Immanuel Kant's Sparrow

An integrative approach to
canary-like singing House Sparrow
(Passer domesticus)

DISSERTATION

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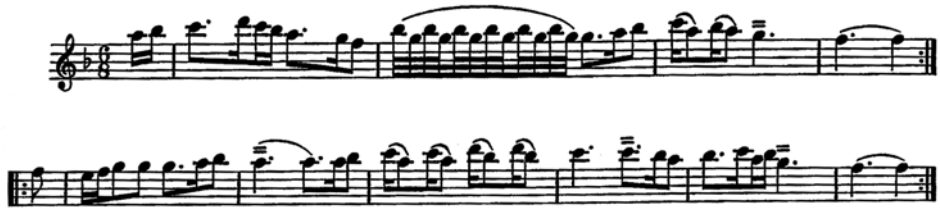
A Tune for the Sparrow

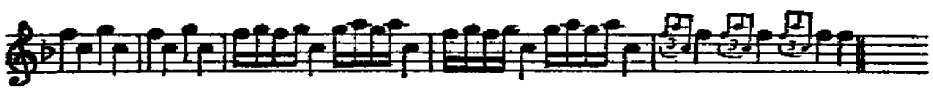


Teaching birds to imitate tunes was a popular and lucrative hobby in the 18th century. The Bird Fancyer's delight was the first collection of tunes, published by the rivals J. Meares (1717) and J. Walsh (1717).

From Godman 1954.

The most famous house sparrow was Clare Kipps' Clarence.

He produced a remarkable song with two sections (see below): first an introduction with the usual sparrow chirping, though less harsh in tone, followed by a several times repeated four note trills. The second more melodious part „opened with an eight-note trill, followed by a high, sweet, plaintive note. Then, descending by an interval of which I am not quite sure, it rose again to a second trill of eight notes a perfect fourth higher than the first. This theme was repeated several times and sometimes ended abruptly but more often returned to the tonic."



From Kipps 1956b.

ABSTRACT

The adoption of foreign song elements occurs under natural conditions in various songbird species including the house sparrow *Passer domesticus*, even though it may go largely unnoticed by humans. House sparrows singing canary song have been known by hobbyists for a long time. My study is the first to analyse the imitative abilities of house sparrows in detail.

I used an integrative approach considering features that are particularly important for the degree of vocal learning that can be displayed by a species. These included (1) a genetic predisposition, (2) body condition of the parents, (3) food availability during early ontogeny, (4) social factors, (5) neuronal mechanisms, (6) hormonal states, and (7) body size and morphology of the vocal tract.

House sparrows provided for 3 generations with food ad libitum could afford a high parental investment already at egg laying; this resulted in significantly higher hatchling weights of male and female neonates in the third breeding season in captivity. However, I could not find indications that hatchling weight influenced nestling growth, song learning, androgen levels or body size in adulthood.

Sparrows are obligate insect eaters in the first two weeks after hatching, and thus suffered from low quality food when they were reared by seed eating canary foster parents. This resulted in a significantly lower body mass gain during the day.

Canary-raised sparrows can learn the canary typical tour (= repetition of one type of syllables), but their songs did not match completely with the model. Tours are significantly shorter in sparrows than in canaries. While canaries sing several tours without a break, sparrows separate tours by a short silent interval. This goes in line with an increased volume of HVc, which codes besides others for syllable identity. However, this alone does not explain, why sparrows include such silent intervals.

House sparrows distinguish between sequences comprising syllables only, or both tours and single syllables: they produce significantly less different syllable types per time in a pure syllable sequence than in a sequence with syllables and tours.

The nucleus hyperstriatum ventrale pars caudale (HVc), a song control nucleus that is thought to coordinate temporal patterns, proved to be significantly increased in size in sparrow males

singing canary-like song compared to no-tour singing sparrows, independent of the rearing parent species. Sparrow-reared sparrows did not differ from canary-reared sparrows, whether singing canary tours or not, in any of the other brain measures.

The sparrow male's song control system undergoes seasonal changes. Nevertheless, it happened that a sparrow produced canary-like tours with appropriate temporal patterning in autumn, when song nuclei are significantly smaller than during the breeding season. This is a surprising result since it has been shown for other birds that song deteriorates with reduced brain area size. Indeed some syllables varied between seasons.

Singing proficiency was not enhanced by artificially elevated androgen plasma levels, nor did canary-like singing males possess naturally higher testosterone plasma levels. Testosterone implantation did not increase the dehydroepiandrosterone (DHEA) plasma levels and tour-singing sparrows did not show naturally higher DHEA plasma levels. But individuals who were kept in a sound-proof chamber for 2.5 days to study IEG response showed significanlty higher DHEA plasma level independend of their origin (wild-caught or bred in captivity) than individuals caged in ordinary rooms.

Canary-raised sparrows were able to learn the canary-typical tour, but their songs did not match completely with the model. Differences between model and imitation may reflect distorted production rather than copying errors, because morphology can act as an interfering factor. When taking into account the birds' body size and beak dimensions, it became probable that the house sparrow's vocal proficiency for singing canary-like tours may be limited by intrinsic jaw mechanics and respiratory demands.

House sparrows singing canary-like songs provide a rich tool for further integrative approaches. I suggest an interpretation combining all the above features under the perspective of female choice. Instead of searching for a „key adaptation" or single explanation for the imitative ability (song learning ability) in passerines, it might be more appropriate to focus on the multiplicity of factors involved in song production that - shaped by different selective forces - promote the highly specific song adaptations.

ZUSAMMENFASSUNG

Schon seit Jahrhunderten sind Haussperlinge bei Vogelliebhabern als gelehrige Imitatoren fremder Laute und Gesänge bekannt. Am häufigsten wird von Sperlingen berichtet, die von Kanarienvögeln aufgezogen wurden und den Kanariengesang lernten. Wissenschaftlern hingegen blieb dieses Wissen bislang weitgehend verborgen.

In dieser Arbeit wird erstmals der wissenschaftliche Nachweis erbracht, daß Sperlinge tatsächlich den Kanariengesang lernen und produzieren. Dazu habe ich einen integrativen Forschungsansatz verwendet, der folgende Aspekte umfaßt:
(1) Einflüsse der Aufzucht durch Kanarienvögel oder Sperlinge;
(2) Gesänge von Haussperlingen, aufgezogen von Kanarienvögeln oder Sperlingen;
(3) Gehirnstrukturen (HVc, RA), welche dem Gesang zugrunde liegen;
(4) Einflüsse von Steroidhormonen (Testosteron, DHEA) auf die Gesangsproduktion;
(5) Einflüsse des Stimmapparates auf die Gesangsproduktion.

(1) Haussperlinge sind in ihren ersten beiden Lebenswochen obligate Insektenfresser, Kanarienvögel aber lebenslang weitgehend Körnerfresser. Spatzenjunge in Kanariennestern erhalten folglich vergleichsweise weniger Protein in der Zeit größten Wachstums als ihre Sperlingsgeschwister im elterlichen Nest. Die unterschiedliche Ernährung wurde u.a. im Körpergewicht deutlich: Sperlingsjunge in Kanariennestern zeigten einen signifikant geringeren Gewichtszuwachs pro Tag als ihre Geschwister unter Fürsorge ihrer Eltern (Kapitel 2).

(2) Männliche, von Kanarienvögeln aufgezogene Haussperlinge kopierten die für ihren Ziehvater typischen Touren (= rasche Wiederholung einer Silbe), wenn auch in modifizierter Form (Kapitel 3). Touren sind bei Sperlingen deutlich kürzer (selten länger als 1 Sekunde) als bei Kanarienmännchen (mehrere Sekunden). Sperlinge trennen aufeinanderfolgende Touren durch eine kurze Stille, während Kanarienmännchen sie ohne Pause aneinanderreihen. Dadurch muten von Spatzen gesungene Touren wie eine komplizierte Einzelsilbe an, die viele (gleiche) Elemente enthält.

Weibchen verschiedener Vogelarten bevorzugen Männchen, die viele verschiedene Silben in möglichst kurzer Zeit singen. Von Kanarienvögeln aufgezogene Sperlinge produzieren sowohl Sequenzen, die nur Sperlingssilben enthalten, als auch Sequenzen, in denen sie Sperlingssilben

und Kanarientouren kombinieren: In kombinierten Sequenzen werden signifikant mehr verschiedene Silben pro Zeiteinheit gesungen als in reinen Sperlingssequenzen. Dies gilt ausschließlich für Sperlinge, die als Nestlinge nicht nur den Kanariengesang gehört haben, sondern auch von Kanarienvögeln gefüttert wurden (Kapitel 3).

(3) Der Gesangskern HVc ist nachweislich zuständig für das Erkennen von Silben sowie für das zeitliche Muster des Gesangs (Kapitel 4). Von Kanarien aufgezogene Sperlinge, die Touren singen, besitzen einen signifikant größeren HVc als Sperlinge, die ebenfalls von Kanarienvögeln aufgezogen wurden, aber keine Touren singen. Die Volumenzunahme kann zum einen auf einer stärkeren Vernetzung der Nervenzellen basieren, wie sie auch von anderen Tierarten bekannt ist. In der neueren Vogelliteratur finden sich andererseits Hinweise, daß auch Gliazellen bei Volumenzunahme eine größere Bedeutung haben als bisher gedacht.

Von verschiedenen Tierarten ist bekannt, daß mehrjährige Gefangenschaftshaltung die Größe verschiedener Gehirnbereiche negativ beeinflussen kann. Bei meinen Haussperlingen konnte ich einen solchen Einfluß nicht finden (Kapitel 4). Wohl aber variierten die Volumina der Gehirnkerne in Abhängigkeit von der Jahreszeit; im Herbst und Winter waren sie signifikant kleiner als im Sommer. Trotz des verkleinerten HVc, zuständig für das zeitliche Muster des Gesangs, konnte ein Sperling Touren auch im Herbst singen, ohne offensichtliche Abstriche in der Struktur (Kapitel 3).

(4) Von verschiedenen Vogelarten ist bekannt, daß Steroidhormone, insbesondere Testosteron, das Gesangskontrollsystem beeinflussen und als Folge davon auch den Gesang. Bei einzeln gehaltenen, aus dem Freiland entnommenen Haussperlingen bewirkte ein künstlich erhöhter Testosteronspiegel im Blut weder eine Zunahme der Gesangsaktivität noch spontane, den Kanarientouren vergleichbare Gesänge. Meine einzeln gehaltenen, von Kanarienvögeln aufgezogenen Sperlinge hatten im Vergleich zu sperlingsaufgezogenen Individuen weder einen erhöhten Testosteronspiegel (Kapitel 5) noch eine erhöhte Expression von Androgenrezeptoren in den untersuchten Gesangszentren (Kapitel 4). Das Singen von Touren kann also nicht auf hormonelle Einflüsse, z.B. als Folge unterschiedlicher Aufzuchtsbedingungen, zurückgeführt werden, sondern muß auf Lernen beruhen.

Eine Vorstufe von Testosteron ist Dehydroepiandrosteron (DHEA). Bei Säugern, einschließlich dem Menschen, wird es intensiv erforscht, bei Vögeln bisher noch vernachlässigt. In dieser Arbeit kann erstmals bei einer Vogelart gezeigt werden, daß länger anhaltender Stress den DHEA-Spiegel im Blut signifikant erhöht, unabhängig sowohl davon, ob das Individuum im Freiland oder in Gefangenschaft aufgewachsen ist, als auch davon, ob es von den eigenen Eltern oder von Kanarienvögeln aufgezogen wurde (Kapitel 5).

(5) Sind Sperlinge morphologisch überhaupt in der Lage, den Kanariengesang exakt zu kopieren? Die Syrinx, das Lautgebungsorgan von Vögeln, erwies sich nicht als mögliches Nadelöhr in der Gesangsproduktion kanarienaufgezogener Sperlinge (Kapitel 6), wohl aber der weitere Körperbau.

Seit relativ kurzer Zeit ist bekannt, daß Vögel den Frequenzverlauf von Silben nicht ausschließlich mit der Syrinx bestimmen, sondern durch Öffnen und Schließen des Schnabels. Der Sperlingsschnabel ist jedoch in allen Dimensionen (Länge, Breite, Höhe) signifikant größer als der Schnabel vom Kanarienvogel (Kapitel 6). Sperlinge wären folglich gehandikapt bei der Produktion von schnellen Silbenabfolgen, wie sie für Kanarientouren typisch sind (Kapitel 5).

Desweiteren ist von verschiedenen Vogelarten bekannt, daß größere Körpermasse die Atmung zwischen Silben beeinträchtigt. Die erwähnten Pausen zwischen den Touren (Kapitel 3) meiner Sperlinge könnten also vor allem eine Folge ihrer größeren Körpermasse sein. Tatsächlich erreichen Touren singende Sperlinge das aus Literaturdaten von mir errechnete theoretische Maximum an Silbenwiederholung pro Zeiteinheit (Kapitel 6).

Summa summarum zeigt diese Arbeit, daß eine Verhaltensweise wie ‚Singen' auf dem komplexen Zusammenspiel vieler verschiedener Faktoren beruht, von denen keiner vernachlässigt werden darf:

- Der ‚kanarisch' singende Hausperling offenbart sich als ideales Subjekt für einen integrativen Forschungsansatz, der - mindestens - Neurobiologie, Endokrinologie, Verhaltensbiologie, funktionale Morphologie, und Life History verbindet;
- Beim Vergleichen des Gesang von verschiedenen Vogelarten sollte zukünftig nicht nur auf phylogenetische Nähe bzw. Ferne korrigiert werden, sondern auch auf die unterschiedliche Körpergröße;

- Gesang sollte folglich nicht mehr nur als eine einheitliche Anpassung betrachten werden, sondern als hoch spezialisiertes Ergebnis vieler verschiedener, in Wechselwirkung stehender Anpassungen, geformt unter unterschiedlichen Selektionsdrücken.

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PRÉLUDE

This thesis was initiated by a paper of my supervisor W. Wickler (1982) „Immanuel Kant and the song of the house sparrow". Working on first lectures on educational theory he read the book „Über Pädagogik" written by I. Kant (1803), the famous German philosopher, and came across the following description: „To become convinced that birds do not instinctively[1] know, but in fact have to learn, how to sing, it is worthwhile to make a test and for instance replace half of a clutch of canary eggs by sparrow eggs, or else exchange their very young for sparrow nestlings. If these are then taken into a room where they cannot hear sparrows from outside, they will learn the canary song and one obtains singing sparrows" (Wickler 1982). Wickler collected some early references of singing house sparrows and concluded: „(1) The fact of song tradition in birds was known even before 1773. The importance of traditive traits (in parallel to genetic traits) in animal behavior was known to Kant in 1803. (2) The house sparrow can imitate foreign sounds, specifically from individuals that he accepts as parents or group members early in life." All this went unnoticed by most modern ornithologists.

To summarise, there exist an unprepossessing, worldwide distributed bird, known for his unmelodious chattering who in literature suddenly turns out to be a capable imitator of various elaborate bird songs such as that of the canary. This would not be suggested to be possible regarding the neuro-ethological background of bird song (e.g. DeVoogd et al. 1993). The study of organisms is split up in research topics, mainly treated as separate units. Considerable research on the neural circuits responsible for the production and development of bird song has focused either on the hormonal influences during development or adulthood or on the innervations of the syrinx, i.e. the motor pathway leading to it via the hypoglossal nucleus of the brainstem (nerve XII) as the pathway for the control of song. Research on the functional morphology and evolution of song in birds has typically targeted syringeal morphology, leaving cranial structure as the province of feeding studies (Westneat et al. 1993). Feeding studies usually fall under the topic of life history.

This is the first study of the songbrain in a cross fostered songbird and it seems to be important to combine all these aspects for a final interpretation of the data. To do so, the General introduction offers a succinct review of the main theories and findings relevant to the following chapters.

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[1] „Instinctively" at that time based on Spalding's famous definition of instinct as „any ability to perform an adaptive behavior without learning" (Spalding 1873).

1 GENERAL INTRODUCTION

There are about 9000 known bird species, among them 5100 species of sparrow birds (Passeriformes), of which roughly 4000 species are song birds (oscines). They are not only characterised by common genetical and anatomical features but also by two peculiarities related to their song: they all[1] learn their songs and they own a special neuronal circuit in the brain that is devoted to song learning and song production.[2] Both song learning and brain might be influenced by different factors during post postnatal growth.

1.1 GROWTH AFTER HATCHING

Postnatal growth up to fledging is thought to be the energetically most demanding period in a bird's life (Ricklefs 1983), due to dramatic changes in mass gain, tissue maturation and anatomical development within a short time period (Lepczyk & Karasov 2000).

A basic premise of life history theory is, that the range of possible phenotypes is constrained by certain structural and physiological limits of the organism; these limits establish conflicts between different functions and requirements (Ricklefs et al. 1998). In the case of growing birds constraint and compromise may occur at three levels (Ricklefs 1969, 1979):
1) limitations arising from a basic antagonism at the tissue- and cellular level between juvenile and mature function, which are thought to be mutually exclusive functions of tissue;
2) limitations of individual capacity to utilise available resources (e.g. the energy uptake of growing chicks is supposed to be limited by the size of the digestive tract); and
3) limitations as a consequence of food availability (e.g. limited by the parents' foraging time, food abundance, feeding strategy; sibling competition).

1.1.1 CONSTRAINTS ON THE TISSUE LEVEL

Altricial birds grow as fast as possible and limitations are set by internal physiological constraints of cell proliferation rate and tissue maturation (Ricklefs & Webb 1985; Starck

[1] The whitethroat (*Sylvia communis*) is the only known exception: when reared in isolation from the egg, individuals produced the species-specific song as an adult (Sauer 1954).

[2] Interestingly, the phenomenon of song learning and an anatomically defined song-related neuronal circuit occurs also in two other, taxonomically unrelated bird groups, the parrots (Psittaciformes) and the hummingbirds (Trochiliformes). This syndrome of characters may include an independent elaboration of neuronal circuits possibly already present in a rudimentary form in the respective ancestral birds (Schlinger & Brenowitz 2002).

1989). Studies on house sparrows, for example, suggest that greatest daily energy requirements may occur early in nestling development during periods of rapid growth and even exceed the maintenance energy requirements of fully-grown young (Ricklefs 1968; Seel 1969, 1970; Blem 1975a). A growth-rate-maturity-trade-off has been suggested for several tissues, including skeleton muscle (Moss & Leblond 1971; Ricklefs et al. 1994), bone (Kirkwood et al. 1989; Carrier & Leon 1990; Swartz et al. 1992) and brain (Ricklefs et al. 1994).

In altricial birds like oscines the hatchling's brain just meets the requirements of a basic regulation of physiological function and maintenance, sense organs are still closed by protective skins and do obviously not function (Weber 1950). The most dramatic postnatal volume increase is due to the production of neurons in the brain. For example in the Java sparrow *(Padda oryzivora)* a factor of 16.34 has been determined for the overall brain volume increase from hatchling to adult; maximum growth has been determined in the hyperstriatum ventrale (an important region for song) and the "wulst region", which together account for a 36-fold volume increase (Starck 1993)!
Brain development, however, does not limit postnatal growth. More probably skeletal musculature is the most critical site of constraint on growth rate on the tissue level (Ricklefs 1979).

1.1.2 DIGESTIVE TRACT

The gastrointestinal tract has a central position in studies of avian ontogenies because of its key function in energy intake (Neff 1973; Lilija 1983; Konarzewski et al. 1989, 1990; Starck 1993; Ricklefs et al. 1998; Caviedes-Vidal & Karasov 2000; Konarzewski & Starck 2000). In house sparrows, for example, the intestine shows an accelerated growth compared to other body parts. Its growth curve reaches an asymptotic size soon at about an age of 6 days (Neff 1973), before their feeding rate and growth rate stop increasing, which occurs by day 9 or 10 (Blem 1973, 1975b; Lepczyk et al. 1998).

1.1.3 FOOD AVAILABILITY

Food availability is generally considered to be the most important aspect of the environment affecting nestling growth and development (reviewed in Martin 1987; Gebhardt-Henrich & Richner 1998). Various factors have been recognized to elicit deviations from a mean

developmental trajectory: rate of food delivery at the nest (Bertram et al. 1991), weather conditions (Bryant 1975; Konarzewski et al. 1989; Keller & van Noordwijk 1994; Brzek & Konarzewski 2001), habitat differences (Richner 1989), and sibling competition[3] (Magrath 1990; Ricklefs 1993). All these factors influence fluctuations in food availability and/or quality (Lepczyk & Karasov 1996) for the individual chick; and this is ultimately the most significant factor shaping patterns of avian growth and development (Gebhardt-Henrich & Richner 1998; Schew & Ricklefs 1998).

The transition from neonate to fledgling is thought to be a relatively fixed, i.e. genetically determined, process (Lack 1968). Thus, in many altricial birds, even a short-term food shortage could cause increased nestling mortality, permanent stunting, reduced immunocompetence or other detrimental effects (e.g. Lees 1949; Cooch et al. 1991; Saino et al. 1997; Lepczyk et al. 1998; Schew & Ricklefs 1998; Horak et al. 1999). Behavioural, physiological, and morphological development nevertheless can continue at the species-typical rate (Lack 1968; Ricklefs 1968, 1983).

However, a growing body of literature indicates that young birds show the ability to adjust growth rate or the time to reach developmental endpoint, to prevailing food conditions. This ability is termed labile development, a developmental plasticity that differs in its expression between species (Lack & Lack 1951; Ricklefs 1976; Emlen et al. 1991). In contrast to food restriction the chick's response to overfeeding may depend on structural and functional limits (Lepczyk et al. 1998), and when an upper ceiling of plasticity is reached, no further growth response will be observed (Starck 1999).

Postnatal growth does not follow a hierarchy of constraints according to the three described levels. Muscles are an intensively studied tissue. The development of the skeleton has frequently been referred to as possible constraints well as the gut's capacity to process energy. The brain and other tissue level constraints have been discussed, but evidence is missing. In fact we don't know anything about the ultimate constraint.

[3] The effects of sibling competition need not express themselves lethally during the nestling period. They may result in weight variations at fledgling that translate into subsequent survival or recruitment into the breeding population (Ricklefs 1993).

1.2 SONG LEARNING

The described constraints are most influential during postnatal growth which lasts for about 15-35 days. Sound production in this period is very simple and sound recognition is rare (Schneid 1995; Godsave et al. 2002). But the situation changes with the time of fledging, when song learning starts.

1.2.1 DEFINITION OF "SONG"

There is a widespread categorization of bird vocalizations into 'songs' and 'calls'. Songs are thought to be relatively long, consisting of complex, well identifiable acoustic structures that have to be learned and are used by males to attract females and to stimulate their reproductive behaviour and physiology. Calls on the contrary are thought to be short, simple, unlearnt and used for other purposes (Catchpole & Slater 1995). In addition songs and calls have been attributed to different taxa of birds, suggesting that production of (learned!) songs could be confined to songbirds, while non-songbirds only produce (unlearned) calls (McGregor 1991). Both distinctions cannot be maintained, however, in view of the unlearned complex song of the whitethroat (Sauer 1954), complex learned vocalizations of the non-oscine humming birds (Baptista & Schuchmann 1990; Gaunt et al. 1994) and the call-like song structure of various songbirds, for example *Laniarius funebris* (Seibt & Wickler 2000).

A review of over 80 definitions of bird song (Spector 1994) shows little agreement as to what defines bird song or differentiates it from calls. Defining criteria have included for example structural (e.g. duration), physiological (e.g. hormonal control), developmental (e.g. learning), functional (e.g. territoriality), affective (e.g. musicality), and taxonomic (e.g. restriction to passerines) attributes of song – and each criterion has been rejected by some authors. The old distinction between songs and calls is therefore abandoned nowadays by more and more authors. Between species the song repertoires, the syntactical structure, the learning style and the function of song vary widely (McGregor 1991; Catchpole & Slater 1995; Seibt & Wickler 2000). A single definition for song, that covers all extant song concepts, is thus not available (Spector 1994).

The characteristic canary song is a rapid sequence of syllables (detailed terminology: see chapter 3) lasting several seconds. The usual, noise-like sparrow vocalizations, however,

are generally of a „call-like“ structure. Supposedly, this song contains as many definite and variable characteristics as the melodious songs of other birds, though they are not as easily recognized by human ears. It is possible that the brief vocalizations of house sparrows are compressed melodies that may contain many characteristics of a melody except its sequential arrangement (Wickler 1982).

1.2.2 PHASES OF SONG LEARNING

Following Konishi (1965) the term “song learning” refers explicitly to song development by auditory feedback control of voice. Only sound patterns that develop without auditory feedback might be called „innate”. Song learning passes through distinct phases (Marler 1997) fitting a two-step model (Konishi 1965). The first phase is the sensitive period of “song acquisition”[4], during which young birds become imprinted on species-specific song by an innate predisposition. Most often this happens prior to any own song production. In the following sensorimotor phase young birds begin to convert their sensory memory into the appropriate motor patterns of song production by subsequent reproduction of that model (Arnold 1975; Bottjer & Johnson 1997; Schlinger 1997). Each of the two main learning events (auditory and motor learning) could be controlled by a separate and different “mechanism”, and the onset and termination of these two sensitive periods could result from separate and different variables (Nottebohm 1999).

Species-specific song learning will not normally be impeded by limits on vocalizing activities (Marler 1976; Marler 1984; Slater 1989; Podos 1996). However, Pytte and Suthers (2000) showed that disruption of vocal motor practice during selected stages of song development by temporarily and reversibly blocking efference to the vocal muscles results in motor defects in adult song production. Permanent vocal aberrations are only noticeable in learned song syllables rather than in non-learned calls.

