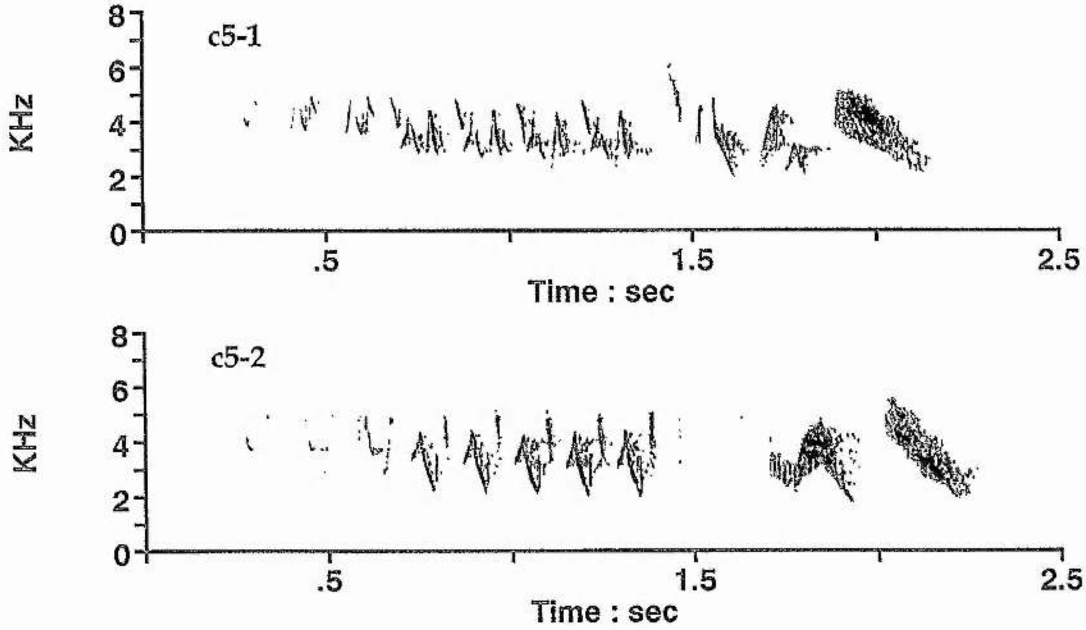


Fig. 1b): Song type repertoire of chaffinch 5.

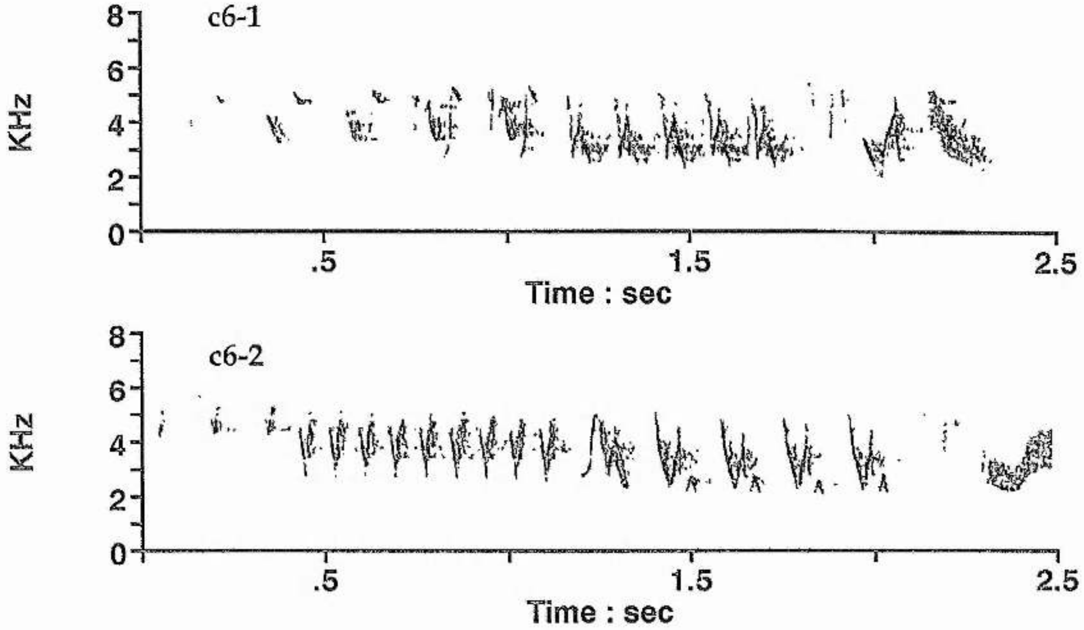


Fig. 1c): Song type repertoire of chaffinch 6.

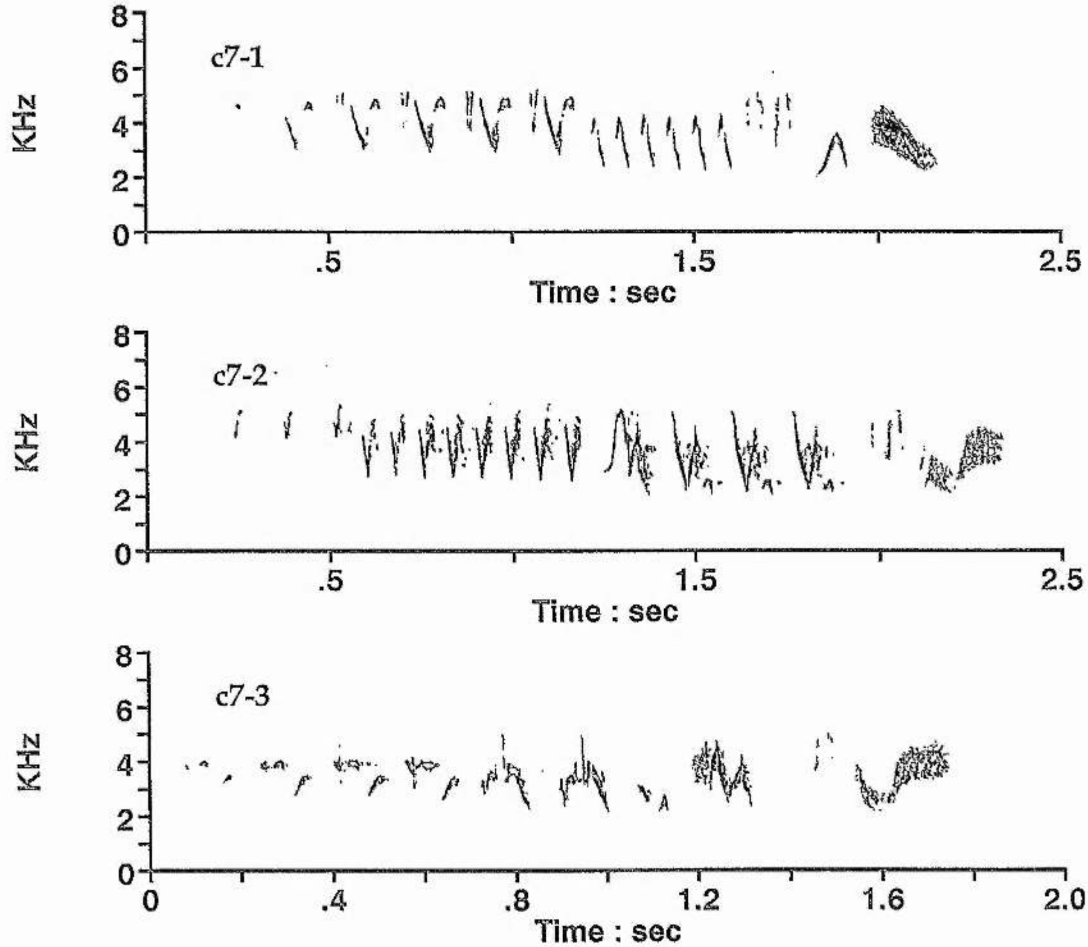


Fig. 1d): Song type repertoire of chaffinch 7.

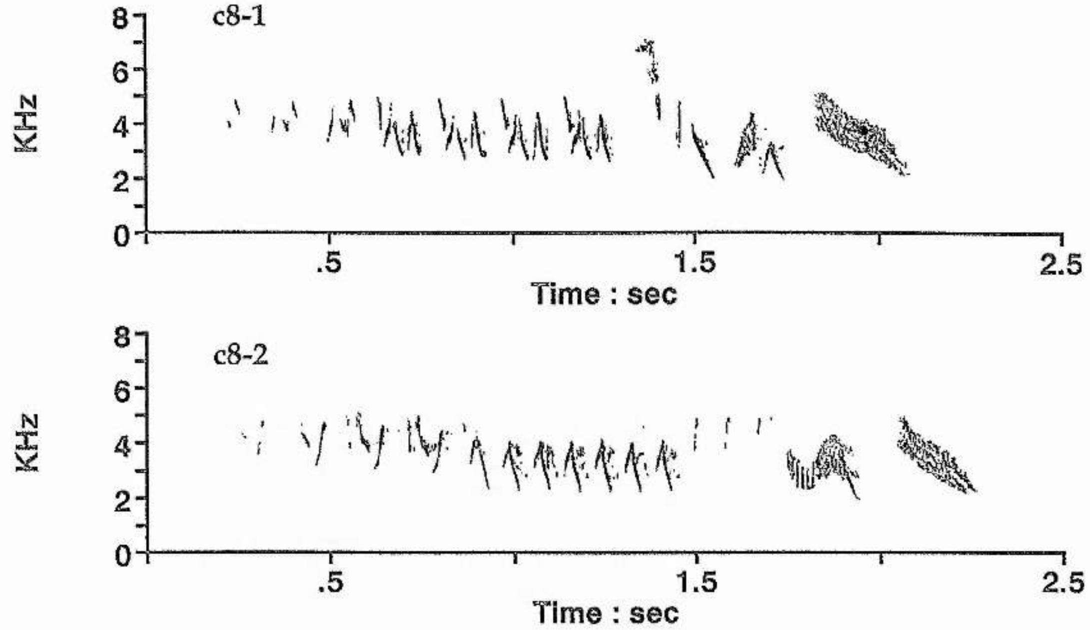


Fig. 1e): Song type repertoire of chaffinch 8.

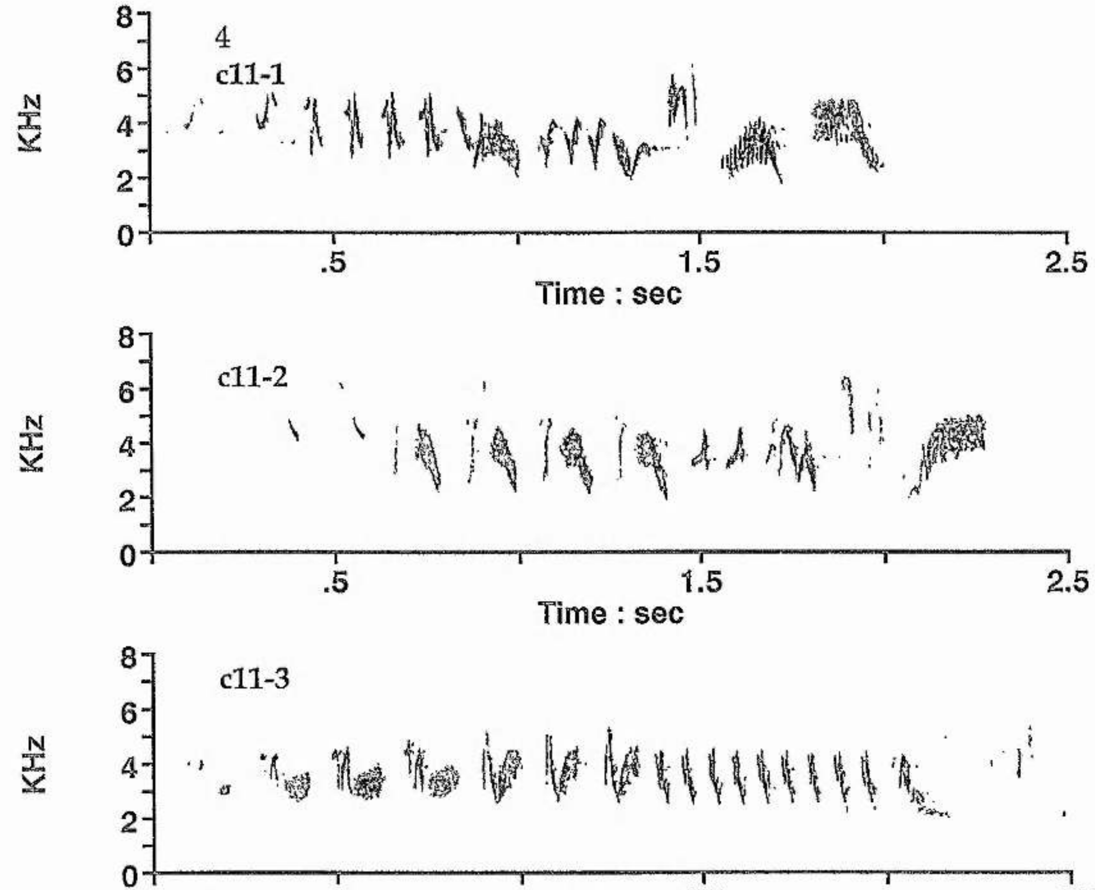


Fig. 1f): Song type repertoire of chaffinch 11.

Definitions of song parts

Definitions used throughout follow those established by other authors (i.e. Slater & Ince 1979, Slater *et al.* 1984) and are illustrated in Figure 2.

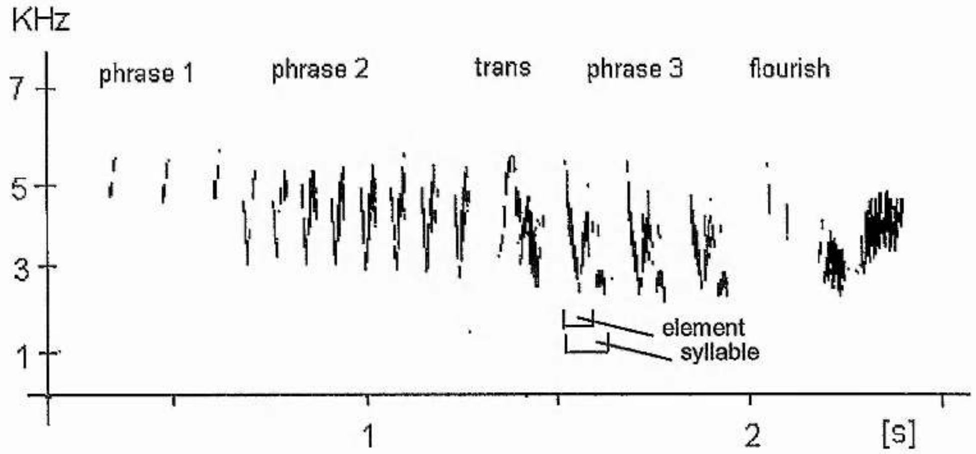


Fig. 2: Typical chaffinch song with three phrases and one transitional element (=trans) between phrases 2 and 3.

Element: smallest unit within song production, continuous trace on a sonagram

Syllable: units of repetition either consisting of a single element or a fixed combination of elements (for illustration see phrase 3 in Fig. 2).

Cadence: duration of one syllable + subsequent silent interval

Phrase: series of successive repetitions of the same syllable

Transitional element: single element or syllable occurring between two phrases

Trill: part of the song consisting of phrases of repeated syllables and the transitional elements between phrases

Flourish: end phrase of every chaffinch song, sequence of non repeated elements

Song type: one specific sequence of phrases and flourish

Song type bout: bout of repetitions of one particular song type

Measured temporal parameters

Sound analysis was made with a Kay DSP 5500 sonagraph (frequency range 0-8 kHz, wide band setting 300 Hz). All measurements were made with cursors on the screen (error ± 7 ms). For all phrases (p_i) the absolute time from the onset of the first (t_ia) to that of the last syllable was measured (t_ib) on the screen (see Fig. 3).

Also the absolute time of onset of a transitional element (tr), of onset of the flourish (tfl) and of the song end were assessed. For all phrases of the trill part of the song the number of syllable repetitions were counted. All the data measured were typed into a spreadsheet on a second computer during measurements as the DSP 5500 has no interface to allow online storage. A code system was used to label songs as complete or interrupted. Only songs that were interrupted before the last element of the flourish were counted as incomplete songs. The relatively frequent shortening of the last element in the flourish was not counted as such.

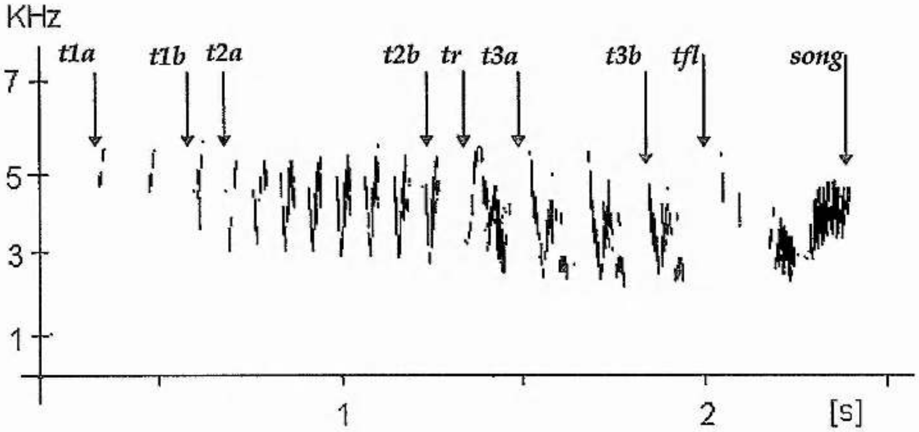


Fig. 3: Measurements taken on screen of the DSP 5500, these were used for the calculations described in Box 1.

Calculated temporal parameters

These absolute time values were used to assess phrase and cadence durations by the following calculations (for overview see Box 1):

1. Cadence: To assess cadence duration (syllable + subsequent silent intersong interval) I followed the methods used by Williams & Slater (1993). The interval between the start of the first and that of the last syllable in each phrase was divided by the number of syllables in that phrase minus one.
2. Phrase duration: The cadence duration for that phrase was multiplied by the number of elements in that phrase.

3. Cadence difference (dc): The calculated duration of a phrase was added to the absolute time value (as originally measured) for the start of that phrase ($t_i a + p_i$). This value was than subtracted from the absolute time value for the start of the next phrase (t_{i+1}) (or transitional element or the flourish). The resulting value could be either negative or positive thereby indicating the direction of deviation for the last cadence from mean cadence duration.

Box 1: Parameters obtained by calculations on first data set

Phrase 1 (p1)

$cad1 = t1b/n - 1 \quad \Rightarrow p1 = cad1 * n1$

$dc_1 = t2a - p1$

Subsequent phrases (p_i)

$cad_i = (t_i b - t_i a)/n_i - 1 \quad \Rightarrow p_i = cad_i * n_i$

$dc_i = t_i b - (t_i a + p_i)$

Transitional elements (tr_i)

$tr_i = p_i - trans_i$

Flourish (fl)

$song\ duration - tfl$

$IPI_{fl} = tfl - (tb + phrase)$

Percent performance time (PPT)

$PPT = song / song + SI$

Statistical analysis

Data were tested for normality with Kolmogorov-Smirnov-one sample tests. The outcome determined whether data were tested with parametric or non-parametric statistics. All tests were performed with the statistical package SPSS (Version 6.1 and 7.0B) and used a significance level of $\alpha=0.05$ and were 2-tailed. Depending on the question, data were pooled either by subject or by song type within a subject. For most questions concerning the interdependency of song components data for the two recordings days were pooled (although some parameters differed between days - see results section) for the following reasons: a) differences within days occurred as well as differences between days (e.g. in song duration), b) the differences between the means or medians were minute in comparison to overall duration and rules guiding the temporal organisation within one subject's repertoire should apply for all the songs of the same type.

2.3 Results

Table 2 gives an overview of the absolute and relative proportions of song types and the occurrence of incomplete songs in the sample. The mean durations for all song parts are summarised in Table 3 which also gives the sample sizes for each day and song type. In the following paragraphs the individual sections of the song will be looked at in greater detail. Incomplete songs are not included in the analyses as it is unclear whether differences between interrupted and complete songs exist. Unfortunately, the sample for interrupted songs was very small for most song types (see Table 2) so that the sample here did not allow a comparison between them and complete songs for all song types.

Table 2a: Frequency distributions of song types in the measured sample (number of songs in complete bouts)

type	chaff		chaff		chaff		chaff		chaff		chaff	
	4		5		6		7		8		11	
	all	icpl	all	icpl	all	icpl	all	icpl	all	icpl	all	icpl
1	186	4	202	7	333	19	204	12	191	4	163	16
2	161	3	211	3	289	16	241	26	205	5	178	15
3	194	2	-	-	-	-	72	5	-	-	142	34
Total	550	9	413	10	622	35	517	33	396	9	483	65

icpl = incomplete songs

Table 2b: Relative frequency of song types in the measured sample [%]

type	chaff		chaff		chaff		chaff		chaff		chaff	
	4		5		6		7		8		11	
	all	icpl	all	icpl	all	icpl	all	icpl	all	icpl	all	icpl
1	34.5	0.7	48.9	1.7	53.5	3.1	39.3	2.1	39.3	1.0	34.2	3.3
2	29.8	0.5	51.1	0.7	46.3	2.6	46.7	5.0	46.7	1.3	36.4	3.1
3	35.6	0.4	-	-	-	-	14.0	1.0	-	-	29.4	7.0
Total	100	1.6	100	2.4	100	5.7	100	8.1	100	2.3	100	13.6

icpl = incomplete songs

Table 3a: Chaffinches with three song types - summary for measured parameters

song type	N	n1 median, range	cadence1 mean, SD [ms]	phrase 1 mean,SD [ms]	n2 median, range	cadence 2 mean, SD [ms]	phrase 2 mean, SD [ms]	Trans II mean, SD [ms]	n3 median, range	cadence 3 mean, SD [ms]	phrase 3 mean, SD [ms]	Trans III mean, SD [ms]	flourish mean, SD [ms]	song mean, SD [s], [ms]	ISI mean, SD [s], [ms]
Chaffinch 4:															
02.05.1994															
1	147	6 4-8	161 7	934 107	7 4-11	77 3	559 95	- -	- -	- -	- -	- -	447 26	2.15 152	7.24 4.01
2	120	4 3-5	175 7	712 96	5 4-7	145 5	781 100	- -	- -	- -	- -	- -	759 61	2.25 137	7.36 2.31
3	147	4 3-7	157 5	678 95	5 4-7	124 3	639 78	- -	- -	- -	- -	- -	752 14	2.32 124	7.36 4.35
08.05.1994															
1	39	6 5-8	155 6	987 100	7 4-11	75 1	516 52	- -	- -	- -	- -	- -	440 17	2.16 114	8.10 2.49
2	41	5 4-6	170 3	851 104	4 4-7	144 2	628 74	- -	- -	- -	- -	- -	746 21	2.19 123	7.37 1.91
3	47	4 3-6	149 8	633 94	5 4-7	120 2	611 62	- -	- -	- -	- -	- -	743 24	2.24 215	7.70 2.78
Chaffinch 7:															
14..05.1994															
1	101	5 4-7	178 7	997 140	7 6-8	70 3	483 40	- -	- -	- -	- -	- -	519 21	1.96 107	9.38 4.34
2	123	5 3-6	132 13	518 78	7 6-8	80 4	577 56	187 26	4 3-5	165 11	630 99	- -	393 55	2.39 144	9.81 3.79
3	29	4 3-4	160 5	578 94	3 6-8	170 9	475 74	- -	- -	- -	- -	- -	690 17	1.72 185	8.46 3.15
16.05.1994															
1	103	6 4-7	181 6	1040 105	7 5-9	70 2	465 50	- -	- -	- -	- -	- -	531 22	2.03 107	9.69 4.55
2	117	4 3-6	133 6	600 80	7 6-10	79 2	582 58	193 7	3 1-5	164 4	566 95	- -	387 25	2.34 145	8.71 4.30
3	42	4 3-5	161 7	637 108	3 2-4	174 15	472 85	- -	- -	- -	- -	- -	690 19	1.79 117	8.72 4.52
Chaffinch 11:															
15.06.1994															
1	57	3 2-3	182 10	520 65	4 3-6	104 6	433 51	221 6	4 3-5	69 3	280 48	164 6	585 81	2.18 103	8.28 4.58
2	66	3 2-3	169 22	465 98	4 3-5	200 6	773 129	- -	2 2	99 7	198 14	193 17	390 17	2.00 182	8.16 4.01
3	29	5 4-6	195 7	930 131	3 3-5	166 3	545 116	- -	9 3-10	70 2	569 101	254 12	332 67	2.64 189	9.41 5.58
19.06.1994															
1	88	3 2-3	183 12	530 68	4 3-5	104 16	429 54	223 28	4 2-5	85 5	286 34	182 7	577 107	2.17 163	5.90 4.20
2	99	3 1-4	169 20	460 104	4 3-5	193 14	735 142	- -	2 2-4	96 7	196 15	172 8	388 62	1.97 179	6.13 3.55
3	75	4 2-6	196 8	876 141	3 2-5	166 4	524 111	- -	9 2-11	70 4	604 99	252 25	354 52	2.56 299	6.91 5.38

typ - song type, n= syllables/phrase, Trans = transitional syllable, ISI = Intersong Interval

Table 3b: Chaffinches with two song types - summary for measured parameters

song type	*N*	n1 median, range		cadence1 mean,SD [ms]		phrase 1 mean, SD [ms]		n2 median, range		cadence 2 mean, SD [ms]		phrase 2 mean, SD [ms]		Trans II mean, SD [ms]		n3 median, range		cadence 3 mean, SD [ms]		phrase 3 mean, SD [ms]		flourish mean, SD [ms]		song mean, SD [s], [ms]		ISI mean, SD [s], ms]	
Chaf finch 5:																											
04.05.1994																											
1	102	4	3-6	166	7	659	93	5	3-6	142	3	644	92	-	-	-	-	-	-	-	-	718	43	2.03	138	6.74	3.60
2	101	4	2-5	159	7	621	90	3	2-5	179	7	618	94	-	-	-	-	-	-	-	-	741	78	2.00	150	7.10	2.76
20.05.1994																											
1	93	5	2-6	161	5	764	123	5	4-7	140	2	727	90	-	-	-	-	-	-	-	-	763	60	2.26	152	6.30	1.86
2	108	4	3-6	153	7	682	102	4	2-5	170	7	627	115	-	-	-	-	-	-	-	-	762	16	2.09	131	6.11	1.72
Chaffinch 6:																											
09.05.1994																											
1	41	5	5-6	204	6	1085	100	5	4-6	127	7	666	58	-	-	-	-	-	-	-	-	572	14	2.33	114	2.33	1.82
2	52	6	5-7	140	6	872	101	8	7-10	80	3	674	65	200	7	4	1-5	170	4	645	76	422	14	2.80	201	2.80	1.90
10.05.1994.																											
1	273	6	1-9	208	8	1163	150	5	4-6	127	4	660	70	-	-	-	-	-		-	-	555	29	2.38	148	2.38	4.74
2	221	6	4-8	139	6	869	105	9	6-12	81	2	707	81	202	10	4	3-5	171	5	677	91	426	26	2.89	149	2.89	4.64
Chaffinch 8:																											
22.05.1994																											
1	88	6	5-7	167	5	935	112	7	4-8	86	2	606	88	-	-	-	-	-	-	-	-	773	116	2.30	200	7.16	4.40
2	121	3	1-4	161	7	525	91	2	3-6	179	7	797	127	-	-	-	-	-	-	-	-	769	72	2.10	181	5.92	2.78
24.05.1994																											
1	99	6	3-5	166	6	923	107	7	5-9	87	8	626	95	-	-	-	-	-	-	-	-	770	145	2.31	205	6.70	3.07
2	79	3	3-5	156	7	519	95	4	3-5	179	3	797	98	-	-	-	-	-	-	-	-	799	77	2.13	129	7.94	4.17

p = phrases, cad= cadence, n= syllables/phrase, trans=transitional element

Variability in duration in the different song components

For each cadence, phrase and song type the coefficient of variation (c.v. = SD/mean x 100) was calculated for its mean duration. Figure 4 illustrates the means for the coefficients of variation of these different units. The amount of variation differs strikingly between song units: cadences, transitional elements and songs show little variation whereas phrases show a great deal of variation. The variation for flourish duration is intermediate.

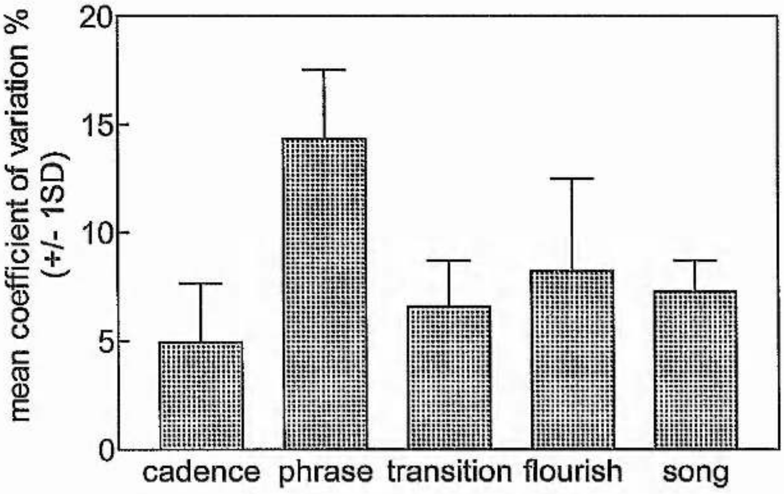


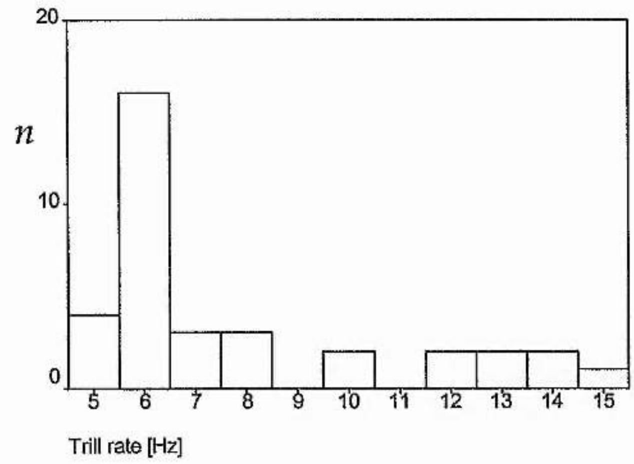
Fig. 4: Comparison between the coefficients of variance of song units (mean +/- 1SD, cadence N=35, phrase N=35, song and flourish N=15, transition N=8; complete songs only).

Cadences

All cadences were highly constant in duration (Table 3) within days. The standard deviation is smaller than the measurement error in most cases (i.e. < 7ms). Median, 1st and 3rd Quartile for each day are given in Table 4. Out of 35 cadences 20 differed significantly in duration between the two recording days. This could not have been due to differences in recording speed as not all of the cadences of a given individual changed (within and between song types). Also, the same cassette recorder was used throughout and occasional calibration (by recording a 440 Hz tone from a tuning fork) showed no changes in tape speed.