Whether cross-fostered individuals which might be limited in morphological features to produce the song of their foster family also show motor defects in adult song production is not known at the moment.

[4] Also called “memory acquisition” or “sensory acquisition”

1.2.3 TIMING OF SONG LEARNING

The timing for vocal learning is known for very few species. The data for different species vary tremendously, not only in respect to species-specificity, but also in conceivable details of methodology. Thus cross-species comparisons are next to impossible (Kroodsma 1982).

The interval between auditory (listen to and memorise a song) and motor (first vocal reproduction) learning can be as long as several months (e.g. swamp sparrows *Melospiza georgiana*: Marler & Peters 1982) or the two periods can overlap such that the bird continues to copy new sounds after the sensorimotor stage has started (e.g. zebra finches *Taeniopygia guttata:* Immelmann 1969; Nottebohm 1999)

Typically song learning ends with the onset of adulthood in age-limited (= closed-end) learners. Their song memorisation phase is restricted to a brief period early in life, usually around the time of fledging, but can extend up to the time when breeding territories are established in the following spring (zebra finches *Taenopygia guttata:* Immelmann 1969; song sparrow *Melospiza melodia*: Marler & Peters 1988; chaffinch *Fringilla coelebs:* Thorpe 1958; indigo bunting *Passerina cyanea*: Payne 1981). After the first year of life, when a central motor program for song has been established and the stereotyped adult song pattern is achieved, no new songs are acquired (Marler & Peters 1987).

However, song learning does not stop with the onset of adulthood in open-end learners. Until now only five species are known, who can develop new song patterns throughout adult life: the European starling *Sturnus vulgaris* (Feare 1984; Adret-Hausberger 1989), the canary[5] *Serinus canaria* (Nottebohm & Nottebohm 1978), the mockingbird *Mimus polyglottos* (Laskey 1944), the nightingale *Luscinia megarhynchos* (Wistel-Wozniak & Hultsch 1992) and the great tit *Parus major* (McGregor & Krebs 1989). Indeed where the house sparrow belongs to is not known yet.

1.2.4 ORIGIN OF SPECIES-SPECIFICITY OF SONG

All songbirds depend on parental care, and it has been suggested that this is the time when the young learn their songs (Payne & Payne 1996). Thus most species have been shown to develop abnormal songs when deprived after hatching (Kroodsma & Miller

[5] A male's repertoire may increase by up to 40% each breeding season (Schlinger & Brenowitz 2002).

1982; Catchpole & Slater 1995; Kroodsma & Miller 1996). With the exception of some groups (e.g. sturnids, menurids, young of brood parasitic widow birds), most young oscines do not copy allospecific vocalizations in the wild (Dobkin 1979). Thus if naïve young are exposed to conspecific and allospecific song in the lab, they selectively learn only conspecific song (Marler 1970; Marler & Peters 1977; Kroodsma 1978).

Models of song learning summarizing these findings suggest a kind of innate auditory filter (innate genetic template[6]) that helps a young bird to focus its attention on conspecific models, and – within a learning and memorisation phase – a rapid installation of a memory trace or engram (neural template) of the heard song (Konishi 1965; Slater 1983a; Marler 1997). When the bird begins to sing, it uses the memory trace to guide its vocal output. The "innate" selectivity may be part of a multifaceted system that ensures normal song development in nature (Konishi 1985). Some authors have suggested that the filtering is on the motor level (Mulligan 1966; Marler & Mundinger 1972; Dietrich 1980), is effected by a "culling" process (Slater et al. 1988; Baptista et al. 1993) and that also social factors may function as filters (Slater et al. 1988).

1.2.5 SOCIAL FACTORS AND VOCAL DEVELOPMENT

Post-hatching social factors are known as important variables in avian song learning, though the roles of auditory and other social stimulations are not clear yet (Chaiken et al. 1997). A social context can affect the selection of the song model to be imitated (Marler 1970; Marler & Mundinger 1972; Baptista & Morton 1981; Payne 1981; Baptista & Petronovich 1984; DeWolfe et al. 1989; Beecher et al. 1994), the timing of song acquisition (Kroodsma & Pickert 1984; Petrinovich 1985; Petrinovich & Baptista 1987), and possibly the timing of motor development (DeWolfe & Baptista 1995).

Species differ considerably in how they cope with standardized laboratory settings and whom their young choose as tutors: some do learn from loudspeakers, but others need a social tutor (social selectivity; overview see Appendix 2, Table A2.1); some readily learn non-natal dialects or even heterospecific song patterns, but others do not (signal selectivity). The choice of tutor (overview see Appendix 2, Table A2.2) can be categorized in three not necessarily exclusive modes (Cavalli-Sforza et al. 1992): some learn from

[6] The concept of templates is largely a short-hand description of observed facts. What it says is that a bird memorises song and reproduces it from memory (Konishi 1985).

(genetic) parents (vertical tradition), some from genetically unrelated adults (oblique tradition), some from age peers[7], but some may not follow exclusively one of these three transmitting modes of song traditions.

Wickler (1982) concluded, that social partners are important early in life for house sparrows, on which of the mentioned levels is not known yet.

1.3 THE SONGBIRD BRAIN: THE VOCAL CONTROL SYSTEM

This very special acoustic communication (including song learning) system of passerines evolved together with its underlying neuronal circuits, the avian song control system (SCS). A preliminary survey has shown that these circuits are large and well-defined in 35 species from eight oscine families (DeVoogd 1991). Despite interspecific variation in the relative sizes of song system nuclei, they clearly form a highly developed, highly specialized neural system across oscine birds. No parallel nuclei have been observed in the forebrains of non-oscine birds (e.g. reviewed by Ball 1990), again with the two noteworthy exceptions: the parrots and the hummingbirds (Gahr 2000).

The SCS is traditionally defined as a set of discrete, inter-connected anatomical nuclei. It includes nuclei in the forebrain (e.g. HVc, RA, Field L, NiF, lMAN, Area X), midbrain (e.g. DLM, Uva) and the brainstem (Am/Ram, nXIIts); the telencephalon contains the hierarchically highest centres for processing sensory information and controlling motor activity (Dubbeldam 2000). The SCS is organized into two pathways, the anterior (rostral or ascendant) and the posterior (caudal, motor, or descendent) pathway (Jarvis et al. 1998). Both pathways[8] originate in the nucleus (n.) hyperstriatum ventrale pars caudale (HVc[9]) and intersect in the n. robustus archistriatalis (RA). I will describe the passerine vocal control system (see Fig. 1.1) with an emphasise on the here analysed nuclei of the motor pathway HVc and RA. The description is based on reviews by Brenowitz et al.

[7] Although experimental studies provide considerable evidence for song learning from age peers, evidence from the field is lacking (Baptista & Gaunt 1997).

[8] Both pathways have mammalian correlates; for details see (Karten 1969; Jarvis et al. 1998).

[9] The acronym HVc derives from the earlier view that this nucleus is located in the hyperstriatum ventrale. It turned out to actually reside in the neostriatum, a dorsal part of the avian pallium neostriatum. To maintain the already introduced and cited abbreviation, Nottebohm (1987) suggested that this nucleus be redesignated as the “high(er) vocal center” HVC. To avoid a functional interpretation, Margolisah et al. (1994) proposed that the acronym “HVc” be adopted as the proper name of this nucleus (Margoliash et al. 1997).

(1997), Margoliash (1997), Wild (1997), Fusani (1999), and Schlinger & Brenowitz (2002).

1.3.1 BRAIN DEVELOPMENT OF THE SONG CONTROL SYSTEM

It has been experimentally shown that light influences brain development in embryos through the egg shell (e.g. Rogers 1982; Güntürkün 1997; Skiba et al. 2002). Until now little is known about acoustic effects on songbirds' embryos through the egg shell. Prior to hatching the acoustic apparatus of oscine embryos seems to be too poorly developed to undergo any acoustical stimulation[10] (DeVoogd 1991; Schneid 1995; Godsave et al. 2002; but see Konishi 1985; Johnston 1988); experimental evidence, however, is lacking.

At hatching, the telencephalon in songbirds is very immature with large germinal zones and relatively few neurons. In zebra finches, none of the telencephalic nuclei of the song system can be identified at hatching (DeVoogd 1991).

After hatching very high levels of neurogenesis, migration and differentiation lead to very rapid brain growth. In zebra finches, RA can first be identified in Nissl-stained brain sections at about day 5, HVc at day 10 after hatching (DeVoogd 1991). The apparent sizes of the HVc and RA increase substantially in the third week after hatching (Bottjer et al. 1985; Konishi & Akutagawa 1985; Kirn & DeVoogd 1989). By about day 25 after hatching, axons from HVc have grown to the dorsal surface of the RA, but HVc and RA become synaptically linked only after about 30 days of age, when young males first start to produce crude song-like vocalizations (Konishi & Akutagawa 1985).

1.3.2 ANATOMY AND FUNCTION OF THE SONG CONTROL SYSTEM

Within the anterior pathway projections (Fig. 1.1) are topographically organized (reviewed by Bottjer & Johnson 1997). Auditory information ascends from the level of the thalamus (location of the inner ear) to several sites in the telencephalon, including the major subdivisions of field L, a high auditory processing centre (Nottebohm et al. 1982), which indirectly projects to HVc (Vates et al. 1996; Gentner et al. 2001; Gentner & Margoliash 2001). HVc sends axons via, Area X, DLM, lMAN (see Fig. 1.1) back to both n. robustus

[10] Embryonic communication some days before hatching is only known from non altricial birds e.g. bobwhite quail (*Colinus virginianus*; Vince 1964), Muscovy duck (*Cairina moschata*; Rumpf & Nichelmann 1993), and little tern (*Sterna albifrons*; Saino & Fasola 1996).

archistriatalis (RA) and Area X. This elaborate neural loop may modulate the activity of the HVc and RA, and thereby ultimately the output to the syrinx (Okuhata & Saito 1987; Bottjer 1989; details see below). The anterior forebrain pathway is suggested to control song learning and song recognition, but it does not seem to be immediately necessary for song production in adult birds (for reviews see Doupe 1993; Vicario 1994; Brenowitz et al. 1997; Doupe & Solis 1997).

The motor pathway (Fig. 1.1) includes the thalamic n. uvaeformis thalami (Uva) which projects directly as well as via the neostriatal n. interfacialis (NIF) upwards to HVc in the forebrain. HVc sends axons to RA. From RA multiple output routes are suggested that can be grouped into four anatomical and functional sets of projections:

1) to the dorsomedial part (DM) of the n. intercollicularis (ICo) in the midbrain (Gurney 1981; Vicario 1991; Wild 1993, 1994), which is also involved in motor coordination and furthermore mediates interactions between forebrain and midbrain systems during singing and calling (Vicario & Simpson 1995);

2) to motor neurons in n. hypoglossus pars trachosyringealis (nXIIts) in the brain stem, which in turn sends axons to the ventral and dorsal muscles of the sound-producing organ, the syrinx (Nottebohm et al. 1976). Ventral and dorsal muscles of the syrinx have distinct functional roles during singing, either gating the expiratory flow or controlling the frequency of vocalization (for details see chapter 1.5. song production);

3) to thalamic nuclei (DMP via mMAN, DML via lMAN) that ultimately project back to HVc and RA (Vates et al. 1997); although sparse in adult birds this loop is well suited to provide internal feedback during singing (Margoliash 1997);

4) to n. retroambigualis (RAm) and n. ambiguus (AM) in the medulla of the brainstem (Wild 1997). RAm consists of many respiratory related neurons that fire in phase with expiration, while AM contains motor neurons which innervate the larynx; they together might provide information about the configuration of the syringeal muscles for respiratory and laryngeal control (Vicario 1993; Wild 1993; Suthers 1997).

The caudal pathway is thought to be involved in song production (e.g. Nottebohm et al. 1976) as well as - with some portions of its circuits - to participate in song learning (Bolhuis et al. 2000). Taking into account that birds produce sound only during expiration

and that the larynx is thought to play a role in filtering sounds produced by the syrinx (Suthers & Goller 1997), the pattern of descendent projections from RA may play an important role in the coordination of respiration, syrinx and larynx activities.

In sum the projections 2), 3) and 4) provide an internal feedback during singing, possibly important during sensorimotor learning (Margoliash 1997) while projections 1) again ultimately strengthen the motor coordination.

Besides song production, HVc seems to play a crucial part for the integration of information, which it then hands on to the two forebrain pathways as described above. In addition to the described auditory inputs, HVc also receives indirect projections from the visual medial pre-optic nucleus (POM), which is known to regulate male courtship and sexual behaviours expressed prior to, and in anticipation of, copulation (Striedter & Vu 1998; Riters & Ball 1999). However a neuronal link between a 'motivational' system, controlling the motivation to vocalize on the one hand, and the song control system, controlling the production of song on the other hand, has still to be identified (Fusani 1999). Nevertheless this route has to be kept in mind when studying androgenic effects on brain and behaviour.

1.3.3 NEUROGENESIS IN THE ADULT BRAIN

The songbird displays widespread neuronal mitogenesis and migration throughout adulthood, most remarkably in HVc (Goldman & Nottebohm 1983; Goldman 1998). This forebrain region generates new neurons within the ventricular/subventricular zone followed by the migration of the new daughter cells into the forebrain parenchyma. Neuronal migration occurs along a system of guide fibres that emanate from radial guide cells of the ventricular epithelium (Goldman & Nottebohm 1983; Alvarez-Buylla et al. 1988; Kirn & Nottebohm 1993). In the target region naïve cells differentiate into physiologically functional, synaptically integrated members of the local neuronal network (Goldman & Nottebohm 1983; Paton & Nottebohm 1984). Many of these cells go on to establish long-distance projections to distant targets (Paton et al. 1985; Alvarez-Buylla & Kirn 1997). These neurons, born in adulthood, are fully active by auditory stimulation like other song system neurons born in developmental stages (Paton & Nottebohm 1984; Burd & Nottebohm 1985).

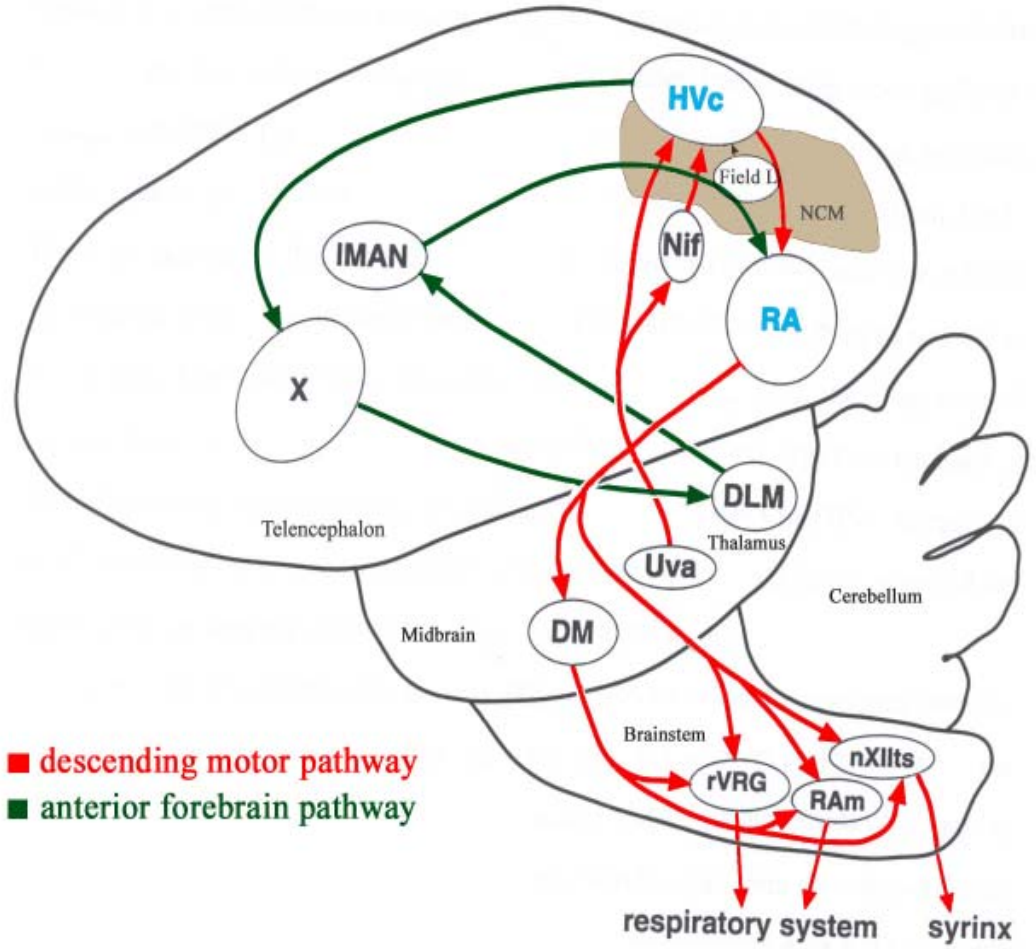


Fig. 1.1: Sagittal scheme of the songbird brain showing projection pathways of major nuclei in the song control system. DLM: nucleus (n.) dorsolateralis anterior thalami pars medialis; DM: n. dorsomedialis of the intercollicular complex; HVc: n. hyperstriatum ventrale pars caudale; lMAN: n. magnocellularis anterioris lateralis; NCM: neostriatum; Nif: n. interfacialis; nXIIts: n. hypoglossus pars trachosyringealis; RA: n. robustus archistriatalis; RAm: n. retroambigualis; rVRG: rostro-ventral respiratory group; Uva: n. uvaeformis; X: Area X (adapted from Brenowitz 1997).

Seasonal changes in the recruitment of new neurons to the HVc (Kirn et al. 1994) and less temporally and spectrally stereotyped song during autumn (Nottebohm et al. 1986; Smith et al. 1997b), were thought to be necessary for learning new songs each year as known from canaries (Nottebohm 1987) or for acquiring new perceptual memories of songs each year as suggested in white-crowned sparrows (Nottebohm et al. 1990; Tramontin & Brenowitz 1999).

But indeed seasonal neuron recruitment occurs in a variety of bird species, including songbirds, that are not seasonal in song production (zebra finches), and non-songbirds,

who do not learn song at all (e.g. doves) (Nottebohm 1984; Nottebohm 1987; Nordeen & Nordeen 1988). Furthermore it occurs throughout the telencephalon, not just in regions involved in vocalization (Nottebohm 1987) and in both sexes independent of singing performances (Goldman & Nottebohm 1983). Thus the functional significance of seasonal neuron recruitment to the adult HVc is not clear.

1.4 STEROID HORMONES: MEDIATORS BETWEEN SONG AND BRAIN

Hormones are secreted in response to internal and external stimuli (Ketterson & Nolan Jr. 1992), and they act among others on the central nervous system to control complex vertebrate behaviours (Schlinger & Brenowitz 2002). Androgens are known to be involved in the production of courtship behaviour and territorial vocalizations in adult males. In the following I focus on two androgens, testosterone and its precursor DHEA.

1.4.1 ANDROGENS AND SEASONAL CHANGES IN BRAIN MORPHOLOGY

In general, the morphology of HVc and RA (for a review see Brenowitz & Kroodsma 1996) and song production in adult birds parallel seasonal changes in plasma androgen levels in most seasonally breeding species examined (Nottebohm 1981; Ball 2000; Tramontin & Brenowitz 2000).

The gonads of songbirds regress outside the breeding season, like in other seasonal reproducing species of the different vertebrate classes (e.g. Ando et al. 1992; Saidapur & Hoque 1995; Kriegsfeld & Nelson 1998; Moyle & Cech 2004). With regressed gonads, plasma androgen levels decrease, which causes an increase of neuronal turnover in the HVc of adult songbirds via incorporation of naïve neurons. In spring, when day length increases, gonads of songbirds increase in females up to 175-fold, in males 360-fold up to 1000-fold (Marshall 1961; Lofts & Murton 1973; Follett 1984). In turn both the survival of HVc neurons and the addition of new neurons increase, while the neuronal turnover decreases; this results in an increase of neuron number followed by rapid HVc volume enlargement (Rasika et al. 1994; Hildago et al. 1995; Tramontin & Brenowitz 1999; Schlinger & Brenowitz 2002). In spotted towhees' *(Pipilo maculates)*, the most extreme known example, HVc volume nearly triples during the breeding season (Smith 1996).

The cellular basis of volumetric growth of the RA differs from that observed in the HVc. While the HVc grows rapidly in response to exposure to breeding levels of testosterone, the RA grows more slowly (Ball 2000; Tramontin et al. 2000). Neuron numbers do not change seasonally in the RA. Thus, volumetric changes during breeding season result from increased neuron size, spacing, dendritic arborisation, and the size of pre- and post-synaptic profiles in the breeding season (DeVoogd et al. 1985; Brenowitz et al. 1991; Hill & DeVoogd 1991; Tramontin et al. 1998; Tramontin & Brenowitz 2000).

1.4.2 PATTERN OF ANDROGEN RECEPTOR (AR) DISTRIBUTION IN THE BRAIN

The distribution pattern of androgen concentrating cells in the brain has been found to be similar in all songbird species studied so far (e.g. Arnold & Saltiel 1979; Nordeen et al. 1987; Brenowitz & Arnold 1990, 1992). Songbirds possess androgen-sensitive brain areas that are a part of their specific telencephalic network (see Table 1.1) as well as in limbic and nonlimbic regions of the telencephalon. In common with non-songbirds ARs are expressed in diencaphalic and mesencephalic regions. Song control nuclei androgen-sensitive cells were also found in the caudomedial neostriatum (NCM), a region thought to be involved in song memories, in several preoptic-hypothalamic areas (HPOA) (Arnold et al. 1976; Balthazart et al. 1992; Riters et al. 2000), in various nuclei in the hypothalamus, and in the midbrain; this corresponds to a common distribution pattern described in all vertebrate classes (Morrell et al. 1975; Pfaff 1976; Stumpf & Sar 1978).

1.4.3 TESTOSTERONE AND SONG

Singing activity is correlated with circulating levels of testosterone (Rost 1990; Kriner & Schwabl 1991; Rost 1992; Gahr 1997; Wada et al. 1999). Testosterone is high during the breeding season at a time when males sing at high rates[11] (Hegner & Wingfield 1986). Outside the breeding season males may sing only occasionally or not at all. However, some species use songs to defend (feeding) territories year round or attract mates during the non-breeding season (e.g. Summers-Smith 1988; Hau et al. 2000; Canoine & Gwinner 2002). Pair formation in house sparrows often begins in autumn (Schifferli 1974) and individuals claim a small region around the nest as a territory (Bent 1958). They do so at

[11] Since DHT often circulates in coordination with T (Wingfield & Farner 1993), it may also contribute to song expression (Schlinger & Brenowitz 2002).

Table 1.1: Overview of song control regions in the songbird brain containing AR cells

nucleus	**brain region**	**selected literature**
HVc	forebrain	Sohrabji et al. 1989; Gahr 1990b; Arnold et al. 1976
RA	forebrain	Arnold et al. 1976
lMAN, mMAN	forebrain	Balthazart et al. 1992; Arnold & Saltiel 1979
Area X	forebrain	Bernard et al. 1999; but see Metzdorf et al. 1999
nucleus taeniae	forebrain	Balthazart et al. 1992
Nif	midbrain	Schlinger & Brenowitz 2002
ICo but not DM	midbrain	Arnold et al. 1976; Balthazart et al. 1992
nXIIts	brainstem	Arnold et al. 1976; Gahr & Wild 1997
RAm	brainstem	Gahr & Wild 1997
rVRG	brainstem	Gahr & Wild 1997

times when the traditional circulating sex steroids, such as E_2, T and DHT are basal (Dittami & Gwinner 1990; Logan & Wingfield 1990; Gwinner et al. 1994; Wingfield & Hahn 1994).

With respect to the neuronal bases several lines of evidence suggest that T (or its active metabolites) is the primary physiological cue that mediates the seasonal changes in the song nuclei. Castration of males severely attenuates the seasonal growth of the song regions (Bernard et al. 1997; Gulledge & Deviche 1997; Smith et al. 1997a), and reduces or eliminates singing (Nottebohm 1969; Pröve 1974; Arnold 1975; Nottebohm 1980; Heid et al. 1985), while T treatment of castrated or intact males in non-breeding status (in fall and winter) induces growth of song nuclei by acting directly on the HVc (Nottebohm 1980; Johnson & Bottjer 1993; Rasika et al. 1994; Bernard & Ball 1997; Wennstrom et al. 2001), and can increase song production (Nottebohm 1969; Pröve 1974; Arnold 1975; Nottebohm 1980; Searcy & Wingfield 1980; Heid et al. 1985; Hunt et al. 1997).

However, the studies of plasma T levels and their effects by using castration and/or T-replacement therapy (e.g. Nottebohm 1980; Marler & Moore 1988a; Marler et al. 1988; Bottjer & Hewer 1992) are problematic. Castration induces an increase of circulating estrogens in several songbird species (Marler et al. 1988; Adkins-Regan et al. 1990), therefore some of the behavioural effects of castration could be due to the increase in E_2, and not to the lack of T. Similarly, T-replacement provides both androgen and estrogen,

as T is aromatised to E_2 within the brain (Fusani 1999). It is thus unclear to what extent the action of exogenous T is due to T itself or to its androgenic or estrogenic metabolites (e.g. Harding et al. 1988; Walters et al. 1991; Panzica et al. 1996).