Table 4: Duration of cadences (Median, 1st and 3rd Quartile, complete songs only)

Bird	Song type	phrase no.	day 1 median [ms]	1st Q	3rd Q	day 2 median [ms]	1st Q	3rd Q	Mann-Whitney-U p	Z	n
11	1	1	185	175	191	187	178	191	0.25	- 1.1	147
11	1	2	104	102	106	102	100	104	<0.0001*	4.8	147
11	1	3	67	67	69	67	66	69	0.36	0.9	147
11	2	1	166	156	175	174	166	181	.076	-5.0	164
11	2	2	200	198	204	196	194	198	<0.0001*	2.1	165
11	2	3	100	94	101	94	94	100	0.016	-6.9	164
11	3	1	196	192	198	197	192	200	0.42	-0.8	108
11	3	2	166	165	169	165	163	168	0.06	- 0.2	108
11	3	3	70	70	71	69	69	70	0.004	- 2.9	106
4	1	1	160	158	164	155	152	156	<.0001*	- 6.7	186
4	1	2	76	76	78	75	74	76	<.0001*	- 6.0	186
4	2	1	175	171	179	170	169	174	<.0001*	- 5.3	161
4	2	2	145	142	147	144	142	146	0.14	- 1.5	161
4	3	1	158	156	160	152	145	156	<0.0001*	0.6	194
4	3	2	124	123	125	120	120	122	<0.0001*	- 8.9	193
5	2	1	167	162	171	162	158	165	<0.0001*	- 6.3	195
5	2	2	142	141	144	140	138	141	<0.0001*	- 6.9	195
5	3	1	158	154	162	152	149	155	<.0001*	- 6.1	208
5	3	2	179	177	182	171	168	171	<.0001*	-11.9	208
6	1	1	205	201	208	208	205	212	0.0001*	- 3.7	313
6	1	2	126	124	128	127	125	128	0.136	- 1.5	314
6	2	1	141	137	142	139	135	142	0.120	- 1.5	373
6	2	2	80	79	80	81	80	82	<0.0001*	- 4.4	373
6	2	3	171	167	172	171	169	173	0.0001	- 3.9	270
8	1	1	167	164	170	166	162	170	0.201	- 1.3	187
8	1	2	86	85	87	86	84	87	0.093	- 1.7	186
8	2	1	160	154	166	156	153	162	0.0037	- 2.9	199
8	2	2	180	177	183	179	177	181	0.734	- 0.3	200
7	1	1	178	175	183	181	178	184	0.001	- 3.3	203
7	1	2	70	69	71	70	69	71	0.14	- 1.5	191
7	2	1	133	127	136	133	129	137	0.069	- 1.8	237
7	2	2	79	78	80	80	79	81	0.004	- 2.9	234
7	2	3	165	163	167	163	161	166	0.002	- 3.1	224
7	3	1	161	156	163	160	159	163	0.37	- 0.9	72
7	3	2	172	166	175	175	169	175	0.07	- 1.8	69



Trill rate

Trill rate was defined as number of syllable repetitions per second. The frequency distribution for the sample analysed here (all phrases of all birds pooled) is highly skewed towards slow trills within the range (Mean ± SD= 8.0± 3.0 Hz, N=35).

Fig.5: Frequency distribution for trill rates in the sample.

Earlier descriptions of chaffinch songs describe an acceleration between phrases as a typical characteristic. This is partly confirmed by the quantitative analysis. The second phrase in a song is faster than the first (phrase 1 mean ± SD = 6.1 ± 0.7 Hz, phrase 2 = 8.8 ± 3.2, t=3.4, p=0.004, N=15). However, third phrases are not generally faster than second phrases (phrase 2 = 9.1 ± 3.5, phrase 3 = 10.3 ± 4.2, t=0.36, p=0.7, N=5) or first phrases (phrase 1 = 6.3 ± 1.1, phrase 3 = 10.3 ± 4.2, t=1.7, p=0.17, N=5). An inspection of Figure 6 reveals that for third phrases two different patterns emerge, some increase in speed (all third phrases of chaffinch C11: c11-1, c11-2, c11-3) while others decrease (c6-2, c7-2).

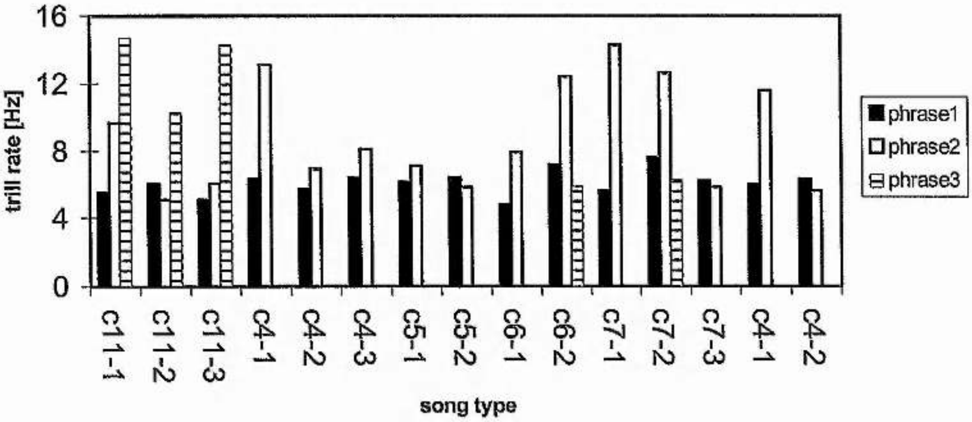


Fig. 6: Comparison of trill rates in phrases 1, 2 and 3 for 15 song types of 6 males.

Intervals between phrases

This analysis tested whether there was a difference between the duration of mean cadence and that of last cadence within a phrase. The relation between the trill rates and this difference is plotted in Figure 7. The graph illustrates two findings. First, in many phrases the last cadence deviated from the mean and was either longer (positive values) or shorter (negative values). Trill rate and the difference between mean and last cadence were positively correlated ($r_s=0.410$, $p<0.014$, $N=35$). The difference between the last cadence and the mean duration for that cadence therefore tends to be longer when the trill is fast. This interval was not influenced by the trill rate of the subsequent phrase ($rs=-0.382$, $p=0.144$, $N=16$).

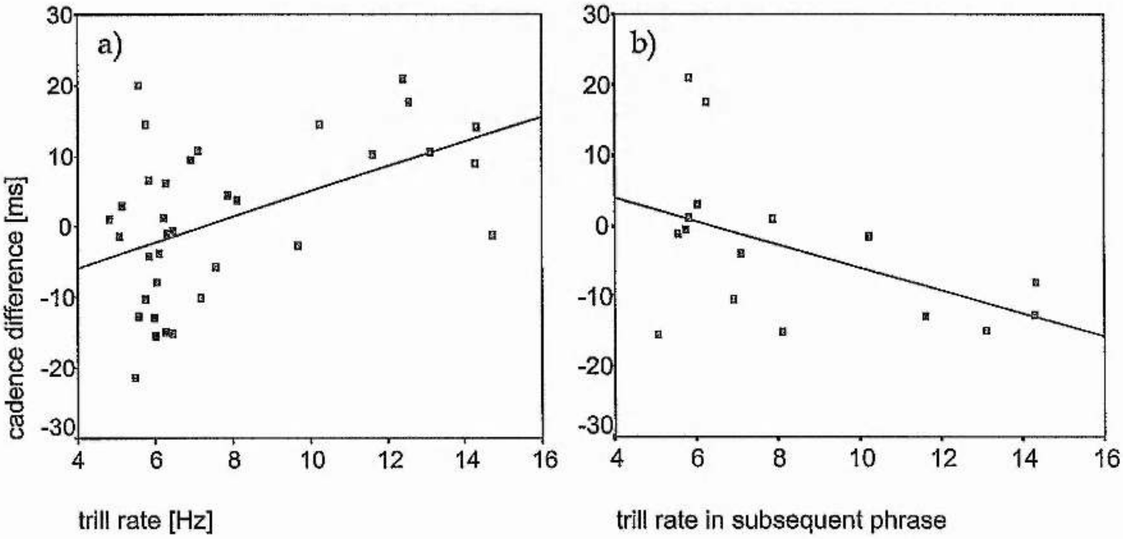


Fig. 7a, b): Cadence difference in relation to trill rate within phrases (a) and to trill rate in the subsequent phrase (b). Only phrases without transitional elements.

Phrase duration and number of syllable repetitions

Phrases showed substantial variation in duration (see Table 3 and Fig. 4). Within song types cadence duration for each phrase is nearly constant (Tables 3 and 4), therefore only the number of syllable repetitions could possibly cause this variation. However, song duration is relatively constant, which means that phrase duration can only vary to a certain extent. If phrase duration is limited by a maximum duration then the coefficient of variation (for number of syllables/ phrase) should be smaller for long cadences as small changes in the number of syllable repetitions cause more variation in phrase duration than they would in a phrase where the cadence for syllables was short. This was not the case: shorter cadences (i.e. faster trill rates) had no higher coefficients of variation for syllable repetitions than longer cadences (Fig. 8, r=.176, p=0.31, N=35).

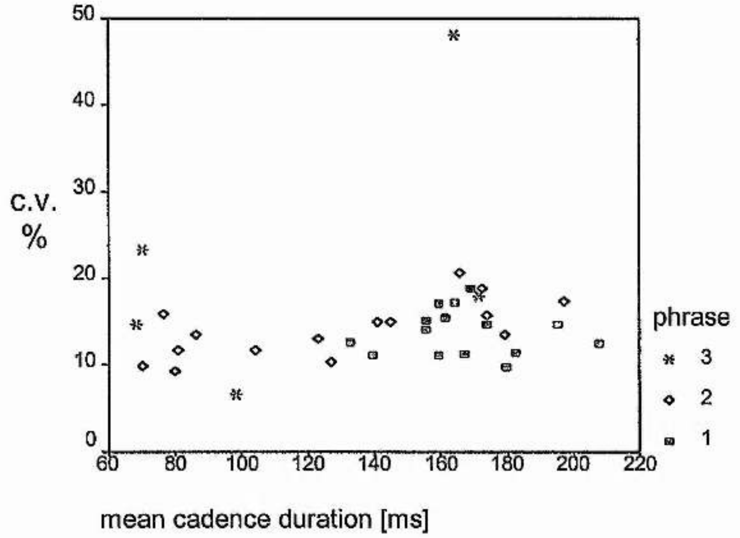


Fig. 8: Coefficients of variation for syllable repetitions in relation to mean cadence duration for each phrase.

If a given phrase had a specific time window, this should manifest itself by a limited 'carrying capacity' acting as a constraint on the possible maximum number of syllable repetitions. This carrying capacity however would be a function of both the duration for the phrase and cadence duration. The mean number of syllables per phrase should be the quotient of the two. Those phrases with many syllable repetitions should show more variation than those with few repetitions only. However, that mean number of elements within a phrase is no predictor of variation either is apparent from Figure 9. The mean number of elements per phrase and the respective coefficient of variation are not correlated (r=-1.59, p=0.36, N=35).

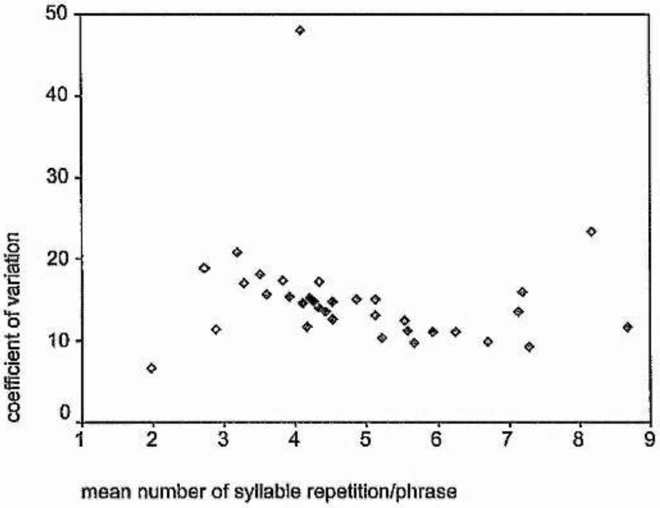


Fig. 9: Mean number of elements per phrase and coefficient of variation.

The only relationship between cadence and phrase duration that could be discovered within the data set was a negative correlation between trill rates and phrase duration (r=-0.49, p=0.003, N=35, see Fig. 10). The faster a trill the shorter the phrase becomes.

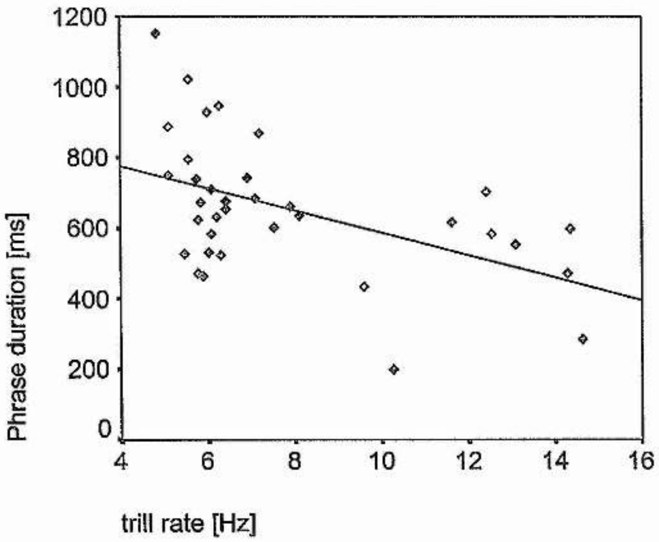


Fig. 10: Trill rate and phrase duration.

Are number of syllable repetitions negatively correlated between phrases?

The durations of phrases within songs should be negatively correlated. i.e. " time overspending" in one of the phrases should lead to a decrease in duration in another phrase in order to maintain the standard song length. Number of syllable repetitions were negatively correlated between phrases 1 and 2 in 5 out of 15 song types (see Table 5). Two were significant between phrases 2 and 3 (one positive, one negative), 2 n.s. and for song type c11-2 no correlation coefficient was calculated as it had a constant number of 2 syllable repetitions. There were no significant correlations between phrases 1 and 3.

Table 5: Correlations between different parts of songs (Spearman's rho)

	correlation between: n1 and n2		n2 and n3		n1 and n3		trill and flourish	
song type	r	p	r	p	r	p	r	p
c11-1	-.005	.96	.08	.32	-.036	.67	-.06	.48
c11-2	-.02	.8	-	-	-	-	.07	.37
c11-3	-.14	.15	-.11	.28	.087	.37	.007	.94
c4-1	.09	.21	-	-	-	-	-.13	.08
c4-2	-.44	<.001*	-	-	-	-	.19	.016*
c4-3	-.11	.14	-	-	-	-	.13	.08
c5-1	.23	.001*	-	-	-	-	.24	.001*
c5-2	-.04	.55	-	-	-	-	.25	<.001*
c6-1	-.21	<.001*	-	-	-	-	.06	.28
c6-2	-.14	.02*	-.13	.09	-.085	.16	.13	.04*
c7-1	-.13	.07	-	-	-	-	-.14	.06
c7-2	-.06	.36	.21*	.002	.12	.08	-.26	<.001*
c7-3	-.19	.14	-	-	-	-	.006	.96
c8-1	-.05	.49	-	-	-	-	.12	.09
c8-2	-.24	.001*	-	-	-	-	.17	.018*

Flourish

As elements within the flourish are not repeated they were assessed as one duration measurement only. The flourish actually showed some variability in duration (see standard deviations in Table 3 and Fig. 4). This is not surprising as the shortening of the last element was not counted as a song interruption and occurred rather frequently. Flourish duration was negatively correlated with the trill duration in 6 out of the 15 different types (see Table 5), so shortening of the flourish could partially have been caused by 'overspending' time in the first song part.

Trill and flourish

If only the mean values for flourish and trill duration for each song type are considered the sample reveals an interesting interaction. There was a negative correlation between mean flourish and mean trill duration for song types (Fig. 11).

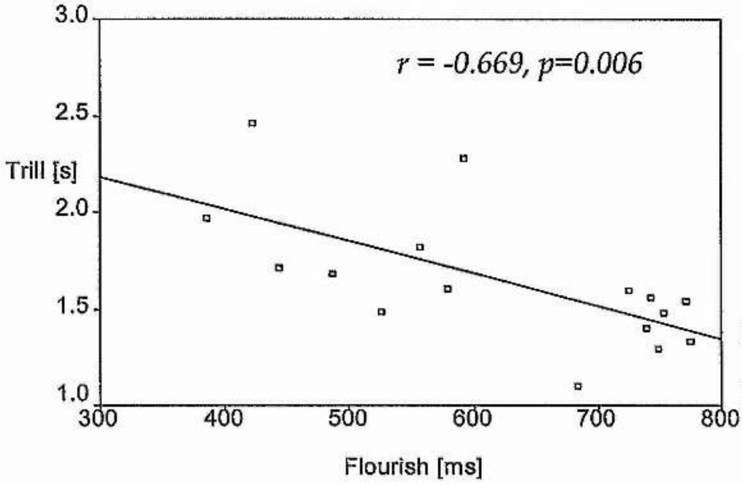


Fig. 11: Correlation between trill and flourish duration.

Song duration

Mean duration for songs was significantly different between the subjects and song types of the sample (Table 6a, b; Fig. 12), but there was also a significant interaction with recording day. These differences might be attributed to days (i.e. shifting with progressing season) or to short term motivational changes such as can also occur within days. This was confirmed when song duration between bouts was also tested. 14 out of 15 song types showed significant differences in duration between bouts (One-way Anova, results in Appendix 2.1).

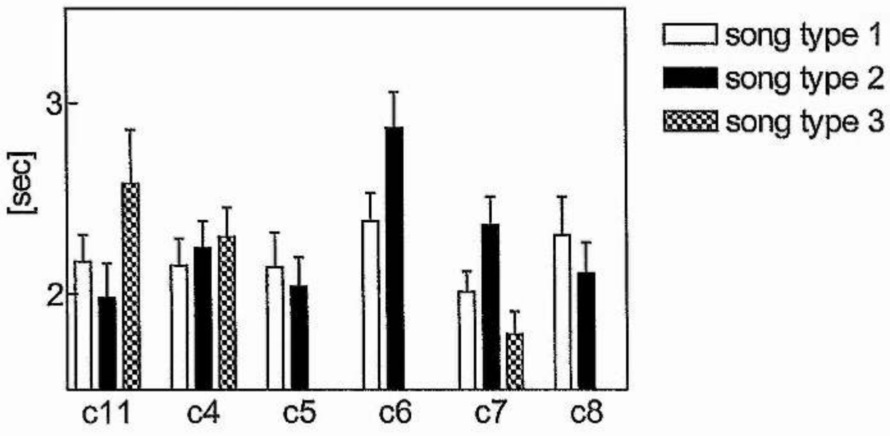


Fig. 12: Mean song duration by subject and song type (± 1 SD).

Table 6a: Anova: song duration by subject with day as nested factor

Source	df	Mean Square	F	p
subject	5	23.1	106.2	<0.001
day	1	0.94	4.3	0.038
subject *day	5	0.51	2.3	0.039
error	649	0.22		

Table 6b: Anova: song duration by song type with day as nested factor

Source	df	Mean Square	F	p
song type	14	12.7	107.7	<0.001
day	1	0.52	4.4	0.036
song type * day	14	0.33	2.8	<0.001
error	2945	0.12		

Number of phrases and song duration

Song types in the sample had either two or three phrases (see Fig. 1 a-f). The sample is rather small: there were only 5 song types with three phrases and three were from one individual (c11), which questions the meaningfulness of this particular comparison. Mean duration of song types with two and three phrases showed no significant difference (2 phrases: mean ± SD= 2.10 ± 0.18, N=10, 3 phrases: mean ± SD= 2.28 ± 0.35, N=5, t=1.3, p=0.21, d.f.=13) within the sample.

Percent performance time

If neuromuscular exhaustion is the reason why birds singing with eventual variety switch to another song type then drift in song duration should also be found in the chaffinch. Figure 13 plots the mean song duration versus the position within the bout. There is no evidence that song duration declines towards the end of very long bouts, but song duration seems to be relatively constant. The illustration depicts pooled data, thus there is the possibility that song duration early in a bout differs between long and short bouts. However both visual inspection of separate plots and the low variance suggest that this is not the case.

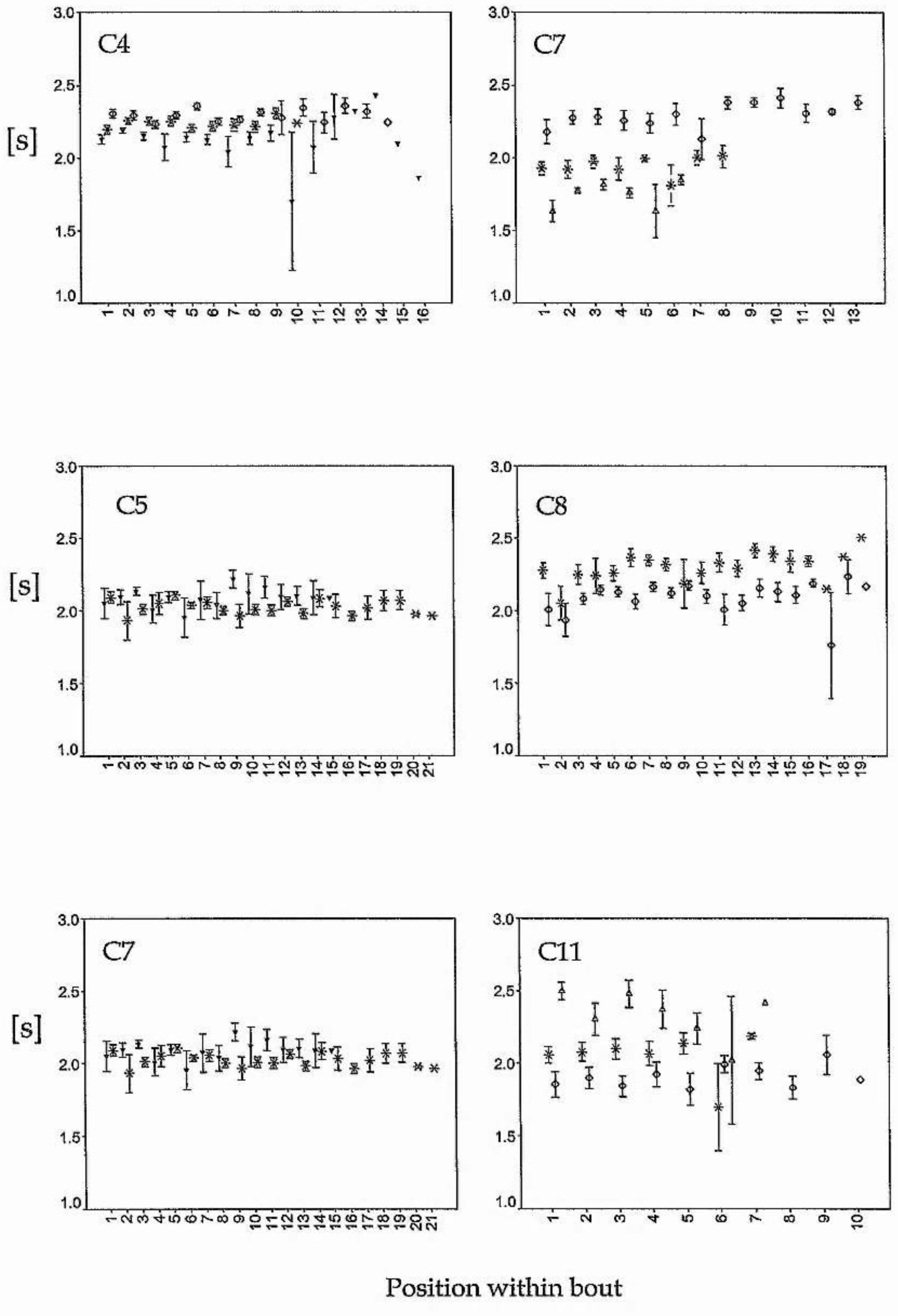


Fig. 13: Song duration (mean ± SE) in relation to position within bouts. Symbols represent song types (▲ = song type 1, ✧ = song type 2, ✳ = song type 3).

2.4 Discussion

This analysis of the detailed fine temporal structure in chaffinch songs revealed that mean duration for syllable cadences is almost invariant. Consequently, the great majority of observed variation in phrase duration is due to varying numbers of syllables. Although changes within a phrase were not assessed, the minute variance for mean cadence duration makes it unlikely that an equivalent to what has been described as drift in great tit songs (i.e. the increase in duration of the silent intervals between syllables towards the end of a song) exists in chaffinch songs. There was some evidence that variation in phrase duration within a song type was limited by the duration of other phrases, as some negative correlations between adjacent phrases and also between flourish and trill were found. This suggests that long preceding phrases lead to shorter following phrases too. However, the results were not clear cut. The idea of a phrase being constrained by a temporal limit is difficult to support in the light of the finding that long and short cadences do not show differences in variation for number of syllable repetitions. By contrast, in cardinals the number of syllable repetitions was found to be inversely related to the syllable duration (Lemon 1975). In the chaffinch, it seems possible that varying numbers of syllable repetitions are an additional, genuine feature of the singing style, thereby being a cause not a consequence of variation in phrase duration. This seems a better explanation than suggesting that all phrase variation is to compensate for time overspending in other parts of the song at least at the within song type level. However, a comparison between song types resulted in the unexpected finding that there is a clear interdependency and negative correlation between the flourish and trill parts of songs. An early playback study suggested that the trill is more important as a territorial signal than the flourish (Brémond 1968). The findings in Chapter 6 suggest that the flourish is more attractive for females the longer its duration. As overall song duration is relatively constant (Figures 4 and 13) an interesting conflict arises as either long trills or long flourishes can only be achieved be shortening the other part of the song.

In contrast to the variability in duration of other song parts, the observed constancy in cadence duration within a day is striking. Unfortunately there are no similar quantitative data available from other species. However, the fascinating studies on song production in the brown-headed cowbird and the mimic thrushes show the respiratory system to produce song type specific patterns of activity with remarkable accuracy (Allan & Suthers 1994, Suthers et al. 1994). The chaffinch data fit in well with the idea of the element or syllable being the unit of production in song birds (Cynx 1990) as has also been suggested for non-songbirds (ten Cate & Ballentijn 1996). The observed differences between days are therefore the more remarkable. They occur for some phrases within a song but not for others and are therefore not a reflection of differences in recording speed. It is hard to see either a functional or causal explanation for this. Perhaps they do reflect differences in motivational levels. Perhaps the respiratory system produces some trills faster or slower at different temperatures. None of these hypotheses seems satisfactory as the suggested mechanisms should affect all phrases and not only some. The constancy within days however clearly shows that no equivalent exists to the drift within songs as observed in the great tit where interphrase intervals of repeated syllables tend to get longer towards the end of songs (see Lambrechts & Dhondt 1987, Lambrechts 1996).

Consistent individual differences in the number of phrases and in song duration have also been reported for other species: great tits (Lambrechts & Dhondt 1987), blue tits *Parus caeruleus* (Bijnens 1988) and chiff-chaffs *Phylloscopus collybita* (McGregor 1988). In the great tit these differences were suggested to reflect either differences in male quality (Lambrechts & Dhondt 1986, 1987) or to be short term indicators of males' motivations to react to territorial intruders (McGregor & Horn 1992). In the chiff-chaff, individual differences in song length in spontaneous song were no predictor of song length observed after playback, therefore making it unlikely that song length indicates male quality in this species (McGregor 1988).

From the point of view of mechanisms, motor constraints have been shown to influence performance and copying of temporal aspects of song organisation

(Podos 1996, 1997). In many other species that repeat long trains of repeated syllables varying amounts of syllable repetition have been reported, for example, in the canary *Serinus canaria* (Wolffgramm 1973) and great tit (reviewed in Lambrechts 1996), but in none of the cases do we know either the function (if any) or the cause of this variation. In the chaffinch songs investigated in this study, fast trill rates tended to result in shorter phrases and longer interphrase intervals suggesting that trill rate could be a constraint on performance and could at least explain some variation between phrase types, albeit not necessarily within them. Whether some syllable types are more difficult to perform, and therefore more exhausting to the vocal apparatus, remains to be seen.

On a functional level, temporal variability within songs has not been studied very systematically within individuals. Differences in temporal organisation have been studied more on a population than individual level and are seen as a possible species cue (e.g. Nelson 1988) or population marker (e.g. Kroodsma & Verner 1987) or as a means of adaptation to a certain habitat (Handford 1988). Thus, all variation between individuals could simply reflect the variation of the trait under selection. However, this does not account for the fact that there is so much variation within individuals. Variation in temporal organisation could possibly play a role in individual recognition (Weary 1990), could be an age indicator (Ballentijn & ten Cate 1997) or a means of increasing variability to delay habituation. However, at present it is not at all clear how much of the observed variations are adaptive or just 'noise' in the interaction between the sound production and song control system. Further studies in this area will be worthwhile as temporal parameters like pulse rates have been shown to change with behavioural contexts (Davis 1988). Furthermore, they are perhaps more relevant for comparisons with taxa lacking song than the standard measurements of song variability like repertoire size and syntactical rules. This chapter has shown that the magnitude of the within song and within subject variability is large enough to be further investigated both on a mechanistic and functional level, which has to show whether this variability is of relevance for communication.

Furthermore, the units of production were highly constant in duration, refuting the idea that the observed variation arises solely because of production inaccuracy.

2.5 Summary

The temporal organisation within the songs of six wild male chaffinches was studied in detail. A sample of about 500 songs was measured for each bird. The variability in phrase duration, already described in the literature, is due to variation in number of syllable repetitions as no changes in mean cadence duration (syllable plus subsequent silent interelement interval) were observed. Song duration varies between song types. Comparing coefficients of variation an interesting pattern arises: the coefficient of variation for mean duration is not correlated with the absolute duration of the component under study. Instead two units - songs and syllables - show very little variation in length. Most of the variation in the temporal organisation of the song is therefore accounted for by variation in phrase length.

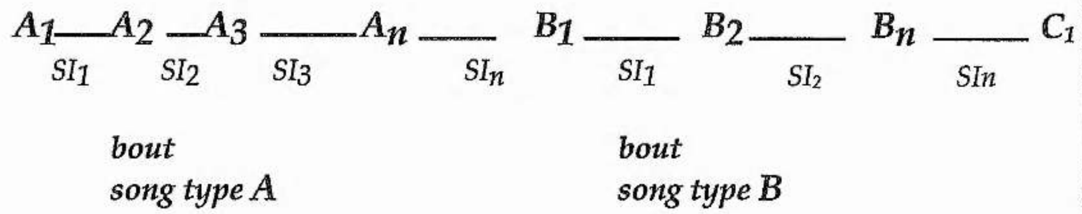
Chapter 3

Song type switches in the chaffinch: Timing or counting?

3.1 Introduction

Song birds show a great variety of singing styles and repertoire organisation (Krebs & Kroodsma 1980, Kroodsma 1982, Catchpole & Slater 1995). Within this great diversity two major groups can be discriminated: continuous and discontinuous singers. Whereas continuous singers show long uninterrupted bouts of varied song, discontinuous singers intersperse songs of a few seconds with silent intersong intervals of slightly longer duration. Species with great song type repertoires tend to sing with "immediate variety", i.e. in general each rendition of a song is a new song type and repetitions tend to be avoided (ABCD..). Species with smaller repertoires tend to sing with "eventual variety", i.e. every song type is repeated a few times before a bird switches to another song type of its repertoire (see Box 1).

Box 1: Bout organisation: song types (AAABBB..) are repeated several times before the bird switches eventually to another song type of its repertoire. Songs are separated by silent intersong intervals (*SI*).



This singing style has been described in many species on an observational basis and different hypotheses have been put forward to explain this singing style both on a proximate and ultimate level (Hartshorne 1956, Krebs 1977, Kroodsma 1978, Slater 1981, Lambrechts & Dhondt 1988). However, studies investigating song switching in detail measuring temporal parameters are rare, if playback experiments are discounted.