1.4.4 DHEA

DHEA is an andrenocortical hormone possessing only weak androgenic properties (Kriegsfeld & Nelson 1998; Lu et al. 2001). It is called "mother steroid" (Regelson et al. 1994), because its major function is thought to be a precursor to many other steroid hormones produced in the adrenal cortex (Rosenfeld et al. 1974; Kroboth et al. 1999). DHEA shows low affinity for intracellular androgen and estrogen receptors, and there is little evidence for a DHEA-specific intracellular receptor (Svec & Porter 1998); but DHEA is thought to have specific membrane receptors (reviewed by Shealy 1995). Thus DHEA actions may depend on its conversion to AE, T and E_2 either in the adrenal glands and testes (Lieberman 1986; Soma & Wingfield 2001; but see Vinson et al. 1978) or by steriodogenic enzymes in the brain (Vanson et al. 1996). Furthermore the brain itself may synthesise DHEA de novo from cholesterol (Robel & Baulieu 1995; Baulieu 1997; Nomura et al. 1998; Schlinger et al. 1999).

Exogenous DHEA has numerous effects on the mammalian CNS (cited by Soma et al. 2002); e.g. DHEA enhances memory in rodents and men (Karishma & Herbert 2001; but see Wolf & Kirschbaum 1999). Also in birds physiological doses of DHEA can have large-scale effects on neuro-anatomical structures. Treatment of non-breeding male song sparrows with physiological levels of DHEA increases the volume of a brain nucleus (HVc) regulating song and singing behaviour (as expression of aggression) by a decrease of the latency to sing and an increase of song rate (Soma et al. 2002).

1.5 SONG PRODUCTION: THE SYRINX AND THE VOCAL TRACT

A further facet in song production is the avian sound producing organ, the syrinx, and the connected vocal tract. The syrinx is as unique to the class Aves as are feathers (Beddard 1898; King 1989). It is found in all known bird species with the exception of New World vultures, who have lost it secondarily (Gaunt & Nowicki 1998). The passerine syrinx varies little around a basic pattern (Suthers 1999), but is endowed with a complex musculature of seven pairs of muscles (Warner 1972b). This basic conformity in pattern and muscular complexity led Stein (1968) to suggest that in passerines who display

considerable vocal versatility, this facility may be attributed to refined neuromuscular control rather than to anatomical complexity.

The classical theory of birdsong production holds that all variation in sound quality (acoustic attributes of song) are determined (i.e. generated and modulated) entirely by the action of the syrinx, and that acoustic properties of the vocal tract play little or no part (e.g. Greenewalt 1968; Gaunt & Wells 1973; Casey & Gaunt 1985). Meanwhile there is growing evidence that the resonance properties of the vocal tract, including trachea and oral cavity, may influence the sound that is produced during song (Westneat et al. 1993). In describing syrinx anatomy, respiration during singing, and differences between left and right syrinx I follow Suthers (1997).

1.5.1 SYRINX ANATOMY

The oscine syrinx, hanging in the interclavicular air sac, is formed from modified cartilages of the caudal end of the trachea and the cranial ends of the two primary bronchi (see Fig. 1.2). The cranial end of each bronchus contains a medial tympaniform membrane (Mtm) and a pair of labia built from connective tissue. The medial labium is located at the cranial edge of the medial tympaniform membrane and opposes the more prominent lateral labium. Endoscopic observations of syringeal configuration during phonation showed that the sound is generated by the labia.

Besides the extreme homogeneity of the oscine syrinx morphology (Ames 1971), there exists a considerable confusion in the literature concerning the tracheal and syringeal muscles (George & Berger 1966). Commonly they are subdivided in extrinsic (= tracheal)[12] and intrinsic (= syringeal)[13] muscles. The maximum total number of paired muscles (excluding extrinsic muscles) varies between four and nine according to the author (Fürbringer 1888; Köditz 1925; Miskimen 1951; Ames 1971; Warner 1972a; Welty & Baptista 1988). For the house sparrow Miskimen (1951) determined 4 pairs of syringeal muscles (Bronchiotrachealis anticus, Bronchiotrachealis posticus, Sternotrachealis, Bronchialis anticus). The left and right members of each muscle pair are separately innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve (King 1989).

[12] Extrinsic muscles: Musculus (M) tracheolateralis and M. sternolateralis

[13] Intrinsic muscles: M. bronchiotrachealis posticus (dorsal), M. bronchiotrachealis anticus (ventral), M. bronchialis posticus, M. bronchialis anticus with two well differentiated fasculi: pars lateralis, pars medialis

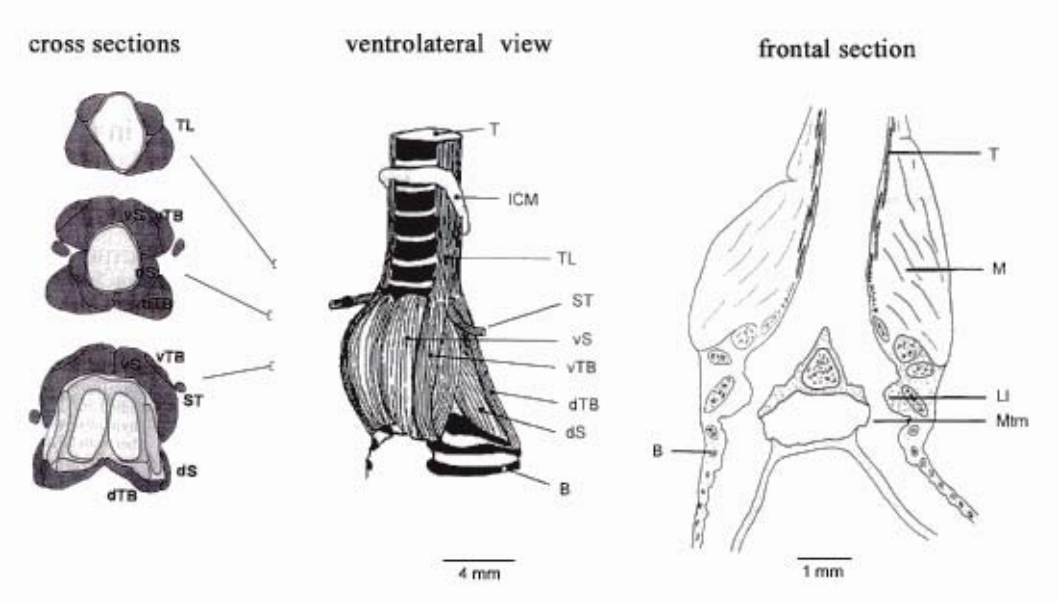


Fig.1.2: Schematic view of a syrinx depicting the main morphological structures.
T: Trachea; M: syringeal muscle; LI: lateral labium; Mtm: medial tympaniform membranes; B: bronchial ring; ICM: membrane of the interclavicular air sac; TL: musculus (m.) tracheolateralis; ST: m. sternotrachealis; vS: m. syringealis ventralis; vTB : m. tracheobranchialus ventralis; dTB : m. tracheobranchialus dorsalis; dS: m. syringealis dorsalis (adapted from Goller & Suthers 1996 a,b).

In addition to the left and right muscle groups of the syrinx the respiratory muscles are particularly important for sound production. They are innervated by branches of various cervical, thoracic, and lumbar spinal nerves and generate the respiratory pressure, the driving force necessary for vocalization. Cranial muscles control the configuration of the vocal tract. The motor activities of syringeal and respiratory muscles must be perfectly coordinated during song to achieve the appropriate vocalization.

1.5.2 RESPIRATION DURING SINGING

Miskimen (1951) demonstrated by forcing air in and out of the lung-air sacs of an anaesthetized house sparrow *(Passer domesticus)*, that sound was produced only when air was withdrawn in the expiratory direction. He therefore concluded, that sound was normally produced only during expiration (Brackenbury 1989). Respiratory pressure is increased and controlled during vocalization to maintain the appropriate rate of airflow across the adducted, sound-generating structures of the syrinx. Respiratory adjustments to singing depend on the tempo of the song (Suthers & Goller 1997). Domesticated

canaries *(Serinus canaria)*, for example, may sing continuously for more than 30 seconds with a syllable repetition rate within a phrase that ranges from a few to more than 40 per second depending on the duration of the syllable (Calder 1970; Nottebohm & Nottebohm 1976; Hartley & Suthers 1989; Brenowitz et al. 1997). Detailed measurements during singing (Calder 1970; Hartley & Suthers 1989) revealed two different respiratory strategies according to repetition rate. In phrases with syllable repetition rates below about 30/s, a small aspiration, called mini-breath, occurs after each syllable. This inhalation is about equal in inspired air volume to the amount expelled to produce the previous syllable and thus replenishes the volume of air in the respiratory system that is available for the next vocalization (Suthers & Goller 1997; Hartley & Suthers 1989). The production of mini-breaths involves a complex sequence of motor acts that requires accurate coordination between the two sides of the syrinx and the respiratory muscles with an accuracy of several milliseconds.

There is an upper limit in syllable repetition rate beyond which the interval between syllables is too short to allow a mini-breath. In this case mini-breath motor patterns seem to be replaced by a syringeal motor pattern of pulsatile expiration: expiratory muscles maintain a positive respiratory pressure and the timing of each syllable is determined by micropuffs of air, which are allowed to escape through the labia. Pulsatile expiration permits very high syllable repetition rates, but the duration of such song phrases is limited, since neither the respiratory volume nor the pulmonary oxygen is replenished (Suthers & Goller 1997).

The limit forcing an individual to switch from mini-breaths to pulsatile expiration is probably determined by the mechanical properties, like mass and compliance of the thoracic and abdominal structures that must oscillate at the frequency of ventilation. Canaries (18g) reach this limit at about 30 syllables/seconds, the larger cardinals (40 g) at about 16 syllables/seconds. With pulsatile expiration canaries can sing trills containing up to about 70 and cardinals 30 syllables/seconds, respectively (Hartley & Suthers 1989; Hartley 1990; Goller & Suthers 1996a). Nothing is known about a cross-fostered species singing a hetero-specific song. But the available data made me wonder about the limits of vocal imitation in house sparrows.

1.5.3 DIFFERENCES BETWEEN LEFT AND RIGHT SYRINX

The oscine syrinx is functionally a two-voice organ, each side separately innervated by the ipsilateral side of the brain (Konishi 1985; Vu et al. 1994; Suthers et al. 1996; Yu & Margoliash 1996). Independent activation of the left and right ventral muscles enables all oscines to use the two sides of the syrinx as independent sound sources ("two-voice-theory"; Greenewalt 1968): the bird may sing with one side, switch back and forth between sides[14], or may generate two-voice syllables with both sides simultaneously. Those few species, whose song production has been studied in detail, show important differences in the way they use the two sides of their syrinx (for details see Suthers 1999). These inter-specific variations in syringeal use have apparently evolved to produce the different characteristic acoustic properties of species-specific song.

Left and right syrinx have somewhat different vocal registers and generate syllables with fundamentals in different though overlapping frequency bands (for an overview see Suthers 1999). However it is not clear whether these differences in frequency range reflect lateral differences in motor control or anatomical asymmetries in the sound-generating structures, i.e. that the right side is slightly smaller in some species (Luine et al. 1980). Thus consequences for vocal imitation are not available yet.

1.5.4 THE ROLE OF THE VOCAL TRACT IN SOUND PRODUCTION

The sound, generated in the syrinx in connection with the respiratory system (Hartley 1990; Suthers 1994), is modified during its passage through the vocal tract - composed of the trachea, larynx, and the beak including the tongue (Podos 2001) - before it is emitted as song. Frequency-dependent acoustic interactions, determined by the dimensions or shape[15] of the vocal tract, may significantly change the amplitude spectrum of the vocalization by allowing some frequencies to pass, but attenuating others. The role of the vocal tract in avian sound production was first demonstrated by analysing songs produced in a helium-enriched atmosphere (Nowicki 1987). Subsequent studies (e.g. Westneat et al. 1993; Fletcher & Tarnopolsky 1999) contradict the classical idea of the syrinx as the only sound producing organ. Not only does the songbirds' vocal tract act as

[14] As shown in northern cardinals, for example, the coordination between the two sides of the syrinx is so precise that the change from one side to the other may not be evident either to the human ear or in the spectrogram (Suthers 1999).

[15] The trachea can be approximated as a tube having a resonance determined by its length (Suthers & Goller 1997)

an acoustic filter, but its filter characteristics are actively coordinated with the output of the syrinx; this is done by cranial movements of singing birds, which modify the physical configuration of the vocal tract, and by prominent beak movements, which often accompany song (Suthers et al. 1999).

Birds posses a so-called kinetic skull. This means that not only the lower jaw, but also the upper jaw rotates around its kinetic joint with the braincase (Bühler 1981; Dubbeldam 2000) during beak opening. The upper and lower jaws are anatomically and functionally separate kinematic units (Bühler 1981). Independent control of simultaneous movements of upper and lower jaw increases the velocity of beak movements (i.e. increases the possibility for fine control during song in oscines; Hoese & Westneat 1996). And with elevated upper jaw less force is required to open the lower jaw (Nuijens & Bout 1998; Bout & Zweers 2001). In fact, in most of the note types analysed from singing swamp sparrows *(Melospiza georgiana)*, white-throated sparrows *(Zonotrichia albicollis)* and Bengalese finches *(Lonchura domestica)*, beak opening (or beak gape, i.e. the distance between the tips of the upper and lower mandibles) was positively correlated with sound frequency; this means an increase in beak gape is accompanied by an increase in sound frequency (Westneat et al. 1993; Podos et al. 1995), but is not strongly correlated with sound amplitude (Westneat et al. 1993). In singing northern cardinals (*Cardinalis cardinalis*) each syllable type was accompanied by a stereotyped pattern of beak gape which in turn positively correlated with the syllable's fundamental frequency (Suthers et al. 1996). But beak gape does not automatically indicate a given sound frequency. In developing the adult note structures, young song sparrows arrive at the adult frequency range already up to mid-plastic song, while the gape-frequency-correlation significantly increases only from the mid-plastic song stage onward (Podos et al. 1995). This suggests, that juveniles produce most of the syllables with modifications on syringeal level. Taking the findings of Westneat et al. (1993) and Podos et al. (1995) together the impression arises, that for the production of a given produced frequency the syrinx and the beak work together, but in juveniles the emphasis lays mainly on the syrinx, in adults on the beak.

Song production is of course constrained in an absolute sense: birds of a given size are physically unable to produce sounds outside of a given frequency range, sound duration

and repetition rate (e.g. Ryan & Brenowitz 1985; Nowicki et al. 1992b). Already Wallschläger (1980) found a correlation between mean song frequency and body weight, showing that bird vocalization is highly dependent on anatomical (length of trachea, resonance capacity, etc.) as well as physiological factors (respiratory rate). He suggested a possible evolutionary link between the ecological niche, the birds' morphology and their song performance. A growing body of literature elucidates that the vocalization in songbirds meets physical limitations (Podos 1996), for instance in that the evolution of trill structure can be limited by motor constraints on vocal production (e.g. in emberizidae; Podos 1997), and that vocal performance capacities vary as a function of vocal tract morphology, in particular of beak morphology (Nowicki et al. 1992a; Podos 1997), due to a suggested intrinsic trade-off between force and velocity in jaw biomechanics, as large (strong) jaws are less able to perform the rapid movements required for the production of certain types of songs (Podos 2001).

1.6 THE BIRD OF THE STUDY: THE HOUSE SPARROW

The house sparrow *Passer domesticus* has the widest natural distribution of any land bird species (Summers-Smith 1988; Bezzel 1993). It belongs to the suborder 'songbirds' (passeri resp. oscines) within the large order of 'sparrow birds' (passeriformes). *Passer* together with further 6 genera constitute a separate family called passeridae (Bock & Morony 1978; Sperl 1988; Bielfeld 1992; Glutz von Blotzheim 1997)

1.6.1 DESCRIPTION

House sparrows tend to be sexually monomorphic in morphological features like hand limb size, cranial morphology (especially the beak), perhaps the legs (Selander & Johnston 1967), and yearly average body weight (Folk & Novotny 1970). Slight differences are found i.e. in lacrimal breadth, height of mandibular (Ruprecht 1968), pectoral and wing bone size (Johnston 1973). Several studies found significant direct correlation between total body weight and wing length for both sexes (Grimm 1954; Löhrl & Böhringer 1957; Folk & Novotny 1970). The secondary sexual characters of the house sparrow are clearly dimorphic (Keck 1932; Johnston & Selander 1973).

Males in warmer regions reach a length of 140 mm while members in the north grow to 180 mm (Summers-Smith 1988). During the breeding season the male's chin, throat and chest base - all together called male bib - turn deep black (see Fig. 1.3). The size of the

male bib is independent of the genetic father, but depends on hatching early in the year (spring) and on the rearing father (Griffith et al. 1999). Because of the grey edges of the feathers (Bezzel 1996) the bib is less clearly visible during winter. Interestingly bill colour depends on testosterone (Keck 1932; Nowikow 1935), changing from horn to black towards the breeding season (see Fig. 1.3), while plumage colour - of both sexes - is largely independent of steroids, but influenced by thyroxin (Witschi & Woods 1936).

Females show a more simple plumage than males. The bill becomes darker in breeding season and a few females have completely black bills (portrait of a female house sparrow: see chapter 6.3).

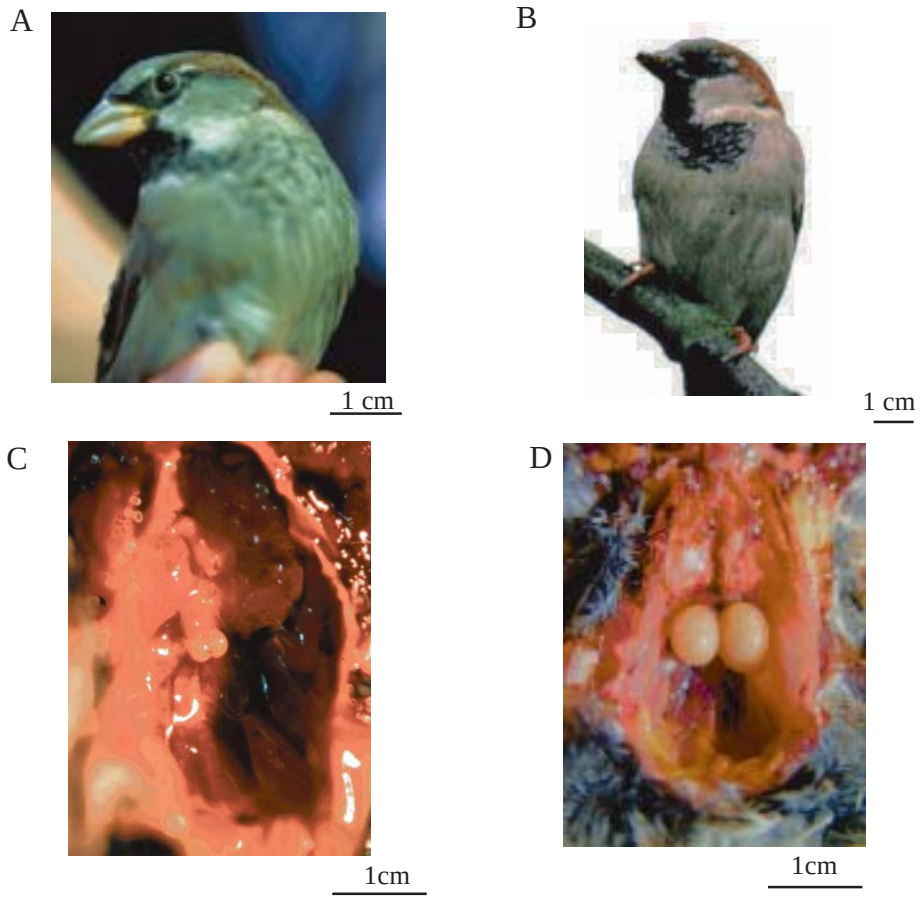


Fig 1.3: During the breeding season, when gonads increased 200-fold (D), the male's chin, throat and chest base - all together called male bib - turn deep black (B). Outside the breeding season, when gonads are small (C) and testosterone levels low, the male beak turns horny (A).

1.6.2 BREEDING BIOLOGY

Pair formation often begins in autumn (Schifferli 1974). Most pairs stay together throughout their adult life (Leugers 1997), though polygamy does occur (Clark 1903; von Boxberger 1930; Brackbill 1969). Individuals claim a small region around the nest (Bent 1958) as a territory. But this does not prevent them from communal nesting similar to weaver bird colonies (McGillivray 1980; Summers-Smith 1963). Generally a given pair occupies a nest site for successive clutches (Summers-Smith 1963).

A clutch contains two to eight eggs, but five is most common (Bent 1958; Anderson 1975; Seybold 1983). Freshly laid eggs weigh between 2.1 and 3.3 g (König 1970). Egg sex was random with respect to laying order (Cordero et al. 2000). The female house sparrow incubates, being replaced by the male only for a brief time for her feeding and drinking (Schifferli 1978). Stable incubation takes 11 to 13 days (Witherby 1949; Novotny 1970), starting with the third or last laid egg (Bent 1958; Novotny 1970). Both parents take an about equal share in brooding the hatchlings (Daanje 1941; but see Weaver 1942).

Duration of the so called “brooding in nest” fluctuates between 12 up to 18 days (Weaver 1942; Summers-Smith 1963; Novotny 1970). After leaving the nest fledglings will still be predominantly fed by the parents up to about day 30 when they become independent.

1.6.3 DESCRIPTION OF THE HOUSE SPARROW’S NATURAL SONG

“Every one knows that the common house sparrow, when in a wild state, never does anything but chirp” (Barrington 1773). Given that simple description it is no surprise that there is little enthusiasm about house sparrows singing abilities. Their voice was described as a monotone, poorly structured, noisy (Witherby 1949) loose sequence of often harsh calls (Howard 1954; Cramp & Perrin 1994), which can be uttered in different situations. Deckert (1969) – like Daanje (1941) – identified a repertoire size of about 25 elements, grouped according to 13 different situations (for detailed description see Summers-Smith 1963, Cramp & Perrins 1994). The house sparrow seems to use only a limited number of elements to attain an “extensive range of calls used at nest and elsewhere” (Cramp & Perrin 1994) by highly flexible element structure (with respect to frequency and duration).

In communal roosts there is often a considerable outburst of social vocalizing. Places where house sparrows gathered for roosting were known as “chapels” in London in the

19th century. Chorusing in the morning is usually much less conspicuous with little social vocalizing; there is more monotonous chirping mixed with several elements of the repertoire (Glutz von Blotzheim 1997). House sparrows have different alarm calls for aerial and ground-predators (details see Hull 1998). And they produce wing burring as instrumental sounds when starting and landing.

House sparrows use low husky flight-notes in flocks, which are very variable and hard twittering (Bergmann & Helb 1982). It occurs during excitement as does a less metallic twittering, which can develop into a fairly regular song of 8-10 notes, with some upcoming of rhythm (Witherby 1943). During individual and communal courtship display males' syllables become more variable. Males and females solicit for copulation with a low voice, nasal sound.

Best known is the male's song or chirrup call, a lasting sequence of rhythmically repeated mostly disyllabic syllables uttered in 1-2 s intervals mainly near the nest ("nest call"). Unmated males sing it daily for several hours, especially in spring. Singing is accompanied by synchronous beak movements and ruffling of the throat and chest feathers (Glutz von Blotzheim 1987). A variable syllable structure encodes the singer's individuality as well as its present motivational state.

The birds often pre-positioned a broad banded, overtone rich impulse that merges into the rising element (additional overtones make the element sound harder). Indeed this scheme is open for much more variable and complex changes. Variations can occur in repetition rate of trill spikes (in chapter 3 called 'vibratos') and formant composition.

Nivison (1978) in his thesis aimed among other "to investigate how [the sparrows] accomplish complex social behaviour with only a few auditory elements" . Using digital spectrograms he found 1) four major groups of cheeps based on the number of peaks, which seems to be an important factor in house sparrow's vocalization, and 2) basically three groups of calls based on a) mate and colony interaction, b) irritation, agitation or conflict and c) alarm calls. With the possible exception of three calls all other calls of the house sparrow contain at least one harmonic. It has to be assumed that house sparrows can control the number of harmonics they emit. The birds can change the meaning of a call by altering its formant's composition and by emitting it in different contexts (Smith

1963, 1965). But there are also 'discrete calls' (Sebeok 1962), for example the contact call, that conveys a fixed message. Nivison (1978) summarized the sparrow song as follows: "context, harmonics, repetition (tonic communication), figure duration, and grading are all methods used by the house sparrow to increase the vocal repertoire and develop a more complex communication system yielding a greater variety of messages, including mood or motivational states as well as discrete information".

1.6.4 HOUSE SPARROWS IMITATING FOREIGN SOUNDS

Teaching birds to sing was a popular and lucrative sport in the 18th century. In addition to well-known singers like the nightingale and canary, Hamersley's collections of bird-tunes (1714, in Godman 1954) also provided a non trivial melody for the house sparrow, and stated that house sparrows "learn any song if short if taken very young out of the nest" (Godman 1954).