The aim of this study was therefore to analyse the temporal aspects of song type switching in a species which sings discontinuously and with eventual variety: the chaffinch. The chaffinch seems very suitable for this investigation: it has a small repertoire (1-6 song types Marler 1952, Slater *et al.* 1980) and song types are easily recognisable and subject to no variation on the phonological level. Its singing style is amply described in the literature (i.e. Hinde 1958, Slater 1983). However, the mechanism that triggers a song type switch remains unclear for any of the species that deliver song type bouts. Furthermore, such studies are of general interest to ethologists: many behaviours occur in bouts and where alternative motor patterns are observed detailed temporal analysis is one way to analyse underlying motivational changes (Slater 1973, 1975). Below, a list of hypotheses for mechanisms possibly controlling song type switches is given and subsequently explained in more detail:

H1: time window (= maximum duration limiting bout duration)
H2: maximum number of repetitions
H3: a combination of H1 and H2
(H4: bout length is copied from tutor)
(H5: bout length developed by bird during motor learning)

The predictions resulting from the first two hypotheses are illustrated in Fig. 1. If a maximum time window was the only factor controlling bout length all bouts should be of the same maximum duration (or shorter). In contrast, if a maximum number of songs limits bout duration then the relationship between number of songs and bout duration should be linear (the more songs the longer the bout). This hypothesis predicts a cut off point at the hypothetical maximum number.

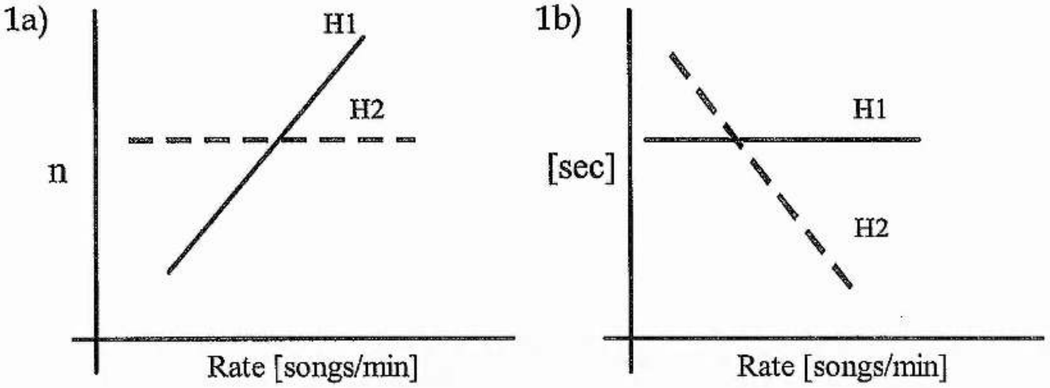


Fig.1: Schematic illustration of the relation between number of songs per bout and bout duration according to hypothesis H1 ("time window") and H2 (max. number of songs).

If the two mechanisms interact (H3) predictions are more difficult as it is unlikely that each would contribute with the same weighting. A switch would occur as soon as either the maximum number or the maximum duration was reached, suggesting that song rate (number of songs per time unit) should be a good predictor for bout duration if either hypothesis H2 or H3 were to be confirmed by the data.

This figure clearly illustrates that bout duration is not influenced by the song rate if a time window controls the durations of bout length. In contrast, if switches between song type bouts are triggered by a max number of repetitions, song rate influences bout duration as bouts sung at a slow rate would potentially be longer than bouts sung at a fast song rate.

The question of whether or not ontogeny influences song type bout length (hypotheses H4 and H5) cannot be investigated with the data analysed here as the ontogeny of the birds under study was unknown, but will be the subject of Chapter 4.

3.2 Methods

Subjects and recordings were identical to those analysed in Chapter 2. For all songs within the sample (for details see Chapter 2) the durations of both the song and the subsequent interval were measured with cursors on the screen of a Kay DSP 5500 sonagraph. Bout duration was the sum of all songs and silent intersong intervals (ISIs) of one song type. Only complete bouts were used for further analysis. A complete bout was defined as starting after a switch from the preceding song type and ending with a switch to the next song type. The maximum silent intersong interval within continuous song was defined not to be longer than 30 s which is the equivalent to a song rate of about two songs per minute, the slowest song rate a chaffinch will perform without stopping singing altogether (own observations).

3.3 Results

Comparison between days

Bout duration and number of songs per bout were tested for differences between the two sampling days for every single song type in the sample. Bout durations for all but one song type in the sample were not significantly different between days (t-test, all $p>0.10$, song type 15, $t=2.19$, $p=0.043$). Differences in the number of songs per song type bout were tested with a Mann-Whitney U test yielding no significant difference for all but one song type (song type 3, $Z=2.07$, $p=0.038$, all other song types $p>0.10$). As the parameters under study - number of songs per bout and bout duration - did not vary between days, data for each bird were pooled for the rest of the analysis. Mean singing rate (songs/min) differed for bird c11 (t-test, song type 1-3, $t_{type1}=3.6$, $p=0.001$; $t_{type2}=2.7$,$p=0.01$, $t_{type3}=3.4$, $p=0.0015$) and for one of c4's song types (type 14, $t=3.3$, $p=0.005$). For all other birds and all other song types the song rate did not differ between days.

Mean bout length - comparison between birds

The mean duration of song type bouts (see Table 1) showed great variation between individuals (One-way Anova, $F_{5,494}=93.9$, $p<0.001$). Multiple comparisons showed most birds to be significantly different from each other (Fisher least significant difference, $p<0.001$). Only two comparisons did not yield significant results (c6 and c4, $p=0.49$; c5 and c8, $p=0.12$).

Comparison within birds

The mean duration of song type bouts were compared within individuals. Individuals with three song types were tested with an One-way ANOVA and individuals with two song types by means of a t-test. In chaffinches 7 and 11 the three song types had different bout durations (c7 $F_{2,123}=27.5$, $p<0.000$; c11 $F_{2,142}=3.95$, $p=0.021$). Durations of song type bouts turned out to be no different in chaffinch 4 ($F_{2,70}=2.34$, $p=0.104$). In all three subjects with two song types no significant differences could be found in the mean duration of song type bouts (c5, $t=1.6$, $p=0.12$, $df=35$; c6 $t=1.9$, $df=83$, $p=0.064$; c8 $t=1.7$, $df=32$, $p=0.097$).

Table 1: Bout length - Mean duration of bouts and mean number of songs per bout

bird	song - type *1	*2	Mean number of songs n	SD	Mean bout duration [s]	SD	n	same song type as	t-test t	p
C11	1	1	3.4	2	30.2	18.8	48			
	2	2	4.3	2.8	36.6	21.1	40			
	3	3	2.6	2.1	25.2	19.3	57			
C4	1	4	7.9	2.8	77.0	26.6	24			
	2	5	6.6	2.0	63.7	20.2	24	C5-2	3.2	0.005
	3	6	8.0	3.9	81.4	40.1	25			
C7	1	11	4.2	1.9	48.3	17.8	48	C6-2	2.3	0.022
	2	12	5.2	2.6	56.7	21.3	46			
	3	13	2.3	1.5	25.2	14.6	31			
C5	1	7	10.1	2.9	85.4	25.1	20	C8-1	3.3	0.002
	2	8	12.4	6.0	106.5	52.6	17	C8-2	.65	0.51
C6	1	9	7.9	2.9	76.2	18.6	42			
	2	10	6.7	3.2	67.5	23.7	43			
C8	1	14	10.6	3.9	97.3	27.6	18			
	2	15	12.8	3.3	112.2	22.9	16	C4-2	4.6	0.001
Total			5.97	4.0	57.3	34.6	500			

*1song type labelling used for analyses within subjects.

*2labelling used for analyses with song types as units.

Bout duration was not influenced by song length. There was no correlation between mean song length and the number of song type repetitions (r =-0.007, p=0.98, N=15) or mean bout duration (r=0.041, p=0.89, N=15). If songs differ in their level of difficulty mean bout duration should be similar in shared song types. However, five of the six possible comparisons between shared song types showed significant differences in mean bout duration (see Table 1). Mean bout duration in birds with 2 song types was longer than in those with three song types (2 song types 90.9 ± 17.5 s, N=6; 3 song types 49.4 ± 21.6 s, N=9, t=3.9, p=0.002).

Number of songs per bout - between subjects

The mean number of songs per song type bout also varies between individuals (see Table 1). Mean number of songs per bout were compared between individuals and this showed significant differences between them (Kruskal-Wallis H, χ^2=222.7, d.f.=5, p <0.001). Multiple comparisons (Siegel & Castellan 1988, N=15) showed all birds to be significantly different from each other with the exceptions of the pairwise comparisons between c5 and c8 and between c4 and c6.

Within subjects

Within subjects the mean number of song type repetitions per song type bout was compared with Kruskal-Wallis H test (repertoire size 3) or a Mann-Whitney-U test (repertoire size 2). Only two of the subjects with 3 song types (c11, c7) showed significant differences in mean number of repetitions between song types within a repertoire.

Table 2: Number of song per song type bout: comparisons within individuals

subject	song types	Kruskal-Wallis H (χ2)	p	N
C11	3	10.5	0.005[1]	145
C4	3	4.1	0.13	73
C7	3	27.8	<0.001[2]	126
		Mann-Whitney-U z		
C5	2	- 1.6	0.099	37
C6	2	- 1.9	0.06	85
C8	2	- 1.4	0.17	34

[1] Multiple comparisons (critical difference): significantly different between C11-2 and C11-3.
[2] Multiple comparisons: number of songs/bout in song type C7-3 is significantly different from song types C7-1 and C7-2.

Number of songs and song rate

Figure 3 illustrates the relationship between number of songs and song rate. Two dotted lines illustrate the cut off points for the maximum number of songs and the maximum song rate observed in the sample. The third line accents the extremely triangular nature of the data. Song type repetitions only increase with increasing song rate. Not a single bout with many song type repetitions occurred at a slow rate. In this context it is important to note that song rate does not influence bout duration, as only in one song type (c7-2, r=0.37, p=0.01, N=48) a correlation was found between bout duration and song rate (all other song types, p>0.05). The maximum song rate observed was about eleven songs per minute with a few outliers all stemming from the same individual. The following calculation gives the mean duration for mean minimal silent intersong interval: (60 s -11 songs x 3 s) = 27 s, 27 s / 11 = 2.5 s. At least for the observed sample a maximum rate of 11 songs/min and a minimal mean silent intersong interval of 2.5 s can be described.

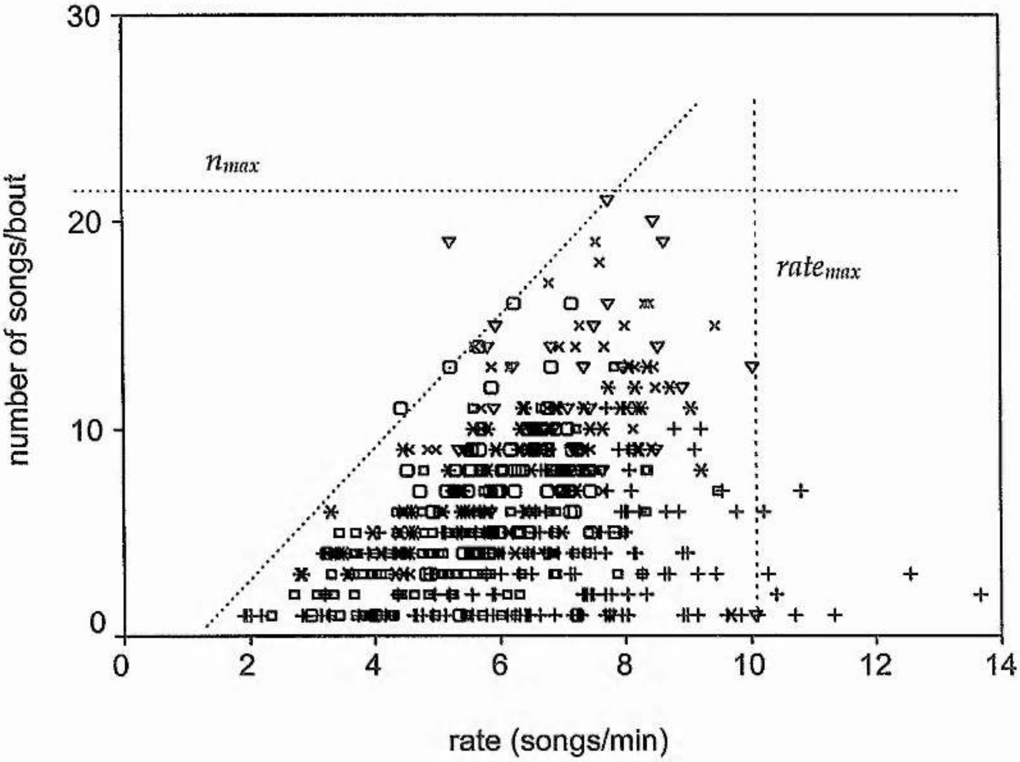


Fig. 3: The relationship between song rate and number of songs per bout. Different symbols represent subjects 1-6. n_{max} = maximum number of repetitions, $rate_{max}$ = maximum repetition rate.

Silent intersong intervals

Mean song rate (songs/min) and mean duration for silent intersong interval both reflect the speed a bird sings with and means for both are plotted in Fig. 4. Here and for further analyses the mean was calculated without the last silent intersong interval, because the last interval tends to be longer (see Table 4). As the effect on mean bout duration is stronger in short bouts than in long bouts, this may mask other differences between the two. Analysis will concentrate on the silent intersong intervals (rather than rate) as they are an immediate reflection of the amount of time between songs whereas song rate reflects both the length of song and of the silent intersong interval. Comparing mean ISI duration by a One-way Anova shows both subjects ($F_{409,14}$=3.97, p<0.001) and song types ($F_{418,5}$=9.2, p<0.001) to be significantly different from each other. Multiple comparisons between subjects (Fisher least significant difference) were significant for 5/15 possible comparisons and between song types for 28 out of 105 possible comparisons.

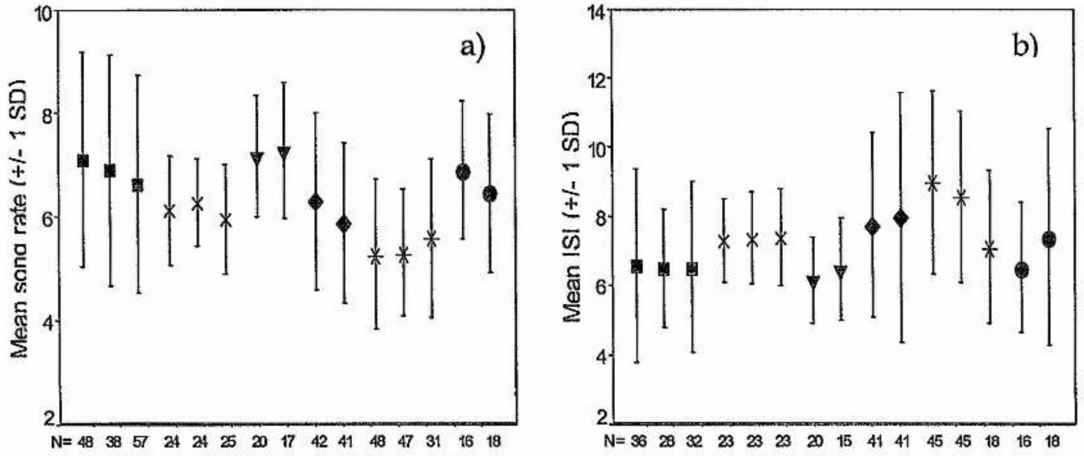


Fig. 4a,b): Mean song rate and mean duration of intersong interval (ISI) for all song types (1-15). Different symbols represents subjects (from left to right: c11, c4, c5, c6, c7, c8).

As song duration is not subject to much variability (see Chapter 2) a singing chaffinch can accomplish changes in bout duration only by increasing or decreasing the duration of silent intersong intervals, i.e. changing song rate. A plot of mean duration of silent intersong intervals in relation to number of song type repetitions within a bout is given in Figure 5, both for the pooled sample and for each individual separately. It shows clearly that bouts with few songs can be sung fast or slowly, whereas song type bouts with many song type repetitions can be sung fast only. This form of distribution is consistent within individuals as shown in the individuals plots for each subject. One bird (c5) sings fast only regardless of bout length. However, this is not in contradiction with the observation that only fast singing allows many repetitions.

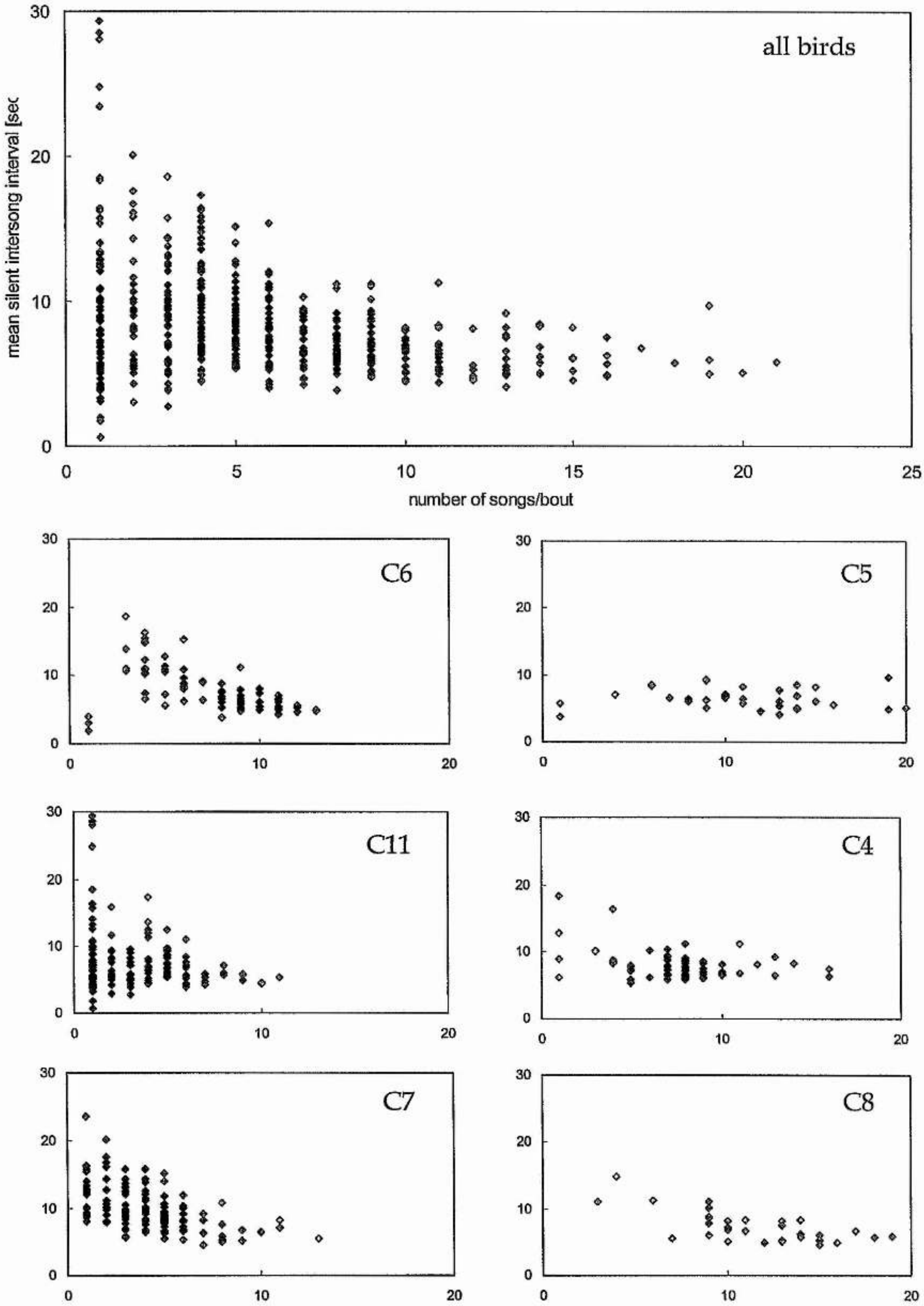


Fig. 5: Mean duration of silent intersong interval in relation to number of songs per bout.

To see whether this trend held true for each song type in the sample, data were split into the two categories slower or faster than mean song rate (see Table 3). The number of songs per bout is smaller in those song type bouts that are sung slower than the mean (Binomial test, p<0.001, N=15). Within song types this difference is significant for 8 out of 15 song types and in all the other seven song types the trend is in the same direction.

Table 3: Mean number of songs / bout tested against song rate for songs sung faster or slower than mean song rate for this particular song type

	Mean number of songs/ bout				
Song type	**slow** (<mean rate)	**fast** (>mean rate)	direction of difference	Mann-Whitney (2-tailed) **p-value**	n
C4 -1	7.0	8.7	slow < fast	0.2	24
C4 -2	6.0	7.2	" < "	0.14	24
C4 -3	7.1	8.9	" < "	0.29	25
C5 -1	9.5	10.8	" < "	0.55	20
C5 -2	11.4	13.3	" < "	0.2	17
C6 -1	6.1	9.5	" < "	**0.0000 ***	42
5C6 -2	5.2	8.5	" < "	**0.0001 ***	41
C7 -1	3.4	5.1	" < "	**0.0017 ***	28
C7 -2	3.4	6.6	" < "	**0.0000 ***	47
C7 -3	1.8	3.0	" < "	**0.024 ***	31
C8 -1	8.6	12.7	" < "	**0.019 ***	18
C8 -2	11.1	14.5	" < "	**0.038 ***	16
C11 -1	3.0	3.8	" < "	0.2	48
C11 -2	3.4	5.3	" < "	**0.044 ***	38
C11 -3	2.2	2.9	" < "	0.27	57

Switch between song types

The SI preceding a song type switch (A-B) was compared with the average duration within the bout (A-A transitions). It was significantly longer than the average duration within the bout in five of the six birds (see Table 4). I also tested the first SI within a bout against the mean duration of other SIs within the bout. Table 4b shows that in five out of six subjects this difference is not significant.

Table 4a: Comparison of mean SI duration within song type bout with mean duration for last SI

subject	mean SI ± SD	last SI ± SD	paired t-test t	p	n
c11	6.5 ± 2.4	7.7 ± 6.0	- 1.96	.053	96
c4	7.3 ± 1.3	9.9 ± 7.4	- 2.9	.004*	69
c7	8.5 ± 2.6	12.0 ± 5.2	- 7.7	<.001*	108
c5	6.3 ± 1.3	8.8 ± 4.5	- 3.4	.002*	35
c6	7.9 ± 3.1	9.5 ± 6.1	- 2.7	.009*	82
c8	7.0 ± 2.6	10.1 ± 6.7	- 2.5	.016*	34

Table 4b: Comparison of mean durations of first silent intersong interval within song type bout with mean duration SI - 1st SI

subject	mean SI ± SD	1st SI ± SD	paired t-test t	p	n
c11	6.9 ± 3.3	6.6 ± 3.6	0.66	.51	95
c4	7.8 ± 2.0	7.4 ± 2.0	1.20	.23	68
c7	10.2 ± 4.1	8.8 ± 4.1	-0.32	.005*	107
c5	6.6 ± 1.4	6.8 ± 3.3	0.69	.75	34
c6	8.3 ± 4.0	8.0 ± 3.7	2.9	.50	81
c8	7.1 ± 2.1	8.0 ± 5.6	0.99	.36	33

Percent performance time (PPT)

In studies on the great tit *Parus major* various authors have used percent performance time (PPT=song duration/song duration + silent intersong interval x 100) and have examined how this varied with position within song type bout in order to assess drift (Lambrechts & Dhondt 1988, Weary *et al.* 1988, 1991). This parameter was calculated for the chaffinch. The means were pooled after checking that the subjects' plots were similar in shape. Fig. 6a plots mean percent performance time against position within bout (independently of the size of the bout). There is no negative drift: if anything PPT increases slightly. If the number of repetitions within a bout is taken into account, mean percent performance time increased with increasing number of song type repetitions within a bout (Fig. 6b).

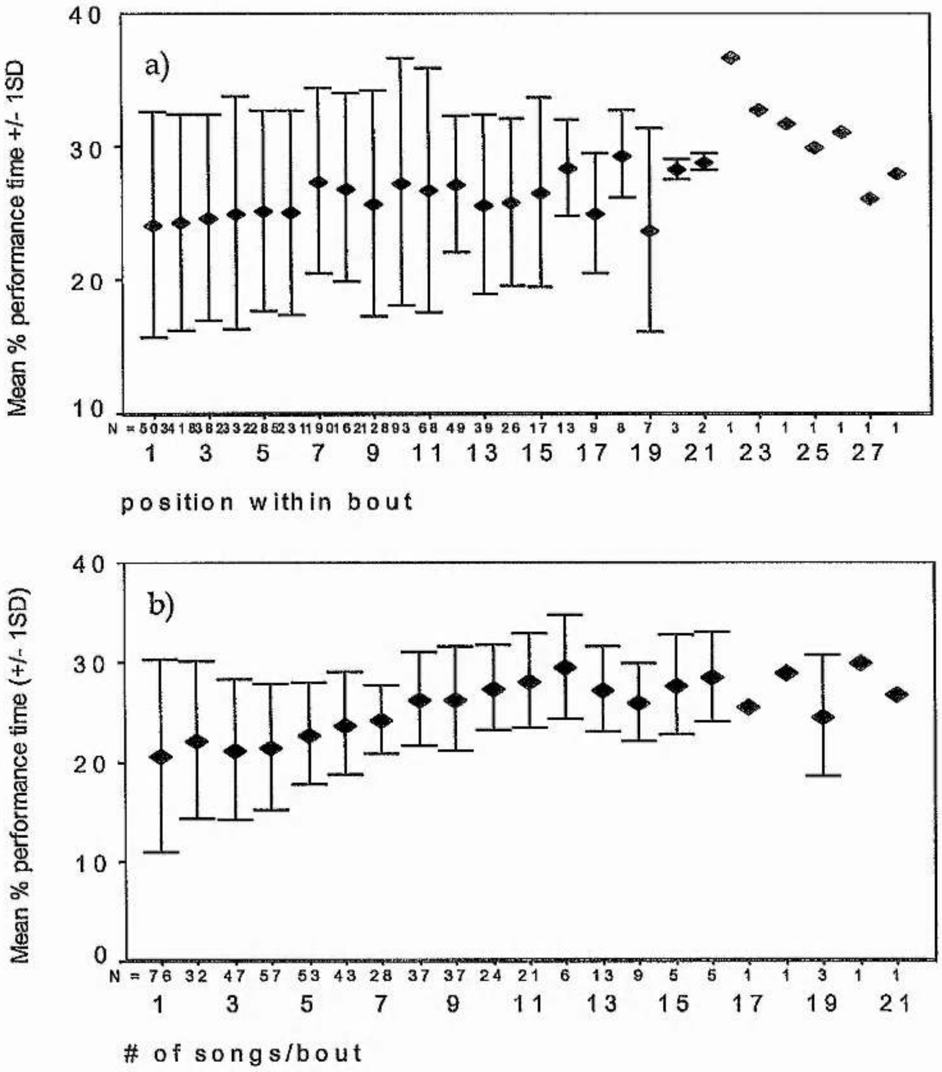


Fig. 6a, b): Mean % performance time (song duration/song + SI) according to position within song type bout (a) and according to size of bout (b). Before data were pooled, separate plots for short and long bouts, song types and subjects were examined and were not obviously different.

Number of incomplete songs and song rate

The number of incomplete songs was compared between bouts sung slower and faster than mean song rate within each subject. Only in one subject (c6) were songs significantly more often interrupted at a song rate faster than the mean (Z=-2.9, p=0.003, Mann-Whitney U, all other subjects p>0.10). If song types were tested independently rather than pooled for all subjects, only song type 10 (c6) was significantly more often interrupted at higher song rates (Z=-2.4, p=0.015), all other song types showed no significant differences.

3.4 Discussion

Song type switching in six male chaffinches was investigated in order to test between two hypothesis for the possible song control mechanisms triggering song type switches, that it is based on the number of repetitions or on a temporal limitation (time window). The data gave strong evidence for a temporal limitation as only song types sung at a fast rate resulted in bouts with high numbers of song type repetitions whereas bouts with few repetitions could be delivered both at a fast or slow rate. These data can be interpreted to favour models based on competition between behavioural patterns, which assume that motivations for alternative motor patterns decrease during performance while patterns that have not been performed for a while simultaneously increase again (Slater 1978, Whitney 1981). However, bout durations and mean number of repetitions were found to vary within and between song types. This strong individual or song type component suggests that the number of repetitions is a song type and repertoire specific characteristic.

Silent intersong intervals

Other authors have reported a relationship between song rate and number of songs per bout (i.e. Hinde 1958, Lambrechts & Dhondt 1988). Interpretations differ (e.g. anti-exhaustion hypothesis, Lambrechts & Dhondt 1988) but most authors interpret the relationship as an indication of high motivation acting both on song rate and on number of song type renditions (Kramer *et al.* 1985, Weary et al. 1988, 1991). This study suggests that there is perhaps an additional constraint: The data support the idea of a temporal limitation of song type duration (a time window). Consequently song type bouts with many repetitions of the same song type can only be sung fast as at a slower song rate this temporal limit is reached after fewer songs. However, bouts with few songs can be delivered at a fast or a slow rate as they might never get near this upper boundary. Also high motivation and the number of song type repetitions do not necessarily have to result in longer bouts: previous results suggest that song type switching is high when birds are aroused. In Eastern and Western Meadowlarks, *Sturnella magna* and *S. neglecta*, song type switches increase immediately after onset of playback of species specific song, but the likelihood of a switch is clearly related to previous bout length as switches are more likely if the song type had been repeated more than just a few times (Falls & D'Agincourt 1982). These data may be taken as support for the idea that motivational levels rise and fall at the onset and termination of this hypothetical time window.

Intersong intervals have been compared by Hinde (1958) in a group of captive and hand reared chaffinches. Silent intersong intervals tended to be shorter within than between bouts. Four out of five birds in his study had been hand reared and tutored with either reversed chaffinch song or tree pipit songs (Thorpe 1954, Thorpe 1958). Hand reared chaffinches tutored with atypical song and the wild chaffinches studied here behave the same in this respect, giving strong evidence that this is a characteristic of the song control system. The longer duration of silent intersong intervals preceding switches are of special interest as they could reflect transitions between two levels or planes of hierarchically organised behaviour (Dawkins 1976). They have also been reported in at least another species singing with eventual variety, the song sparrow *Melospiza melodia* (Podos *et al.* 1992).

Hinde (1958, Fig. 4) reports also a strong positive correlation between songs per minute and songs per bout for three different song types of three different birds. The larger sample size in this study (see Fig. 5, plotted in the same way) shows an extremely triangular data set or an upper bound distribution. Upper bound distributions have been discussed as an indication for ecological or behavioural constraints (= the upper bound) (Blackburn *et al.* 1992, Podos 1997). It seems likely that this graph indicates a temporal limitation on bout duration, as slow bouts never occur where there are many song type repetitions. These results suggest that song type specific differences in bout length are a characteristic of chaffinch song organisation, which is not culturally transmitted. Even if not copied from a specific tutor, the observed differences in bout length could still be influenced by other developmental processes either during motor development or memory formation. Either way, intrinsic mechanisms leading to song types seem to differ resulting in different motivational levels for different song types, influencing number of repetitions. Upper limits however are set by a temporal constraint.

Subject and song type specific bout durations

Differences between song type bout durations could be observed both within and between individuals. Different numbers of repetitions per bout within individuals are also reported for wild chaffinches in Orkney by (Slater 1981) and for captive birds by Hinde (1958). This could either mean that bout durations are perhaps learnt just as song types (Williams & Slater 1990, Slater & Williams 1994). Also, young chaffinches could develop a preferred number of repetitions for each song type during the motor phase of the song learning process. Number of song type repetitions then could or could not be related to relative difficulty of the song and its syllables.

The results obtained here and those reviewed in the preceding paragraph suggest that song type specific differences in bout length are a characteristic of chaffinch song organisation. The question whether bout length is copied from a tutor will be tested in a song tutoring experiment where numbers of repetitions per song type bout vary across song types (see Chapter 4).

Comparison with other song birds

Among the European song birds that sing with a comparable singing style the great tit is perhaps the best studied. A male great tit has a repertoire of up to 8 song types consisting of a single repeated phrase. These song types are delivered in bouts at varying song rates (reviewed in Lambrechts 1996). Lambrechts and Dhondt's (1988) anti-exhaustion hypothesis states, that the faster birds sing the more likely they are to switch as the vocal apparatus tires. Results obtained in this study point in the opposite direction: bouts with a great number of song type repetitions are only delivered at fast rates. The results add further doubt to the anti-exhaustion hypothesis, for which contradicting data within the great tit are also accumulating (Weary et al. 1991). In the data reported here the chaffinch, another bout singer, shows as many or more songs in fast as in slow bouts which have lower song percentage performance time. Also, chaffinches with only one song type are not at all rare. They can be found delivering long continuous bouts. However, nobody has so far measured the duration of silent intersong intervals of chaffinches performing with only one song type and compared them with chaffinches having two or more song types in their repertoire.

Some additional indirect evidence for the suggested timing mechanism may be derived from studies in which authors investigated the communicative function of song. In eastern and western meadowlarks, song type switches increase immediately after onset of playback of species specific song, but the likelihood of a switch is clearly related to previous bout length as switches are more likely if the song type had been repeated more than just a few times (Falls & D'Agincourt 1982). Langmore (1997) reports that song type switching rates are higher at slow than at fast singing rates as occur in the different contexts of mate attraction and of territory defence in the dunnock *Prunella modularis*. The observation that switching occurs after fewer repetitions at a slow rate fits in exactly with our observations on the chaffinch and suggests that further comparative studies would be fruitful.

Although we cannot make any suggestions about possible neurophysiological processes regulating the suggested time window, it seems interesting to notice that timing processes have also been suggested in some other aspects of song control. For example, numbers of syllable repetitions are negatively correlated with syllable durations in the song of the cardinal *Cardinalis cardinalis* (Lemon & Chatfield 1971). In the nightingale *Luscinia megarhynchos*, the temporal spacing of a tutor song sequence influences the number of songs clustered in song type association groups in later performance (Hultsch 1992).

The results obtained here and in other studies suggest that there are at least two motivational components acting on song type bout length. First different contexts influence motivational levels. Second, at least in the chaffinch, intrinsic mechanisms leading to song types seem to differ, resulting in different motivational levels for different song types, influencing number of repetitions. This leads to song type specific differences in bout length, which are an additional characteristic of song organisation in the chaffinch. However, the main finding of this study has been that, within a song type, upper limits for bout duration are set by a temporal constraint.

3.5 Summary

Chaffinches sing with eventual variability. A singing male repeats each song type in its repertoire a few times before switching to another type. The mechanism triggering these switches is not known. Long continuous recordings of six wild males were investigated in order to test between two hypotheses: 1) a maximum number of repetitions limits bout length or 2) a switch occurs after a maximum duration for a song type bout ('time window'). Strong evidence for a temporal limitation could be found: song type bouts with many repetitions were delivered at a fast rate only, whereas bouts with few songs in them could be delivered fast or slowly. However, numbers did matter too - number of song type repetitions differed both between song types within and between individuals. The results are interpreted as pointing towards a song type specific motivational component, its magnitude being reflected in the mean bout duration for this particular song type. A design for a song tutoring experiment emerges, with the aim to test whether number of song repetitions in a song type bout is copied as well as the form of the song type itself.

Chapter 4

Song acquisition: Are bout length and song sequencing acquired during ontogeny?[1]

4.1 Introduction

Young song birds need exposure to conspecific song in order to produce the species specific phonology and syntax in their songs as adults (for review see Slater 1989). To date studies on song learning have focussed on sensitive phases and social factors affecting song acquisition. However, recently, studies on the nightingale *Luscinia megarhynchos* have shown that the tutors' song type sequencing could clearly influence the tutee's (reviewed in Hultsch & Todt 1996). Furthermore, the versatile singing style of this species, which tends to deliver a different song type with each rendition, could be influenced towards more repetitions if the tutor program had had an artificially increased number of repetitions (Hultsch 1991).

The chaffinch's and nightingale's song organisation differ dramatically. The nightingale is a classic example of a versatile singer with a large repertoire of up to a few hundred song types. In the chaffinch a small repertoire (1-6 song types) is delivered with eventual variability: each song type is repeated a few times before the bird switches to another type. However, birds do not just cycle through their repertoire, but certain transitions are preferred over others and not all song types in the repertoire occur with the same frequency (Hinde 1958, Slater 1983). A detailed analysis of bout size and duration (see Chapter 3) has shown that individual chaffinches can deliver different song types in their repertoire in bouts that differ both in the number of song type repetitions and duration.

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[1] Parts of this chapter have been accepted for publication in *Journal für Ornithologie*.

To test whether these differences are acquired in the song learning process, two groups of hand reared chaffinches were exposed to a set of four different songs. The sequencing and the number of repetitions of the songs differed between the two groups. It was predicted that the mean number of repetitions of a song type in the tutee should reflect that of the tutor's, if song acquisition also determines differences in the bout sizes of different song types.

4.2 Methods

Subjects and housing conditions

Birds were taken from the wild at age 5-9 days under license from the Scottish Natural Heritage office (for origin of nests see Appendix 4.1) and hand reared in the laboratory, where siblings were kept together in artificial nests until fledging (see Table 1). Birds from the same nest had the same colour for the left leg ring (orange, black, pink, no ring); subjects' individual identities were coded by a second colour ring on the right leg.

From day 1 in the laboratory birds were separated into two groups which were kept in two different rooms. Group 1 consisted of all the birds from nest orange and nest no-ring. Group 2 consisted of the birds from nests black and pink. After fledging birds from the same nests were kept in the same cage for another two weeks until they started to feed themselves. After reaching independence (at around 30 days of age) two siblings were kept together in a cage (35 x 40 x 130 cm, see Table 1). Day length was controlled by artificial light and automatic time clocks which followed light conditions outside and were adjusted weekly (for details see Appendix 4.2). Water for drinking and bathing was provided, as well as dried and soaked seeds ad libitum. In addition, some live insects and greens or grated carrot were given twice a week.

Table 1: Housing conditions for the period July 1995 - 14.11.1995

	nest (ring left leg)	fledging date	cage	
Group 1 (room 1)	no ring	24.6.1995	1	B4 (blue/yellow), B5 (white/red) + 1 female
	orange	17.6.1995	2	2 females
	- " -		3	B6 (orange-blue/orange) + 1 female
Group 2 (room 2)	pink	1.7.1995	1	2 females
	black	1.7.1995	2	B2 (black-pink) + 1 female
	- " -		2	2 females
	pink		4	B1 (pink-red/blue), B3 (pink-blue/yellow)

From 14 November 1995 males were housed individually in sound-proof boxes (internal dimensions 76 x 79 x 46 cm) where they remained until moved into outdoor aviaries in the University gardens in June 1996.

Tutor songs

Four songs from four different males, but the same location (Kippo Wood), were chosen as tutor songs (see Fig. 3). All songs were digitised using the SIGNAL sound analysis system (Engineering Design, Belmont), band filtered (100 Hz above and below the highest and lowest frequency measured on the screen) and then averaged in amplitude. The average amplitude for each song was assessed by using enveloped amplitude waveforms. These average values were used to calculate an overall mean. Song amplitudes were subsequently increased or decreased to match the overall mean. In addition, songs were ramped (relative amplitude gradually increased from 0 to 1 over 50 ms) so that switching noise at onset was avoided.

For the playback the songs were re-recorded onto cassette with a Marantz CP430 recorder to give a presentation rate of six songs/min (for song and silent intersong interval durations, see Table 3) and played back via a Nagra DSM amplifier/speaker preset to an amplitude of 60 dB at 1.5 m from the cages for 30 min (i.e. five repetitions of the sequence). For subjects B3-B6 (group 1) this first playback period lasted from 20 July until 14 August with a total of 25 playback sessions between 0830-1000 h and 1600-1800 h. Playbacks for the subjects of group 2 (B1, B2, B3) started one week later and lasted from 26 July until 19 August.

Before each playback session the equipment was brought into the room and playback of song would start approximately 2 min after the tape was switched on and after I had left the room. In March 1996 tutor songs were played back in the sound proof boxes for a period of three weeks once a day with a single Sony SRS A20 loudspeaker and a Sony professional walkman (group 2) or with the sound track of a Panasonic videoplayer (group 1).

Table 2: Tutor program for the two different groups

Group 1 (subjects B4, B5, B6) Song type sequence	# of repetitions	bout duration [sec]	Group 2 (subjects B1, B2, B3) song type sequence
tut1	10	100	tut2
tut3	2	20	tut4
tut4	15	150	tut3
tut2	10	100	tut1
Corsican calls	2 x 5		Scottish calls

Table 3: Duration of tutor songs and silent intersong intervals

song	duration [ms]	silent intersong interval [ms]
tut1	3064	6933
tut2	2927	7073
tut3	2266	7734
tut4	2155	7845

Call tutoring

Nottebohm observed that hand reared chaffinches did not develop raincalls (Nottebohm 1972). In the wild, rain calls vary on a small geographical scale (reviews in Baptista 1990, Bergmann 1993). Both observations suggest that rain calls are learned. To test this hypothesis both groups were exposed to different rain calls. Group 1 was tutored with rain calls and chinks recorded in Corsica (British Wildlife Sound Library, Recording no. 20721, see Fig. 6 for illustration) and group 2 was tutored with rain calls and chinks recorded in Kippo Plantation near St. Andrews (Scottish calls, see Fig. 6). Repetitions of the call combinations were separated by 2 s and were played back 5 times 30 s before and after the tutor song sequence for the last 10 playback sessions in summer 1995 and for all of the playback sessions (n=25) between 25 February and 28 March 1996.

4.3 Results

Figures 3a-c show the song types copied by males of group 2. B1 copied all four tutor songs. Alterations consisted of omitting phrase 3 and the transitional phrase preceding it in type 1, a slight shortening in the last element of the flourish in type 2 and 4, and the change of phrase 3 in song type 4 into a transitional element. B2 copied tutor song 1 and 2. Again, song type 1 is performed without the third phrase and a transitional element of the tutor's is used as the flourish. A third song type consists of the first two phrases of tutor type 3 and phrases 1-2 of tutor song 1 again with the transitional syllable as flourish. This type will be referred to as 31. Bird 3 copied all four song types, but type 4 was hardly ever performed. Song 3 and 4 were not exact copies. In song 3 the flourish differed and in song 4 the transitional element between phrases 2 and 3 is missing. In addition to correct copies of type 1 and 2, this bird also performed a hybrid between types 1 and 2 (type 21), consisting of the first two phrases of tutor type 2 and the third phrase of tutor type 1 plus the transitional element instead of the flourish.

Learning success in group 1 was poor in comparison. Siblings B4 and B5 developed isolate songs (see Fig. 3d). B4's song improved slightly between May and June eventually showing at least some chaffinch like trill structure. Both birds were found to perform continuous song during any of the recording sessions and these songs crystallised and were delivered at very high amplitudes in a highly stereotyped manner (see B5-a and B5-a2 as example) alternating with silent intersong intervals. Only one male (B6) of this group performed any of the tutor songs. In early recordings B6 showed incomplete songs of tutor type 3 and an incomplete hybrid of one phrase each of tutor songs 4 and 1 (see Fig. 3e). In later recordings after full crystallisation song 2 was the only type this subject sung for the remainder of the season.

In the second breeding season in spring 1997 recordings of all males were made, albeit on a less regular basis then in 1996. Analysis of the recordings showed that in 1997, both males B4 and B5 underwent much more prolonged plastic song phases than other males in the aviaries. Interspersed with quiet unidentifiable warbling sequences, each bird developed one song from the tutor program. B4 developed a copy of type 3, B5 of type 1 (phrases 1 and 2 only, see Fig. 3d). There was also a change in B6's repertoire: a hybrid between song types 3 and 1 (see Fig. 3e) showed up occasionally. This song was much shorter and always sung more quietly than song type 2, which remained the prominent song of B6.

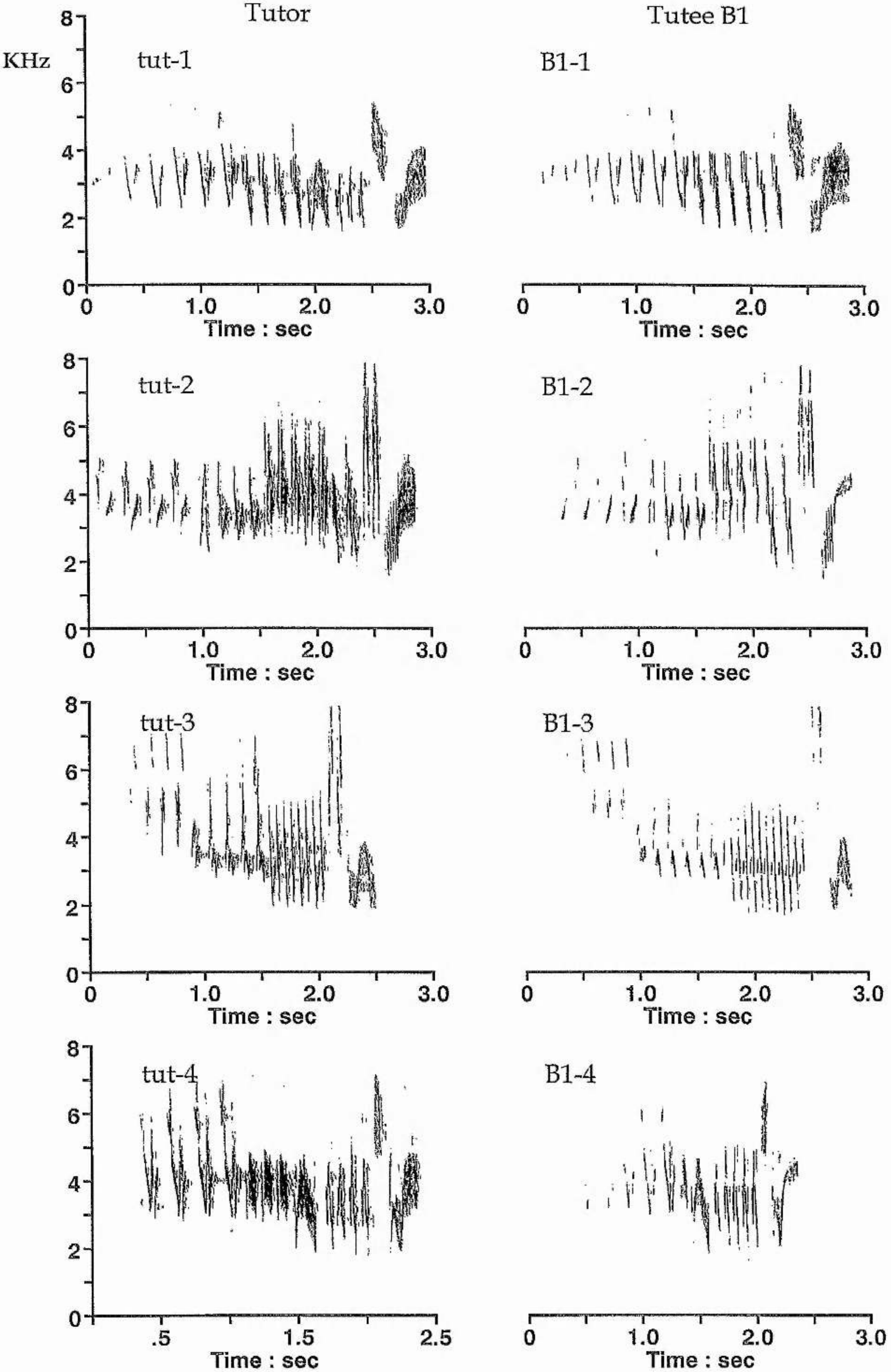

Fig. 3a): Tutor songs (left column) and songs of tutee B1 (right column).

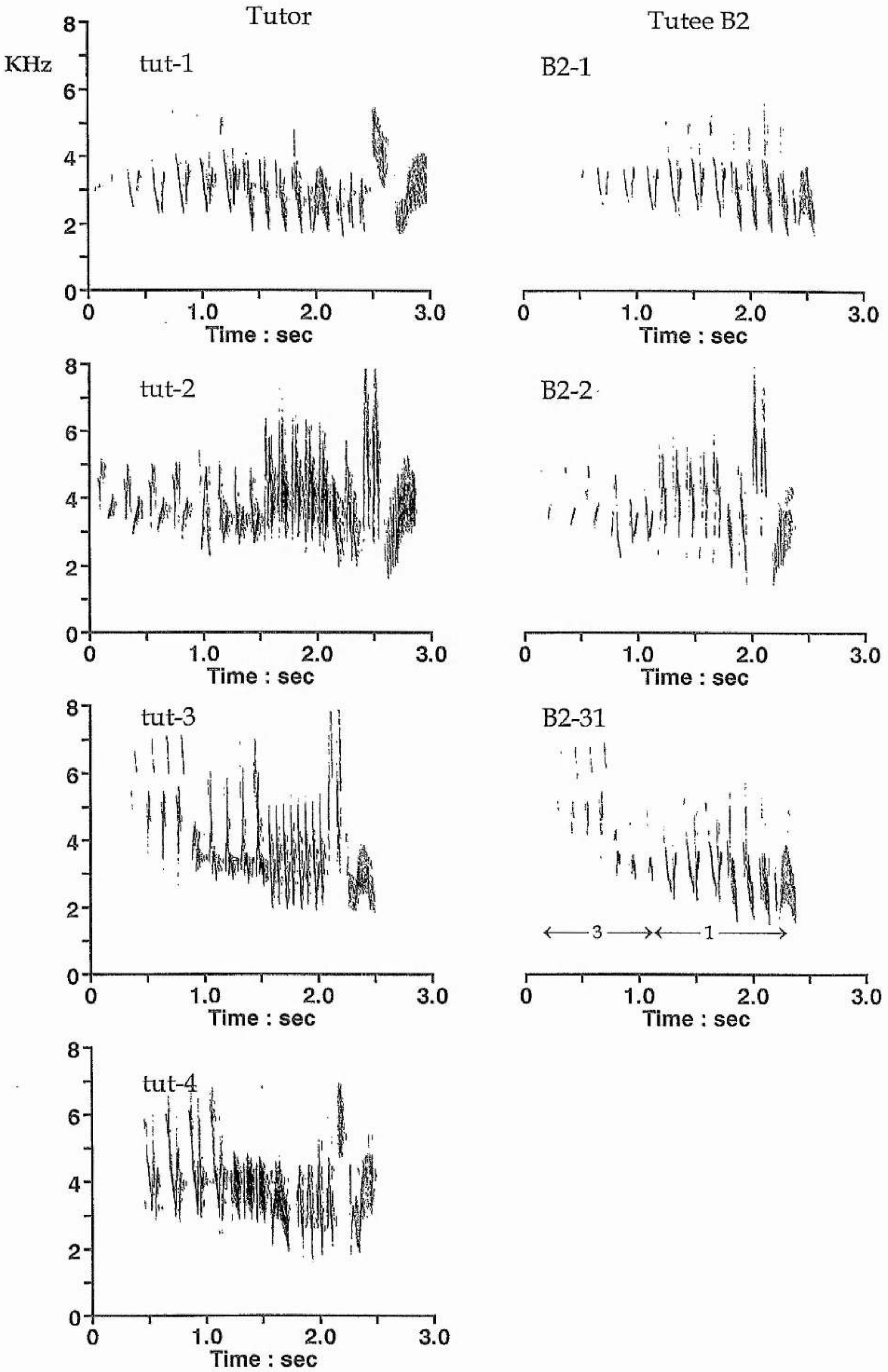

Fig. 3b): Tutor songs (left column) and songs of tutee B2 (right column).

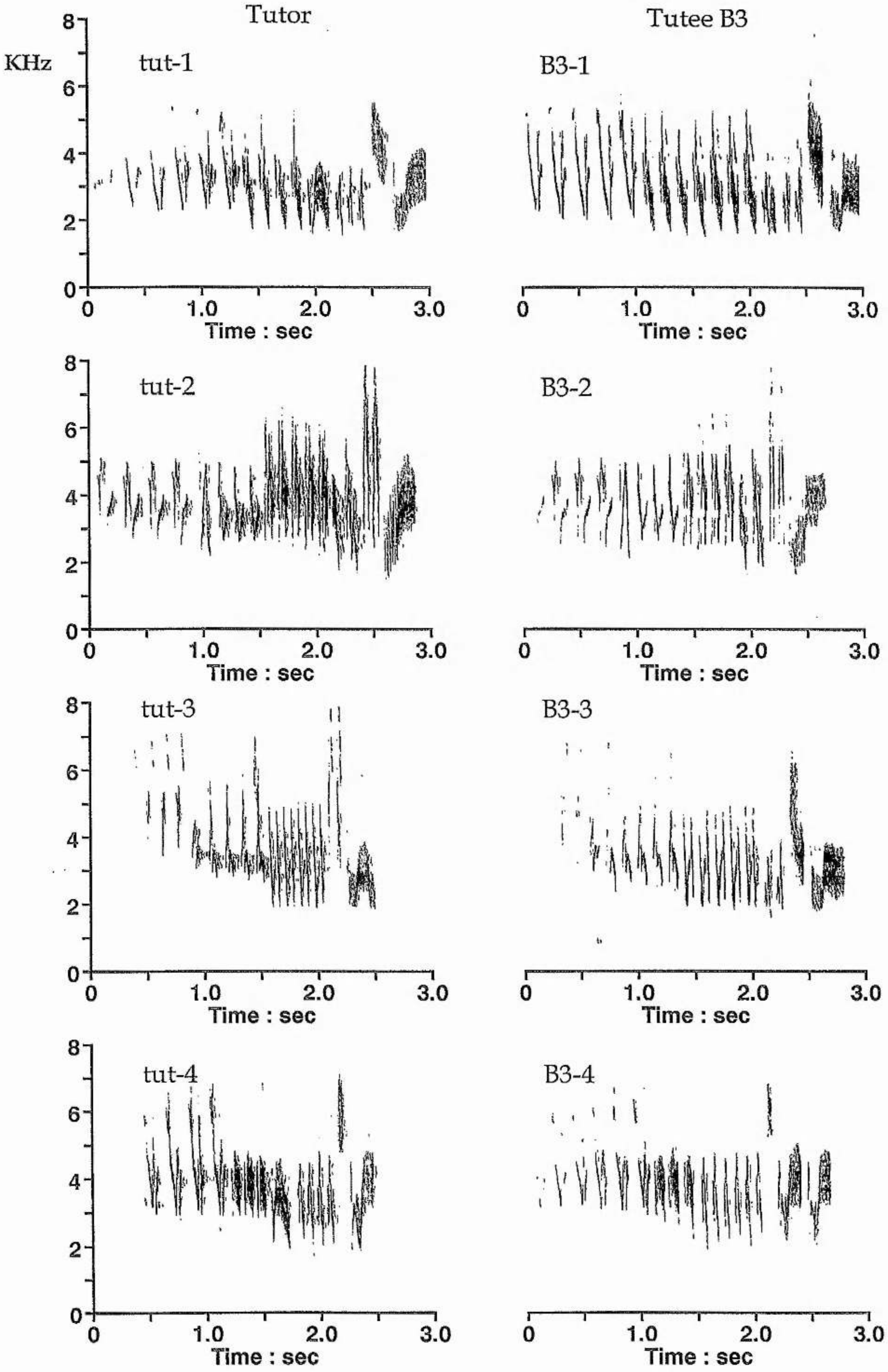

Fig. 3c): Tutor songs (left column) and songs of tutee B3 (right column).

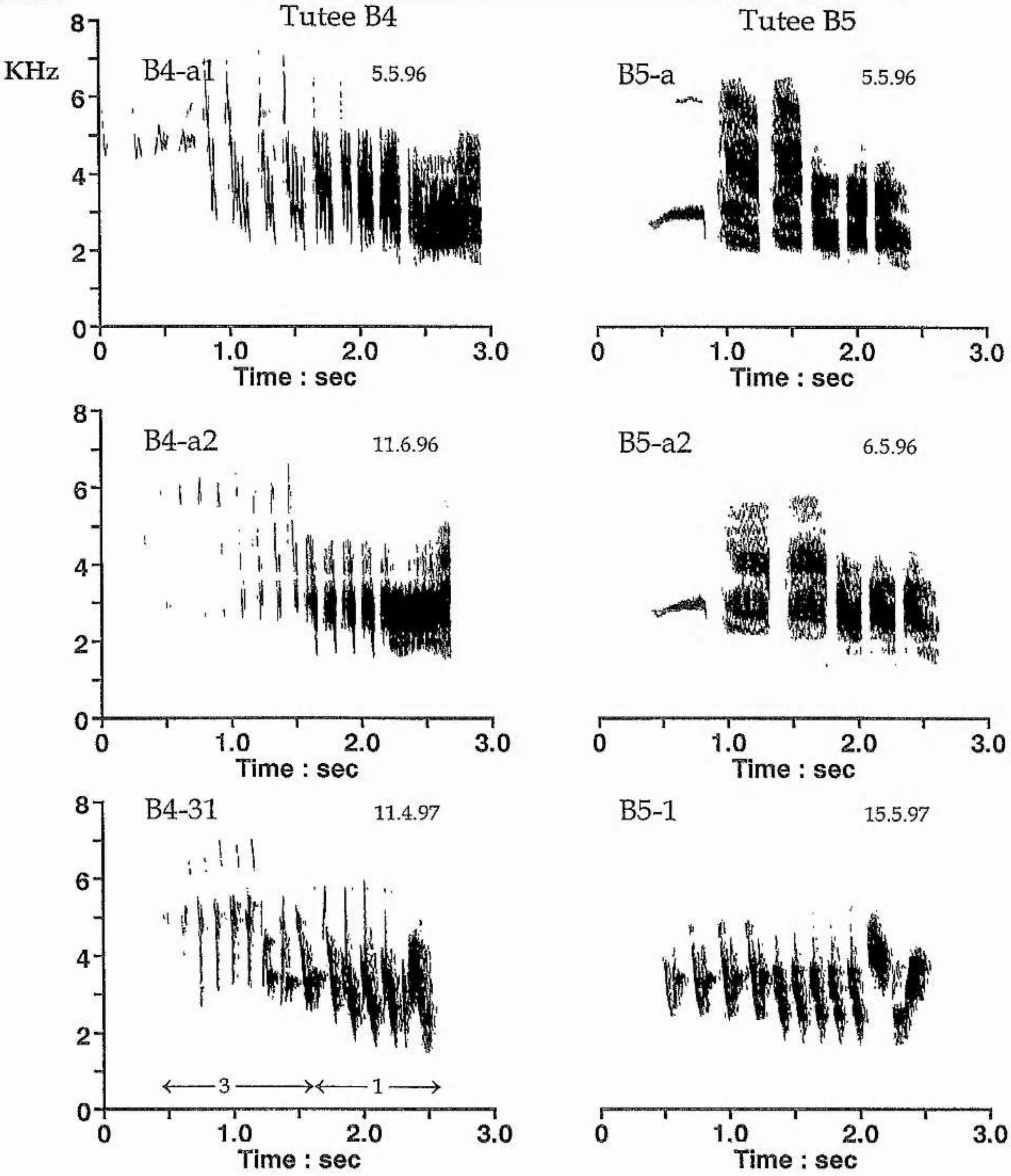

Fig. 3d): Songs tutee B4 (left column) and tutee B5 (right column). Both subjects developed only one isolate song in 1996. However, in 1997 both started singing one song of the tutor program. B4 produced a hybrid of song 3 (phrases 1 + 2) and song 1 (3rd phrase and flourish). B5 performed an incomplete copy of tutor song 1 (without 3rd phrase and without the original flourish).

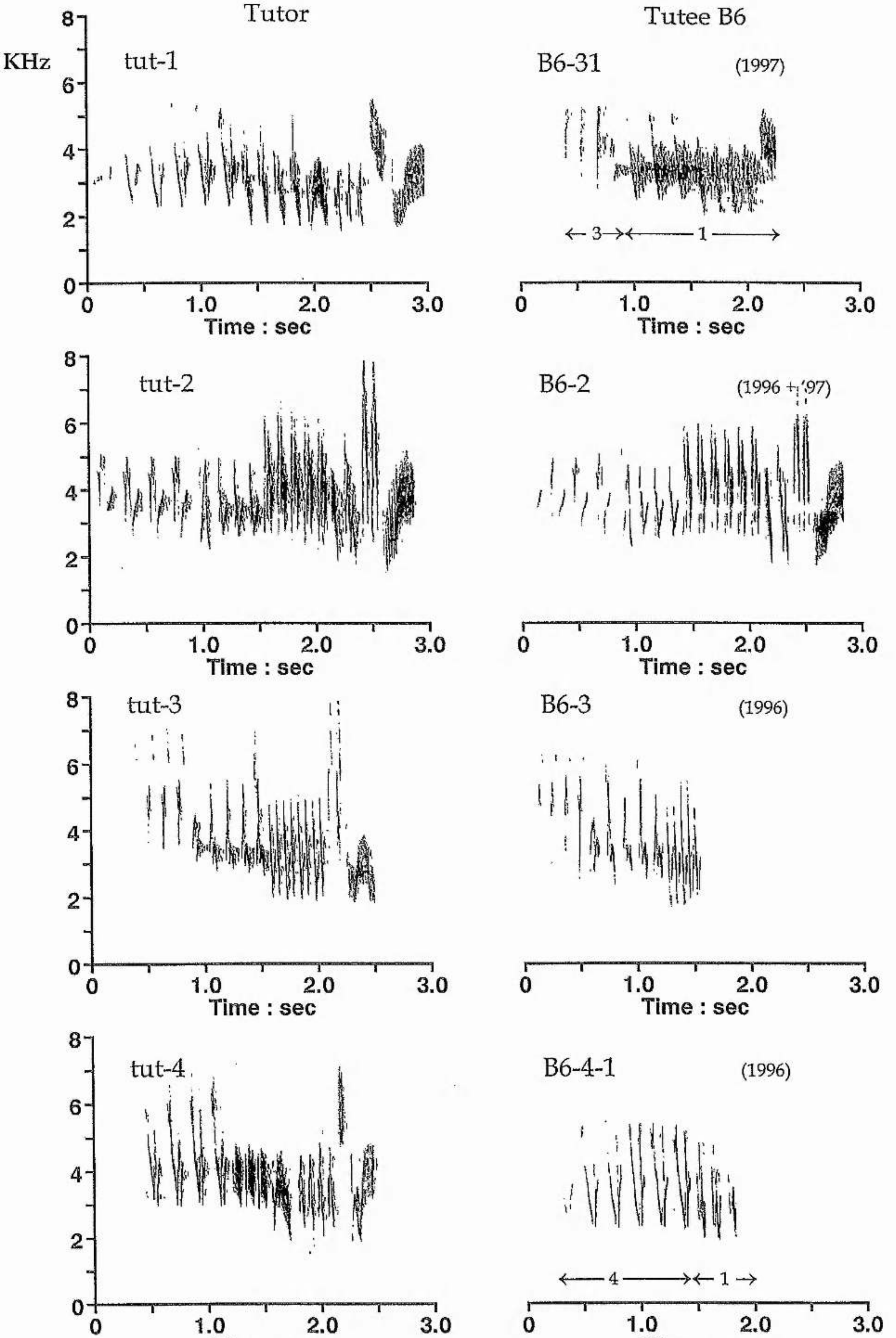

Fig. 3e): Tutor songs (left column) and songs of tutee B6 (right column)

Bout length

There were significant differences between subjects both for bout duration (One-way Anova, $F_{2,344}=42.8$, $p<0.001$) and number of repetitions per song type bout (Kruskal-Wallis H, $\chi^2=48.2$, d.f.=2, $p<0.001$, N=347). Figure 4 illustrates the bout duration and number of song type repetitions for each subject and each song type in comparison to the tutor tape. There is no clear relationship between tutor's and tutee's bout length.