Moreover, for a long time it had already been known that the house sparrow was able to imitate foreign sounds. Barrington (1773) performed an experiment to demonstrate the learning ability of house sparrows. He took a common sparrow from the nest when fledged and educated him with a linnet. By accident the young individual also heard a goldfinch, thus the sparrow's song became a mixture of linnet and goldfinch songs. Barrington summarized "though the scholar imitated the passages of its master, yet the tone of the sparrow had by no means the mellowness of the original". 100 years later Witchell (1896), following the singing of a male house sparrow for several years concluded that "if reared under birds of another species in a cage, the sparrow has their notes, and not sparrow notes, though he retains the sparrow tone of voice "(cited by Conradi 1905). Witchell (1896) in addition mentions sparrows imitating the alarm-cry of starlings, of blackbirds, the whistle of the chaffinch and even the song of a skylark. Coupin (1901) claimed that his house sparrow, caged next to a box with grasshoppers, imitated the stridulation of the grasshoppers and produced a polyglot mixture of the insects' and of other birds' songs.

Some sparrow male individuals are reported to produce in the wild the song and calls of the tree sparrow (Daanje 1941; Hansen 1975 cited by Glutz von Blotzheim 1997), the song of a whitethroat (Bent 1958) and the greenfinch call, this one also perfect in tune (Huber 1983).

The most famous house sparrow seems to be ‘Clarence’ described by Clare Kipps (1956a). Clarence’s range and variety of notes and calls must have been remarkable. The list of sparrows imitating foreign birds’ song increases when one takes into account sparrows housed with other birds in aviaries (e.g. Dost 1954).

1.6.5 CANARY-LIKE SINGING HOUSE SPARROWS

Most reports of house sparrows singing foreign species songs concern their imitation of canaries. Ernest Thompson Seton (1901, cited in Bent 1958) mentioned in his book “Lives of the Hundreds” a sparrow who produced “a loud sweet song, much like that of a canary”. Conradi (1905) seems to be the first who wanted to document clearly the house sparrow’s imitation ability, when canaries hatch the sparrow eggs and rear the young. Most of his sparrow hatchlings died or were crippled. One bird was only able to produce a “violent, confused song which consists of rapid repetition of single notes and which was not very musical but rather harsh”, while two others “imitated the canary perfectly except that their voice did not have the musical finish“. Surprisingly, when the two canary singing house sparrows were placed close to a window, where they could hear wild sparrows, they produced only sparrow chirps; but they switched back to produce canary songs after being placed again in a room with canaries. Sanborn’s sparrow (Sanborn 1932), unlike Conradi’s good singer, did not learn the canary song but produced ”merely a rather continuous succession of sparrow chirps or trills” (Sanborn also failed to train other birds to sing foreign songs!). Ten years later Stoner (1942) wrote about a hand-reared house sparrow, that had ”acquired a remarkable proficiency in singing ability through the medium of two canaries which were his companions – in separate cages – for about six years. [The sparrow’s] imitations of the ‘rolling´ notes of the one and the ‘chopping´ notes of the other were sometimes well done as to deceive even his mistress”.

The remarkable proficiency of house sparrows to produce the canary trill was often reported from captivity (Heinroth & Heinroth 1926; Stoner 1942; Radtke 1961; Wotkyns 1962; Schröder 1964; Bergmann et al. 1983), but not from wild house sparrows (Radtke 1961). Barrington (1773) argued this is because young house sparrows listen only to their parents’ notes.

The German Philosopher Immanuel Kant (1803) was the first who realized the scientific potential of house sparrows singing the canary song, in particular for the existence of non-genetic traditions in animals.

1.7 AIMS OF THE WORK

The aim of my work was to study how far house sparrows can imitate the complex canary song; and then to analyse possible neuronal differences between canary- and sparrow-like singing sparrows. In particular I investigated the following problems:

(1) Is the house sparrow able to sing the most characteristic feature of the canary song, the tours? If yes, how similar are the original and the imitation? (Chapter 3);

(2) Does complex song learning result in measurable differences in brain structures already known to be sensitive to intra-specific individual song differences? (Chapter 4);

To get a more comprehensive (integral) view on possible correlations between (1) and (2), I controlled for possible side effects from my raising routine (Chapter 2, 4), for potentially elevated androgen levels (Chapter 5) and for morphological constraints (Chapter 6).

2 INFLUENCES OF THE RAISING ROUTINE ON THE EARLY DEVELOPMENT OF YOUNG HOUSE SPARROWS

2.1 INTRODUCTION

The voice of a house sparrow will barely encourage a naïve listener to classify him as a songbird. But this underrated songbird is reported to learn melodies taught by sopranino (treble) recorder (Mears 1717, in Godman 1954) and piano (Kipps 1956) or to sing like greenfinches (Huber 1983) and canaries (Kant 1803).

To test Kant's assertion, that there are canary-like singing house sparrows (chapter 3), and to study possible neuronal consequences (chapter 4), I raised sparrow young in canary nests. Sparrow parents feed their young during the first 8 - 10 days insects only and then change to a mixture of seeds and insects (Pinowksa 1975; see Fig. 2.1), while canaries are seed eaters throughout life.

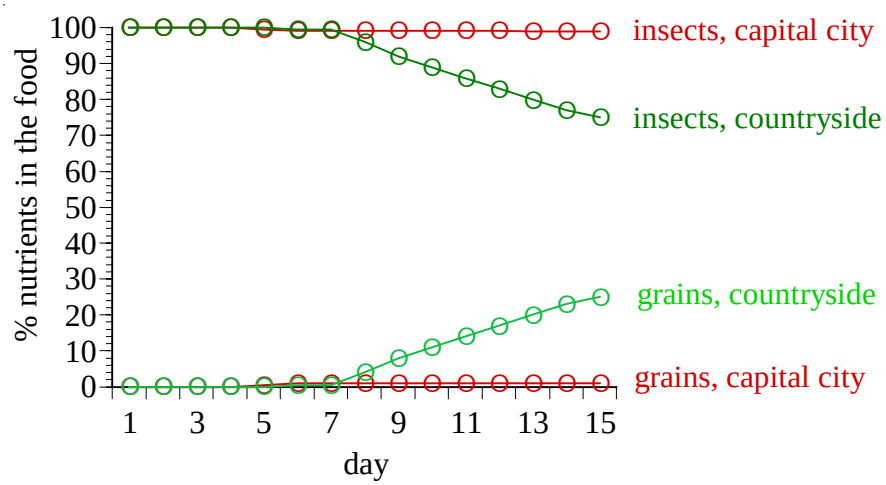


Fig. 2.1: Percentage of animals and plants in house sparrow nestlings' food in two different biotopes (capital city: red; countryside: green) (adapted from Encke 1965).

Thus I had to feed young house sparrows in canary nests additional food (mealworms, grasshoppers and bee maggots) to guarantee a house sparrow specific minimum of protein. This manipulated feeding regime could change the developmental conditions of canary-fostered young in relation to sparrow-raised house sparrows a) either to the better by additional food or b) to the worse by low quality food due to a higher proportion of seeds but lower proportion of protein. An increased growth rate, possibly indicative of better supply, could lower constraints for cell proliferation and result in an improved physiological, morphological or/and motivational condition at the time of song learning

which in turn may lead to a more elaborate song production. A reduced growth rate (i.e. lower growth rate constant (K), reaching the point of maximal growth at a later day), possibly indicative of a shortened supply, could have the opposite effects. The house sparrow indeed displays, to some extent, a labile growth rate[1] (North 1973) resulting in a prolonged nestling period under poor food conditions (Lepczyk & Karasov 2000).

To decide whether singing abilities in canary-raised house sparrows can be explained by privileged developmental conditions, I compared hatching weight, growth rate (point and day of maximum growth), fledgling weight and fledgling age for house sparrows bred in captivity and raised either by their own or by canary foster parents.

2.2 METHODS

2.2.1 ANIMAL SUBJECTS

All house sparrows, *Passer domesticus domesticus,* were bred in our institute. Sparrow clutches contained 5, seldom 4 eggs. Wild house sparrow hatchlings weigh 2.0 – 3.1g (Novotny 1970; Schifferli 1974) and are completely naked (without natal dune). The bill shows bulges on both sides (Fig. 2.1A), which change from white to lemon-yellow by the fourth day after hatching (details see Weaver 1942).Weight of young increases about two grams per day during the first thirteen days (Weaver 1942; Blem 1975a; Fig. 2.4).

As foster parents I used domestic colour and song canaries, *Serinus canaria.* Male and female canary parents feed their young with soaked seeds from their crops. Canaries start breeding in March and, with nest boxes available, may continue to lay eggs until August. A canary clutch contains 4-6 eggs laid one per day. While wild canaries start incubation after the last egg is laid, domestic canaries start with the first egg. Canary young hatch after about 13 days of incubation. Canary hatchlings have dune feathers on their back and head (Fig. 2.2A), and weigh about 1.4 to 1.6 g. They posses a bill with sharp edges, typical for seed eaters, without bulges on either side. Around day 20 post hatching young of both species will leave the nest and are still fed predominantly by the parents up to about day 30 when they become independent.

[1] A flexible growth rate, i.e. a plastic developmental program (Schmalhausen 1949) is typical for aerial insectivores, whose food supplies are unpredictable in time and space (Konarzewski & Starck 2000). Labile growth rates are documented especially in gallinaceous birds (Schew and Ricklefs 1998) and swallows/martins (Brzek and Konarzewski 2001).

2.2.2 AVIARIES

I kept two house sparrow groups, both with five females and five males. They all were hatched in captivity in May 1998. Each group lived in an aviary with an inner and an outer compartment. The inner compartment contained wooden perches and fresh branches, its floor was covered with sand**.** The outside compartment contained small living trees or thicker branches with horizontal twigs; the floor was covered with shredded bark. A water bath was available throughout the year. For breeding we supplied wooden nest-boxes as used for budgerigars (23 x 15 x 14.5 cm^3) on the walls of the inner sparrow compartment. Coco-fibres, dry mosses, chicken and duck feathers, horse hairs, straw and dried grass as nest materials were scattered on the floor. The birds used mainly the coco fibres for the outside of the nest and preferred mosses and hairs for the inner lining.

Outside the breeding season canary females and males were housed in separate aviaries, each comprising an inner and an outside compartment, furnished like the sparrow aviaries. During the breeding season male and female canaries were united and kept in five aviaries containing 4, 5, 6, 6 and 10 pairs respectively. I only used those females as foster mothers who either did not leave the nest (Fig. 2.2B) while I was present or returned straight to the nest after I had left the aviary. The aviaries were acoustically isolated. Three canary groups lived in two-compartment aviaries, as described, the two remaining groups inhabited inner compartments only. As a nest basis we offered them so called 'Kaisernests´ (plastic baskets: 11.2 cm, depth 5.3 cm; wired cube: 11.2 x 11.4 x 12 cm^3). All birds were offered white cotton fibres (Scharpie weiß) and various mosses as nest material.

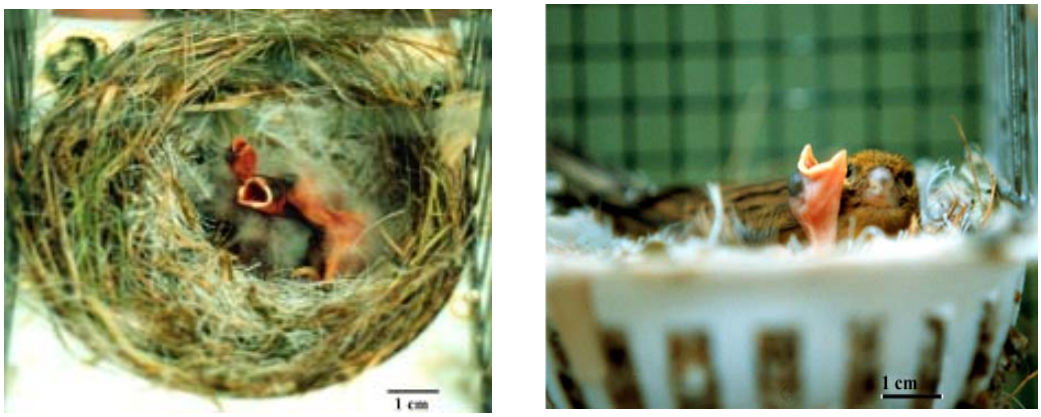


Fig. 2.2: two days old house sparrow hatchlings in canary nests. Left: the sparrow (middle) is larger as his canary foster siblings of the same age; right: a begging young sparrow and his (tame) female canary foster parent. In B the back side of the wired cube of the 'Kaiser-nest' is visible. For a detailed description of the young, see text.

2.2.3 FOOD

Free-living *house sparrows* are both opportunists and generalists. Their basic food includes several kinds of grain, seeds of grass, herbs and weeds. In addition they take berries, fruits, buds (Deckert 1969) and other green parts of plants. During the breeding season when feeding young the proportion of insects (arthropodes) and their larvae rises to a minimum of 50% of their food, often up to 70%. In fruit gardens the insect proportion can reach 95.5% (Deckert 1969; Encke 1965).

In the non-breeding season we tried to cover the wide spectrum of adult wild sparrows' food by using a commercial mixture of grains for canaries and forest birds, salad, cucumber, grated carrots, pieces of fruits (apple, orange, banana), and berries. Mealworms and crickets were offered every second day. During breeding time, between April and August, we enriched the parents' menu, offering a 1:2:1 mixture of fat-, honey- and parakeet's food (Aleckwa Tiernahrung, Postfach 25, D-67163 Waldsee) with some dog's flakes added. We also offered canary rearing-food, mealworms and/or crickets daily.

Throughout the year our *canaries* were daily fed a special canary grain mixture, sliced apple and cucumber, salad, and twice per week mealworms. During the breeding season we offered in addition daily germinated seeds, canary breeding food, mealworms and a special homogenated „insect-paste" (consisting of house crickets, mealworms, bee-maggots mixed with hard boiled egg yolk; see below).

All birds were regularly supplied vitamins and minerals, either mixed in the food or in water.

2.2.4 RAISING YOUNG HOUSE SPARROWS

2.2.4.1 BY THEIR SPARROW PARENTS

Three sparrow broods, each with three or four young, were raised by their own parents as a control group. During my nest inspection in the morning the parents waited in the outer compartment of the aviary until I had left and then immediately returned to their nests.

2.2.4.2 BY CANARY FOSTER PARENTS

To avoid a possible acoustic influence of the embryos while still in the egg, I transferred each sparrow egg on the same day it was laid to a canary nest. Whenever possible I used

a nest with at least 5 days old canary eggs, to compensate for the fact that sparrow hatchlings are bigger, grow faster and may endanger their canary nest mates. At the 5th day of incubation I checked the sparrow eggs with a small light for existing veins; an egg without any sign of development was replaced by a new one.

Although young house sparrows differ from young canaries in their outer appearance and their begging behaviour, the canary parents accepted them even in a mixed brood. A major problem resulted from the fact that canaries, although they like to eat the innards of mealworms, do not feed insects to their young; they feed them boiled yolk, however. I therefore enriched the food of canary parents with a freshly homogenised mixture of boiled egg yolk and insects (1/2 chicken-egg yolk mixed with 30 - 40 crushed cricket abdomina). That was sufficient for the young house sparrows if both parents cared for the young. Young sparrows that did not get enough food very soon became weak and stopped begging. I then fed them insects by hand, complementing canaries' provisioning. From days 1 to 5 I used to offer either the abdomen of a house cricket or half of a white mealworm every 30 – 45 minutes. I slowly lengthened the intervals up to 2 hours according to the nestlings' begging, age and developmental state. All young sparrows, even those hand-fed from their first day onwards, turned shy towards me for a while when the eyes opened. During that period it may take quite some time until they take the food offered. About this time (mean 10 days of age) additional feeding was terminated.

When about 12 - 14 days old the young sparrows left the canary nest. Although they began to take food by themselves with 17 - 20 days, they still were fed by the foster parents up to day 30. With that date I transferred them to cages (alone or with male canary foster siblings) or to other aviaries (e.g. if the fledgling was a female).

For song analyses I needed canary-reared males only. In the third[2] breeding season I could sex the hatchlings on day one or two (see 2.2.6 bird sexing). I grouped females together in one artificial nest and raised them by humans, while sparrow males were left in the canary nests. Nestlings were weighed when freshly hatched, and then daily between 7.00 – 7.30 am and 7.00 – 7.30 pm (this means that sparrow young were weighed in a 12 hours rhythm). The birds were housed in different buildings. To ensure that each bird

[2] In the first two years it was not possible in our facilities. To give the blood samples to an external lab, however, would have needed too long time.

was weighed at a definite time, I followed a constant route (of about 30 minutes) from one aviary to the next. All young were weighed by myself with the balance Kern 162-41 (to measure to the nearest 0.1g) until they fledged.

2.2.5 BIRDS USED FOR LATER ANALYSES

As in the first year (1999) there was no indication that cross-fostered female sparrows produced canary-like songs, the study of song, brain, hormones and vocal tract focuses mainly on males. Individuals who eventually died either during the nestling phase or later were excluded from growth analyses. I obtained canary-raised house sparrows who learned the canary song (especially the canary-typical tours) as well as birds who did not, although some had been raised by the same foster parents as the tour producing ones and thus had the same opportunities for learning. From the control group (sparrow-raised young) I selected first hatchlings, if males, being the largest in the clutch to parallel the fact that house sparrows are the largest young in the brood of canaries. (A detailed description of groups is given in chapter 3).

2.2.6 BIRD SEXING

The procedure followed an universal method for molecular sexing of non-ratite birds (Fridolfsson & Ellegren 1999). This method is based on the detection of a constant size difference between two introns, called CHD1W and CHD1Z. Blood samples (30µl) were taken from the wing or foot vein with a 50µl capillary and stored in the refrigerator in Queens lysis buffer for at most 24 hours. DNA was extracted using the GFX^{tm} blood extraction method (Extraction kits, GFX Genomic blood DNA purification, Nr. 27960301). All PCR reactions were performed

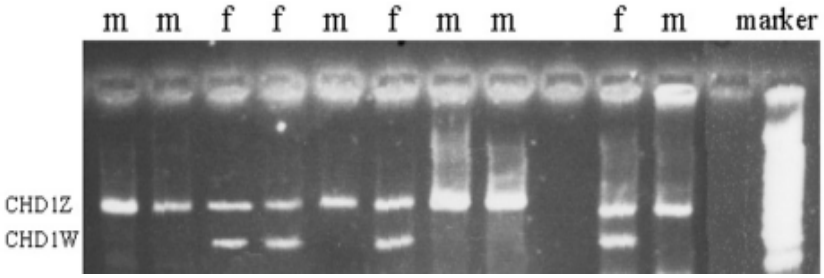


Fig. 2.3: DNA sex identification of birds using PCR amplification of the CHD1 genes followed by 3 - 4% agarose electrophoresis. The primers 2550F and 2718R give one fragment in males (CHD1Z) and two fragments in females (CHD1Z and CHD1W). Females of some species sometimes also show only one fragment (CHD1W) (Fridolfsson & Ellegren 1999), but this never happened in my samples. The sex of each house sparrow individual is indicated by f = females (two bands) and m = male (one band).

in 10µl volumes, containing 5µl DNA-sample and 9.5µl PCR-mix on Gene Amp PCR System 9600 and Perkin Elmer PCR System 2400. Two different primer sets were used: CHD3007 & CHD 3112 (Ellegren & Fridolfsson 1997) or 2550F & 2718R (Fridolfsson & Ellegren 1999; DNA sequences are given in Appendix 1). Also the thermal profile followed Fridolfsson & Ellegren (1999). 0.8µl of PCR products were separated in 3% agarose gels, run in standard TBE buffer and visualized by ethidium bromide staining (Fig 2.3).

2.2.7 COMPARATIVE STUDIES OF GROWTH

The postnatal period (from hatching to adulthood) is a phase of body growth and learning. Postnatal developmental time can be described using growth functions with postnatal growth rate as a function of adult body size (Starck 1993). Data are usually presented as the weights recorded each day throughout the youth period (Ricklefs 1979). In most extant animals as well as for example in dinosaurs, mass changes with respect to age show a sigmoidal pattern (Erickson et al. 2001). Thus growth curves start with a slowly, then rapid rising part followed by a period of slowing growth as the chick approaches adult weight. Based on comparative analysis of growth functions in birds, Ricklefs (1967, 1983) suggested a scale of growth units based on the time required to increase body mass from 10% to 50% of asymptotic size. This growth function is described by the logistic equation: **W(t) = A/(1 + exp(-k*t)).**

This is one of three most widely used mathematical descriptions of postnatal avian growth (Starck 1993). The logistic equation adequately describes the growth of most avian species:

W(t) is the weight at age *t*;
A is the asymptote (the 'final' weight) of the growth curve;
k is the growth rate constant; and
$t_{i,}$, the inflection point, is the age at maximum growth.

The rate constant (k), whose unit is days^{-1}, is an overall measure of rate of weight increase, directly comparable between species. A comparison of the analyses of exponential growth among the major groups of extant vertebrates indicates that growth rates generally increase with respect to body mass and that each clade has a characteristic rate (Case 1978). Growth rate constants of fitted logistic equations vary from 0.024 days^{-1} in the Laysan albatross *(Diomedea immutabilis)* and domestic turkey *(Meleagris gallopavo)* to 0.680

days^{-1} for the painted redstart *(Setophaga ruticilla)*. The house sparrow is expected to lie in between.

2.2.8 STATISTICAL ANALYSES

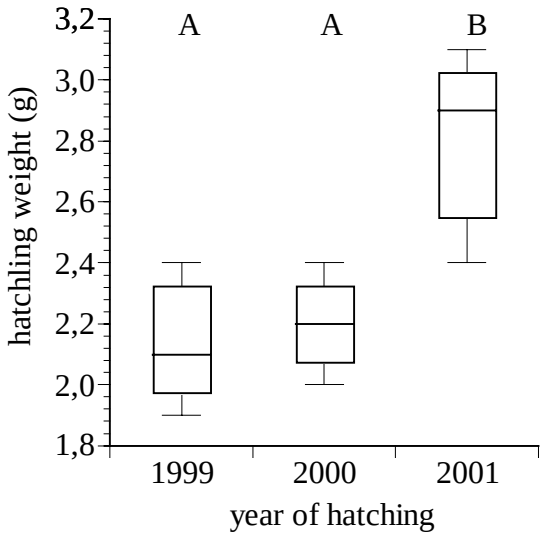
For statistical analyses I used Systat 9.2 (Systat Software Inc., Richmond, CA) and SSS for Windows 2000. First, all data were tested for normal distribution (Kolgomorov-Smirnov Lilliefors test) and equality of variances (Levine test). If both tests did not show significant differences ($p > 0.05$), one-way-ANOVA, followed by Bonferroni post-hoc-test, was performed to detect differences between several groups, or the pooled variances t-test to detect differences between two groups. When the assumption of equal variances (but not distributional shape) was violated, I conducted the separate variances t-test to compare two groups.

To compare not normally distributed data sets (hatching weight) the Kruskal-Wallis-Test for independent data sets was used. All tests were two-tailed and the significance level was $p = 0.05$. Usage of statistical tests followed Conover (1980), Sokal & Rohlfs (2000), and Lamprecht (1999). If multiple analyses were conducted with the same data sets (e.g. hatching weight) the significance level α was adjusted following the sequential (sequ.) Bonferroni method (Rice 1989).

2.3 RESULTS

2.3.1 HATCHING WEIGHT OF HOUSE SPARROWS

In 2001 the weight of hatchlings (males and females) was significantly higher than in the preceding years, while for 1999 and 2000 hatchling weight did not differ significantly ($n = 113$, Kruskal-Wallis-Test, $H = 81.252$, $p << 0.001$, Dunn's Test, sequ. Bonferroni post hoc $\alpha = 0.013$) (Fig. 2.4). The result also holds for both groups of birds, sparrow- and canary-raised sparrows, selected for further analyses (sparrow-raised: $n = 28$, Kruskal-Wallis-Test, $H = 19.503$, $p << 0.001$, Dunn's Test, sequ. Bonferroni post hoc $\alpha = 0.025$; canary-raised: $n = 38$, Kruskal-Wallis-Test, $H = 25.915$, $p << 0.001$, Dunn's Test, sequ. Bonferroni post hoc $\alpha = 0.016$).



Hatching weight (g)

year	1999	2000	2001
n	32	35	46
maximum	2.4	2.4	3.1
3. quartile	2.3	2.3	3.0
median	2.1	2.2	2.9
1.quartile	2.0	2.1	2.6
minimum	1.9	2.0	2.4

Fig. 2.4: Hatching weight (g) of house sparrows bred in captivity in subsequent years (1999-2001). Data are presented as box plots showing median, 1st and 3rd quartiles, minimum and maximum; in addition the absolute values are given in the included table. Similar letters above boxes represent non-significant different medians from *post hoc* multiple comparisons.

2.3.2 GROWTH RATE OF SPARROW YOUNG

I compared the growth rates of canary-raised (n = 38) and sparrow-raised (n = 28) male young, using morning and evening data separately. Growth rates based on morning weight did not differ significantly between years (1999 - 2001) neither for canary- nor for sparrow-raised young (canary-raised: one-way ANOVA, $F_{2,35} = 0.246$, $p = 0.783$; sparrow-raised: one-way ANOVA, $F_{2,25} = 0.009$, $p = 0.992$); the same was true when using evening data. Thus year cohorts were grouped together.

2.3.2.1 GROWTH CURVES OF SPARROW NESTLINGS

Growth curves from literature (Weaver 1942, Blem 1975a; Fig. 2.5) and from my birds (Fig. 2.6) were nearly identical. Sparrow- and canary-reared house sparrows weighed about the same in the morning of a day. Until day 10, however, both weighed less than data from literature suggest (Fig. 2.6a, morning). Growth curves using evening weight fit better with data from literature indicated by one reference (Blem 1975a). Sparrow young raised by their parents were clearly heavier in the evening of a day than canary-raised young (Fig. 2.6b, evening).