It seems unlikely that the differences between song types are caused by different levels of difficulty as no song type was performed in short or long bouts in all subjects. Within all the variability between subjects it is interesting to note that song type 1 was not copied completely by any of the subjects. All of them failed to copy the third phrase, all stopped after the transitional element following the second phrase and used it as a flourish instead (see Fig. 3).

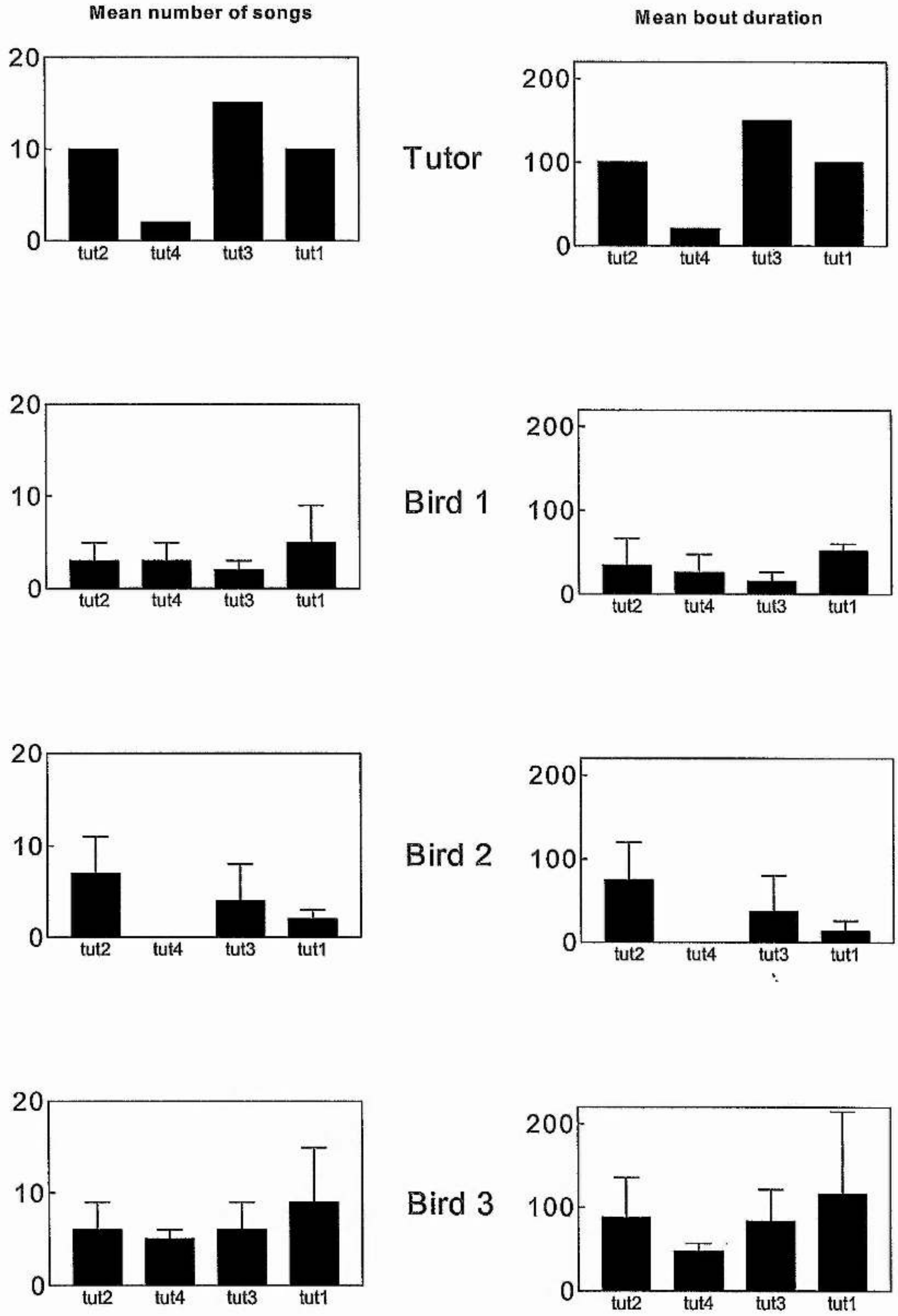

Fig. 4: Mean bout duration [s] and mean number of repetitions per bout for all subjects with more than one song type (number of complete bouts included: B1 n=110, B2 n=97, B3 n=67).

Sequencing of song types

The frequencies of transitions between different song types are illustrated in Figure 5. The framed cells above the diagonal indicate the transitions as played back on the tutor tape. The observed frequencies in these cells were combined and compared with the combined frequencies for all other transitions. Expected values were calculated under the assumption that all transitions should be equally frequent. Expected values were obtained by first dividing the sample size by the number of cells. For the category tutor's transitions (matrix cells framed in bold) this value was multiplied by the number of cells representing the tutors' transitions. Expected values for the category non-tutor transitions were obtained the same way. In bird B1 almost all transitions involving song type 31 went either 3 -31- 1 (n=9) or 1 -31 -3 (n=1). For testing the 31-1 transitions were pooled with transitions from 3 to 1 and those from 1-31 with those from 1 to 3. There were two additional cases which went 4-31-1, rather than having an extra class these were counted as 4-3 transitions as the type actually started with the first phrase of song type 3. The hybrid song type 21 of bird B3 occurred twice in the sequence 2-21-1 and is treated in the same manner for testing (see second matrix in Fig. 5a) and 5c) respectively).

In B1 the cell frequencies were higher for transitions between songs that succeeded each other on the tutor tape (χ^2=49.5, p<0.001, df=1). In B2 with only three song types three out of the six possible transitions matched those of the tutor, but they were not more frequent than the others (χ^2=0.01, n.s.). In B3 two transitions (3-1 and 1-2) matching the tutor's were quite high, but the differences were not significant as the opposite transitions (1-3 and 1-2) were frequent too (χ^2=2.81, n.s.). Sequential analysis in other song birds (Hultsch & Todt 1996) suggests that all first order transitions in either direction are evidence for an associated memorisation. If first order transitions in both directions between sequentially associated tutor songs (2-4, 4-2, 4-3, 3-4, 1-2, 2-1, 1-3, 3-1) are tested against the remaining transitions (1-4, 4-1, 2-3, 3-2) the singing of B3 seems highly influenced by the sequential association of the tutor's songs (χ^2=13.8, p<0.001, df=1).

5a) B1 (n = 110 transitions between bouts)

leading type	following type				
	4	3	31	1	2
2	7	0	0	0	■
4	■	27	2	3	0
3	7	■	10	14	1
31	0	0	■	13	0
1	17	5	0	■	4

4	3	1	2
7	0	0	
■	27	5	0
7	■	27	1
17	5	■	4

5b) B2 (n = 97 transitions)

leading type	following type		
	31	1	2
2	24	2	■
31	■	20	24
1	23	■	4

5c) B3 (n = 67 transitions)

leading type	following type				
	4	3	1	21	2
2	1	6	8	2	■
4	■	1	1	0	0
3	1	■	17	0	1
1	0	13	■	0	14
21	0	0	2	■	0

4	3	1	2
1	6	10	■
■	1	1	0
1	■	17	1
0	13	■	16

Fig. 5a-c): Transitions between song type bouts for tutees of group 2 (Tutor sequence **2 - 4 - 3 - 1 - 2 - 4 - ...**), the bold framed matrix cells above the diagonal mark the expected transitions (i.e. the transitions of the tape tutor). The second matrix for B1 and B3 pooled transitions for hybrid songs with the matching start phrase (i.e. 21-1 pooled with 2-1).

Call copying

In group 2 rain calls and chinks of B2 and B3 clearly ressembled the Corsican version (see Fig. 6). No rain calls could be identified for B1 and its chinks did not resemble the tutor's. In group 1 only B4 developed a rain call. This call and the chinks of all subjects match the Scottish more than the Corsican tutor.

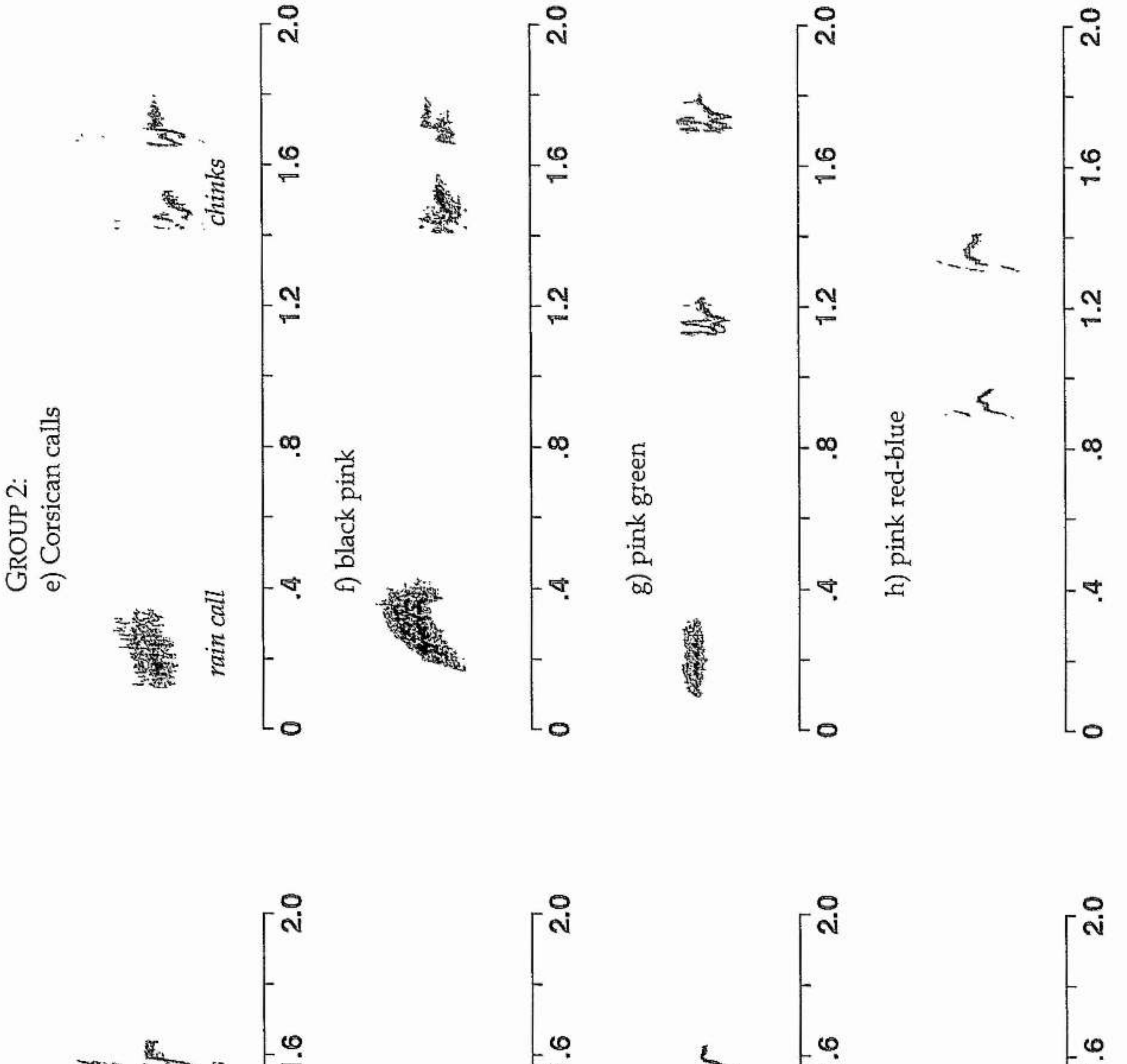

Fig. 6: Rain calls and chinks Group 1 (left column) and Group 2 (right column).

4.4 Discussion

For those subjects that developed more than one song type from the tutor program no evidence could be found that the number of repetitions or mean bout duration were copied from the tutor. There was great variability within and between subjects just as observed in the wild birds (see Chapter 3). As all exposure to song in these subjects was controlled it seems likely that the number of song type repetitions was developed by each bird individually. If findings in this small sample can be generalised at all, some interesting comparative questions arise. In the nightingale tutor sequencing, song type spacing, and context influence performance in adult birds (reviewed in Todt & Hultsch 1996), but also an increase in frequency of repetitions increased the repetition rate in this versatile songster (Hultsch 1991). Results obtained here suggest that in the chaffinch number of repetitions in the tutor does not influence the number of repetitions in the tutee. In order to know whether similarity in singing style or phylogenetic distance predicts similar effects of memorisation on later performance more comparative studies are needed. But at least one (B1) of the three subjects copying several song types also copied the sequencing of the song types and it seemed to be clearly influenced by the tutor in a second bird (B3). As the number of birds with a sufficient number of song types was very small, no conclusions can be drawn before data for more birds are available, but the data here suggest an influence to be likely.

Some interesting observations on plasticity of song development were made. Altogether three out of the six birds showed changes in their repertoires between the two years. One subject (B6) showed precursors of the other song types before song was fully crystallised, but not thereafter. This shows that songs were memorised but not incorporated in the subject's performance. Furthermore, a new phrase combination forming a hybrid song could be observed in the second year. Subjects B4 and B5, the two siblings that only sang isolate songs in their first breeding season in 1996, produced one song each in their second breeding season in 1997 and these consisted of copied tutor song phrases.

The chaffinch has been described as a species that learns its song in the first year of life only (Thorpe 1958, Slater & Ince 1982), and does not change it subsequently. However, evidence is accumulating that they do show some plasticity over the years. Nürnberger et al. (1989) report changes within one season like dropping or adding songs to repertoires, but there was good evidence that the individuals were first year birds. Goodfellow and Slater (1990) made similar observation in first year wild males but found at least one that sung a new song type in its second year. One could argue that all these cases but the last could be caused by selective attrition (Marler & Peters 1982, Nelson 1992) following overproduction during ontogeny. Marler and co-workers coined the expression action based learning for a possible mechanism controlling the selection (Marler & Nelson 1993, Nelson & Marler 1994). Song types that match songs of adult males with which they interact during development or settling are kept, the others discarded. However, both studies on repertoire changes in the chaffinch (Nürnberger et al. 1989, Goodfellow & Slater 1990) report no clear relationship between the observed subjects and neighbours' songs. Nonetheless, it is quite likely that all the observed changes only included songs that were memorised during the sensitive phase, but not sung as is argued by Nelson (1997) to be a likely alternative hypothesis to learning of new songs at least in some species. The three cases observed here seem to be in line with this idea: all newly arising song types were part of the tutor program. Furthermore, the housing in the aviary meant exposure to at least two wild males that were observed singing nearby, but their song types were not copied. In the chaffinch, only one laboratory case has been reported where all song input was known and where a song was copied in the second year. However, this was a male that had been castrated before maturation. It only developed song after testosterone injections in its second year, and copied two songs from a tape tutor at that stage (Nottebohm 1969).

To summarise, data obtained here, and those in the literature, show that chaffinches can modify their repertoires in their second year, i.e. after what is considered the normal sensitive phase for song learning in this species. However, none of the reported cases so far shows conclusively that songs were newly *acquired* after the first year. Chaffinches copy songs within locations at random (Slater & Ince 1982) rather than maximising their song type sharing with neighbours, thus it is hard to imagine why in this species song learning should continue throughout life. On the other hand, the adaptive value of repertoire changes between years, which are clearly occurring in some other species, for example the canary *Serinus canarius*, (Nottebohm & Nottebohm 1978), are not at all clear either. All this strongly suggests that further studies investigating both the extent of learning later in life and its possible functions are needed.

The call tutoring experiment revealed further plasticity and learning dependency in chaffinch acoustic communication. Not all birds copied rain calls but two clearly copied the rain call recorded in Corsica which was not found in any of the Scottish study sites. This is the first confirmation that the rain call is learned in the chaffinch. Reports on the small scale regional differences between rain calls (Bergmann *et al.* 1988, Baptista 1990) and the fact that they were not developed by handreared birds (Nottebohm 1972) have provided indirect evidence. However, no case has been reported previously of the actual copying from a tutor. This adds further support to the idea that the traditional dichotomy between calls (not learned) and songs (learned) is too simplifying and rigid. The chinks developed by the subjects were clearly individually distinct. However, their matching with the tutor is less clear. Two of the hand reared birds had Scottish chinks resembling the tape tutor, but in this case the tutor matched the calls of the native area. The chinks shown by B2 and B3 were clearly not typical but did resemble the Corsican tutor. Chinks have been reported to be developed by hand reared birds without exposure to tutors too (Nottebohm 1972). This suggests that learning is not crucial for their development but might play a modifying role as seen in the two birds that developed chinks resembling the Corsican tutor. This parallels an interesting finding by Lynch (1996) in males transferred between two New Zealand islands.

Two of the three birds that had been transferred in autumn and were sighted again in the subsequent spring had modified their contact calls towards the local variant.

The observations on call and song development made here have shown that the influence of learning on song type sequencing and call notes would be worth studying further in this and in other songbird species. Both parameters are likely to be important in inter- and intrasexual communication. However, to study the possible function of observed individual differences, the role the song acquisition process plays in modifying or establishing these differences needs to be understood.

4.5 Summary

This experiment investigated whether the number of repetitions in song type bouts of the tutor had an influence on later performance of the tutees. In the three subjects that developed more than one copy of tutor songs, no evidence could be found that the number of repetitions or mean bout duration was influenced by the tutor. There was significant variation within and between subjects for these parameters just as was observed in wild birds (cf. Chapter 3). However, in two out of the three subjects with more than two song types, there was some evidence that their song type sequencing was influenced by the tutor's. Some interesting plasticity could be observed in song development: two tutees that crystallised abnormal songs each developed one song from the tutor program one year later. The call tutoring clearly influenced the vocalisations of the tutees, some chinks and rain calls resembling their respective tape tutors.

Chapter 5

Testing the flexibility of bout length control with single song playbacks

5.1 Introduction

Many hypotheses have been brought forward to explain the functional significance of song type switching and matching (reviews in Nielsen & Vehrencamp 1995, Dabelsteen *et al.* 1996). These phenomena have been suggested to be important in communication between males, used for example to address particular other individuals (McGregor *et al.* 1992), to deceive conspecific receivers on the number of individuals present in a territory (Beau Geste hypothesis, Krebs 1977), to signal levels of aggressiveness (Kramer *et al.* 1985), as a means of delivering graded responses (Krebs *et al.* 1981) or to reduce habituation by the receiver (the anti-habituation or anti-monotony hypothesis, Hartshorne 1956, 1973).

In species in the order Passeriformes that sing with immediate variety (Krebs & Kroodsma 1980) males tend to match song types played back with the same or a similar song out of their repertoire (e.g. blackbird *Turdus merula* Todt 1970, 1975). In Passerine species which deliver their song types with eventual variety song types are delivered in bouts before a switch occurs. In the Western meadowlark *Sturnella neglecta,* the likelihood for switching depends on the number of song repetitions since the last switch (Falls & Krebs 1975). This suggests that singing with eventual variety could decrease the potential for immediate song type matching in countersinging contexts (i.e. if a bird just switched from song A to B, it is perhaps less likely to switch immediately back to A than it would in another sequential position). This points out the importance of proximate constraints not only acting on the acoustic quality of a signal but also stresses the way a species specific song control mechanism can reduce the degree of freedoms in employing and arranging signals in a sequence.

But in contrast to its possible function, the mechanism underlying song type switching has been little studied. This is surprising as the interpretation of observed differences in the singing behaviour in different contexts should be related to base line data in spontaneous singing. Given the great differences between species in song organisation it is rather obvious that song type matching on a song to song basis might be achieved by a species singing with immediate variety but not in a species with a small repertoire in which every song type is repeated a few times before a bird switches to another type. However, a countersinging conspecific underlies the same constraints, therefore one could argue that each individual might switch each time the other switches and so match it. The great variability in bout duration observed in spontaneous singing between individuals (see Chapter 3) makes this unlikely. However, no systematic studies exist on whether spontaneous singing is a predictor for individuals' performances in interactions.

Chaffinches have been reported not to immediately match song types played back to them (Slater 1981) and not to adjust the timing of their song in order to alternate with or overlap playback songs (Marler 1956, Hinde 1958). Investigating spontaneous singing in chaffinches provided evidence that bout length seems to be restricted by an upper temporal limit and that therefore overall bout duration rather than the number of song type repetitions within a bout is responsible for song type switching (see Chapter 3). The data on the chaffinch suggest a motivation based mechanism leading to the externally measurable time window for bout length.

However, playbacks do alter the relative frequencies of song types (Slater 1981), suggesting that the auditory input facilitates motivation for a particular song type. To test this idea further and to obtain an estimate of how flexible this hypothetical motivation based time window is, wild chaffinches were exposed to playbacks of songs out of their own repertoire. If the upper temporal constraint was motivation dependent bout duration should be subject to short term changes. Only single songs of a male's own repertoire were played back, and always from outside the territory, in order to have a single controlled event rather than simulating the continued presence of a conspecific leading to a possible escalation. If changes of motivational levels are influenced at all by external stimuli the playback should either lead to premature and increased switching or increase in bout duration.

5.2 Methods

Individual males were chosen for observation if they showed a high song output and were without vocally active neighbours. The territory boundaries were estimated by observing song post choice and birds were considered as possible experimental subjects especially if their territories were adjacent to open habitat. This was because chaffinches react to playbacks within their territories by attacking the speaker rather than countersinging (Slater 1981). Placing the speaker outside the territory in open habitat not occupied by a territory holder avoids this.

For a potential experimental bird, long continuous recordings were made the day prior to the first trials. Recordings were then screened on a DSP 5500 Kay elemetrics sonagraph to assess the repertoire size and to select a good quality recording of each song type. These songs were digitised in the SIGNAL sound analysis system (Engineering Design, Belmont), band filtered (100 Hz below and above the lowest and highest frequency measured on the screen) then averaged in amplitude. Furthermore, songs were ramped (relative amplitude gradually increased from 0 to 1 over 50 ms) to avoid switching sounds on the onset of songs. Songs were re-recorded on a 1 min loop tape separated by one second in a random order but with equal numbers for each song type. The bird was tested the next day or the earliest day thereafter, weather permitting and provided it was showing song activity.

Playback trials

A Nagra DSM amplifier/loudspeaker was placed outside the territory in open habitat 10-20 m away from the observer and at least 10 m away from the outmost singing post of the territory. Songs were played back from a Sony WM-D6C cassette recorder which was connected to both the loudspeaker and a second cassette recorder (Marantz CP 430) which recorded the playback on one channel and the bird's singing with a Sennheiser Me 80 microphone on the second channel. Single songs were played back to the bird. If the bird kept interrupting singing to fly over to the loudspeaker and did not resume singing but called instead, the loudspeaker was moved to another position. If the bird kept reacting with such strong territorial responses it was discarded as a possible subject. For subjects that reacted only briefly with orienting movements or short interruptions of singing, sessions were continued until a minimum of 10 playbacks of each song type had been presented. Birds were subjected to playbacks either on one or two mornings (for details see Appendix 5.1). Vocalisations were recorded continuously but if singing did not start again within 60 s after a playback the tape was stopped until the bird resumed singing again. After such stops the earliest time for the next playback was after a bird had sung at least two complete song type bouts (assessed by ear). In continuous singing, two playbacks were separated by a minimum of one undisturbed song type bout longer than 1 min. In most cases however this interval was much longer as several bouts and/or breaks in singing separated the playbacks.

Data analysis

The tape recordings from each session were digitised and analysed with Rts/SIGNAL software. Song type bouts were split into three categories a) no playback (NONE), b) bouts with a playback song of the same type as last performed by the subject (SAME) and c) playback song different from the song performed last by the subject (DIFFERENT). Only complete bouts which were preceded and followed by a different song type were used for the NONE category. For all song type bouts exposed to playback the first song after a playback decided whether this bout belonged to the category SWITCH (first song after playback a different song type than before) or NO SWITCH (first song after playback the same type as before). This categorisation only included immediate switches and might therefore underestimate the number of switches caused by the playback.

However, this approach seemed safer than trying to distinguish later occurring switches from switches that were about to happen anyway. For all bouts the number of song types (complete and incomplete), the song type bout duration (from the onset of first song until the onset of the first song of the next type) were measured. For bouts with a playback the time of the playback (as measured from the beginning of the bout), the interval from the onset of the playback song until the onset of the next song of the subject (delay), the number of songs between playback and switch and the interval until the switch were assessed.

Statistical analysis

Tests for normality were conducted with a Kolmogorov-Smirnov One-sample test ($p>0.10$). According to the outcome, statistical tests applied are parametric or non-parametric. All tests were performed with the SPSS statistical package (version 7.5). In those subjects ($n=4$ out of a total $n=7$) where data were collected on two days, bout duration was compared between days. Mean bout duration differed only in one subject between days (t-test, $t=1.45$, $p = 0.028$, d.f.=65). Data within subjects were therefore not split by day, but pooled (see also Chapter 3, where mean bout duration in spontaneous song did not differ between days either).

5.3 Results

Reactions to playback exposure

Latencies longer than 30 s were counted as stops. This value was chosen as prior field observations showed this to be the longest interval that occurs between songs during continuous singing. This cut off point is of course arbitrary, but a survivor function (Fig. 1) shows the distribution of delays to decrease exponentially approaching zero before the 30 s mark. For delays longer than 60 s temporal measurements are lacking as tapes were switched off after this interval in the field. Occasionally, subjects did not switch but stopped singing after a few repetitions of the same song type. These events were also counted as (delayed) stops. Out of $n=268$ playbacks 18 resulted in stops (5 of them delayed). These cases were not included in the analysis. In the majority of cases birds did not switch to another song type (165=66%). About one third of playbacks (85=34%) resulted in an immediate switch. The number of switches differed only in one subject between the SAME or DIFFERENT playbacks (c1: 2x2 matrix χ^2 corrected for continuity, χ^2=29.1, d.f.=1, p<0.001), in all the other subjects there were no differences (χ^2 or Fisher-Exact respectively, all n.s.) For further analysis of the data set another 5 cases (see Table 1 for details) were excluded because the recording quality was not sufficient to assess all analysis parameters, leaving a total of 245.

Table 1: Reactions to playback of single song types

	ALL		SAME		DIFFERENT	
	n	%	n	%	n	%
no switch	165	54.3	79	78.2	86	51.5
switch	85	28.0	16 (-1)*	15.8	69 (-4)*	41.3
stop	13	15.8	6	5.9	7	4.2
delayed stop	5	2.0	-	-	5	3.0
Total	268	100%	101	100%	167	100%

*no. of cases that had to be discarded

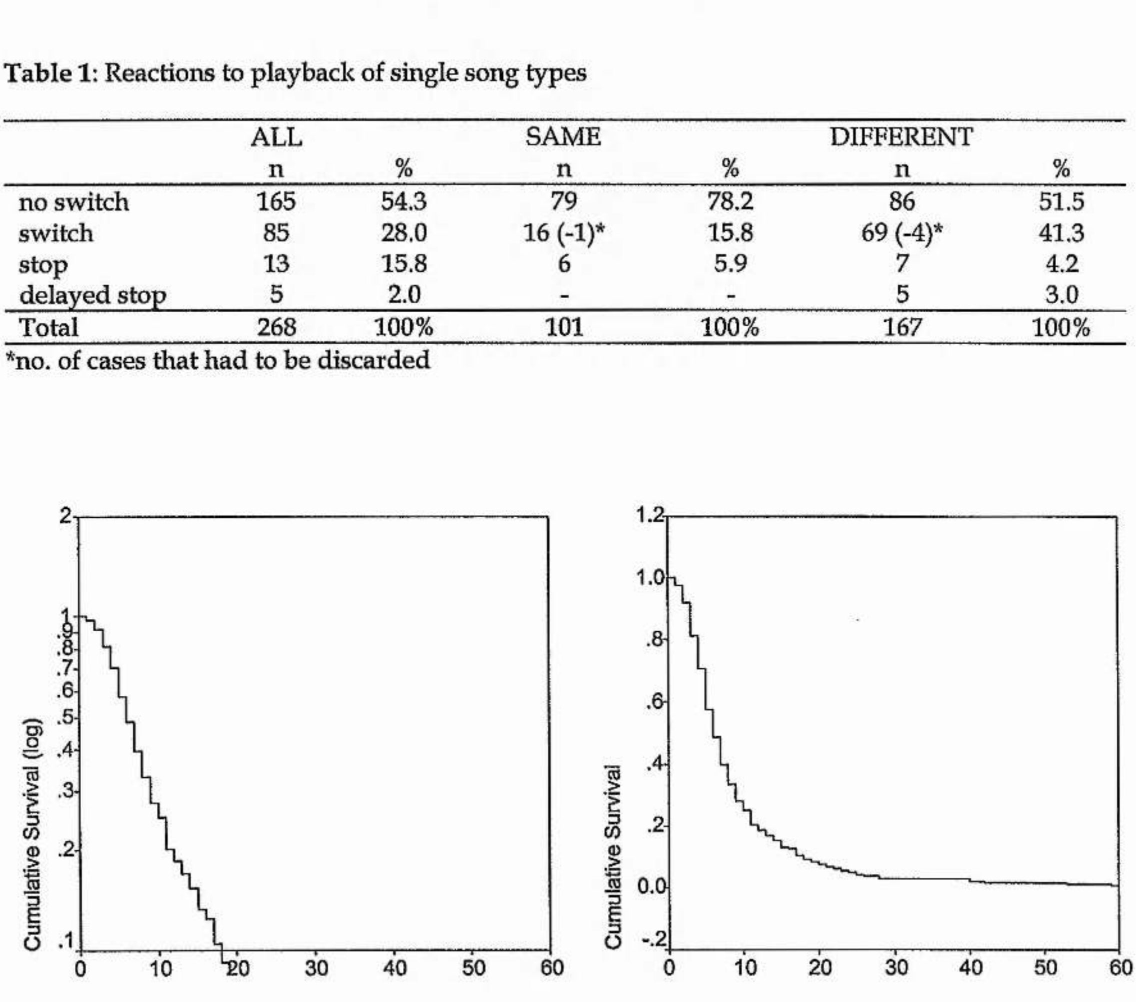

Fig. 1: Interval between onset playback and the subject's first subsequent song plotted as survivor function. Left: cumulative frequency on a logarithmic scale, right: absolute cumulative frequency.

The number of incomplete songs was not significantly different between conditions in all but one subject (c2: Kruskal-Wallis H, χ^2=7.2, p=0.027; all others: n.s.). Playbacks of same or different song types did not result in significant differences in the interval between the onset of the playback and the next song performed in any of the subjects (t-test, all n.s.).

Song rate

Although song rate is likely to be affected by the playback it was not analysed. The main aim of this study was to test whether a playback could lead to short term changes in bout duration thus testing the flexibility of the hypothetical time window. Furthermore, to assess changes in song rate before and after the single song playback is a statistical problem. First, the silent interval within which the playback took place cannot be categorised. Second, the last silent interval within a bout tends to be longer, an effect with more impact if only few songs follow a playback.

Bout duration

Only bout duration rather than number of song type repetitions was considered as this parameter is the more relevant in bout length control (see Chapter 3). Furthermore, both parameters were highly correlated in all subjects (range r_s=0.556-0.919, all p<0.001). To check for additive effects of repeated playbacks, bout duration was regressed on playback number (for those subjects tested on two days only the first day was included). Neither the analysis nor visual inspection of scatter plots revealed any changes over the duration of sessions (range r=0.047-0.285, all n.s.). Bout duration differed between subjects (One-way Anova $F_{6,447}$=30.4, p<0.001) in the control bouts (playback NONE). Four out of seven subjects also showed significant differences between their song types (Table 2).