Table 2.1: House sparrow data from Weaver (1942) , Blem (1975a) (for details about growth curves of different body parameters see Novotny 1970)

	Weaver 1942	Blem 1975a	
day	**weight [g]**	**weight wild[g]**	**weight lab[g]**
1	2.8	3.0	3.0
2	4.8	5.0	5.3
3	6.9	7.5	6.6
4	10.2	10.1	10.0
5	11.7	12.1	12.9
6	13.8	14.9	14.0
7	16.4	17.1	16.6
8	18.0	18.7	18.0
9	20.3	19.4	19.3
10	20.4	21.2	21.3
11	22.7	22.1	21.6
12	22.7	23.1	22.7
13	25.6	24.1	23.8
14	25.2	25.5	24.5
15	23.9	26.3	25.4
16	26.0	24.9	24.0
17	22.5	24.0	23.8

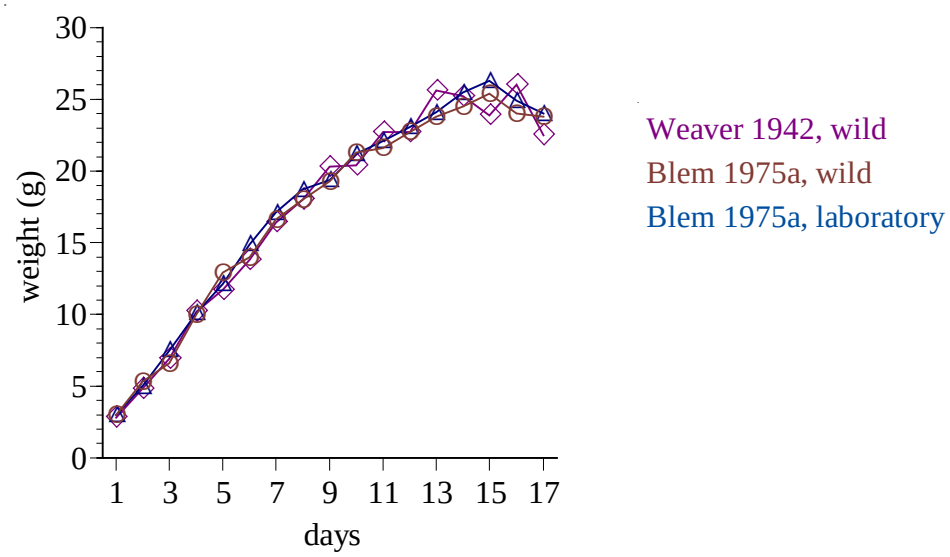


Fig. 2.5: Growth curves of house sparrow young using data from the literature. Data are given in Table 2.1.

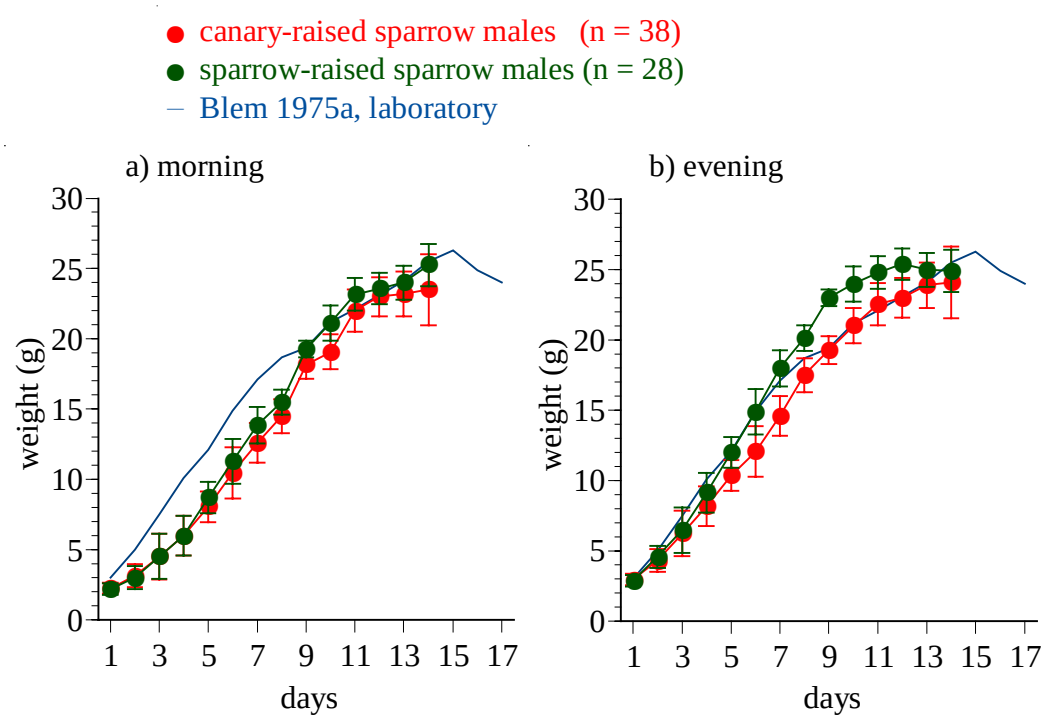


Figure 2.6: Growth curves of canary- and sparrow-raised house sparrow young based on a) morning or b) evening weight. My data (red and green curves) are presented as mean (weight) ± sem and data from Blem 1975a (blue line) serve as a reference (data values of Blem 1975a are shown in Table 2.1).

2.3.2.2 POINT OF MAXIMUM GROWTH (K)

In the evening sparrow-raised individuals were significantly heavier than canary-raised house sparrows (separate variance t-test, t = -3.335, df = 44.7, p = 0.002, sequ. Bonferroni post hoc $\alpha = 0.016$). But canary-raised and sparrow-raised males did not differ significantly in morning growth rate (pooled variance t-test, t = 0.003, df = 64, p = 0.998) (Fig. 2.7).

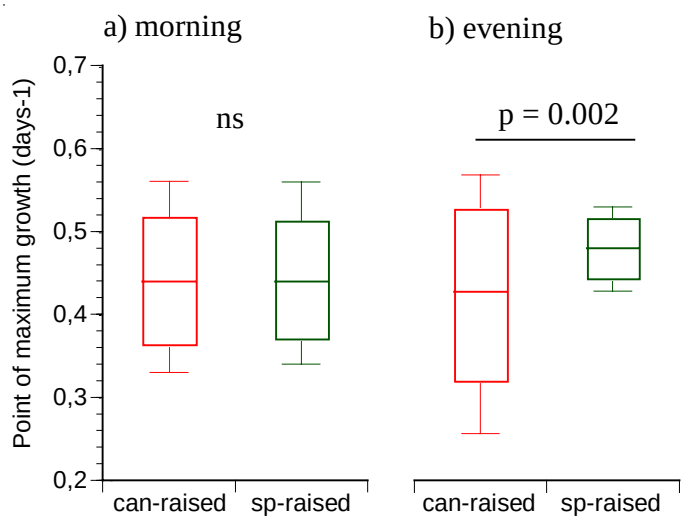


Fig. 2.7: Point of maximum growth of house sparrow nestlings raised either by canary (can) foster parents or by their sparrow (sp) parents, calculated from morning and evening weight. Canary-raised: n = 38, sparrow-raised: n = 28. P-values of the respective statistical tests (details see text) are presented in the graphs, ns = not significant. Data are presented as box plots showing mean ± sem, minimum and maximum values.

2.3.2.3 BODY MASS ALTERATION

Body mass gain during daytime was significantly higher in sparrow- than in canary-raised individuals (separate variance t- test, t = -3.048, df = 55.2, p = 0.004, sequ. Bonferroni post hoc $\alpha = 0.016$). But the two groups showed no significant difference in body mass alteration during the night (pooled variance t-test, t = 1.280, df = 64, p = 0.206) (Fig. 2.8).

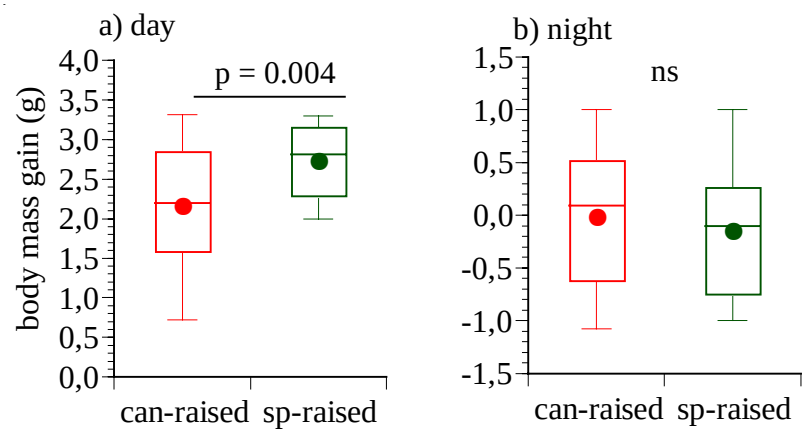


Fig. 2.8 Body mass alteration (g) of young house sparrows in canary (can) or sparrow (sp) nests during the day (differences between morning and evening) and during the night (differences between evening and the following morning). Canary-raised: n = 38, sparrow-raised: n = 28. P-values of the respective statistical tests (details see text) are presented in the graphs, ns = not significant. Data are presented as box plots showing median (line), mean (dot), 1st and 3rd quartiles, minimum and maximum values. (Although data show normal distribution, this type of graph was chosen to show the large range.)

2.3.2.4 DAY OF MAXIMUM GROWTH

Based on nestlings' weight in the evening sparrow-raised young reached the day of maximum growth significantly earlier than canary-raised young (pooled variance t-test, t = 3.180, df = 64, p = 0.002, sequ. Bonferroni post hoc $\alpha = 0.013$). However, the day of maximum growth was similar in both groups, if calculated with data of morning weight (pooled variance t-test, t = -0.513, df = 64, p = 0.610)(Fig. 2.9).

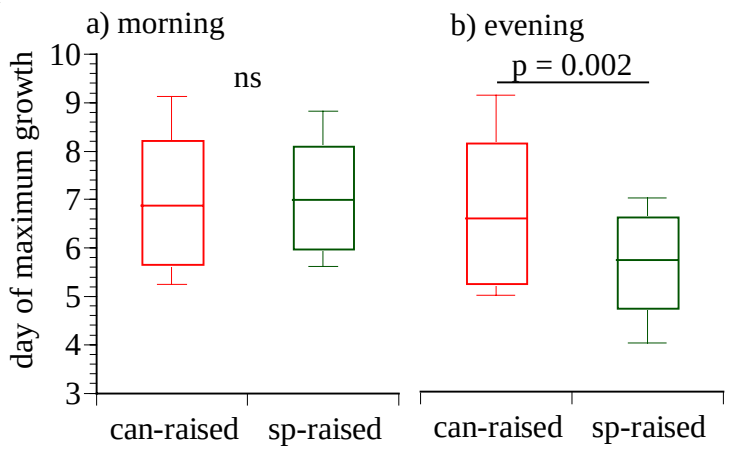


Fig. 2.9: Day of maximum growth of house sparrow nestlings raised either by canary (can) foster parents or by their sparrow (sp) parents, calculated from morning and evening weight. Canary-raised: n = 38, sparrow-raised: n = 28. P-values of the respective statistical tests (details see text) are presented in the graphs, ns = not significant. Data are presented as box plots showing mean (line) ± sem, minimum and maximum values.

2.3.3 AGE AND WEIGHT OF FLEDGLINGS

Canary- and sparrow-raised house sparrow young showed no significant difference in fledgling age (pooled variance t-test, t = 0.171, df = 64, p = 0.865) and in fledgling weight, although sparrow-raised fledglings tended to be heavier (pooled variance t-test, t = -0.956, df = 64, p = 0.055) (Fig. 2.10).

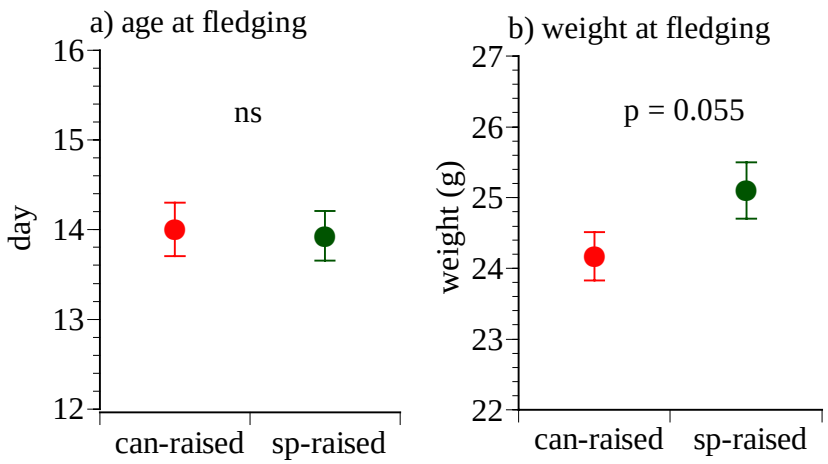


Fig. 2.10: Age and weight, when house sparrow young left the nests of their canary foster and sparrow parents. Canary-raised: n = 38, sparrow-raised: n = 28. P-values of the respective statistical tests (details see text) are presented in the graphs, ns = not significant. Data are presented as means ± sem.

2.4 DISCUSSION

In altricial passerines parental post hatching investment is much greater than the initial investment in eggs (Walsberg 1983; O'Connor 1984). Egg mass commonly varies intra-specifically in wild birds (Boag & van Noordwijk 1987; Perrins 1996). Embryonic development is constrained in different ways, e.g. by genetic factors that influence embryonic metabolic efficiency (Magrath 1992), as well as by nutriment absorption, gas exchange, amount of yolk and size of the egg (Starck 1998), in detail by the amounts of protein, lipids or essential vitamins and minerals present in the egg (Royle et al. 1999).

Our parental house sparrows provided with well-balanced food ad libitum throughout the years improved their physiological conditions such that they could afford a high parental investment already at egg laying; this resulted in the significantly higher hatchling weights of male and female neonates in 2001.

Food availability ad libitum, much above a minimum threshold necessary for normal post-hatching development, does not affect nestling growth because of preset limits to tissues' intrinsic growth capacities, once some properties of the egg initiated a specific developmental track (Ricklefs et al. 1998). This is compatible with the fact that hatching weight of our neonates did not influence growth rate, age/weight of fledging, singing ability (see chapter 3) nor brain morphology (chapter 4).

The genetically determined species-specific growth rate of the young balances factors favouring slower growth (e.g. rate at which energy and nutrients are required by the chick) against factors favouring more rapid growth (e.g. factors which cause mortality and competition of young; Lack 1968). Canary-raised and sparrow-raised young did not significantly differ in morning growth rate, suggesting that there is no factor shifting the balance to more rapid growth. Mortality by predators or weather conditions were excluded in our aviaries.

Based on morning weight I did not find any difference in growth rate or body mass gain within sparrow-raised house sparrow groups of always three to four siblings left in the parental nest. Also Seel (1969, 1970) found maximum feeding rates of house sparrows in broods of 3 young and only slight variation in individuals' weight within a brood. Sparrow-raised and canary-raised sparrows grew at the same rate. This is not self-evident. Canary-raised house sparrows, also faced with 2-3 (canary foster) siblings, can easily out-compete them: young sparrows are larger, grow faster and are heavier than their canary foster siblings. Thus canary-raised house sparrows may not be exposed to sibling competition as are sparrows in their parental nest. Furthermore, canary-raised sparrow young were fed additional food by humans. Nevertheless I could not find evidence for a better food supply of canary-raised young nor any support for a sibling competition situation in one of the groups. One can conclude that canary-raised sparrows did not grow under better conditions than sparrow-raised young.

Based on the evening weight, sparrow-raised young were significantly heavier than sparrow young raised in canary nests; this is because body mass gain during daytime was significantly higher in sparrow- than in canary-raised individuals. Therefore, when calculating growth curves using evening weights, the two groups differed in that sparrow-raised sparrows had a higher growth rate. This suggests that house sparrows in canary nests suffer from low quality food or food shortage respectively. That the two groups showed no difference in body mass alteration during the night suggests a 'catch up growth' during late evening (after light was switched off) and/or early morning (before light started). However the difference in the result calculated from morning and from evening weight remains puzzling. Young sparrows were weighed every 12 hours ± 10 minutes. Sparrow-raised young were the last to be weighed in morning as well as in the evening. If problems had been arising while feeding sparrows in canary nests, it could happen that young in sparrow nest were weighed with a latency of up to 30 minutes. On the

one hand this time could have been used by sparrow parents for feeding; on the other hand as weighing and feeding routine always starts at the same time in the morning, this possible time latency in the evening is missing in the morning. Another reason might be that sparrow parents feed better during the day (by higher rate of feeding and higher portion of protein) but stop with dawn, while humans continued to feed sparrows in canary nests until 8.30 pm. Furthermore, canary parents may start feeding earlier while house sparrows perform social singing. This 'nocturnal catch up' is consistent with the fact that young house sparrows of both experimental groups did not differ significantly in age and weight, in contrast to what Lepczyk & Karasov (2000) would suppose due to the daily difference in body mass gain.

Growth rates of both, sparrow-raised and canary-raised young in my study fit nicely into the range of growth rates known for house sparrows under field and laboratory conditions (Weaver 1942; Blem 1975). And in all parameter measurements canary-raised sparrows were equal to or below those of sparrow-raised sparrows. Thus my data do not support the idea that a potentially better singing performance of canary-raised house sparrows could result from better developmental conditions relative to their sparrow-raised siblings.

3 SONG IN CANARY-REARED HOUSE SPARROWS

3.1 INTRODUCTION

Diversity and versatility are key features of singing in birds (Nowicki & Marler 1988; Todt & Hultsch 1996) which might result from song learning. Song learning has been extensively studied both in the field and the laboratory (for books see e.g. Kroodsma & Miller 1982, 1996; Snowdon & Hausberger 1997; Hopp et al. 1998)[1].

From the field several passerine species, e.g. sturnids, menurids and brood parasitic widow birds, are known to imitate foreign sounds. With the one exception of widow birds (for details see Nicolai 1964, 1974), nothing is known about the individual's benefit from imitating. Speculations deal with possible female preferences for elaborate songs, but conclusive evidence is lacking.

In the lab many cross-fostering studies demonstrated a preference for conspecific over heterospecific song in a choice situation (e.g. Konishi 1985; Eales 1987). White-crowned sparrows, for example, did not copy the song of a song sparrow whether it was presented alone or together with a white-crowned sparrow song (Marler 1970). This was true for birds collected in the wild as nestlings who presumably had heard their fathers and/or other adults singing. But if young white-crowned sparrows were raised from the egg in nests of foreign species, they imitated alien songs or produced modified versions of them (Konishi 1985). Although five to ten days old nestlings do not copy (or produce) songs, hearing them seems to bias the choice of songs in the memory acquisition phase. Furthermore using live tutors, young white-crowned sparrows selected the song of a visible tutor song sparrow over conspecific songs heard from hidden white-crowned tutors (Baptista & Petrinovich 1986); these findings show that a live tutor can override the white-crowned's innate predisposition for the conspecific song.

The house sparrow, too, has already been known for a long time to be able to imitate foreign sounds (e.g. Hamersley 1714; Barrington 1773; Coupin 1901; Godman 1954; Schröder 1964; Bergmann et al. 1983). Most authors focussed on the sparrow's surprising

[1] O. Koehler (1951) was the first to use the tape recorder and W. H. Thorpe introduced the sound spectrograph (borrowed from the marine) in the study of avian song development. When he was informed that the British navy had a sonagraph, he rang them up to ask if he could borrow it. They were very upset that he knew about such a top secret piece of equipment, as they were using it to identify the „signatures" of submarines!

vocal skills in copying domestic canaries (Kant 1803; Witchell 1896; Seton 1901; Conradi 1905; Sanborn 1932; Stoner 1942; Kipps 1956; Bent 1958; Wotkyns 1962). Vocal mimicry in wild sparrows (Bent 1958; Huber 1983) seems to be rare. The natural voice of common house sparrows is described as a monotone, poorly structured, noisy (Witherby 1943), loose sequence of mostly harsh calls (e.g. Howard 1954; Cramp & Perrin 1994). The house sparrow's acoustic communication is poorly studied (see chapter 1). The most detailed study about the vocal behaviour and display of wild house sparrows comes from Nivison's PhD thesis (1978). He concluded that under normal conditions learning does not play an important role for sparrows. The cases of canary-like singing house sparrows point to the possibility that the acquisition of the vocalizations from social partners is of importance in the normal life of a sparrow (Wickler 1982). No systematic study on canary-like vocalizations of house sparrows has been done so far. In my work I examine the vocal skills of canary-like singing house sparrows, analysing their vocal performances, their canary-typical tours in particular, in comparison to a) domestic canaries, b) canary-raised house sparrows who did not produce canary-like songs and c) sparrow-raised house sparrows. My analyses of song characteristics concentrated on total vocal repertoire, syllable features (length, frequency, bandwidth) and syntax (tour composition). Thereby I add new knowledge on the proportion of learned and innate features in house sparrows' song production, the necessity of social bonds (social selectivity; choice of tutors), and inheritance of song learning skills.

3.2 METHODS

3.2.1 ANIMAL SUBJECTS

All birds (canaries and sparrows)[2] were bred in our aviaries. Details about rearing conditions and song exposure are given in chapter 2. Sparrows were housed either separately or together with a male foster sibling in cages (Joko, Bramstedt/Bassum; 122cm x 50cm x 50 cm) in ventilated rooms or sound reduced chambers. In rooms a single caged canary male was positioned opposite to the sparrow cage. Light/dark (LD) regime varied with season; to simulate breeding season birds were kept under LD 16h/ 8h, to simulate non-breeding conditions birds were kept under LD 10h/14h. All animals

[2] The species are defined in chapter 2, 2.2.1 Animal subjects

were in reproductive state (indicated by the completely black bill; see chapter 1) during tape recordings. Food (seeds, insects, salad and fruits) and water were available ad libitum.

From 66 male sparrows hatched in canary nests 8 died within the first 3 days and 4 had crippled feet getting not enough minerals (due to badly feeding females). The remaining 54 canary-raised sparrows can be divided into three main groups:

a) young raised in sound-proof chambers: 11 males were raised in cages in sound-proof chambers by a female and a male canary; a tape with the song of a male canary was played to them three times a day. After independence of the young the canaries were removed.

These sparrows only vocalized very rarely, if at all. Thus the required tape recordings for song analyses could not be obtained. In any case the rare vocalizations of these birds did not comprise tours.

b) young that had to be raised (in the very first year of this study) in normal laboratory rooms where humans were also working: 5 male sparrows were raised in cages by a female and a male canary; a tape with the song of a male canary was played to them three times a day. After independence of the young the canaries were removed.

Though these young vocalized frequently, none of them produced tours. As a consequence of human presence these birds did not hear only the canary song, but other species trough the open window and also some music, whistling and talking humans. The birds produced some not identifiable sounds: neither sparrow- nor canary-like. They thus could not be compared to the other canary-raised birds and have been excluded from further analyses.

c) young raised in canary aviaries (as described in detail in 2.2.4.2): 38 male sparrows were raised in canary nests (for details see chapter 2). After independence they were transferred - if possible with male canary foster siblings - to normal laboratory rooms were they were separated from other sparrows but could hear and see a caged male canary tutor. In addition a tape (à 45 minutes) with the song of a male canary was played to them three times a day.

As a control I raised 28 male house sparrows in their parents' nests. In the neighbouring aviary these sparrow-raised young could hear and see male canaries but had no direct contact with them.

3.2.2 TAPE RECORDINGS

For tape recordings (Uher tape recorder, Uher and Sennheiser microphones) birds were kept isolated in cages (Joko, Bramstedt/Bassum; 122cm x 50cm x 50 cm) in ventilated, sound reduced rooms under long day light regime LD 16h/8h. Canary males and canary-raised sparrows had a male canary, sparrow-raised sparrows another male sparrow in the background (separate cage; visible for the tape-recorded individual). On two subsequent days from each bird 45 minutes of vocalizations were taken on tape; one in the morning (between 9 and 12.00 am), the other in the afternoon (between 15.00 and 18.00 am). Following Nivison (1978) these time intervals comprise peak periods of cheeping activity. If an individual made a pause longer than 8 seconds between vocalizations an Uher acoustomat automatically switched off the tape recorder and started it again with the first sound.

Sparrow-raised sparrows were not used to cages, thus vocalized only rarely. They had to be tape recorded for several days at the given times (morning or afternoon) to obtain the records required.

3.2.3 SONG ANALYSES

3.2.3.1 TERMINOLOGY FOR SONG ANALYSES

The digital spectrogram is a graphic representation of a 'sound' and describes the frequency course in time (frequency is represented on the abscissa, the time on the ordinate; for details see Hopp et al. 1998). To compare song features which house sparrows may have learned from canaries I follow in the description the terminology used to describe canary song (e.g. Voigt 1997):

• Element/Note

A note (or element) is a physically distinguishable unitary vocalization, the shortest, uninterrupted structure in a digital spectrogram (Güttinger 1979; Voigt 1997; Brenowitz et al. 1997). A note can be a pure tone (Fig. 3.1A), characterized as just one horizontal bar in the digital spectrogram. A frequency-modulated note is an upward- or downward sweep in pitch, visible as a correspondingly upward or downward trace in the digital spectrogram (Fig. 3.1B). A very rapid rhythmic frequency modulation is called vibrato (Voigt 1997, Fig. 3.1C, marked by a black arrow). Several notes can occur with different

types of overtones, which determine the timbre of the sound: musical notes contain overtones that are integral multiples of the basic (lowest) frequency (Fig. 3.1D), while noisy, harsh sounds contain many parallel frequency bands (broad-banded notes) (Fig. 3.1E).