Table 2: results of One-way Anova bout duration by song type for each subject

subject	repertoire size	d.f.	F	p
c1	3	2, 147	13.9	<0.001
c2	3	2, 23	2.36	0.117
c3	2	1, 54	.24	0.63
c4	2	1, 47	.05	0.83
c5	3	2, 39	22.1	<0.001
c6	3	2, 65	12.7	<0.001
c7	3	2, 60	5.9	0.004

The aim of this experiment was to test whether the single song playbacks had an influence on bout duration. Further analysis was therefore conducted with the difference values obtained by subtracting the appropriate song type mean duration (as obtained in the NONE condition for each song type separately) from the observed bout durations in SAME and DIFFERENT trials. To control for the differences within and between individuals these differences were standardised, i.e. expressed in numbers of standard deviations.

The effect the playback had on bout duration is illustrated in Figure 2 which depicts the grand means for standardised difference values for the three playback conditions. Playbacks lead to an increase in bout duration which is higher in the SAME than in the DIFFERENT condition.

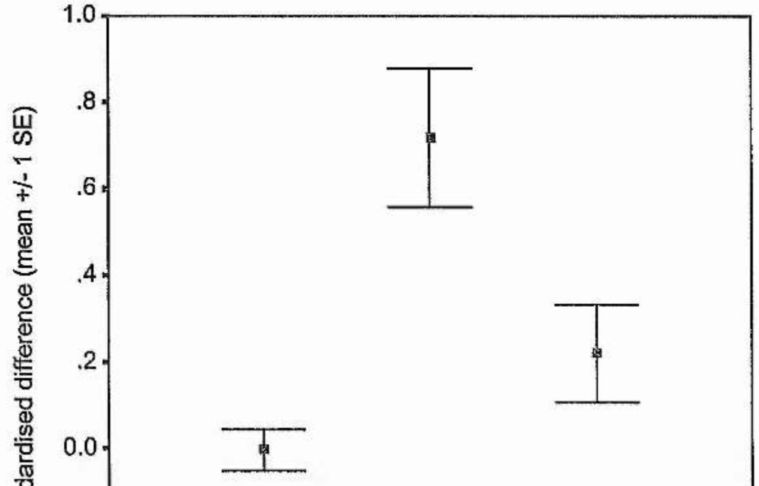

Fig. 2: Mean standardised differences (observed bout duration song $type_i$ -mean bout $duration_{NONE}$ $type_i$ / SD_{NONE} $type_i$) for bouts not exposed to single song playbacks (NONE), to a playback of a single song of the same type (SAME) and of one single song of a different type (DIFFERENT) from the subject's own repertoire.

An Anova in which subjects were nested within playback condition was used for statistical testing. Playback conditions differed significantly (Table 3a) and multiple comparisons revealed all three conditions to be different from each other by pairwise comparisons (protected t-test (Welkowitz *et al.* 1991), all p<0.001). The means for each subject are given in Table 3b, and the standardised differences in Table 3c (for single song types see Appendix 5.2).

Table 3a: Anova with factors playback, bird, song type (Hierarchical Method, song type nested within bird nested within playback)

	d.f.	Mean Square	F	p
(Combined)	10	6.067	4.5	<0.001
playback	2	20.872	15.5	<0.001
bird	6	2.703	2.006	0.063
song type	2	1.352	1.004	0.367
Model	10	6.067	4.503	<0.001
Residual	688	1.347		
Total	698	1.415		

Due to empty cells (number of song types differ), higher order interactions have been suppressed.

Table 3b: Mean bout duration for each bird and each of the three test conditions

	NONE		SAME		DIFFERENT	
bird	mean ± SD	n	mean ± SD	n	mean ± SD	n
c1	44.6 ± 22.7	150	61.6 ± 25.1	23	42.7 ± 27.4	39
c2	78.8 ± 32.3	26	93.2 ± 35.2	19	101.2 ± 42.2	22
c3	70.7 ± 23.5	56	88.4 ± 25.1	17	84.8 ± 22.2	26
c4	57.3 ± 13.1	49	61.0 ± 11.7	4	63.7 ± 14.1	7
c5	74.3 ± 22.4	42	80.2 ± 20.1	9	73.0 ± 23.4	16
c6	60.7 ± 21.1	68	71.4 ± 22.5	12	60.2 ± 20.2	28
c7	35.4 ± 18.3	63	74.1 ± 31.7	10	45.2 ± 30.0	13
Total	55.1 ± 25.7	454	77.2 ± 29.1	94	66.1 ± 34.1	151

Table 3c: Mean standardised differences for SAME and DIFFERENT playbacks

	SAME		DIFFERENT	
bird	mean± SD	n	mean± SD	n
c1	0.60 ± 1.05	23	-0.21 ± 1.36	39
c2	0.56 ± 1.60	19	1.26 ± 1.85	22
c3	0.75 ± 1.04	17	0.62 ± 0.91	26
c4	0.25 ± 0.88	4	0.46 ± 1.05	7
c5	-0.30 ± 1.34	9	-0.15 ± 1.41	16
c6	0.63 ± 0.99	12	-0.13 ± .99	28
c7	2.45 ± 2.69	10	0.03 ± 1.36	13
Total	0.72 ± 1.54	94	.22 ± 1.39	151

Timing of playbacks within song type bouts and switching

There were no significant differences in the temporal positioning of SAME and DIFFERENT playbacks in any of the subjects (t-test, all $p>0.10$). Therefore the differences in bout duration following SAME and DIFFERENT playbacks are not due to differences in the positioning of playbacks. To test whether playbacks that resulted in switches were in different relative positions within bouts than those not followed by switches, I calculated the differences between the position of the playback and the mean bout duration for a given song type (to control for differences between subjects and song types). As a consequence of differences between individual bout durations this parameter was significantly different between subjects (One-way Anova, $F_{6,238}=4.17$, $p=0.001$). To control for these differences this interval was expressed as a percentage of mean bout duration (NONE condition) and this does not differ between subjects (One-way Anova $F_{6,238}=1.34$, $p=0.24$). Playbacks resulting in a switch occur later than those that do not (NoSWITCH mean ± SD = 45.4 ± 8.2, SWITCH = 83.4 ± 11.5, paired t-test, $t=6.1$, $p=0.001$, $n=7$, for subjects' means see Table 4).

Playbacks presented late within a song type bout are of course more likely to coincide with a switch that is about to happen anyway. Therefore all cases were discarded in which the playback occurred later within a song type bout than the observed mean duration for a particular song type in the NONE condition. The differences remained significant (NoSWITCH mean ± SD = 39.6 ± 4.7, SWITCH = 60.4 ± 14.6, paired t-test, $t=3.38$, $p=0.015$, $n=7$).

Table 4: Time of playback (expressed as percentage of mean bout duration) compared between 5cases followed by switches and not followed by switches

	all playbacks				time of playback ≤ mean bout			
bird	n	NoSWITCH mean ± SD	n	SWITCH mean ± SD	n	NoSWITCH mean ± SD	n	SWITCH mean ± SD
c1	29	53.7 ± 37.7	33	69.5 ± 51.4	27	45.9 ± 22.3	23	42.1 ± 33.6
c2	31	56.1 ± 39.8	10	78.3 ± 57.9	26	43.5 ± 28.4	7	46.6± 30.2
c3	38	51.2 ± 31.6	5	88.5 ± 28.2	34	43.3 ± 22.4	4	78.9 ± 21.0
c4	8	37.9 ± 23.4	3	81.3 ± 24.1	8	37.9 ± 23.4	2	68.4 ± 13.2
c5	18	35.2 ± 24.4	7	81.0 ± 19.8	18	35.2 ± 24.4	5	71.3 ± 13.3
c6	31	43.4 ± 31.6	9	78.8 ± 35.5	29	38.3 ± 25.5	8	68.4 ± 18.5
c7	10	40.6 ± 37.1	13	106.3 ± 87.6	9	33.2 ± 30.5	8	47.3 ± 34.4

I continued working with this sample to assess whether the relative influence on bout duration differed for SAME or DIFFERENT depending on the position of the playback. Cases were classified into playbacks occurring in the first half of the interval between the start of a particular bout and the mean duration for this particular song type and in those occurring in the second half of this interval. A comparison between the pooled sample and NoSWITCH cases only (Figure 3a and b) clearly solves the apparent paradox that playbacks lead to early switches and yet increase bout duration. This resulted from a different response to SAME and DIFFERENT playbacks. The increase in bout duration after SAME playbacks is not dependent on the positioning of the playback. DIFFERENT playbacks however a) lead to relatively more switches and b) their bout increase effect depends on the relative position of the playback as becomes apparent if only NoSWITCHES are analysed. The difference between the two categories is significant, (paired t-test on subjects' means, t=7.04, p<0.001, n=7), for the SAME condition there were no differences between the two (t-test, t=1.18, p=0.28, n=7).

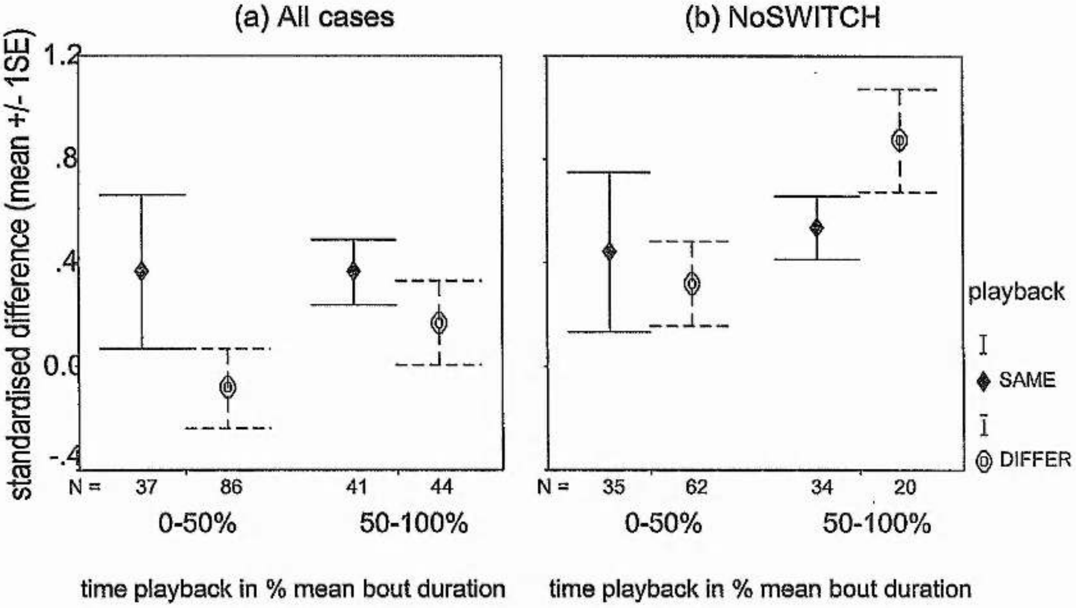

Fig. 3: Mean (± 1SE) standardised differences for song type bouts exposed to a single playback of either the same or a different song type in relation to playback position which is expressed as a percentage of mean bout duration (of each song type).

5.4 Discussion

Male chaffinches responded to playbacks of single song types from their own repertoire with an increase in song type bout duration. A different response towards playbacks of a song type matching (SAME) or not matching (DIFFERENT) the one performed by the subject was observed with a stronger increase for playbacks of the same song type. In general, playbacks early in a bout were less likely to be followed by a switch. However, the relative importance of the timing of the playback differed again between SAME and DIFFERENT, with the latter showing less of an increase if the playback occurred early and more if it occurred late.

The study here was concerned with the proximate causation of behaviour. The data strongly suggest that bout duration is controlled by a motivational component. Its level can rise on a short term basis during performance due to external stimulation, here consisting of playback of a single song. I shall first relate these findings to other playback studies in the chaffinch. Then, I shall compare them with the findings of other playback experiments on species singing with eventual variety.

In a different design from that used here, but also using subjects' own songs, Hinde (1958) played back each song type in a bout of 15 repetitions (separated by 15 s), waited 1 min and then switched to the next type. This was repeated a few times with each subject in each session, the experimental description is unfortunately no more precise than this. Reactions were measured in total number of songs replied during playback. Song types differed in the amount of response they triggered, but the bird's most frequent song type elicited the highest number of songs. The songs replied during playback were described as randomly distributed over the 15 s intervals between playback songs, confirming earlier findings that chaffinches do not temporally co-ordinate counter singing (Marler 1956). Hinde (1958) stressed this point as evidence that playbacks in the chaffinch do not lead to song matching because the bird imitates the song that it hears but as a consequence of a more general facilitation process which favours one of its motor patterns. His argumentation is not quite clear at this point, but I suppose he would have expected a more uniform latency for the 'imitation mechanism'. The facilitation hypothesis seems to be further supported by the findings here, which used a single playback song only and measured the overall duration of bouts rather than the number of songs used in reply. The overall duration of the current bout increased which suggests that playbacks work to facilitate by influencing motivational levels. It is interesting that a single song type was sufficient, as earlier playbacks were continuous and an increase in bout length of the type matching the playback song could have resulted from repeated efforts to match the playback.

More surprisingly, song type bouts also increased in length after playbacks of a different song type, a finding not reported in other playback studies of the chaffinch (Hinde 1958, Slater 1981). If facilitation via auditory feedback is thought to explain the changes in singing behaviour, this increase is perplexing. Only the birds' own song types were played back. On the facilitation hypothesis, a playback should stimulate the matching type and lead to a switch or at least to a decrease in bout duration for the non-matching type. There actually was an increase in switching after DIFFERENT playbacks although the statistical comparison between number of switches after SAME and DIFFERENT playbacks was not significant. This is due to the very conservative approach which took only immediate switches into account. However, switching did increase as indicated by the overall lesser extent to which bout duration increased after DIFFERENT playbacks (cf. Figure 2). It shows very clearly in the comparison between SAME and DIFFERENT in relation to playback positioning (Figure 3a and b), where it is obvious that the early DIFFERENT playbacks lead to a decrease in duration (i.e. switching) in comparison with control bouts. Nonetheless, in particular with DIFFERENT playbacks positioned later in the bout, increases in bout duration were also observed: this cannot be explained by facilitation by a matching song type although this could be an explanation for the increase in bout duration after the SAME playbacks.

It seems that both matching and non-matching playbacks can result in a motivational increase for the song type being performed at the time of the playback. In a model based on competition between alternative motor patterns (Hinde 1958, Slater 1973, Todt 1975, Todt & Wolffgramm 1975, Whitney 1981, 1983) this type would be seen as performed for longer as it remained at a higher level than competing song types for a longer period. In such models, a song type is thought to be inhibited just after performance (for experimental evidence for this inhibition see Todt 1975, Whitney 1985). Such a mechanism could account for the cases were playbacks of different song types did not result in a switch as they occurred perhaps within the interval where the matching song type was still inhibited. However, whether the concept of self-inhibition applies to the chaffinch in this way must be tested first. Also, this interpretation does not provide an explanation for the observation that facilitation by DIFFERENT playbacks was stronger towards mean bout duration than at the beginning of a bout.

Falls and his co-workers conducted a series of studies on proximate causation of bout length and its signal value in Eastern and Western meadowlarks *Sturnella magna* and *S. neglecta* (Falls & Krebs 1975, Falls & D'Agincourt 1982, D'Agincourt & Falls 1983, Falls 1985, Horn & Falls 1988) both of which sing with eventual variety like the chaffinch. *Magna* has a repertoire of 50-100 song types, *neglecta* 5-12. In order to test proximate factors influencing song patterning in the western meadowlark, Falls & Krebs (1975) subjected three males to 2 min playbacks. These were separated by 10 min and played back from inside the territory consisting of 12 repetitions of one of a pool of neighbours' song types. An increased switching rate was observed after playback but no matching of song types. Very interestingly, two out of the three subjects showed a significant increase in bout duration after playbacks, a result which is unfortunately not discussed by the authors, who focus on switching and sequencing only. This is one of the few studies where bout length in response to playback has been measured as duration rather than number of repetitions. Their findings parallel the observation of increased mean bout duration made in this study in the chaffinch. Unfortunately, the follow-up studies both in *magna* and *neglecta* only used number of songs as a measure for bout length (Falls & D'Agincourt 1982, D'Agincourt & Falls 1983), but these further confirmed that playback increased switching. Moreover, they showed that the likelihood for a switch depended on the positioning of a playback, with an increase towards the end of a bout. In this study the authors found bout length of *neglecta* to be normal (as measured in number of song type repetitions) and that of *magna* to be shorter. As switching increased, bouts not followed by a switch must have increased in *neglecta* in order to maintain average bout length and this way would be in concordance with the findings of Falls & Krebs (1975) and also with this study, both reporting an increase in duration for bouts exposed to playbacks.

To test the signal value of bout duration in the Western meadowlark, Horn & Falls (1988) played back long or short song type bouts. The subjects showed no difference in response between the two treatments in number of songs and song rate. However, higher numbers of flights were observed in response to shorter bouts, suggesting a different signal value. It is possible that there were also other more short term reactions which were masked by the design of the playback. Data were collected in a way that is common for playback studies on the communicative function of song. A number of behaviour patterns are recorded for a few minutes before, during and after a playback. With this sort of design it is possible to miss a) short term responses during playback or b) responses occurring after a long delay. In the Carolina wren *Thryothorus ludovicianus*, reactions like approach and inspection of a loudspeaker may occur as long as 45 min after playback of a single song (for examples see Naguib 1995, 1997).

The study presented here further confirms that exposure to a single song can have quite strong and long lasting effects. Another example is a study by Todt (1975) on the European blackbird *Turdus merula*, a versatile singer, in which exposure to single songs can substantially decrease the recurrence interval for that particular type. The results of these different experiments suggest a great advantage of single song playbacks: temporal and sequential relationships between a vocal answer and a previous playback are easier to relate to a single playback event than to long continuous stimulation, where the first, the last or the sum of all the songs could have triggered the response.

Differences in the design make it difficult to compare the results obtained here with the majority of other playback studies which have studied territorial responses by means of prolonged playbacks mimicking intruders. As most of them were interested in the strength of territorial responses, the parameters measured differed and included non-vocal behaviour as well as calls and songs. Still, some interesting comparisons are possible. Studying proximate causes of song type switching in the great tit, Weary *et al.* (1988, 1991) found that song type matching playbacks could lead to recovery of performance parameters that had waned, like number of phrase repetitions within a song and increasing interphrase duration. These results also point towards motivation playing a more important role in controlling bout length than anti-exhaustion (switching to prevent neuromuscular fatigue, Lambrechts & Dhondt 1988). However, in another study song duration remained constant when males were presented with a playback stimulus (Lambrechts & Dhondt 1987).

In the North American song sparrow *Melospiza melodia* song type switching has also been suggested as a graded aggressive response as it correlated with a more aggressive response by subjects exposed to playbacks (Kramer et al. 1985). A more recent study on the same species used interactive playback (Nielsen & Vehrencamp 1995). Shared or non-shared repertoires were presented in three regimes (no switching, synchronised and unsynchronized switching). In contrast to previous findings in this species, the switching rate was not correlated with aggressive behaviour and, if the playback consisted of shared song types which were switched synchronously with the focal bird, they resulted in long bouts of matched type countersinging (as with findings in the blackbird by Todt 1981). This increase in bout duration contrasts with the increased switching rates as a response to playback reported earlier for this and many other species. In the present study every effort was made to keep the acoustic stimulus as distinct from a threatening intruder as possible by using single songs instead of prolonged playbacks and by placing the loudspeaker outside the territory in open habitat. There seems to be a good case for arguing that the playback was indeed not received as a strong threat as a strong territorial response in the chaffinch involves attacks to the loudspeaker rather than song (Slater 1981). My results combined with Hinde's (1958) and Slater's (1981) findings suggest that facilitation via auditory feedback leads to an increase in song type bout duration for playbacks of both the same and a different type, although the latter can also lead to premature switching. The results do not seem to support the idea that switching rate is primarily a graded aggressive signal in the chaffinch.

To summarise, from the results obtained here and the evidence from other studies it seems that song type switching is influenced by short term motivational changes. They clearly show that the time window claimed to be the mechanism to control bout length (see Chapter 3) is subject to motivational influences and therefore a relative rather than an absolute unit. Results support the model suggesting that there is competition between song types (Slater 1978, 1983), but the question of why song types differ in their bout durations and whether this entails a possible communicative function remains open. It seems likely that any potential signal value of song type switching has to be based on a receiver's ability to discriminate between these changes and to the sender's base line, an idea that seems unlikely as individuals differ so much. Rather, the idea that competing song types are activated for motivation based time windows, but also open to short term changes induced by external stimulation, seems to provide a good way of organising a small repertoire with maximal variety and unpredictability. An adaptive consequence of such a singing style on the intrasexual level could be the avoidance of habituation (sensu Hartshorne 1956, 1973).

5.5 Summary

Chapter 3 provided evidence that bout length is subject to an upper temporal limit in the chaffinch. In this experiment the idea that this temporal limitation is motivation based is tested further. Male chaffinches were exposed to playbacks of single songs from their own repertoire. The playback increased duration of the song type bout exposed to the single playback. If the song type played back was different to the song type the subject was performing at the time, the increase was smaller than the increase caused by playback of the same song type. The short term changes induced by the playback show that a switch can be delayed suggesting a motivational rather than a physiological component controlling bout duration. The results support models assuming competition between different song types and facilitation via auditory feedback as the mechanism causing short term changes in motivational levels for specific song types.

Chapter 6

Testing female chaffinch song preferences by operant conditioning[1]

6.1 Introduction

Mate attraction is thought to be one of the primary functions of bird song (Searcy & Andersson 1986, Kroodsma & Byers 1991, Searcy & Yasukawa 1996). Evidence is now accumulating that females choose between different songs in various species, but the song attributes that have been found to be important differ between species (for review see Searcy 1992b, Searcy & Yasukawa 1996). Investigating female song preferences is further complicated by the fact that song in song birds results from a complex learning process, but females of most of temperate zone song birds do not sing making it very difficult to know what exactly they have learned. Clear proof that females have learned song stems from experiments in which they have been induced to sing with hormone treatment (white-crowned sparrow *Zonotrichia leucophrys,* Konishi 1965, chaffinch, Kling & Stevenson 1977, yellowhammer *Emberiza citrinella,* Baker *et al.* 1987). Also females of some species have been shown to respond with higher call rates to tutored than to novel songs (i.e. zebra finch *Taeniopygia guttata,* Clayton 1988, white-crowned sparrow, Nelson *et al.* 1997).

Testing female preferences in the laboratory it is possible to separate song from other mate choice influencing factors like territory quality, and assessing the frequency of copulation solicitation displays in females given oestradiol implants is the most frequently used approach. Using this technique preferences for large versus small repertoires and preferences for home versus alien dialects have been shown in a majority of species tested (Searcy 1992a, Searcy & Yasukawa 1996). However, in most of these studies the females' ontogeny was unknown and in a majority of studies the 'alien dialects' used for stimulus tapes were recorded in great geographical distances to females region of origin to ensure that they had

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[1] Parts of this chapter have been accepted for publication in *Animal Behaviour*.

not heard it before. This way song often stemmed from two subspecies, which leaves the question open whether preferences are due to learned or unlearned biases. If discrimination between home and alien dialects is learned then the home versus alien distinction should be the same as familiar versus unfamiliar in a species like the chaffinch where songs vary considerably in different locations, but where there are no systematic temporal and phonological differences between particular areas (Slater *et al.* 1984). Local variation is thought to arise as a by-product of a small percentage of copying errors during the learning process (Slater *et al.* 1980, Slater 1986, Williams & Slater 1990). Given that such differences arise and that song is known to be a factor in mate choice, it is important to know the extent to which females' song preferences are influenced by early exposure to song. There is some evidence in the zebra finch, where exposure to a live tutor makes females preferentially approach playback of this song over unfamiliar song (Miller 1979, Clayton 1988). Also, in the white-crowned sparrow (Casey & Baker 1992) and in the canary *Serinus canaria* (Nagle & Kreutzer 1996) tutored songs elicited more copulation solicitation displays than unfamiliar songs.

In the experiment described here the influence of early song tutoring on female song preferences was tested by using an old technique as a new tool: Operant conditioning has been widely used in bird song research to test for perceptual thresholds and discrimination abilities (for review see Weary 1992), but surprisingly not for preference tests. The most usual design is a Go-NoGo procedure, in which subjects are exposed to stimuli and depending on stimulus category they either have to perform the operant task or refrain from doing so. Correct performance is rewarded either by food or by the avoidance of time out periods. However, song alone can act as a reinforcer as demonstrated in studies by Stevenson (1967, 1969, Stevenson-Hinde 1973) in the chaffinch. Recently song as a reinforcing stimulus has been taken up in song learning experiments (ten Cate 1991, Adret 1993a, b). The experiment described here tested the suitability of song as a reinforcer in a female song preference test which, in contrast to other laboratory preference test designs, leaves the control over stimulus exposure with the subject. A first experiment tested whether song tutoring during the known sensitive phase for males in this species would influence females' choices in favour of either familiar or unfamiliar songs in their first breeding season. In a second experiment, females were given a choice between unfamiliar songs with and without its terminal flourish, the complex end phrase of each chaffinch song which follows the trill part. Both the trill and the terminal flourish trigger territorial responses in males, but the trill elicits stronger responses (Brémond 1972). However, it is unclear whether this is due to different releasing qualities of the two song parts as suggested by Brémond or to the longer duration of the trill as differences in signal duration were not controlled for. In the red-winged blackbird *Agelaius phoeniceus* another species with clearly two part structured songs, females showed more solicitation displays towards the full song consisting of introductory notes and trill than towards the trill only (Searcy & Brenowitz 1988, Searcy 1990), whereas males show territorial reactions towards both full songs and trill portions only (Beletsky *et al.* 1980, Brenowitz 1982). Searcy and Brenowitz (1988) argue that females should use cues ignored by males as errors in species recognition are more costly to females choosing a mate than to males defending a territory. In line with this, I predict that female chaffinches should prefer songs with the terminal flourish over songs without. As song duration is controlled for in this experiment, observed differences in choices can be directly assigned to the syntactical differences between the two stimulus songs.

6.2 Methods

Experiment 1

Subjects and housing conditions

Subjects were the nine female chaffinches from the handrearing and tutoring experiment described in more detail in Chapter 4. In November 1995 when the young males were moved into sound-proof boxes all females were moved into the same room (see Table 1). Water for drinking and bathing was provided, as well as dried and soaked seeds *ad libitum*. In addition, some live insects and greens or grated carrot were given twice a week.

Table 1: Housing after November 11th, 1995 until May 1996 (all females in room 2)

cage	females
1	pink-pink, pink-white/green
2	orange-purple, orange-green
3	orange-blue/yellow, green
4	black-green, black-red
5	black-white

Subjects experienced their shortest day (8L:16D) during the week from 18.12.95 to 25.12.95 and from then onwards day length was increased by 15 min per week until a daylength of 16 h was reached in April. At this point lights went on at 0640 and off at 2240 both in the housing room and the experimental rooms, in which the Skinner boxes were operational from 0700 until 2200. All females were assumed to be in good breeding condition as they had well developed brood patches, and this was confirmed as they all started laying eggs during the experiment. The 16 h daylength was maintained until the end of the experiments, when they were transferred into outdoor aviaries in July 1996.

Skinner Boxes

Two cages (91x 35x 68 cm), custom built in the university workshops (see Adret 1993b), were used for the experiment. The top and the sides of the cage were wire mesh. Four perches were evenly distributed over the length of the cage. Each cage was placed on a table in the middle of one of two identical rooms (3.60 x 2.50 m base area) evenly illuminated by artificial lights from the ceiling. Thus the experimental set up controlled for possible side preferences caused by cage design or light differences. One end of each experimental cage (see Fig. 2 for illustration) incorporated a loudspeaker (Goodmanns, 15 W, 4 ohms) mounted on a wooden board. The other end consisted of the experimental panel, a metal plate which originally had only two white plastic disks with infrared detection systems. In pilot studies prior to this experiment subjects failed to learn to peck the keys to elicit song, thus confirming the report of Stevenson-Hinde (1973), that this is not a suitable method for chaffinches (although it works well in other species: see review in Adret 1993b). The experimental panel was therefore modified by fixing two short lengths of dowling (7 cm, 0.5 in diameter, subsequently referred to as the experimental perches) to the original pecking disks. If a bird landed on this perch its weight pushed the perch down with a clicking sound. The original pecking disk was thus pushed back thereby interrupting an infrared beam at the back of the experimental panel.

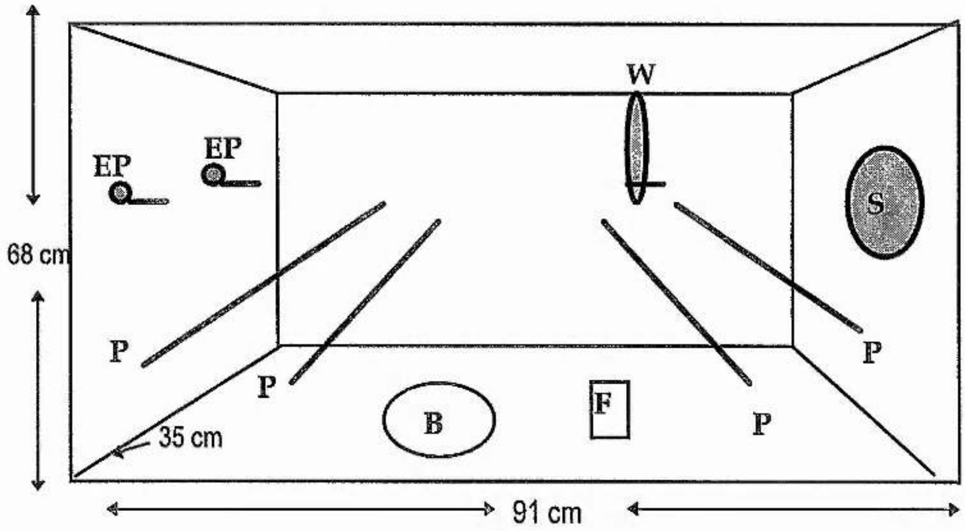

Fig. 1: Sketch of the experimental cage. EP-Experimental perch, P-Perch, B-Bath, F-Food, W-Water, S-Speaker.

Each subject was observed several times a day (from outside the experimental room via a small gap in an obscured window in the door) until the first operant responses were seen. Birds were never observed to sit on the experimental perches. Presumably their shortness, close proximity to a smooth metal surface and sloping angle made them somehow less preferred over the normal perches in the cage. Subjects either hopped onto the experimental perch from the ground, the next nearest perch or by flying over to it. During all observations made subjects left the perch immediately after it had given in to their weight. Triggering the mechanism via the experimental perches switched on a tape recorder (Sony TCM-818) for 15 s. Sound pressure level at the perch opposite the loudspeaker was preset to 56 dB. A computer (Zenith 2-86PC) registered the number of hops per hour on each of the experimental perches.

Stimulus tapes

Three minute cassette loop tapes (type TDK EC 3M) were recorded with songs of a single type falling into one of two categories: one of the four tutor songs from the previous spring (= familiar songs) and songs the females had not experienced prior to the experiment (= unfamiliar songs, see Fig. 2). These songs were from different males and recorded in a forest from which none of the fledglings had originated and where none of the tutor songs had been recorded. As the females were kept without any exposure to conspecific song other than the tape tutors, the assumption that every song other than the tutor songs was an unfamiliar song seemed justified. Unfamiliar songs 1 (U1) and 2a (U2a) were clearly different song types (see Fig. 2); song U2b was the same song type as song U2a, but recorded from another male. Stimulus songs were presented at a rate of six per minute, yielding silent intersong intervals ranging from 4436 to 5345 ms (see Table 2). Preparation of the stimulus songs followed the same procedure as described for the tutor songs (see Chapter 4).