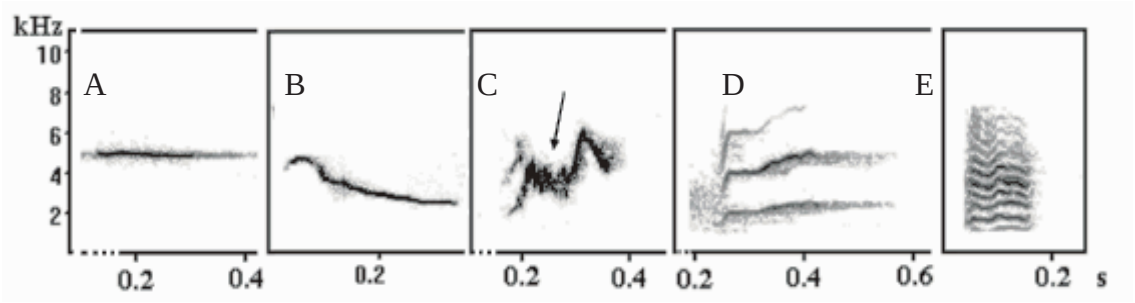


Fig 3.1: Digital spectrograms of different note types sung by canary-raised house sparrow males. For details see text. A: pure-tone note; B: frequency-modulated note; C: frequency-modulated note with vibrato (marked by the arrow); D: harmonic note; E: broad-banded note.

• Syllable

A series of one or more notes that co-occur in a regular pattern during song is referred to as a song „syllable“ (Brenowitz et al. 1997) (Fig. 3.2).

• Tour (phrase)

A phrase („motif“) is a sequence of several - same or different - syllables that are rapidly repeated (Brenowitz 1997). Characteristic for the song of domestic canaries are phrases containing just one type of syllable; Güttinger (1979) called this canary-typical phrase-type ‘tour’ (Fig. 3.2)

• Song type

A particular combination of tours that occurs repeatedly constitutes a song type (Brenowitz 1997). A song type in domestic canaries lasts at least 1.5 seconds and contains no interval longer than 0.4 seconds (Leitner 1999) (Fig. 3.2).

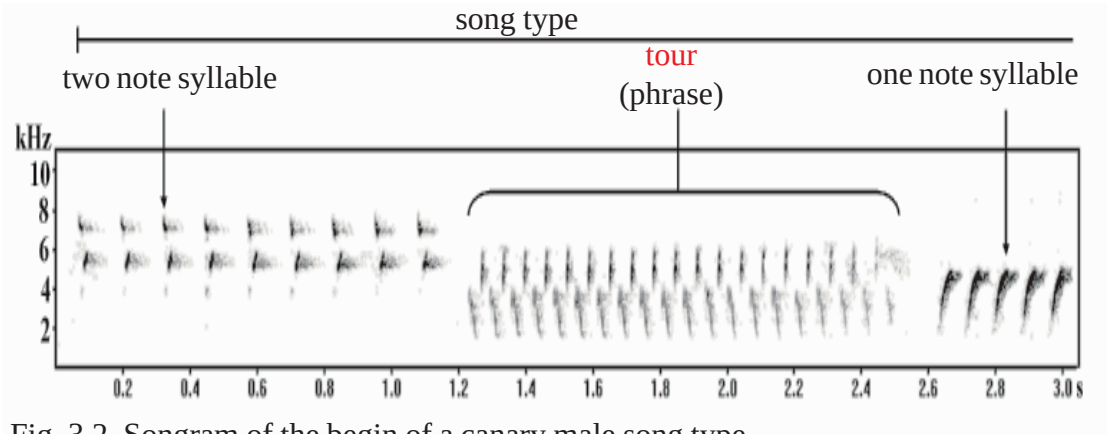


Fig. 3.2. Songram of the begin of a canary male song type.

3.2.3.2 ANALYSES OF DIGITIZED SONGS

Tapes were numbered, thus the analysing person could not know anything about a respective tape's content. Songs of sparrows and canaries were digitised at 22.050 kHz (= sampling rate) using a Hamming window. The acquisition and the analyses were carried out with the digital sound analysis system Avisoft SaslabPro (Specht 2000, Avisoft Bioacoustic, Germany) using a Dell computer (Dell OPTILEX GX 150) and Microsoft Windows 2000. Spectograms of songs were generated using a Fast Fourier Transform (FFT) of 256 points, a Filter Bandwidth of 300 Hz and time resolution of 8,931 msec (Frame). Tours and syllables were classified and catalogued (*see below: repertoire catalogue) by visual inspection, based on discontinuities in their morphologies (Lynch et al. 1989), in Powerpoint (Microsoft Office 2000). To assess syllable similarities in cases of doubt I superimposed spectrogram copies using Adobe Photoshop. For quantification spectrograms with measure options of Saslab32 (Specht 2000, Avisoft Bioacoustic, Germany) were used; the data were automatically transferred to a prepared Excel 2000 sheet. Quantification parameters for tours and syllables were length (= duration), frequency range, and intervals between syllables resp. tours. For a tour the number of syllables and their repetition rate (Hz) were determined. Syllables and tours to be analysed were randomly selected excluding immediately subsequent syllables. To correct for measurement inaccuracies each syllable and tour was measured twice; for statistical analyses I used the mean value of both measurements. Separate measurements were taken for each comparison (inter-specific; intra-specific).

* *Repertoire catalogue*:

Communication works because different signals mean different things, and the communicators share the code (Green & Marler 1975; Smith 1977; Horn & Falls 1996). If notes are visually clearly distinct, they are supposed to have different meanings. My birds had no social input from conspecific birds during tape recording, thus I cannot be sure that all recorded syllables contain meanings, nor can I suggest any function. To be on a safe side, I boiled the number of identified syllables down to an arguable minimum syllable repertoire size in two steps:

a) Each counted syllable has to occur at least 10 times during the 2 x 45 minutes tape recordings of one year. Rare syllables (1-3 times) might occur accidentally or by vocal exploration and thus were excluded from further analysis;

b) If morphologically different syllables (occurring at least 10 times) show gradual intermediates (including rare syllables), they were thought to be variants of one syllable, thus handled as synonyms.

3.2.4 ABBREVIATIONS IDENTIFYING THE DIFFERENT GROUPS

- can: domestic song canaries (n = 5); these males were used as live tutors for canary-raised house sparrows fledglings;
- ca-sin: canary-raised sparrow males, producing canary-like tours (n = 10);
- ca-nosin: canary-raised sparrow males; they have never been heard or tape recorded to produce canary-like tours (n = 21);
- sp-nosin: sparrow-raised sparrow males, who have never been heard or tape recorded to produce canary-like tours (n = 9).

3.2.5 COMPARISONS ON DIFFERENT LEVELS

For inter-specific and intra-specific comparisons of syllables and tours the following measures were taken (Fig. 3.3):

(1) syllable duration: time interval from start to the end of the syllable;
(2) syllable frequency range: interval between highest and lowest frequency within a syllable;
(3) interval between syllables: time interval between the end of the preceding and the beginning of the following syllable; a) within tours; b) between single syllable and the following tour;
(4) tour duration: time interval from start of the first to the end of the last syllable;
(5) tour composition: total number of syllables within a tour;
(6) repetition rate: number of syllables per time (Hz).

Different sets of syllables/tours were used for measurements indicated above. From each data set (details see below) the minimum, average and maximum values were determined for comparison.

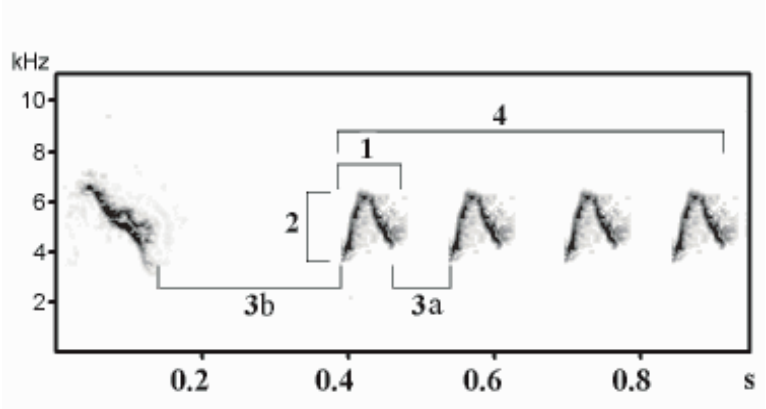


Fig. 3.3: A single syllable followed by a tour of a house sparrow male comprising 4 one-note syllables. Numbers are explained in the text (see 3.2.5).

Individuals from ca-sin fledged in two successing years. Thus some individuals I could tape record in two, most birds only in one year. To provide comparable conditions for analyses I used from all birds the tapes of their first summer.

3.2.5.1 INTERSPECIFIC COMPARISON

A) Is the canary repertoire size different from that of canary-like singing house sparrows? How many syllables of the sparrow total repertoire have been learned?

For each individual of can and ca-sin a syllable catalogue was prepared from 2 tapes à 45 minutes of one year (see 3.2.3.2). From this the individual total syllable repertoire size was calculated. Comparing these catalogues revealed copied and not copied syllables.

B) How similar are canary- and sparrow tours?

From the repertoire catalogue (3.2.3.2) the total number of different tours per individual was determined. Of each type of tour produced by an individual, 5 examples were measured and averaged. From each individual an average value of its different tour parameters (duration, frequency range, minimum number of syllables, intervals between syllables, duration of syllables within tours) was used for interspecific comparisons. From tour duration and syllable number the repetition rate (syllables per seconds, Hz) was calculated.

C) Do sparrows produce tours with a similar frequency range - repetition rate correlation as their canary tutors?

Kinematic studies in different species provide evidence that vocal tract activity during song production differs between slow trills and faster trills. In particular, vocal tract

movements cycle during the production of slow trills (with each cycle corresponding to the production of a syllable), but do not cycle during faster trills (Podos 1997). For this study I included both types of tours, as slower tours might elucidate constraints by the vocal tract and faster trills constraints of body mass (for more details see chapter 6).

As the maximum value of frequency bandwidth regularly decreases with increasing repetition rate (Podos 1997), I first determined for each individual that tour which showed *maximum repetition rate*. Then I determined that tour, which contained syllables with *maximum frequency bandwidth*. For both sample sets, I measured duration of the respective tours, counted the number of syllables and determined the mean of the respective syllable frequency bandwidth or respective repetition rate. To compensate for insurgencies each parameter (frequency, duration) was measured twice; for statistical analyses I then used the mean value of both measurements.

D) Do tour-singing sparrows produce song macro structures like the canary song type?

To analyse song structure I used the program Luseq written by my colleague Dr. H.-U. Kleindienst. In the total repertoire catalogue I listed all produced syllables and tours of all ca-sin individuals, and gave a number to each syllable. In digitized sequences (at least 60 seconds long, containing a minimum of 30 syllables, for both types of sequences) the syllables and tours were replaced by the corresponding numbers (a given tour as a unit was replaced by one number!). The resulting number columns of the sequences were analysed separately in the following way: The program uses a defined sequence length (mask) of 2 up to 10 syllables. Starting with the 2-syllables mask, the initial 2 syllable numbers of a column constitute the first master sequence. The program then checks how often this master sequence with this strict order of syllable-numbers reappears in the column and prints the sum out. The same procedure is repeated with the other masks (3 -10). In a similar way, the program can look separately for the following variations of the master sequences: permutations of a given master sequence (e.g. 1, 2, 17), i.e. all syllables have to occur, but their order is optional (e.g. 1, 17, 2 or 2, 1, 17; etc.). It furthermore singles out „errors“ in a strict order sequence where just one foreign note either replaces a master sequence note (e.g. 1, 5, 17) or is filled into the sequence (e.g. 1, 4, 2, 17).

3.2.5.2 INTRA-SPECIFIC COMPARISON

While analysing it turned out that canary-like singing house sparrows (ca-sin) produced either sequences containing only syllables but no tours, or sequences containing both syllables and tours (Fig. 3.4B and C). Thus measurements were done separately for syllables from pure syllable sequences as well as from sequences that contained both syllables and tours. Individuals of the ca-nosin group were randomly assigned to one of the two groups for comparisons B and C respectively.

A) Do ca-sin's syllables sung separately in tour-comprising sequences differ from syllables in pure - syllable - sequences?

Each type of syllable produced by a given ca-sin individual either between tours or in pure syllable sequences was measured 10 times and averaged.

B) Do ca-sin and ca-nosin differ in their total syllable repertoire size? Do single syllables and pure syllable sequences differ between ca-sin and ca-nosin?

For each individual its total syllable repertoire size was determined from the syllable catalogue already described. Each type of syllable produced by an individual was measured 10 times and averaged

C) Do syllables sung by canary- and by sparrow-raised house sparrows differ?

Tape recordings of sp-nosin were problematic, because most birds, captured from an aviary, vocalized only rarely and produced relatively short continuous sequences when caged. Thus from these tapes I got several syllable types and sequences for comparisons, but cannot say anything about the total repertoire size of sparrow-raised sparrows.

Each type of syllable produced by an individual was measured 10 times and averaged.

3.2.5.3 THE CUMULATIVE CURVE

For canary song analyses often a cumulative curve (also called repertoire curve) is plotted to demonstrate how fast males expose their total repertoire (see Leitner 1999). The repertoire curve is characterized by a steadily decreasing number of new syllables produced, and can be adequately described by an exponential curve without an inflection point. The most frequently used model nowadays is the very flexible Richards curve (Richards 1959), a generalization of the classical (growth) curves,

(1) $W_i = A(1-b*e^{(-Kti)})\text{^}M$.

For a decreasing exponential curve M = 1. Thus the formula (1) becomes

(2) $W_i = A(1-b*e^{(-Kti)}) =$ **$A - Ab*e^{(-Kti)}$**,

where W_i = number of syllables at time i (t_i);

A = asymptote; this is the 'final' number of different syllables of a particular repertoire curve;

b = scaling parameter smoothing the actual to the best fitting curve

K = syllable production index expressed as a function of the ratio of the maximum number of different syllable to the elapsed time interval.

Formula (2) is identical with the second Brody equation (Brody 1945)[3]

(3) **$W_i = A - B*e^{(-K*ti)}$**,

where B (Brody) = Ab (Richards)

= A-W(0);

W(0) is the starting point of the curve. The cumulative curve starts with 0 syllables at time 0, thus B = A. For the ideal repertoire curve B = A, the second Brody equation can thus be modified as follows:

(4) $W_i = A - A*e^{(-K*ti)} =$ **$A\,(1 - e^{(-K*ti)})$.**

(5) At $t_i = 1/K$: $W_{(1/k)} = A*(1 - e^{(-K*1/K)}) = A*(1 - e^{(-1)}) = A*(1 - 1/e) =$ **$A*\ 0.63$.**

Thus K, whose unit is seconds^{-1}, stands for the time a bird needs to produce 63% of its individual final number of different syllables (graphically shown in a repertoire curve, see Fig. 3.13). The curve-specific feature K can be used to compare individuals' abilities to recall their respective syllable repertoire within a certain time interval; K is here referred to as 'recall rate'.

The repertoire curve was determined for can (n = 5) and ca-sin (n=10). Ca-nosin (n = 21) and sp-nosin (n = 5) however produced too few different syllables, thus the repertoire curve did not follow an ideal exponential curve and in turn the results from Richards and Brody equation differed too much. Thus the latter groups were excluded from this analysis.

[3] Püttner suggested this function already in 1920, but published it in German.

To get a first impression how variable K might be within and between species the repertoire curves of male white-browed sparrowweavers *Plocepasser mahali* (n = 4) and wild canaries, *Serinus canaria* (n = 4) were determined; unpublished data were kindly offered by Conny Voigt and Dr. Stefan Leitner.

3.2.5.4.1 USING NUMBER OF NEW SYLLABLES

Is a ca-sin's repertoire curve when singing sequences comprising tours or pure syllables sequences respectively more similar to the canary or to the sp-nosin repertoire curve?

From a sequence of 150 seconds continuous vocalization (silence between syllables was not longer than 8 seconds; thus the acoustomat did not have to stop and start again the tape) the numbers of new syllables within 10 second steps were determined. Then all produced syllables during the 150 seconds were counted. Tours were treated as one new syllable because they comprise only one syllable type.

It has to be taken into account that both sparrows and canaries were analysed as described above. These data are not directly comparable to other canary studies because silences between song types were not excluded!

3.2.5.3.2. USING NUMBER OF NEW SYLLABLES AS PERCENTAGE OF TOTAL REPERTOIRE

Is a singer's repertoire curve in percentage of its calculated total repertoire, when singing sequences containing tours or pure syllables only, more similar to their canary tutors' (can) or sparrow siblings' (ca-nosin) proportional repertoire curve?

The total repertoires of sparrow-raised house sparrows were not available, thus data from ca-nosin were used! For a sequence of 150 seconds continuous vocalization (silence between syllables was not longer than 8 seconds; no acoustomat) the numbers of new syllables within 10 second steps were determined. Each value was divided by the total number of different syllables produced; the result was multiplied by 100.

3.2.5.3.3 COMPARISON OF THE RECALL RATE *K*

The characteristic feature K of the repertoire curve, calculated with the Brody equation (formula 4), can be interpreted as the recall rate relative to the produced set of different

syllables at the end the 150s sequence of continuous song production (details see 3.2.5.4). Knowing K one can determine how long an individual needs to produce 63% of its total repertoire (final niveau of the repertoire curve). In turn if K is constant within a species, a listener can at this point of time after the start of a song estimate the final niveau of the repertoire curve of the respective singer. Thus the listener need not wait until the singer finished.

3.2.6 STATISTICAL ANALYSES

Statistical analyses were performed with Systat 9.2 (Systat Software Inc., Richmond, CA.) following Lamprecht (1999). All data were first tested for normal distribution (Kolgomorov-Smirnov Lilliefors test) and for equality of variances (Levine test). If both tests did not show significant differences ($p > 0.05$), one way-ANOVA, followed by Bonferroni post-hoc-test was performed to detect differences between several groups, or by the pooled variances t-test for two groups. If the assumption of equal variance (but not distributional shape) was violated I conducted the separate variances t-test to compare two groups.

The recall rate K of each curve was determined using both the Richards model (2) and the second Brody equation (4). This is the first study to compare recall rates. To be on the safe side I used for statistical analyses only recall rates where K calculated by the Richards model and the Brody equations did not differ by more than 5% and the Brody function fits the calculated curve to 98%. Statistics were done with the results from the Brody function only.

If the same syllable or tour was used for different measurements (e.g. frequency range and syllable length) I adjusted the significance level of $\alpha = 0.05$ following the sequential Bonferroni (Rice 1989); the same was done for repertoire composition and recall rate. All results refer to two-tailed tests.

3.3 RESULTS

3.3.1 CONCERNING THE BIRDS

Out of my 58 canary-raised and 28 sparrow-raised house sparrows I identified 10 individuals that produced clear canary-like tours (ca-sin).

All ca-sin had been raised in canary nests in aviaries. None of the sparrow-raised young appeared to produce tours although they had had also the chance to hear canary song from neighbouring aviaries. Only two of ca-sin ('Les' and 'Balo') shared the same parents, but hatched from subsequent clutches[4]. Except for vocal performance ca-sin were not conspicuous in any way (see Table 3.1): they did not hatch earlier in the year, nor from the first laid egg of a clutch, and they were not heavier in hatchling or adult weight than other house sparrows (also see chapter 2 and 4).

Table 3.1. Data of ca-sin.
aviary: two separated house sparrow populations;
box: nestbox within a certain aviary;
clutch: in which clutch of a sequence of clutches within a year a bird hatched;
position: position of an egg according to the laying order within a clutch;
weight (h): hatching weight (g) of an individual;
weight (a): adult weight (g) of this individual.

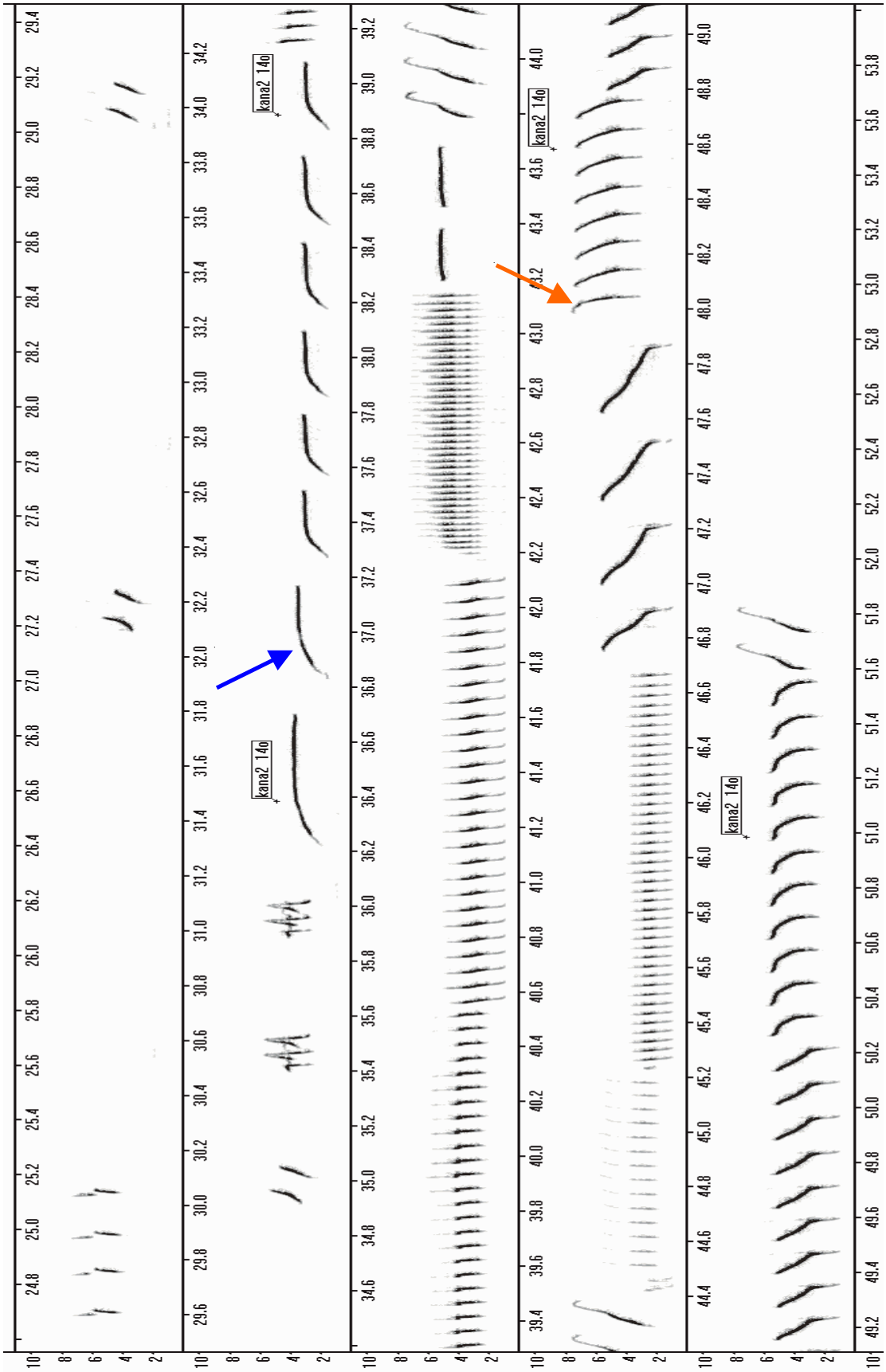
bird	year	aviary	box	clutch	position	weight (h)	weight (a)
Or	1999	A	1	2	1	2.1	27.98
Ro	1999	B	3	2	4	2.3	25.48
Hbli	1999	A	4	1	2	2.2	24.47
Hb	1999	A	5	2	5	2.1	34.50
G	1999	A	3	1	4	2.3	33.35
Rw	2000	B	1	3	2	2.5	25.96
Les	2000	A	2	1	1	2.9	25.86
Balo	2000	A	2	2	3	2.4	24.44
Bun	2000	B	5	1	4	3.0	24.02
Wh	2000	B	4	3	2	2.9	27.11

[4] At the time, when I did the raising experiments, it was not yet possible to determine the paternity of young on the molecular level in our facilities.