Table 2: Duration of songs used for stimulus tapes (F - Familiar, U - Unfamiliar)

	song F1	F2	F3	F4	U1	U2	U2b	
Experiment 1								
duration [ms]	3064	2927	2266	2155	2719	2635	2642	
pause [ms]	4436	4573	5234	5345	4781	4865	4858	
	song							
Experiment 2	1	2	3	4	5	6	7	8
original song [ms]	2392	2482	2456	2654	2439	2425	2408	2589
flourish [ms]	597	458	708	544	536	465	613	897

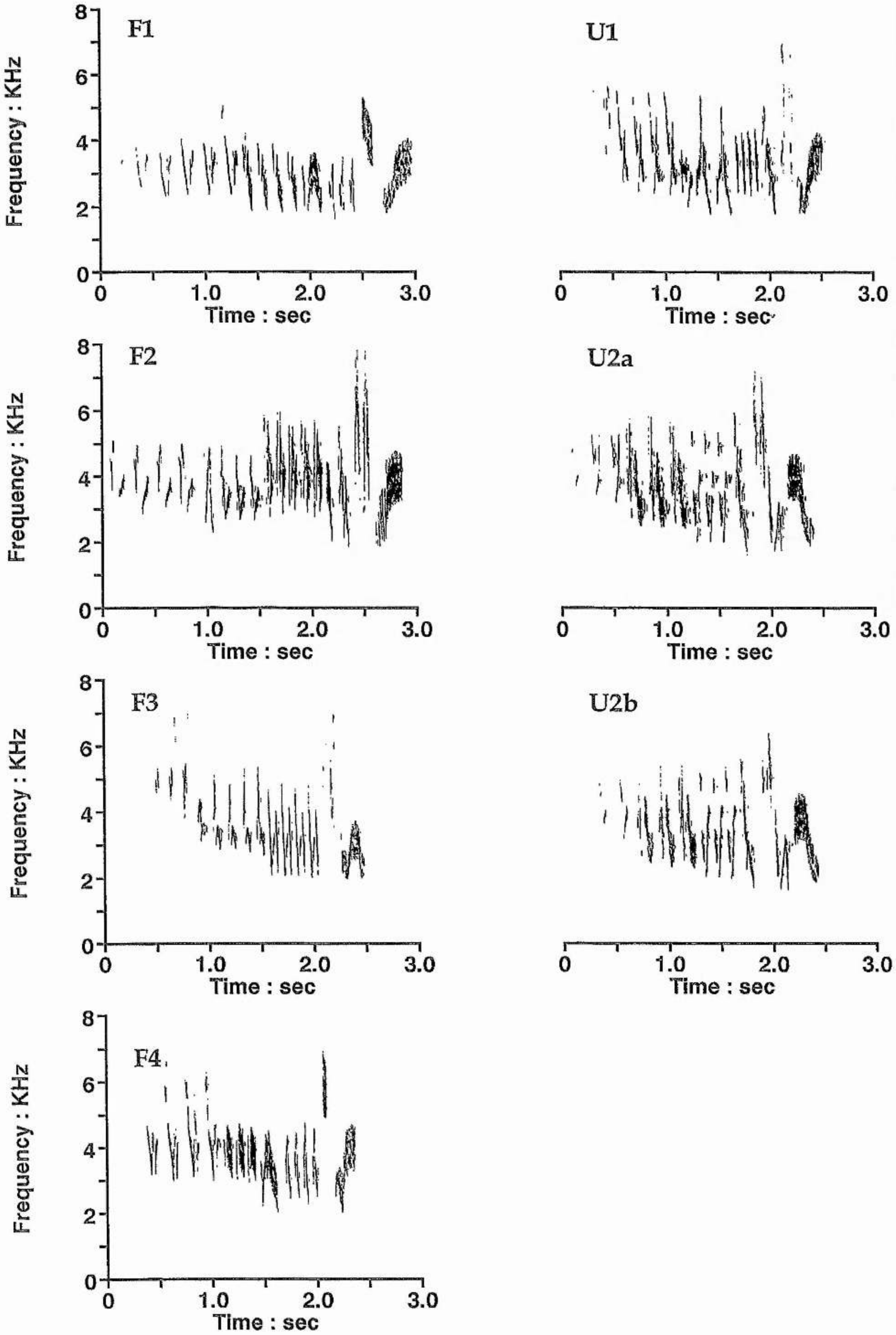

Fig. 2: Sonagrams of familiar songs F1-F4 and unfamiliar songs U1, U2a and U2b.

Testing procedure

Females were caught and placed in one of the two experimental cages and returned to their home cages at the end of each trial. On average birds spent 29.9 h in the experimental cage (range 9 - 78 h) with an intertest interval of 7.5 d ± 2.9 SD (between trial 1 and 2: 8.5 ± 3.7, trial 2 and 3: 7.5 ± 2.3, trial 3 and 4: 6.6 ± 2.5). Each trial consisted of a choice between one familiar and one unfamiliar song, assignment of each to the left or right was randomised, but in total there was an equal amount of exposure on each side for each category (see Table 5) and each of the two experimental cages in the two rooms. During trials birds were provided with water, as well as dried and soaked seed *ad libitum*.

Experiment 2

The same subjects as in the first experiment (carried out the previous year) were used except for one female (pink-pink) which had died during the winter. Subjects had spent the time since the end of the first experiment in July 1996 in outdoor aviaries where they were kept with males from the same hand reared generation. On 16 March 1997 the females were caught and moved from the aviaries back indoors into the same room as the previous year, where they were kept individually in laboratory cages (40x 40x 150 cm). Between 16 March and 25 April daylength was increased to 16L:8D (lights 0830-2430 hrs). After a settling in time of 4 weeks the first two females were moved into the experimental cages on 11 April.

Stimulus tapes

Eight different song types were picked from recordings made from two different woods outside St. Andrews after comparison with tutor songs, their male companions' songs and song types recorded in the university gardens revealed no similarities between stimulus songs and songs females had experienced before. Stimulus songs were sampled and digitised with SIGNAL software as described for experiment 1. With aid of the sound editing facilities of the program two new manipulated versions of each song were produced: a) NoFLOURISH had the terminal flourish deleted and b) FLOURISH was the same song with the terminal flourish but shortened by the duration of the flourish by deleting part of the first phrase (for examples see Fig. 3). Original song duration varied between 2392 and 2654 ms, flourish duration between 458 to 897 ms (see Table 2).

Experimental procedure

The experimental procedure was very similar to the one in experiment 1, but with the following changes. The same experimental panel was fixed on the rear wall end of a normal housing cage, which had bars at the front side only. This cage was identical to the ones in which the females were kept when not being tested in an effort to reduce settling in times. 10 min after lights went on in the morning, the females to be tested were moved in one of the two experimental rooms. Each bird remained there several days with the panel switched on between 0900 and 2200 (lights 0830 to 2430). Every morning at 0850 food and water were exchanged and the test stimuli swapped between left and right side. To compare females' preferences between the two tapes the two consecutive days of highest response were compared (see Fig. 6 and Table 6). Possible side preferences were accounted for by the tape swap between the sides and preferences could be assessed by simply comparing relative frequencies. Three females were tested a second time (see Table 3 for dates). Two had not started triggering the tape the first time they were placed in the experimental cage and one (black-green) had to be re-tested after the first trial was interrupted for technical reasons.

Table 3: Experiment 2 - schedule

subject	start date	stimulus	room
orange-green	11.4.1997	1	1
green	1st 11.4., 2nd 21.5.	2	2, 1
black-green	1st 18.4., 2nd 29.5.	3	1, 1
black-red	21.4.	4	2
pink-white/green	2.5.	6	1
orange-blue/yellow	7.5.	8	2
black-white	15.5.	7	2
orange-purple (no learning)	1st 29.4., 2nd 9.6.	5	1, 2

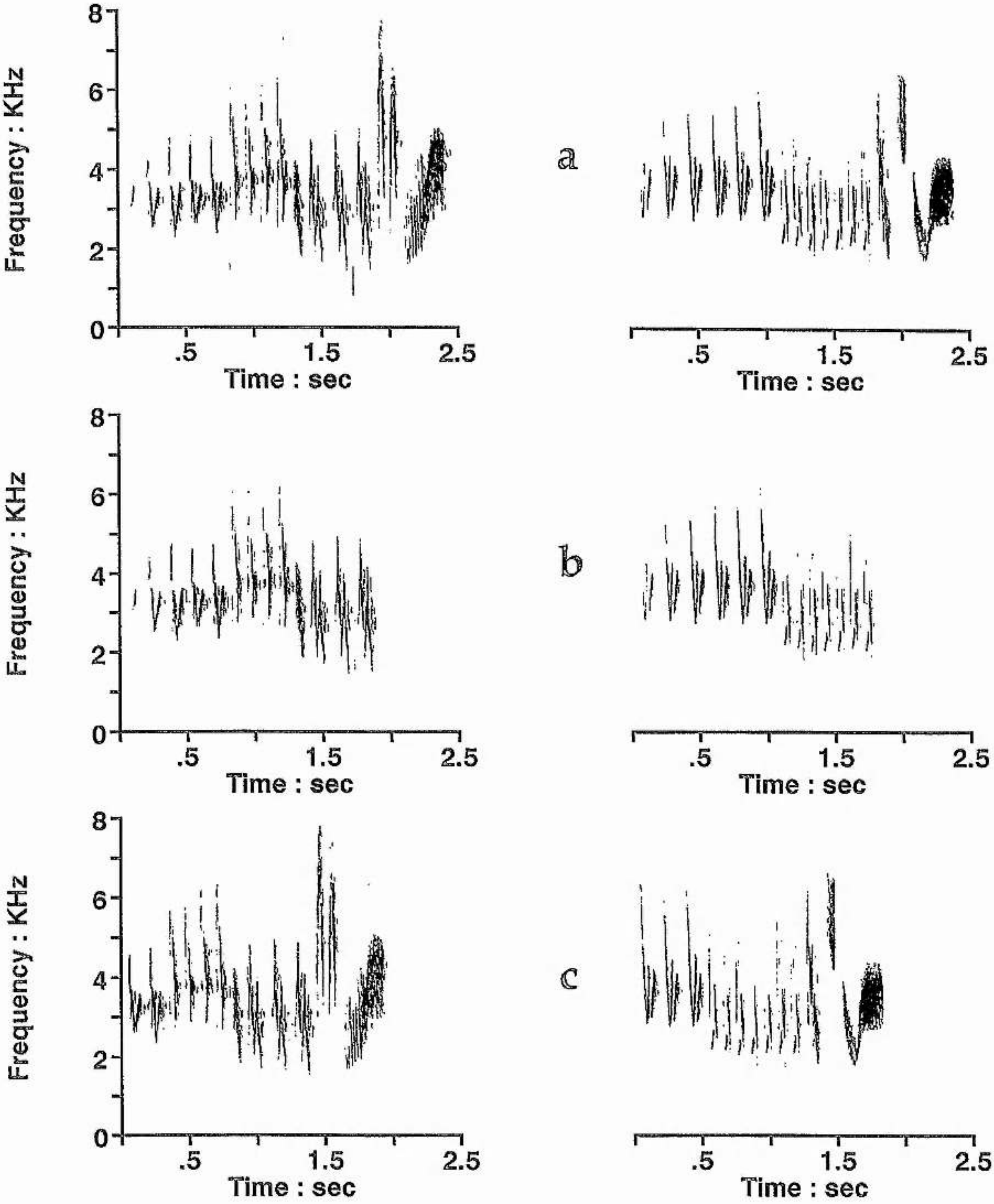

Fig. 3: Examples for song manipulation in experiment 2.
a) original song, **b)** NoFLOURISH, flourish has been truncated, **c)** FLOURISH, song with flourish, but beginning shortened by flourish duration.

6.3 Results

Experiment 1

Eight of the nine females learned to trigger the tape and continued to do so over the four trials. Female black-white did not learn to trigger the tape by perch hopping and is subsequently excluded from the analysis. Subjects varied substantially in the number of times they triggered songs, their activity hours and the time they needed to learn the task (see Figs. 5 and 6). Some birds learned very fast during the first trial and mastered the operant task while others did not. For these two reasons subjects were not tested for a standardised time. Instead they were left in the experimental cages until multiple triggering occurred in a series of hours. However, birds that did not show any or few responses were taken out of the Skinner Box after 3-4 days in order to keep variation for inter-test intervals low.

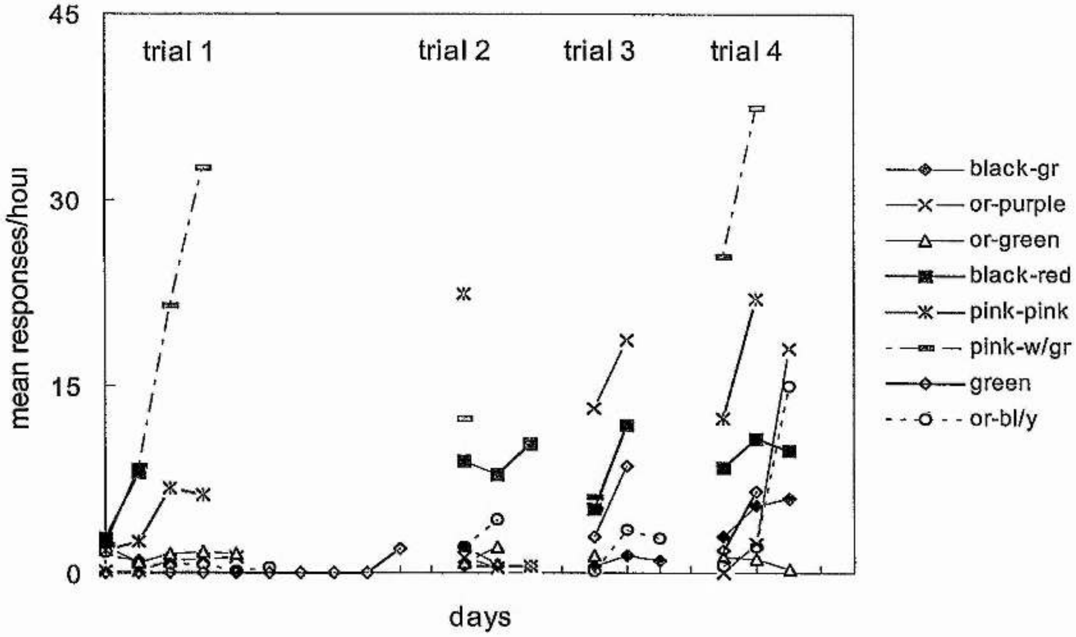

Fig. 5: Mean responses/hour in trials 1-4 for the eight responding subjects.

No habituation could be observed over the four trials, but instead subjects showed more perching in trial 4 (see Table 4, Fig. 6) than in trials 1, 2 or 3 (Friedman two-way analysis of variance by ranks, Fr = 13.28, $p<0.01$, multiple comparisons (Siegel & Castellan 1988) differences between rank sums larger than critical difference R1-R4, R2-R4, R3-R4: $|Ru-Rv|>13.62$, $p<0.05$; all other comparisons: $|Ru-Rv|<13.62$, $p>0.05$).

Table 4: Perch hopping rate (number/hour)

Female:	Trial: 1	2	3	4
pink-pink	3.9	33.7	5.1	12.5
pink-white/green	13.1	17.5	5.9	20.6
black-green	1.2	1.5	1.1	4.6
orange-purple	0.7	0.5	5.0	5.3
orange-blue/yellow	0.6	2.3	3.5	4.7
black-red	4.5	9.8	7.3	11.2
orange-green	1.6	0.3	1.7	1.0
green	1.0	0.7	3.3	3.8
black-white	0	0	0	0

Details of the number of choices for each side and song for all four trials for each subject are given in Figure 6 and in Table 5. Most subjects exhibited a side bias as expressed by very high or very low values for the ratio between left side and total choices (see Table 5), although the experimental set up controlled for symmetry in the apparatus and the experimental rooms. Furthermore, the design was balanced by presenting familiar and unfamiliar songs on different sides at each trial. However, during the course of the experiment it became evident that individual females were either preferring single song types or sides independently of category.

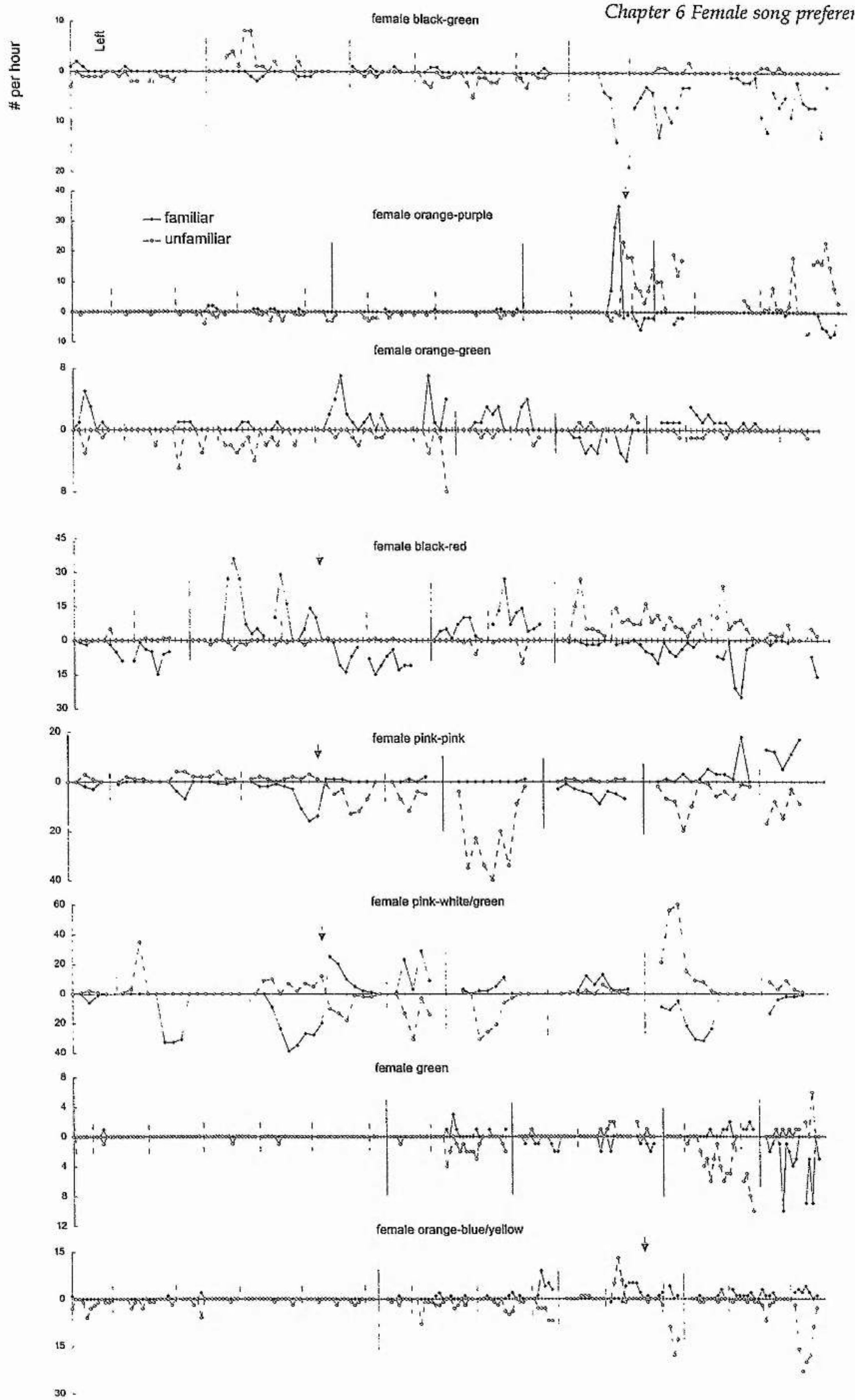

Fig. 6: Number of tape triggering per hour, trials 1-4 separated by solid vertical lines (dashed vertical lines = nights), arrows indicate tape swaps between sides.

Table 5: Absolute numbers of choices for each side and song type for each subject, trials 1-4 and duration of trials. The sequence of cage numbers given beneath each female's name indicates the experimental set up used in the trial sequence 1-4.

Female	Trial 1		Trial 2		Trial 3		Trial 4		Trial 1-4	
	L/R choices	[h]	L/R choices	[h]	L/R choices	[h]	L/R choices	[h]	L/ total	F/ total
pink-pink	U1/F1	16	F4/U2B	9	U1/F3	10	F2/U2A	17	.24	.36
cage 2-2-1-2	40/72		1/201		5/41		93/120			
pink-w/green	U2A/F2	29	F3/U1	9	F4/U2B	10	U1/F1	17	.47	.50
cage 1-1-2-1	95/286		23/89		41/12		195/156			
black-green	F3/U1	18	U2B/F2	36	F4/U2A	32	U1/F1	34	.11	.77
cage 1-2-1-2	5/16		10/43		7/29		7/148			
orange-purple	F4/U1	61	U2B/F1	44	F3/U2A	15	U1/F2A	31	.77	.37
cage 1-2-1-2	10/32		17/5		70/5		136/28			
or.-blue/yel.	U2A/F3	78	F4/U1	44	U1/F2	15	F1/U2B	31	.25	.36
cage 2-1-2-1	2/48		33/67		27/2		35/110			
black-red	U1/F1	16	F4/U2A	44	F3/U1	18	U2B/F2	41	.65	.53
cage 2-1-2-1	64/8		194/131		122/9		263/196			
orange-green	F3/U1	61	U1/F2	49	U2B/F1	13	F4/U2A	24	.35	.60
cage 2-1-1-2	46/53		1/16		5/17		17/6			
green	F4/U2B	34	U2A/F1	40	F3/U1	24	U1/F1	16	.20	.41
cage 2-2-1-1	8/24		10/17		10/70		13/48			
black-white	U2B/F3	16	F2/U1	49	U2A/F1	34	F4/U1	40	-	-
cage 1-2-1-1	2/0		0/0		0/0		0/0			
Mean duration		36.5		36		19		27.9		

To see whether the side bias was completely overriding any preferences five subjects were subjected to a tape swap between the two sides within trials (see Fig. 6, vertical arrows). Two females kept on triggering one song more often even after the sides had been swapped (black-red, orange-blue/yellow). One showed a tendency to alternate between sides and both sides are triggered almost equally often before and after the tape swap, with the song preferred before the swap being slightly higher just after the swap only. Another two kept triggering the preferred side more often after the swap had taken place (orange-purple, pink-pink). The side bias was taken into account by calculating an expected ratio between choices for familiar and unfamiliar instead of assuming a ratio of 0.5 which would have been the value under the assumption of no side bias. For each subject the total number of choices to each side was divided by the grand total, so giving a proportion to the left and to the right. These proportions were multiplied by the total choices in a given trial to obtain the expected values (fe) for left and right choices within that trial. These expected frequencies were subtracted from the observed frequencies (fo) and summed over all four trials to form one difference value between choices for familiar and unfamiliar songs for each subject:

Σ trial 1-4 [(fo familiar- fe familiar) - (fo unfamiliar - fe unfamiliar)]

Having obtained this difference value for each bird, a Wilcoxon's signed rank test was carried out. This showed no preference for familiar over unfamiliar songs (T+=24, p=0.46, n=8, 2-tailed). The data points obtained after tape swaps within trials were not included in this calculation.

Song types

No indication could be found that any of the song types was consistently chosen as the preferred song by all the females. In order to reveal whether some songs were more motivating to females in general, mean choices per hour were compared by an analysis of variance. There were no differences across song types (One-way Anova, $F_{6,49}$=0.78, p=0.55, data log transformed, SPSS Version 7.0, only first exposure to U1 included). As song duration has been shown to influence females' preferences in other species, the duration of each song type was correlated with the overall mean of each bird's mean choices per hour as obtained from the eight responding subjects. No correlation was found between song duration and mean number of choices (r_s=0.643, p=0.119, n=7, 2-tailed).

All subjects had the unfamiliar song type U1 presented in two trials (combined with a different familiar song) and U2 in two versions (U2a and U2b, same song type, but recorded from two different males). Table 6 lists the choices made during first and second exposure to these two different song types. No clear trend is recognisable if these choices are compared with the expected frequencies for a particular side in a particular subject as calculated above. Song type U1 was preferred by five females during the first exposure, but only by three females at the second exposure. U2 was preferred by two different females each during first and second exposure.

Table 6: Comparisons between choices made during the first and second exposure to song types U1, U2a and U2b. ("+" song preferred, "-"unpreferred, "=" no preference after comparison with corrected expected value, $\chi2 > 3.84$, $\alpha = 0.05$)

subject	U1 1st	U1 2nd	choice repeated	U2 1st	U2 2nd	choice repeated
pink-pink	+	-	no	+	-	no
pink-white/green	+	+	yes	-	-	yes
black-green	=	-	no	-	+	no
orange-purple	+	+	yes	=	-	no
orange-blue/yellow	-	+	no	-	+	no
black-red	+	-	no	-	=	no
orange-green	-	-	yes	-	-	yes
green	=	-	no	+	-	no

Experiment 2

Seven out of the eight females learnt to trigger the tapes. The time spent in the cages before they started to trigger the tapes was much longer in this second experiment (compare Fig. 5 plotted in hours and Fig. 6 plotted in days). However, once the birds started to respond, the learning curves were much steeper.

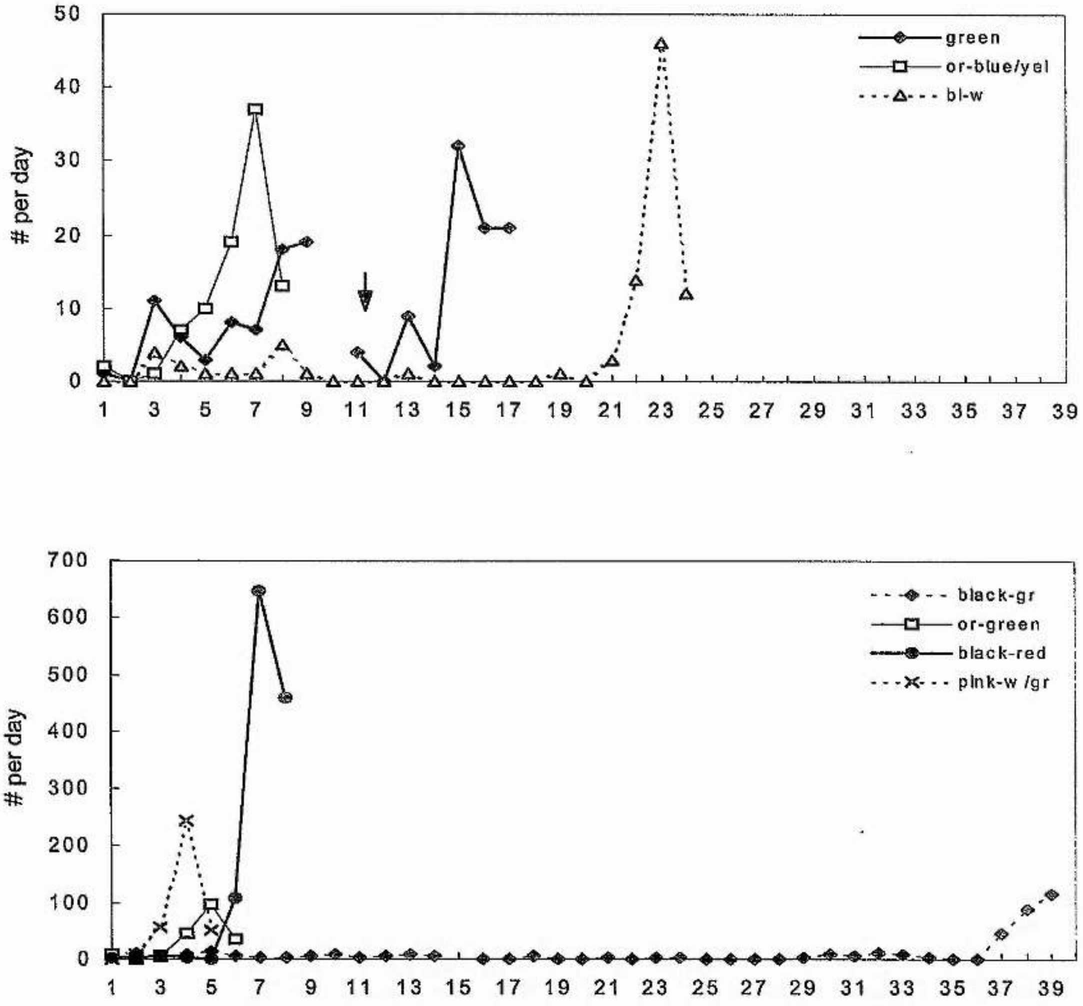

Fig. 6: Absolute number of responses/day in experiment 2. Arrows indicate the start of the second test (female green after a break of 39 days, black-green after 40 days). X-axis: days from start, day 1= first day for each female in the Skinner Box.

A comparison of relative frequencies (for absolute and relative frequencies see Table 7) showed most of the females to prefer the FLOURISH tape (Paired t-test, t=1.96, p=0.048, n=7, one-tailed). Furthermore, the strength of females' preferences was correlated with flourish duration (r_s=0.86, p=0.014).

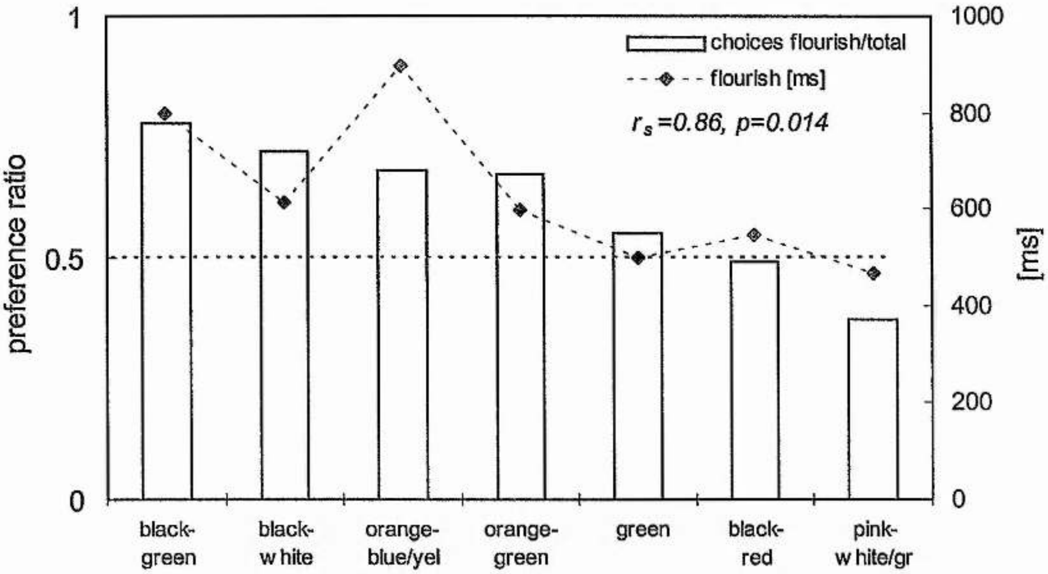

Fig. 7: Preference ratio for FLOURISH (choices for FLOURISH/ total choices) for each subject. The duration of the flourish of the test song is plotted on the second y-axis.

Table 7: Absolute number of choices for FLOURISH (+) and NoFLOURISH (-); L- Left, R-Right

	day 1		swap				
subject	L	R	L	R	total	total	flourish
	+	-	-	+	+	-	/total*
orange-green	6	49	1	96	102	50	0.67
green	14	18	6	15	29	24	0.55
black-green	44	2	28	61	105	30	0.78
orange blue/yellow	1	18	0	37	38	18	0.68
black-white	0	14	3	43	43	17	0.72
	-	+	+	-			
black-red	559	88	453	5	541	564	0.49
pink-w/green	21	36	71	162	107	183	0.37

* For an alternative data treatment and additional data considerations see Appendix 6.