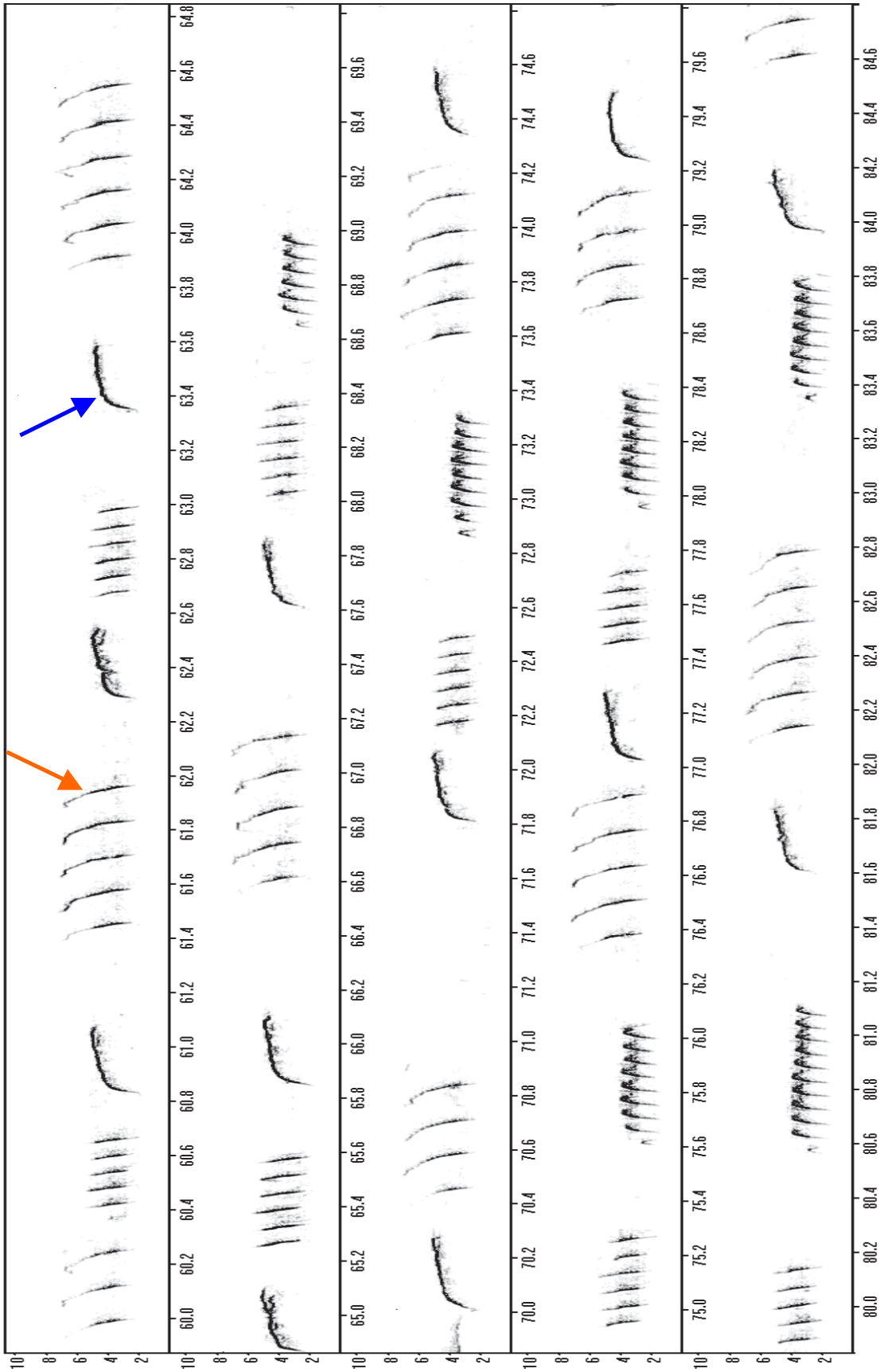
Fig. 3.4: Sequences of continuous vocalizations of
A) can tutor (page 64),
B) ca-sin orange right+left (or) producing a sequence comprising tours (page 65) or
C) a pure syllable sequence (page 66), and
D) a sp-nosin (page 67).

(A) can males produce song types lasting several seconds. It is charaterized by a succession of tours defined as fast repetition of one syllable (3.2.3.1).
(B) The ca-sin orange right+left (page 65) clearly learned from its canary tutor (page 64) syllables and the tour-like structure (orange arrow), which does not occur naturally in the sparrow song. Some syllables which canaries used in tours were sung by the sparrow male orange right+left as a single syllable. The syllable marked with the blue arrow (page 64 and 65) is one type of syllables which also occur in a very similar pattern in the native sparrow vocalization (though normally with at least one overtone); it is not clear whether this syllable has been really learned or not.
(C) The ca-sin orange right+left - like all ca-sin individuals - also produced sequences lacking canary-like tours. These pure syllable sequences sound like native sparrow vocalization and were dominated by separated syllables. Very characteristic for all sparrows of all groups was the disyllabic chirping syllable with the general pattern of two-folded frequency sweep, up-down-up-down (page 66 and 67, green arrows). This syllable was produced by all captivity-raised as well as by wild-caught individuals with inter- and intra-individual variations (see also Fig. 3.9C).
(D) In this digital spectrogram the sp-nosin bird gave short examples of syllable sequences including silent intervals shorter than 0.4 seconds (Fig 3.4D, page 67, pink bars). Though these sequences look and sound far different from canary songs and canary-like singing sparrows, the temporal structure is similar to tour-comprising sequences when seeing tours as units. Only short examples can be presented, sequences, however, could last several seconds.

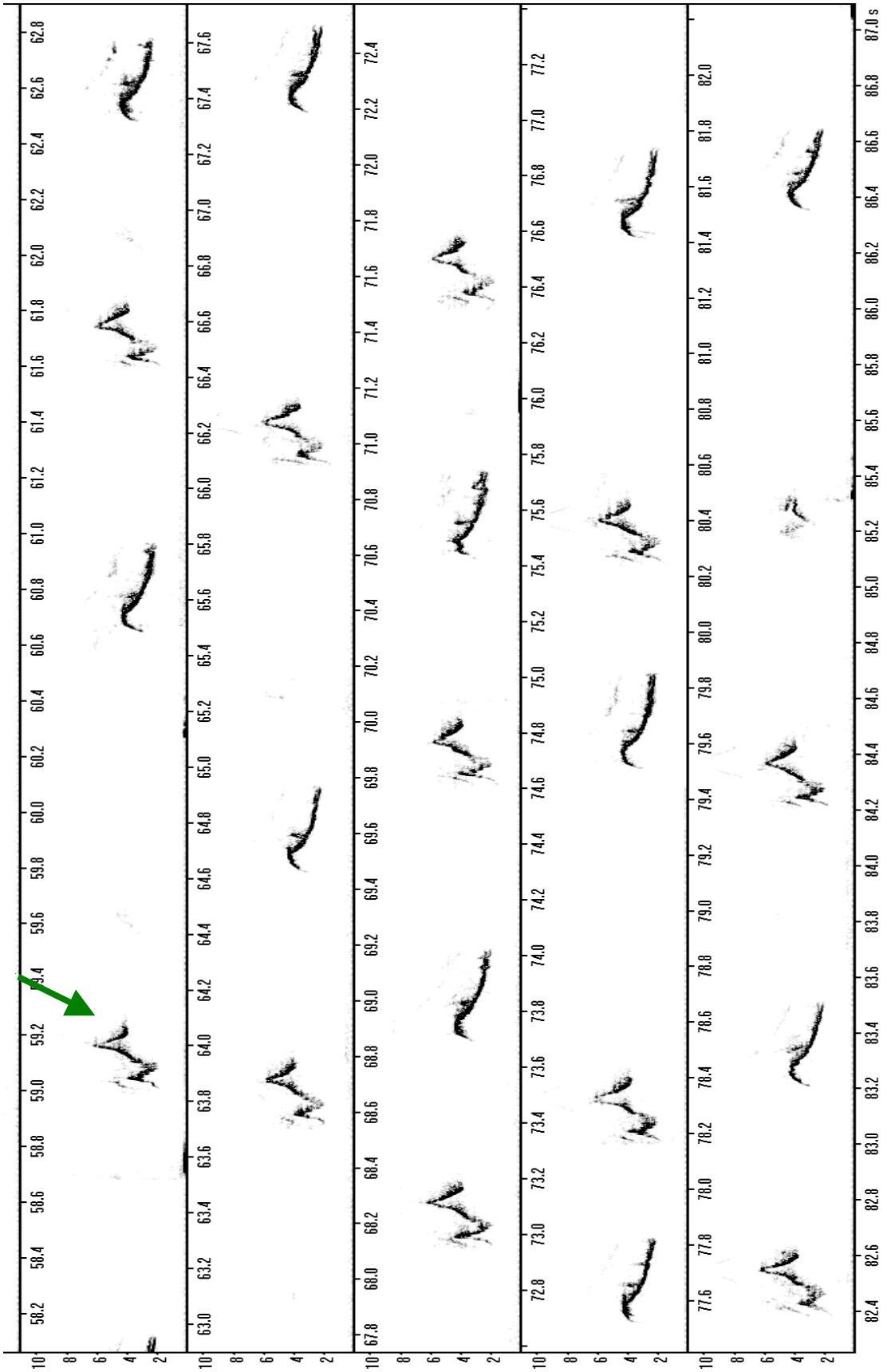
A) male canary tutor kana



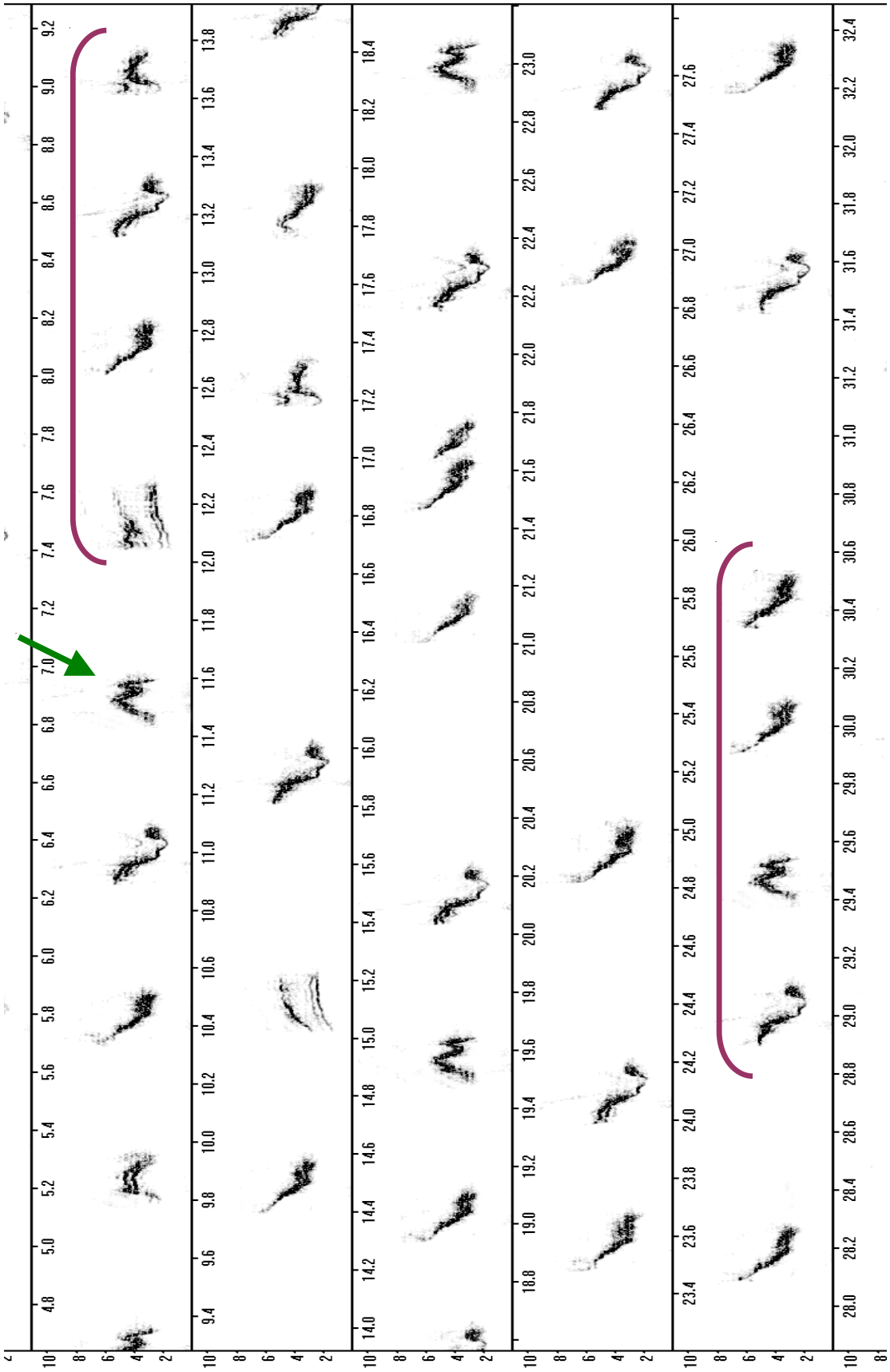
B) ca-sin orange right + left



C) ca-sin orange right + left



D) sp-nosin w40



3.3.2 DESCRIPTION OF THE REPERTOIRE OF CANARY-RAISED BIRDS

The total vocal repertoire of all canary-raised house sparrows taken together comprised about 200 syllables. The groups (ca-sin: n = 10, ca-nosin: n = 21) did not differ in the size of their respective total (syllable) repertoires (pooled variance t-test, t = -0.900, df = 29, p = 0.375) (Fig. 3.5A). A single individual of both groups would own 32 to 42 syllables. I was surprised to find that tapes of one individual from two different days, each with 45 minutes of vocalization without a break longer than 8 seconds, only shared a few corresponding syllables. So I may have recognized only a portion of an individuals' real total repertoire (for details see Table 3.2 and Table 3.3).

3.3.2.1 The total repertoire (copied and not-copied syllables)

The repertoire of both groups (Fig. 3.5B) contained syllables which
a) did not occur in any of the canary-tutors' repertoires and thus cannot have been copied;
b) were produced by at least one canary tutor and by some, though not all canary-raised sparrows, but were never produced by any of the sparrow-raised young; thus these syllables clearly must have been copied;
c) could not be assigned to sparrow- or canary-like vocalization because they were too similar between these groups („similar").

The not-copied syllables (a) can be further subdivided into
a1) „free" syllables, so called because they were particular for one individual, thus were not copied from canary tutors and also did not occur in one of the other sparrows' repertoire and
a2) „common" syllables, 12 in number, which were produced by all canary-raised sparrows (Fig. 3.4B); some of these 12 were also produced by some sparrow-raised sparrows.

Only about 1/3 of ca-sin's total repertoire consisted of copied syllables, significantly more did not come from their canary tutors (paired t-test, t = -15.82, df = 9, $p << 0.001$, $\alpha = 0.012$); this result is even stronger for ca-nosin (Fig. 3.5 C). The percentage of not-copied syllables in an individual's total repertoire was significantly higher for ca-nosin than for ca-sin (pooled variance t-test, t = 5.80, df = 29, $p < 0.0001$, $\alpha = 0.016$; Fig. 3.5 C). This was based on a significantly higher number of „free" syllables in ca-nosin (separate variance t-test, t = 3.927, df = 23.3, p = 0.00066, $\alpha = 0.025$; Fig. 3.5 D).

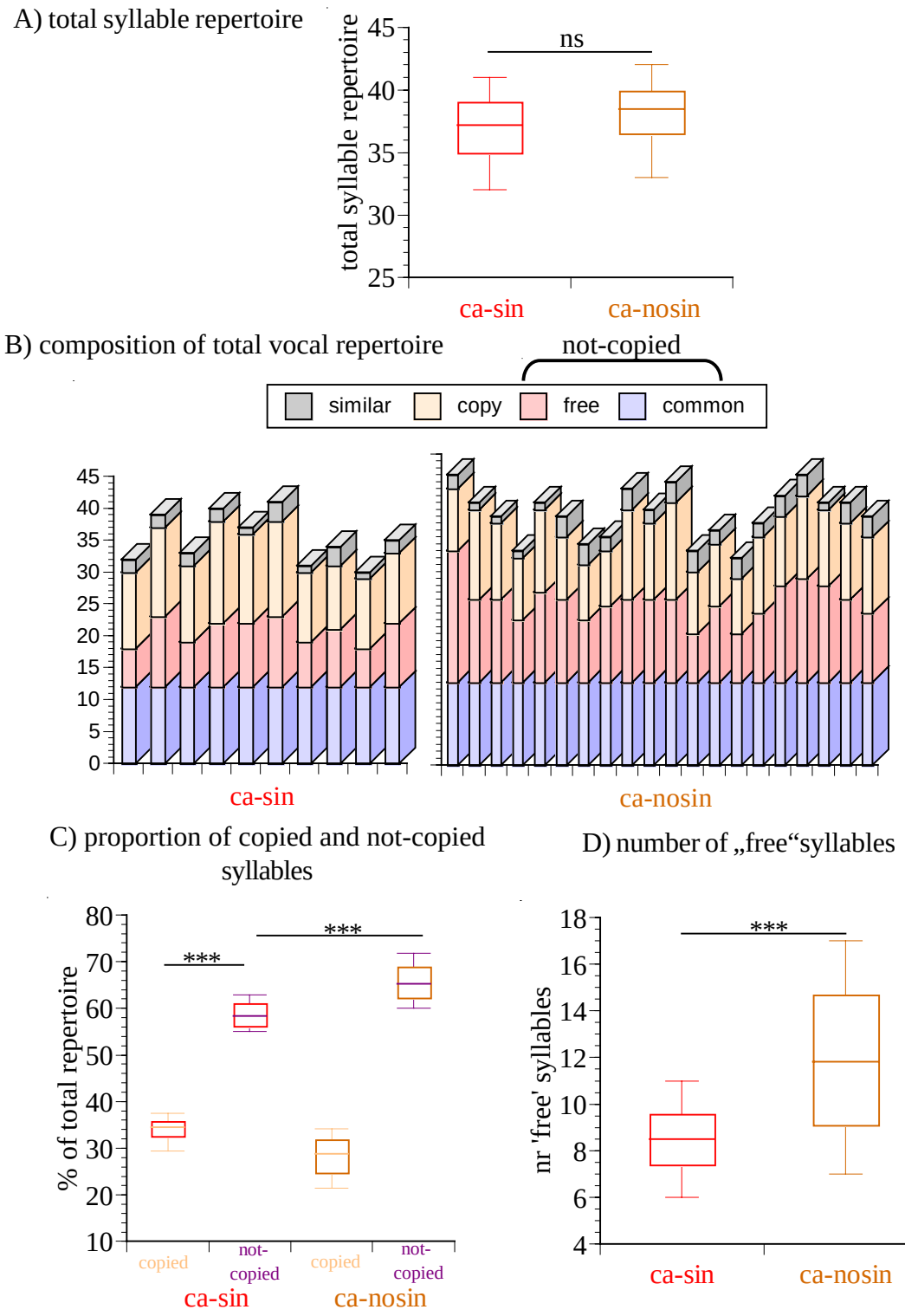


Fig.3.5: Canary-raised house sparrows' (A) total syllable repertoire, (B) composition of total syllable repertoires, (C) percentage of copied and not-copied syllables relative to their total syllable repertoire, D) number of „free“syllables. Ca-sin (red): individuals singing tours (n = 10); ca-nosin (beige): individuals never producing a canary-like tour (n = 21). Lines indicate mean (middle) ± sem (upper or lower line of the box), whisker caps give minimum and maximum values. Statistical results are indicated by *** = $p < 0.001$, ns = not significant. For details about statistics see text.

3.3.2.2 Canary-like tours

Both ca-sin and ca-nosin received the same treatment from the same foster parents, nevertheless only ca-sin produced canary-like tours. Ca-sin mostly did not use tour-syllables separately as single syllables; if this happened then it occurred between tours. A ca-sin individual produced between 8 to 15 different tours, which covers between 26 to 38% (mean ± sem : 31.85 ± 1.4) of its total repertoire (Fig. 3.6). Tours consisted mainly of copied and „similar“ syllables, but two individuals also used „free“ syllables (Fig. 3.7A). However, the latter tours did not sound melodious like canary tours.

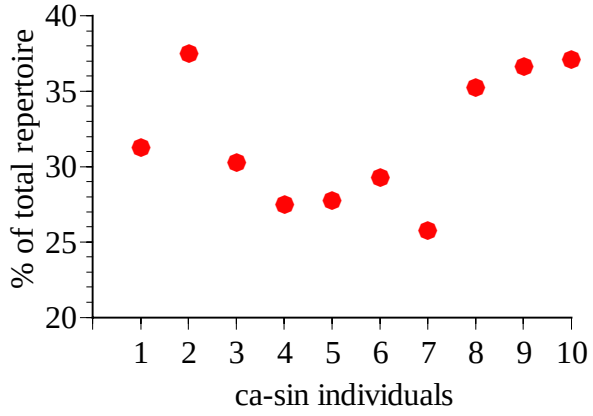


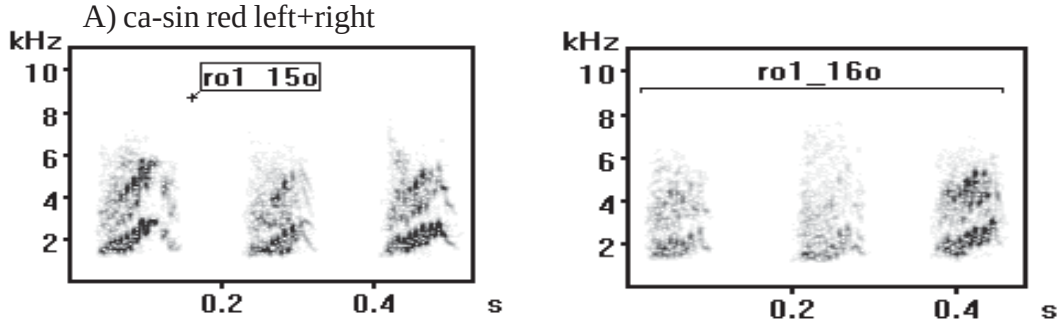
Fig. 3.6: Syllables produced in tours as % of a ca-sin individual's total vocal repertoire. Tours consisted of only one syllable type and were thus counted as one syllable in the total syllable repertoire.

3.3.2.3 Tour-resembling vocalization in agonistic context

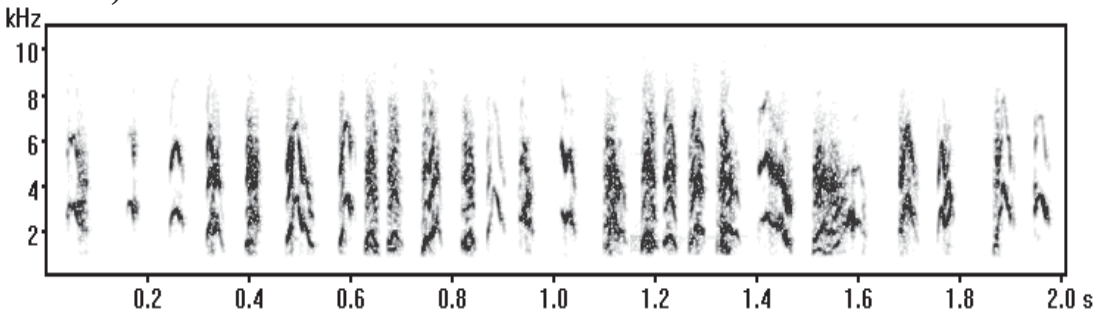
Furthermore in aggressive behaviour (towards conspecifics, or e.g. when kept in the hand) both sparrow sexes naturally produce a tour-resembling vocalization (see Fig. 3.7B-D). Interestingly, these sequences were longer than canary-like tours. Most syllables sung within tours were shorter than syllables sung in agonistic sequences; in addition the

Fig. 3.7: Digital spectrograms of house sparrow vocalizations: sequences of harsh syllables.
A) Two examples of a „tour“ which consists of a 'free' syllable. This tour mainly contains three syllables, only occasionally two.
B1+B2) Agonistic vocalizations: the examples were taken from ca-nosin, because the digital spectrograms are clearer, but such sequences were also produced by sp-nosin. (To get these rapid sequences I kept the birds in one hand, tickling their ventral side with a finger of the other hand).
C) Begin of a sequence of harsh syllables sung by a ca-sin from ordinary tapes; intervals were much longer than in canary-like tours or in agonistic sequences (see 3.7. B). Please note the different time scale of this digital spectrogram example.
D) Agonistic vocalization of a sparrow female (for personal observations I kept two pairs of sparrow-raised house sparrows in a small inside-aviary for one summer).