6.4 Discussion

Female chaffinches were successfully trained to use small lever-type perches to trigger song. This method was used to test preferences between tutored song and unfamiliar one and in a second experiment, between songs with and without a terminal flourish. In the first experiment, subjects showed no preferences for either familiar or unfamiliar song. Within given trials several subjects seemed to show individual preferences (see Table 5), but it is unclear whether the preference was for a particular song type or perch. However, several females did not consistently choose the same side, suggesting that in some cases it was the particular song type that made a particular female more motivated to perch on that side. This is supported by the two females where a tape swap between two sides within a trial lead to an increased use of the previously less preferred side. In the second experiment most females preferred songs with the species specific terminal flourish. Interestingly, the strength of the preference was correlated with the overall flourish duration. As overall song duration was controlled for in the choice test, this results seems further to support the idea that the terminal flourish is important in intersexual communication.

The results of the first experiment have to be interpreted carefully as little is known about song learning in female chaffinches, so it is possible that females did not memorise the songs played back to them during their fledging phase. However their male counterparts exposed to the same regime did (Chapter 4) and the only evidence for different sensitive phases for males and females has shown the female sensitive phase to be closed earlier (Nelson et al. 1997). Subjects were tutored directly after fledging, which is a sensitive phase for song learning in many songbirds species studied of the temperate zones. It is therefore unlikely that failed memorisation caused the outcome of the first experiment.

Views differ on whether females should prefer their familiar dialect or not when choosing a mate (for review of hypotheses see Baker & Cunningham 1985). On the one hand, females might not prefer the local dialect to avoid inbreeding (Jenkins

1978). On the other, they might prefer mates which have similar adaptations to a given habitat as this might secure higher viability for their offspring (Nottebohm 1969). If so they should prefer males with songs of their natal area either because of genetic predispositions or due to a learned preference. In line with this, song tutoring in the female white-crowned sparrow (Casey & Baker 1992) and in the canary (Nagle & Kreutzer 1996) has been shown to increase the number of copulation solicitation displays shown to tutored song types. However, the latter experiment also revealed that some of the unfamiliar song types could elicit as many displays, provided they contained the fast trills, which had proven very attractive to female canaries in previous experiments (Vallet & Kreutzer 1995).

Within the species specific range songs of more dominant males in the brown-headed cowbird *Molothrus ater* (West *et al.* 1981) and songs of longer duration in the great reed warbler *Acrocephalus arundinaceus* (Catchpole *et al.* 1986) elicit more copulation solicitation displays. The first experiment provided no evidence that the overall duration of songs influenced the choice and it is unknown whether anything comparable to what King *et al.* (1981) termed "song potency" exists in the chaffinch. None of the songs in the first experiment was consistently chosen as the preferred song suggesting that in this experiment it was not overall quality of the song types that differed but females' individual preferences. However, the second experiment showed that taking away a species specific cue from the eight otherwise distinctively different song types tended to move females' responses in one direction. This was the case although both song versions were shorter than the average chaffinch song, which is important to notice as longer songs have been shown to be more attractive in various species (Searcy & Yasukawa 1996). It is important to stress that both song versions were equivalent to sound impressions likely to be encountered occasionally in the wild too. The first part of a chaffinch song is quieter, it does not transmit very far in noisy conditions and songs without flourish occur during normal singing as chaffinches often interrupt their songs (Heymann & Bergmann 1988, Nürnberger *et al.* 1989).

Early exposure to tutor songs did not influence female choices in this experiment. This agrees with results from the few field studies in which the populations have been so well known that choices of females could be related to their natal area and their fathers' songs. Chilton *et al.* (1990) found that female white-crowned sparrows chose males with the same dialect in successive years no more often than expected by chance and discovered no influence of the father's song on female choice. Also, when females of the same population were tested in the laboratory, their mates' dialects did not elicit more copulation solicitation displays than another dialect from the area, even though most of the females sang their mates' song when induced to sing by testosterone implants (Chilton & Lein 1996). Other comparisons between fathers' and mates' songs have also shown random relationship to dialect in female corn buntings *Emberiza calandra* (McGregor *et al.* 1988) and Darwin's finches *Geospiza fortis* (Millington & Price 1985). Male corn buntings learn local dialects after dispersal, suggesting that his dialect would not necessarily indicate the origin of a singer. In chaffinches males have sensitive phases for song learning after fledging and at the start of their first breeding season (Thorpe 1958, Slater & Ince 1982), arguing that in this species also song is not necessarily an indicator of natal area.

These field studies contrast with laboratory ones in which preferences for local dialects have been found when the number of copulation solicitation displays in response to playbacks were measured. As few species have been studied so far under both conditions, it remains unclear whether this is a consequence of differences between species or of different conditions in the laboratory and in the field. The white-crowned sparrow is an exception as it is well studied in the laboratory and in the field, but the results obtained have been highly varied (reviewed in Kroodsma *et al.* 1984) due to the different methods, study populations and definitions used by the researchers involved. In as much as female choices are concerned, apparent contradicting results may also suggest that female preferences are perhaps more flexible and context related than previously thought. Furthermore, some of the experiments that have most clearly demonstrated a strong preference for home versus alien dialect have involved separate subspecies, i.e. the white crowned-sparrow *Zonotrichia leucophrys nutalli* and *Z. l. orianthe* (Petrinovich & Patterson 1981, Tomback *et al.* 1983) and the zebra finch *Taeniopygia guttata guttata* and *T. g. castanostis* (Clayton & Pröve 1989, Clayton 1990). This makes comparisons with other species more difficult as it is hard to tell in these cases whether song is already established as a prezygotic isolation mechanism.

Summarising, it is difficult to decide whether the lack of clear preferences between familiar and unfamiliar songs is a consequence of the experimental set up or whether functional explanations like the lack of distinct dialects in this species (Slater et al. 1984) apply, as none of the previous studies can be compared directly with the results obtained here. As the second experiment showed females to choose more uniformly when the songs were manipulated, the results of the first experiment could be interpreted as an indication that within the reduced experimental environment lacking other cues females showed arbitrary individual preferences for songs that are within the conspecific range. Such individual differences in preferences have been postulated by theoreticians as prerequisite to make sexual selection work (for review see Searcy & Yasukawa 1996). The experiment reported here was not designed to test such differences specifically, but the results suggest that using operant conditioning tasks with song as a reinforcer could be the way to systematically test such individual preferences in the future.

It seems strange that to date operant techniques have been widely used to test the perceptual abilities of songbirds, but have been neglected as a tool to examine the preferences of birds given control over exposure to songs. The results obtained here are interpreted to favour the method, despite its elaborate logistics and the long time spans involved in single experiments. Active choices performed by subjects allow greater confidence in interpreting non-responses than for example subjects that do not move in phonotaxis experiments as they could either be equally attracted by both stimuli or ignore them both. Experiments of this type could be used in future to test systematically for individual song preferences which so far have not been conclusively demonstrated for song (Searcy & Yasukawa 1996).

6.5 Summary

Hand reared female chaffinches were tape tutored just after fledging. In the subsequent spring (i.e. their first breeding season) they were successfully trained in an operant conditioning task where exposure to song could be triggered by perching on either one of two short lever type perches. In a given trial one of the four songs that had been used for tutoring was paired with a song type unknown to the subject. No overall preference for either the familiar or unfamiliar song types was found. Instead, females preferred either song types or sides. In a second experiment one breeding season later, the same females were confronted with two versions of one song with and without the species specific terminal flourish. More females preferred the version with terminal flourish. Results of this preliminary study suggest, that at least in our small laboratory sample, female song preferences vary individually for songs within the species specific range and that exposure to a particular song type early in life plays a minor role, if any, in forming their preferences. Operant conditioning with song as a reinforcer can be used as an alternative method to test for approach in the laboratory to test individual females' song preferences with the great advantage that the control over the stimulus is left with the subject.

Chapter 7

Summary and Conclusions

This thesis has combined the investigation of the mechanisms underlying temporal control and pattern choice in chaffinch song, the influence of the song acquisition process on pattern choice and its influence on female song preferences. All these questions concerned aspects of the proximate causation of chaffinch song usage and perception that had not been studied before.

Variation differed between parts of the song. Syllable cadences were the least variable. Variation in phrase duration was therefore caused because the number of syllable repetitions varied, but not their duration. Trill and flourish duration were traded off against each other to achieve relatively invariant song duration. Song types are delivered in bouts of variable duration. Upper limits however are set by a timing not a counting process. The song acquisition process does not seem to be the cause of the observed difference in bout length within and between individuals, but it seems likely to influence the sequencing of song types. The hypothesised time window is likely to vary in length with motivation and single song playbacks have a facilitating effect, which lead to an increase in duration, revealing the song control system to be very flexible. Females did not prefer songs they had heard early in life over unfamiliar ones, but they preferred songs with flourishes to those without and longer flourishes over short ones. It was shown that males' calls are influenced by early experience, adding further doubt to the long maintained distinction between calls and songs.

Within song variability as measured by variation in phrase and flourish duration was shown to be caused mainly by variation in the number of syllable repetitions, whereas the unit of a syllable and the subsequent silent interval (i.e. cadence) was remarkably constant. This makes it unlikely that the variation arises because the production is inaccurate. Elements have been suggested as the units of production (Cynx 1990, ten Cate & Ballentjin 1996). However, this is a relative concept. On the one hand elements can be interrupted, although this is rare (Cynx 1990, ten Cate &

Ballentjin 1996, Riebel & Todt 1997). On the other hand, in many species fixed element combinations (syllables) occur. Investigating in detail how elements are grouped into syllables in the song sparrow *Melospiza melodia,* Podos *et al.* (1992) suggested that those element combinations always occurring together were in fact minimal units of production (MUPs). Within the trill parts of chaffinch songs, the fixed element combinations termed syllables seem to be the chaffinch's equivalent to this phenomenon, they are fixed sequences and the unit of syllable duration plus the subsequent interval is very constant in duration. To recapitulate, there is constancy in timing (this study) or syntax (song sparrow) on the level of production units, but the phrases made up of these units show considerable variation. Which motivational changes at higher hierarchical levels lead to the variation in the output can only be subject to speculation at this point. However, recent neurobiological findings suggest that temporal control is hierarchical and precision in generating patterns is highest at the lower levels within this hierarchy (Yu & Margoliash 1996).

The interesting contrast between highly variable and relatively invariant units also occurs at another level within the song organisation hierarchy: songs vary rather little in duration, whereas song type bouts show great variation. Although temporal parameters have been described to be significantly different between subjects in various species, at least at the within song level (Lambrechts & Dhondt 1987, Nelson 1988, Weary *et al.* 1990), they have received rather little attention to date as differences in song type phonology seem to be more striking and relatively more important in many species (Nelson 1988, Weary 1990). Also, birds are sensitive to much smaller changes in frequency than timing (Dooling 1982). However, these measurements relate to absolute differences, but the sensitivity of perception mechanisms does not necessarily change on a linear scale. All the experimental chapters on male song showed a strong component of individuality for temporal parameters of song organisation. Since Falls & Brooks (1975) conclusively demonstrated neighbour-stranger discrimination in a song bird more and more evidence has accumulated for the ability of songbirds to discriminate individuals by their vocalisations (review in Falls 1982). However, the base of this recognition is not fully understood. Both the songs in the repertoire and individual voice characteristics have been suggested as cues (Weary & Krebs 1992). Temporal aspects as a means of individual recognition have been little discussed in this context although they seem important in other taxa e.g. colonial seabirds like penguins (Jouventin 1972). Most of the temporal parameters measured here showed differences between subjects. They could contribute to coding of individuality in two ways. First, relatively invariant features, like cadence duration could be assessed by conspecifics and used for discrimination. Second, more variable features like mean bout duration could also be used, if variances do not overlap between individuals as was indeed the case with most of the shared types. Two chaffinches sharing the same song types make themselves more distinct if they deliver them in different patterns. Also, if a small repertoire of 2-3 songs types only is sung with immediate variety it leads to predictable cycling (ABAB...), if delivered with eventual variety a small repertoire results in greater variability (AAABABBB..), and even more so if phrase duration is also varied.

Species recognition is most likely to be based on several different features (Date *et al.* 1991), making this likely for individual recognition too. Although relatively invariant features have been suggested to be more relevant both in species and individual recognition (Marler 1960, Emlen 1972, Becker 1982), this seems not to hold true generally, as species recognition has been shown to rely on multiple cues both including variable and relatively invariant features, the weighting depending on the species (Peters *et al.* 1980, Nelson 1988), but within the species also on age (Peters et al. 1980) or sex (Searcy & Marler 1981). It can actually be a species characteristic to vary a certain feature. This is what we observe in species singing with eventual variety: songs are repeated a variable number of times before a bird switches to another song from its repertoire. At least in the chaffinch, units are relatively constant and variability arises at some levels more than others. I conclude that the observed variations are a general characteristic of the song of the subject or species under study rather than a general production 'noise'. However, some noise may arise in the song control centres of the brain as a consequence of changing outcomes in competition between alternative motor patterns. A good reason why the variation in number of syllable repetition is likely to be intrinsic is that handreared birds tutored with a song with a constant number of repetitions show a coefficient of variation for this parameter comparable to those of wild birds (Slater & Ince 1982).

Although bout length varies between the song types of an individual, there were also clear differences between subjects. Chapters 3, 4 and 5 all showed individuals to differ in mean bout length both if measured in duration or in number of repetitions. Although the different numbers of repetitions for different song types have been mentioned in the literature (Hinde 1958, Slater 1981), duration of bouts was not measured so that these differences could also have been a consequence of different song rates. Chapter 3 provides strong evidence that duration rather than number of repetitions trigger switches and it also shows this parameter to be significantly different between subjects, as well as within subjects to some extent. This suggests that this feature is a genuine part of chaffinch song organisation. However, whether this variation has any communicative function, must be tested with playback experiments with constant versus varying bout length. The relative importance of song features is often tested with playback experiments, but these usually involve only the territorial response of males. However, the relative importance of certain song features may differ between males and females (Searcy & Marler 1981, Searcy & Brenowitz 1988). Clearly, more comparisons are needed.

The song tutoring experiment described in Chapter 4 was designed to test one possible hypothesis on the causation of these individual differences. Different song types were presented with constant rate but with varying numbers of repetitions so that bout duration varied for each tutor song type. It is questionable whether final conclusions should be drawn with such a small sample size. However the great variation in song type bout length found within and between subjects that copied songs from the tutor mirrored the observations made in the wild but did not suggest that bout length had been copied from the (tape) tutor. In contrast, the sequencing of song types did seem to be influenced by the tutor. This seems odd, as varying bout length is a more prominent feature of chaffinch song and, with a small repertoire, possible transitions between song types are very limited. Nonetheless, preferred transitions definitely occur (Slater 1983 and Chapter 4). A preference amongst sequences is normally associated with species with large repertoires which sing with eventual variety and has been shown to be copied from the tutor in the nightingale *Luscinia megarhynchos* (for review see Todt & Hultsch 1996). Such questions have been tested in too few species to date to generalise, but the fact that the nightingale and the chaffinch are very distinct in their song organisation and are from two different families, suggests that sequence copying may be a more widespread phenomenon and possibly a consequence of the way the memory formation takes place (Hultsch & Todt 1992, 1996). Together with context memorisation (Kroodsma 1988, Hultsch & Todt 1989) these phenomena deserve further study and might help us explain how individual repertoire organisation is achieved.

This leads directly to one of the most puzzling questions of bird song research: why is so much variation generated within individual repertoires (Krebs & Kroodsma 1980, Kroodsma 1982) in the first place? This study tried to assess some of the mechanisms underlying temporal organisation and pattern choice in the chaffinch. Although, the communicative functions of aspects of chaffinch song have not been examined, the results obtained on mechanisms are a necessary underpinning for any such study. Any hypothesis about the adaptive function of a specific singing style has to take into account species-specific constraints on song production as they limit the degrees of freedom for signal production and delivery (Podos 1996, 1997).

The anti-exhaustion hypothesis brought forward to explain switching in the great tit *Parus major* as being a result of neuro-muscular exhaustion (Lambrechts & Dhondt 1987, 1988) is one of the few hypotheses suggesting a mechanism controlling bout length. However, subsequent studies suggested as alternative explanation that motivation rather than exhaustion guides switching in the great tit (Weary *et al.* 1988, 1991).

In the chaffinch a maximum duration could be identified as a constraint on bout length, and this was both individual and song type specific, but little influenced by the model's bout length. This suggests a song type specific component resulting in different motivational levels for different song types. The experiment described in Chapter 5 clearly showed this system to be extremely flexible, with the facilitating effects of single songs, causing an overall increase in bout duration. This clearly stresses the motivational basis of this time window. It would be interesting to know whether this also applies to other species that deliver their songs in bouts as a facilitating mechanism has of course repercussions on styles of communication.

The functions of song type repertoires, and of the great variation in repertoire size and in singing style between species, are not at all clear and many hypotheses have been put forward to explain them (for review see Krebs & Kroodsma 1980, Slater 1981). The single most influential idea was probably Hartshorne's (1956, 1973) anti-habituation (or anti-monotony) hypothesis, which suggests that variety in repertoires and their delivery reduces habituation on the receiver's side. Continuous singing is possible with a large repertoire and a versatile singing style, but species with a small repertoire must sing discontinuously to delay habituation. I would suggest that the variation in syllable or song repetitions possibly also adds to more varied signals in a species with a small repertoire like the chaffinch. It increases unpredictability in song matching and could also reduce habituation in male and female listeners.

This leads on to the question of the role female chaffinches play in the way signals are shaped and employed. Tests of intersexual communication in the field are extremely difficult as, during the breeding season, when song occurs, females are extremely inconspicuous and elusive as is necessary to successfully complete breeding under high predation risk. The conduction of playbacks in the field which have been so successful in testing the signal value of song to male conspecifics has been less successful in testing non-singing females. However, mate recognition and phonotaxis experiments have successfully demonstrated intersexual communication in the field. In the laboratory, approach tests (two-loudspeaker designs) and the copulation solicitation display have been used to assess females' preferences, but their drawbacks have been described in detail in Chapter 6. It was for this reason that I attempted to test female preferences with a new technique.

It was shown that the use of Skinner boxes is a possible new way to test for female song preferences, which allows one to test the relative importance of different cues and the influence of early exposure to song on such preferences. Song recognition learning clearly occurs as shown by mate recognition on the basis of vocalisations alone (for examples see Falls 1982), but does early exposure to song result in a preference? No evidence could be found for a strong preference for familiar over unfamiliar songs in the experimental birds. Two interpretations are possible. First, the experimental set-up may be unsuitable to detect such preferences, because they are irrelevant in the laboratory contexts. Second, side biases were possibly stronger than other preferences, perhaps partly because the two perches were not associated with two different sound sources. However, the choice between songs with and without a flourish led females to choose in a more homogeneous manner. This suggests that songs heard in the first summer do not have a strong influence females preferences in their first breeding season. As discussed in more depth in Chapter 6 the breeding and dispersal patterns in this species make it unlikely that song is an indicator of natal site, so its value as a cue in mate choice is questionable. More interestingly, despite the small sample size a strong correlation between flourish duration and the strength of females' preference could be found. In male chaffinches, length of the trill and flourish part of a song were negatively correlated (see Chapter 2), but trills are more effective in eliciting strong territorial responses (Brémond 1968) than flourishes (though signal length was not controlled for in Brémond's study). This suggests that in this species inter -and intrasexual selection may act in two opposing directions. These are only preliminary results, but the method can well be used to take these questions further. As a next step, it would be important to systematically test whether certain phonological structures are more attractive. Results in another Fringillid, the canary *Serinus canaria,* show that females are more attracted to fast trills (Vallet & Kreutzer 1995, Vallet *et al.* 1998). Direct and indirect evidence suggests that fast trills are difficult to produce and are a possible species specific constraint on sound production (Podos *et al.* 1995, 1996). However, there seems to be an unlearned bias towards fast trills in young swamp sparrows, which will actually try to copy and produce tutor songs presented with trill rates faster than the species range (Podos 1996). The sample in the present study was skewed towards slower trills (see Chapter 2). Phrases with a faster trill rate were shorter and were separated by longer intervals from the subsequent phrase than phrases with slow trills, providing indirect evidence that trill rates may be a constraint in the chaffinch also. As a follow-up it would be very interesting to vary both flourish duration and trill rates systematically in further choice experiments, both by using examples found in natural songs at the limits of their variation and by editing songs so that they are just outside the boundary for trills and flourishes observed in the wild in order to assess the direction in which females may be indirectly shaping signal characteristics.

To conclude, the temporal analysis has determined the degree of variability of different song parts and the interaction between them. In some instances, data suggested possible constraints on signal production. Some of the observed variability, like varying number of syllable repetitions and varying song type bout length, seems to be a species specific characteristic and is likely to arise from competition between alternative motor patterns rather than simply reflecting production noise. However, the flexibility of such features would make them suitable for graded signalling. Whether they are employed as such needs further research. Further combined investigation of temporal organisation and female preferences seems very promising: they might, for example, prefer features males find difficult to produce (i.e. fast trill rates) or signals that are perhaps less effective in male-male interaction (i.e. a longer flourish). The role that song learning plays in this respect has to be studied in more detail both in males and females. Do male chaffinches preferentially copy a certain type of song (i.e. long trill, short flourish) if given a limited choice between songs from the extremes of the observed distribution? Are females' preferences influenced by features of songs they were exposed to early in life? Do these channel general preferences rather then a preference for a specific type of song? Research on song learning needs to shift towards an integrated approach which looks at usage and organisation of learned information as well as copying success, and takes into account the modifying influences that learning may have on behaviour which may develop without learning (i.e. chaffinch calls). Any such contribution will help us to understand how male-male and male-female interaction shaped the signals we observe today, so that one day the origins of vocal learning might be retraced.

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Appendices

Appendix to Chapter 2

Appendix 2.1: ANOVA (Song duration within-between bouts, only complete songs)

song type	Source	Sum of Squares	d.f.	Mean Square	F	p
1	Between	1.461	51	2.865E-02	2.446	.000
	Within	1.136	97	1.171E-02		
	Total	2.597	148			
2	between	1.928	37	5.212E-02	2.179	.001
	Within	2.942	123	2.392E-02		
	Total	4.871	160			
3	between	4.478	53	.085	1.230	.225
	Within	3.709	54	6.869E-02		
	Total	8.187	107			
4	between	1.112	23	4.833E-02	2.837	.000
	Within	2.760	162	1.703E-02		
	Total	3.871	185			
5	between	.951	24	3.963E-02	2.709	.000
	Within	1.990	136	1.463E-02		
	Total	2.941	160			
6	between	1.131	24	4.711E-02	2.292	.001
	Within	3.473	169	2.055E-02		
	Total	4.604	193			
7	between	3.684	19	.194	11.694	.000
	Within	2.902	175	1.658E-02		
	Total	6.586	194			
8	between	1.404	16	8.772E-02	5.365	.000
	Within	3.123	191	1.635E-02		
	Total	4.527	207			
9	between	2.459	41	5.998E-02	3.921	.000
	Within	4.161	272	1.530E-02		
	Total	6.620	313			
10	between	2.817	40	7.042E-02	2.458	.000
	Within	6.646	232	2.865E-02		
	Total	9.462	272			
11	between	.824	47	1.752E-02	1.815	.004
	Within	1.390	144	9.655E-03		
	Total	2.214	191			
12	between	1.948	46	4.235E-02	2.708	.000
	Within	2.627	168	1.564E-02		
	Total	4.575	214			
13	between	.486	27	1.801E-02	1.784	.050
	Within	.384	38	1.010E-02		
	Total	.870	65			
14	between	1.542	17	9.070E-02	2.536	.001
	Within	6.044	169	3.577E-02		
	Total	7.586	186			
15	between	2.279	15	.152	9.439	.000
	Within	2.962	184	1.610E-02		
	Total	5.242	199			

Appendix to Chapter 4

Appendix 4.1: Origin of nests and fledging dates

nest	date	location	chicks (+ infert. eggs)	tree, nest height	development	eyes open	fledged
orange	16.6.95	Tentsmuir	4	spruce 2m	eyes open, feahered		17.6.95
no ring	16.6.95	Tentsmuir	3 (1)	spruce 1.8m	eyes closed, few dounes	18-20.6.95	24.6.95
black	23.6.95	Tentsmuir	4 (1)	Scot's Pine 3m	2 birds with eyes open, 2 eyes closed	24.6.95	1.-5.7.95
pink	26.6.95	University gardens	4	Oak 4m	eyes open, dounes		1.7.95

Appendix 4.2: Food mixture

Food mixture for hand rearing insectivorous birds
(Recipe most kindly provided by Henrike Hultsch, Freie Universität, Berlin)

1 tin good dog food (450 g)
4 boiled eggs
2 handfuls dried insects
2 handfuls dry dog food
optional: 300 g beef heart (if species needs a lot of iron)

blend all ingredients in an electrical grounder until homogenous mass,
form meatballs,
deep freeze

defrost daily rations, than add:

1 pinch multi vitamin powder
1 pinch gelatine powder
1 pinch grounded cuttle fish
2-3 spoons fromage frais (very low fat)

Feeding (every 30 min):
put some food on the end of a little stick, than offer fledgling
feed some drops of water after meal

Appendix 4.3: Light regime for handreared chaffinches

Date	light	hrs L/D	days	remark
16.6-14.8.1995	0600-2200	16 /8		±0′ handrearing
14.8	0600-2130			-30′
21.8	0600-2210		7	-20′
28.8	0600-2050		7	-20′
4.9	0600-2030		7	-20′
11.9	0600-2010		7	-20′
19.9	0610-2000		8	-20′
25.9	0620-1950		6	-20′
2.10	0635-1935	13/11	7	-30′
9.10	0640-1915		7	-25′
17.10	0650-1905		8	-20′
23.10	0750-1950	12/12	6	-15′ wintertime clock +1h
26.10	0750-1940		3	-10′
30.10	0750-1915		4	-25′
6.11	0750-1850	11/13	7	-25′
10.11	0750-1840		4	-10′
13.11	0750-1810		3	-20′ birds moved into sound proofed boxes
20.11	0800-1730		7	-50′
27.11	0800-1700	9/16	7	-30′
4.12	0830-1700		7	-30′
11.12	0830-1630	8/16	3	-30 ′ shortest day
25.12	0830-1700		14	+30′
1.1.1996	0830-1730		7	+30′
8.1	0830-1800		7	+30′
15.1	0845-1815		7	+15′
22.1	0845-1830		7	+15′
23.1	0845-1845	10/14	1	+15′ time shift forward start
29.1	0900-1915		6	+15′
4.2	0915-1930		6	+15′
5.2	0915-1945		1	+15′
11.2	0915-2000		6	+15′
18.2	0915-2015	11/13	7	+15′
25.2	0915-2030		7	+15′
3.3	0915-2045		7	+15′
8.3	0915-2100		5	+15′
11.3	0915-2115	12/14	3	+15′
15.3	0915-2130		4	+15′
18.3	0915-2145		3	+15′
22.3	0915-2200		4	+15′
29.3	0930-2230		7	+15′
1.4	0945-2300	13/11	3	+15′
5.4	1000-2330		4	+15′
8.4	1000-2345		3	+15′
12.4	1000-0000	14/10	4	+15′
15.4	1000-0020		3	+20′
19.4	1000-0040		4	+20′
22.4	1000-0100	15/10	3	+20′
27.4	1000-0120		5	+20′
1.5	1000-0140		4	+20′
5.5	1000-0200	16/8	4	+20′

Appendix to Chapter 5

Appendix 5.1: Details regarding playback subjects, dates and locations

	bird	location	song types	day 1	bouts n	play back n	day 2	bouts n	play back n	bouts total	play back total
95 c1	1	Kippo E-Spruce	3	4.5.95	119	31	5.5.95	108	31	227	62
95 c2	2	Kippo Thermometer	3	16.5.95	61	29	18.5.95	28	16	79	45
95 c3	3	Kippo S-Therm.	2	31.5.95	71	32	1.6.95	34	12	105	44
95 c4	4	Magus Muir Rhodedron	2	14.6.95	75	20	-	-	-	75	20
96 c1	5	Magus Muir Fallen Tree	3	17.5.96	73	26	-	-	-	73	26
96 c2	6	Magus Muir B1	3	28.5.96	121	44	-	-		122	44
96 c3	7	Kippo E3/E4	3	3.6.96	41	9	8.6.96	61	19	102	28

Appendix 5.2: Standardised differences for each song type for each playback condition

		NONE		SAME		DIFFERENT	
bird	song type	mean±SD	n	mean±SD	n	mean±SD	n
c1	1	0 ± 1	35	0.28 ± 0.92	10	-0.70 ± 1.35	17
"	2	"	59	1.34 ±. 096	7	0.15 ± 0.99	11
"	3	"	56	0.25 ± 1.04	6	0.19 ± 1.54	11
c2	4	"	11	1.09 ± 1.89	9	3.10 ± 1.14	9
"	5	"	7	-0.34 ± 0.56	2	-0.35 ± 0.42	5
"	6	"	8	0.19 ± 1.30	8	0.21 ± 1.12	8
c3	7	"	30	1.13 ± 0.89	10	1.06 ± 0.49	10
"	8	"	26	0.21 ± 1.04	7	0.34 ± 1.00	16
c4	9	"	26	-	-	0.44 ± 1.15	6
"	10	"	23	0.25 ± 0.88	4	0.55	1
c5	11	"	13	0.36 ± 1.71	3	-0.12 ± 1.20	6
"	12	"	13	-0.71 ± 1.26	5	-0.33 ± 2.29	5
"	13	"	16	-0.25	1	0.00 ± 0.60	5
c6	14	"	25	0.69 ± 1.09	5	-0.26 ± 1.24	7
"	15	"	23	0.49 ± 1.00	5	-0.04 ± 0.87	8
"	16	"	20	0.82 ± 1.37	2	-0.11 ± 1.00	13
c7	17	"	19	0.86± 1.13	5	0.75 ± 1.18	8
"	18	"	18	1.05	1	-1.25 ± .66	4
"	19	"	26	4.79 ± 2.79	4	-0.66	1

Appendix to Chapter 6

Appendix 6.1: Data analysis - female song preference Experiment 2

Table 7 in Chapter 6 presents the preference ratio based on the number of absolute choices for stimulus songs with flourish. This analysis is based on the assumption that any differences observed between days and sides are due to increased motivation if preferred side and song coincide. However, levels of motivation to trigger songs may vary between days and over the course of the experiment, as is apparent by the onset of habituation towards the end of trials. In this case it would be more appropriate to calculate a preference ratio for each day and then assess the mean (see Table 1 below). A comparison of the last two columns in Table 1 shows that with either type of analysis five females show a preference ratio over 0.5. However, one female changes in each direction when the means are used and the paired t-test is not significant ($t=1.56$, $p=0.089$, one-tailed). However, the correlation between preference and flourish duration remains significant ($r_s=0.811$, $p= 0.027$, $n=7$). It is difficult to decide which of the two analyses is more appropriate without more experiments. It is worth noting however, that those subjects using one side almost exclusively (orange green, orange blue/yellow and black-white) are those where one would expect activity increases if preferred side and song coincided. In those subjects that use both sides in a more balanced way a decrease in activity is perhaps more likely to reflect a general decrease in motivation to trigger tapes, in which case the other analysis should be more appropriate. Reassuringly, the correlation between strength of preference and flourish duration is significant with both analyses strongly suggesting that females do prefer the songs with flourish.

Table 1: Absolute choices for FLOURISH (+) and NOFLOURISH (-) and comparison between preferenc ratio either based on mean of day 1 and day 2 or based on absolute number of choices.

	day 1		swap				preference ratio	
subject	L	R	L	R	day 1	day 2	mean $_{\text{day 1, 2}}$	total flourish
	+	-	-	+	+/total	+/total	flourish/total	/grand total
orange-green	6	49	1	96	0.11	0.99	0.55	0.67
green	14	18	6	15	0.44	0.71	0.58	0.55
black-green	44	2	28	61	0.96	0.69	0.82	0.78
orange blue/y.	1	18	0	37	0.05	1.00	0.53	0.68
black-white	0	14	3	43	0.00	0.93	0.47	0.72
	-	+	+	-				
black-red	559	88	453	5	0.14	0.99	0.56	0.49
pink-w/green	21	36	71	162	0.37	0.70	0.47	0.37