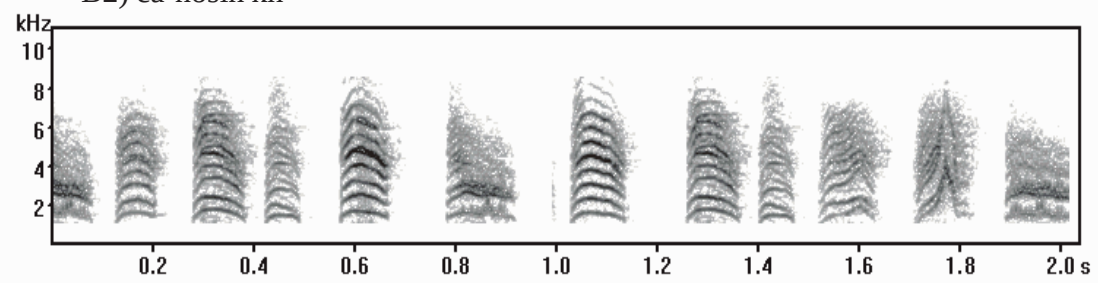
A) ca-sin red left+right



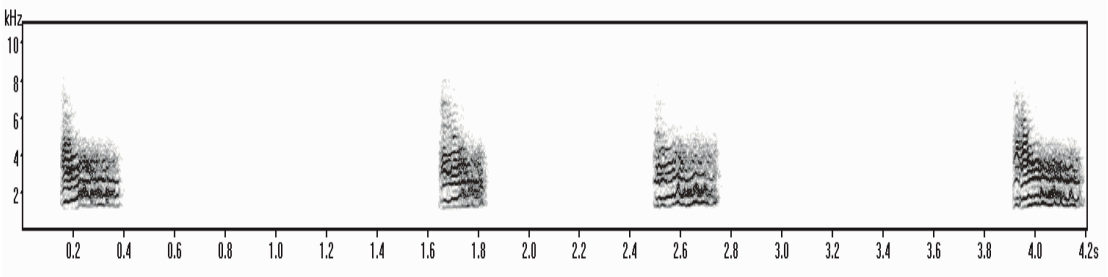
B1) ca-sin balo



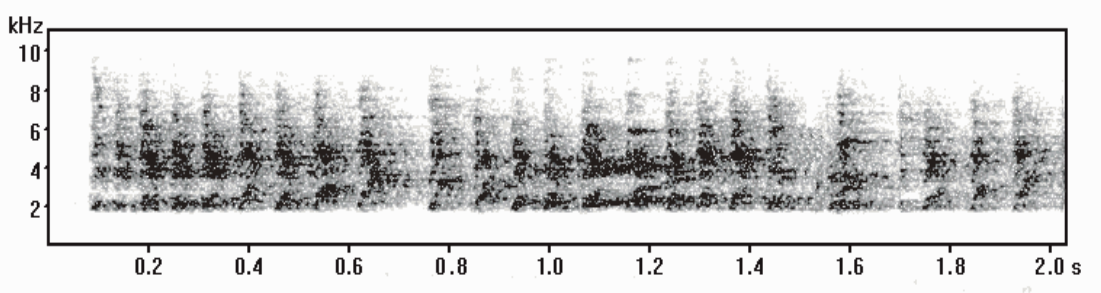
B2) ca-nosin kh



C) ca-sin or



D) sparrow-raised female



latter often contained vibratos and mostly overtones; thus they sound very harsh and very unlike canary syllables or canary tours respectively. Ca-sin produced these harsh syllables also, but with larger silence intervals between the syllables (see Fig. 3.7C).

3.3.2.3 Daily and seasonal syllable repertoires

The first tape recordings of two subsequent days were taken in the morning, the second ones in the afternoon (for details see 3.2.2). Syllable types differed highly, but there was no obvious difference in either the total number of syllables produced, the amount of tours, or the proportion of pure syllable sequences in relation to sequences comprising tours (Table 3.2). A correlation between syllable type and time of day cannot be drawn, this would require more tape recordings.

Table 3.2: Comparison of two tape recordings à 45 minutes without a break longer than 8 seconds of a ca-sin (or) and a ca-nosin (hi).
⟶: „out of“;
Δ syll.: number of different syllables; ≅ syll: number of concurrent syllables;
Δ trs.: number of different tours; ≅ trs: number of concurrent tours.

	tape 1		tape 2		sum tapes 1+2			
bird	Δ syll ⟶	Δ trs	Δ syll ⟶	Δ trs	**≅ syll ⟶**	**≅ trs**	sum Δ syll ⟶	sum Δ trs
or	23	10	20	8	**11**	**4**	32	14
hi	25	0	21	0	**8**	**0**	38	0

Some birds I could tape record in their second year, and again tape recordings from two successive days were very different. The number of new syllables (mainly of no-tour-syllables) in the second year relative to their first year varied from 6 to 13 (Table 3.3). However, this is in the range of the difference between two successive days. Thus I cannot assess the sparrows' ability to learn new syllables in subsequent years.

Table 3.3: Comparison of four tape recordings à 45 minutes without a break longer than 8 seconds of the sparrow Ramses (only the summer tapes were used!). This bird has been chosen because he is the most extreme example for syllable diversity between two subsequent years. More details about Ramses are given in 3.3.5.
Δ syll.: number of different syllables, ≅ syll: number of concurrent syllables;
Δ trs.: number of different tours; ≅ trs: number of concurrent tours.

	year 2000			year 2001			sum years 2000 + 2001	
	tape 1	tape 2	tape 1+ 2	tape 3	tape 4	tape 3+ 4	tape 1+2+3+4	
Δ syll	24	26	45	24	18	31	**(new: 13)**	**58**
≅ syll			**5**			**11**		**18**
Δ trs	8	9	15	8	1	8		**16**
≅ trs			2			1		7

3.3.2.4 Syllables similar in both species

Canary syllables are generally poor in overtones of any kind, while overtones are characteristic for sparrow syllables**.** However some syllables are almost identical in both species (see also Nivison 1978). Canaries can produce the 'similar syllables' as single syllables (see Fig 3.7 A) or within tours (see Fig 3.7 B). A given canary-raised sparrow produced 1-3 syllables of this type either separately or - in the ca-sin group - as a tour. Not all canary-raised individuals, but also some sparrow-raised sparrows, produced these syllables. In sum I cannot show conclusively whether they were copied from canaries or belong to sparrows' native vocal repertoire.

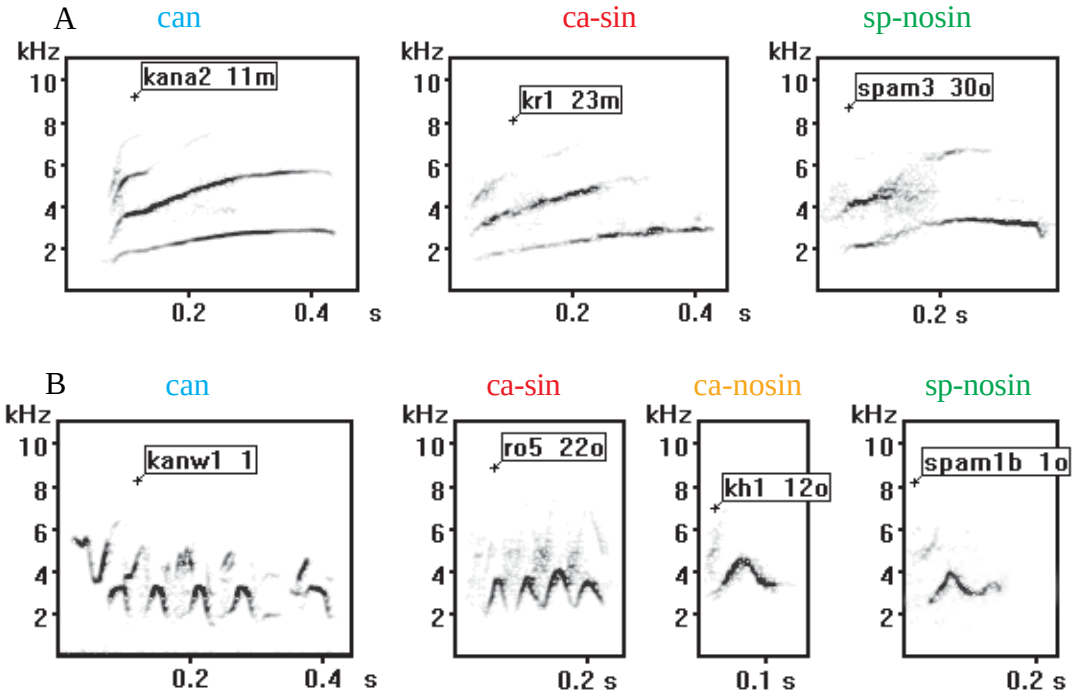


Fig. 3.8: Similar syllables, which occurred in canary and in sparrow vocalization.
A) A syllable never used for a tour by can, nor by ca-sin; however this syllable was also produced by sp-nosin.
B) A syllable which can and ca-sin used in tours, but which also occurred as a single syllable in ca-nosin as well as in sp-nosin repertoires.

3.3.2.5 „Free" syllables

A so-called „free" syllable is owned by a single canary-raised sparrow individual. These syllables were characterized by a high portion of small frequency modulations either produced at a moderate time scale or very rapidly (vibratos) (see Figure 3.8). Only two ca-sin used them within a tour or a tour-comprising sequence (see Fig. 3.7 A). House

sparrows (canary- and sparrow-raised) varied many syllables by including different portions of vibratos or changing their position within a given syllable. Nevertheless „free“ syllables looked quite similar regardless whether produced within one sequence or in different sequences (Fig. 3.9).

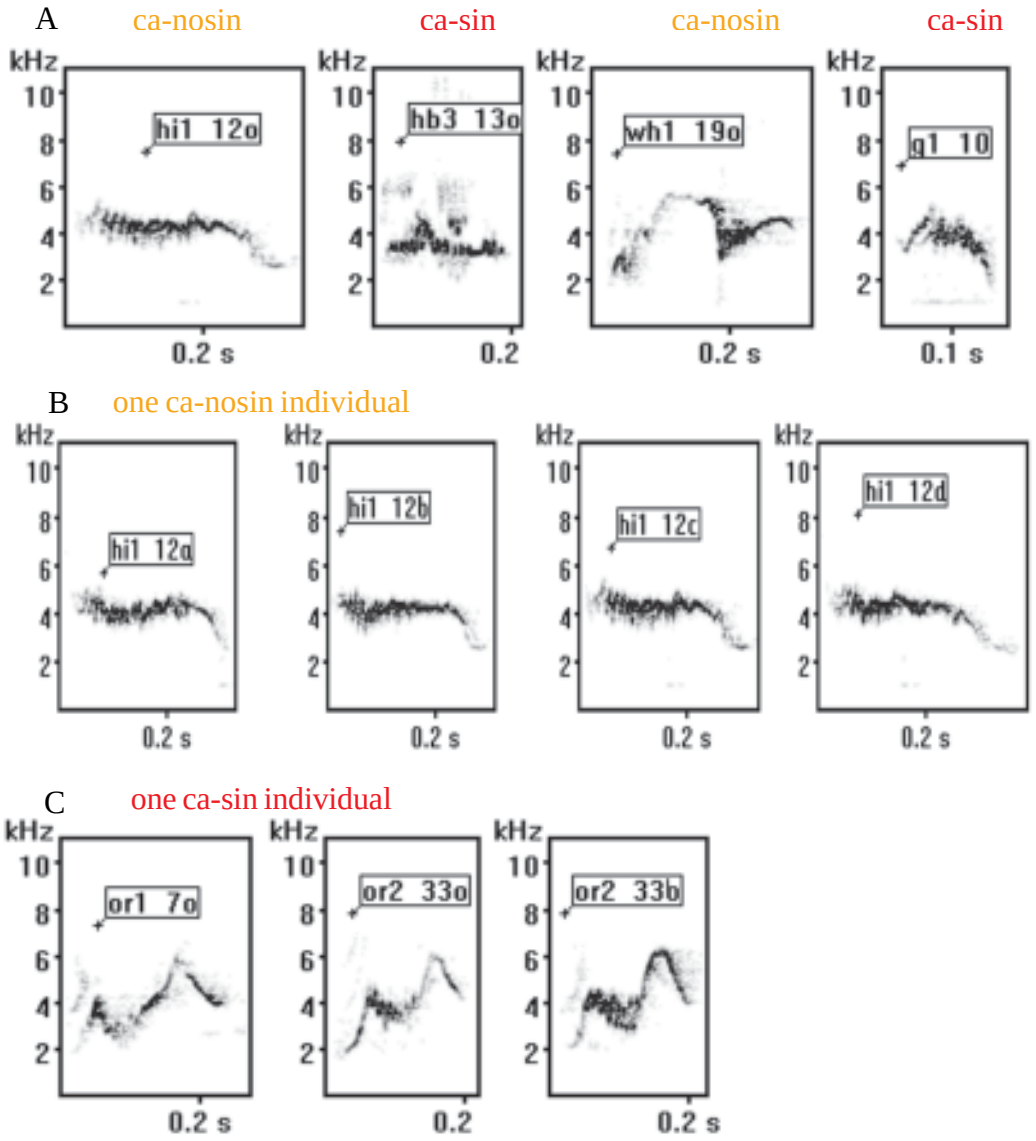


Fig. 3.9: Syllables of canary-raised house sparrow males.
A) Examples of „free“ syllables of different birds;
B) Examples of a given „free“ syllable vocalized by the same individual several times. Any „free“ syllable was produced by only one of the canary-reared individuals and did not occur in the canary repertoire (or in the vocalizations of sparrow-raised sparrows).
C) Examples for the sparrow-typical two-folded chirp with different portions of vibratos within the first part of the syllable.

3.3.2.6 „Common“ and two-voice syllables

„Common“ syllables were produced by all canary-raised sparrows. That only some, but not all sparrow-raised sparrows produced them might be a consequence of rare vocalizing while tape recording. I think they belong to the natural sparrow calls described by several authors (see chapter 1, 1.6.3).

Each sparrow produced two-voice syllables. About 8% of the total repertoire of house sparrows consisted of two-voice syllables that were recorded more than 10 times (Fig. 3.10). The majority of two-voice syllables occurred only up to four times and were thus excluded from this analysis. As canaries only seldom produce two-voice syllables and none occurred in my own tape recordings, but all sparrows produced them, it is reasonable to assume that this syllable type was not learned from canary tutors but belong to the natural sparrow repertoire.

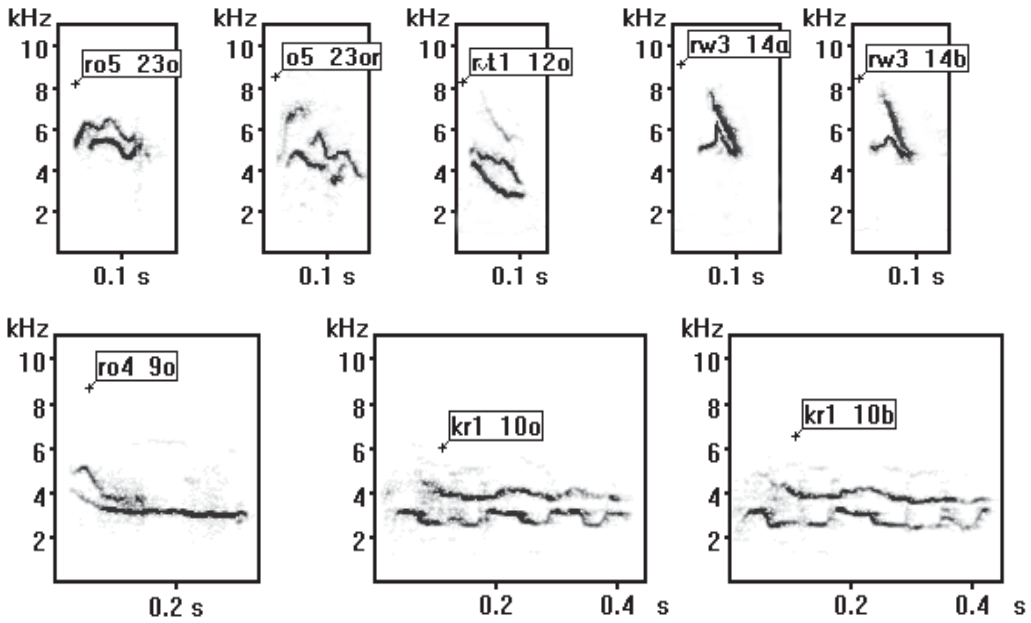


Fig. 3.10: Two-voice syllables of ca-sin and ca-nosin. The upper row gives examples for short, the second row for relatively long syllables. In each row, the last two examples came from the same individual at different times, showing that two-voice syllables did not occur by accident, but were reproduced in a recognizable form. Please not the different time scale in the second row.

3.3.3 COMPARING SEVERAL PARAMETERS OF TOURS AND SYLLABLES

3.3.3.1 INTER-SPECIFIC COMPARISON: TOURS PRODUCED BY CANARIES AND BY SPARROWS

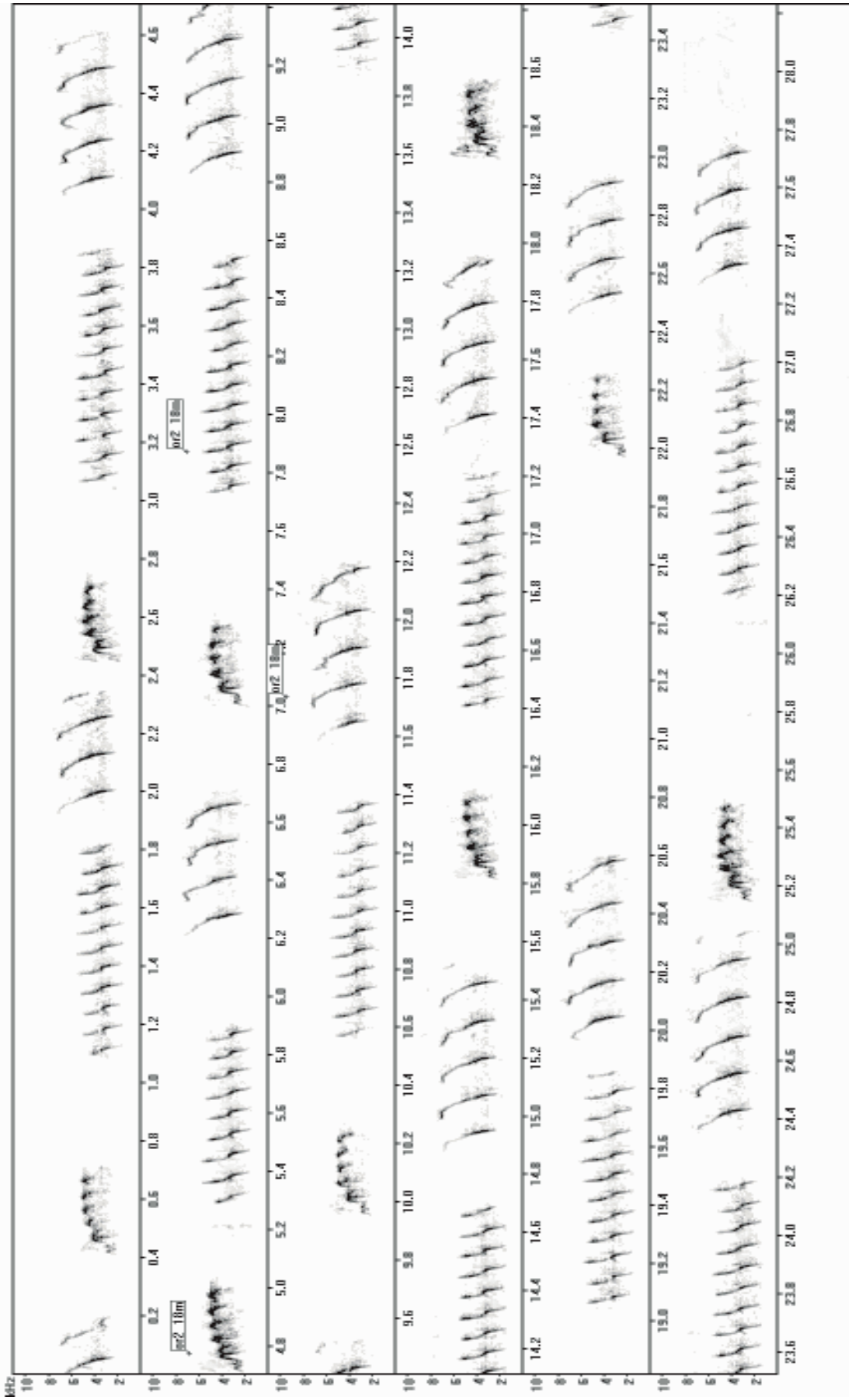
Most often a tour of ca-sin was followed by maximun 2 further (same or different) tours, then at least one lone syllable occurred (see Fig. 3.4B). However two individuals sometimes produced longer successions of several tours (Fig. 3.11). Ca-sin separated successive tours by intervals longer than those between syllables within a tour, while canaries did not increase intervals between two subsequent tours relative to intervals between syllables within the tour (Fig. 3.4A).

Canary males sang song types which were characterized by a stable composition and succession of syllables. A comparable song structure could not be detected in sparrows for mainly two reasons. First of all, sparrow vocalizations had an instable composition in that many syllables occurred in one half of a tape but not in the other one. Furthermore if a syllable occurred in several sequences it was sung with different basic frequencies. For example the bird yellow sung two sequences without tours. Sequence A was 149 syllables long, sequence B contained a total number of 191 syllables. The syllable nr. 47 occurred 89 times in sequence A and was mostly combined with syllable nr. 139 (from all found combinations 83% contained both syllables). However in sequence B syllable nr. 47 only occurred 11 times and syllable 139 disappeared completely. In sequence B there was no comparable combination of two syllables like 47-139 found in sequence A.

Another obvious difference between both species was in tour composition: even the minimum number of syllables which canaries repeated within a tour was significantly larger than in ca-sin (pooled variance t-test, $t = 8.694$, $df = 5.2$, $p << 0.001$, $\alpha = 0.01$; Fig. 3.12A), which in turn resulted in a significantly longer total tour duration in canaries (pooled variance t-test, $t = 9.380$, $df = 13$, $p << 0.001$, $\alpha = 0.012$; Fig. 3.12B).

Fig. 3.11: Sequence of continuous vocalizations of the ca-sin orange right + left singing a succession of different tours.

ca-sin orange right + left



Tour syllables of can comprised slightly significantly larger frequency ranges, i.e. frequency modulation within a syllable (separate variance t = 2.946, df = 12.9, p = 0.011, α = 0.016; Fig.3.12C) than the syllables of ca-sin.

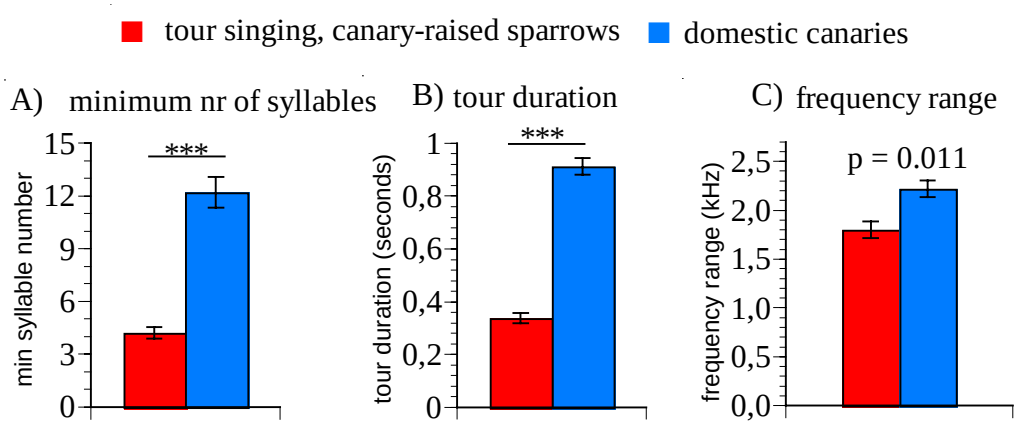


Fig. 3.12: Comparisons between tours sung by ca-sin (n = 10) and can (n = 5). P-values of the respective statistical tests are presented in the graph, *** indicates p < 0.001. In all graphs means ± sem are given; for details about statistics see text. Measurements are explained in 3.2.5. It has to be taken into account that sparrows and canaries were separated from their respective conspecifics.

Syllable duration, however, was of comparable length in both species (pooled variance t = -1.720, df = 13, p = 0.109, α = 0.05) (Fig.3.13A). The same was true for silence interval durations between syllables within a tour (pooled variance t = 1.961, df = 13, p = 0.072, α = 0.025; Fig.3.13B).

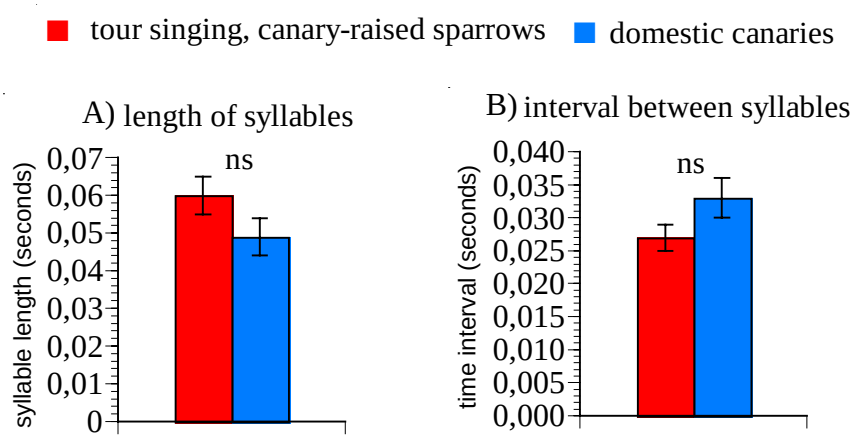


Fig. 3.13: Comparisons between tours sung by ca-sin (n = 10) and can (n = 5).
A) Length of syllables used within tours.
B) Length of silence intervals between syllables within tours (measurements are explained in 3.2.5). P-values of the respective statistical tests are presented in the graph, ns = not significant. In all graphs means ± sem are given; for details about statistics see text.

The specific number of repetitions of a syllable within a particular sparrow tour varied only by 1 or 2 syllables. For example tour 20, sung by ca-sin orange left+right, always contains 8 to 10 syllables (see Fig. 3.14A). The canary tutor kana2, however, repeated a syllable much more often and varied the specific number of repetitions of a given syllable within a particular tour much more. In the given example, the canary male repeated the syllable from 21 up to 34 times.

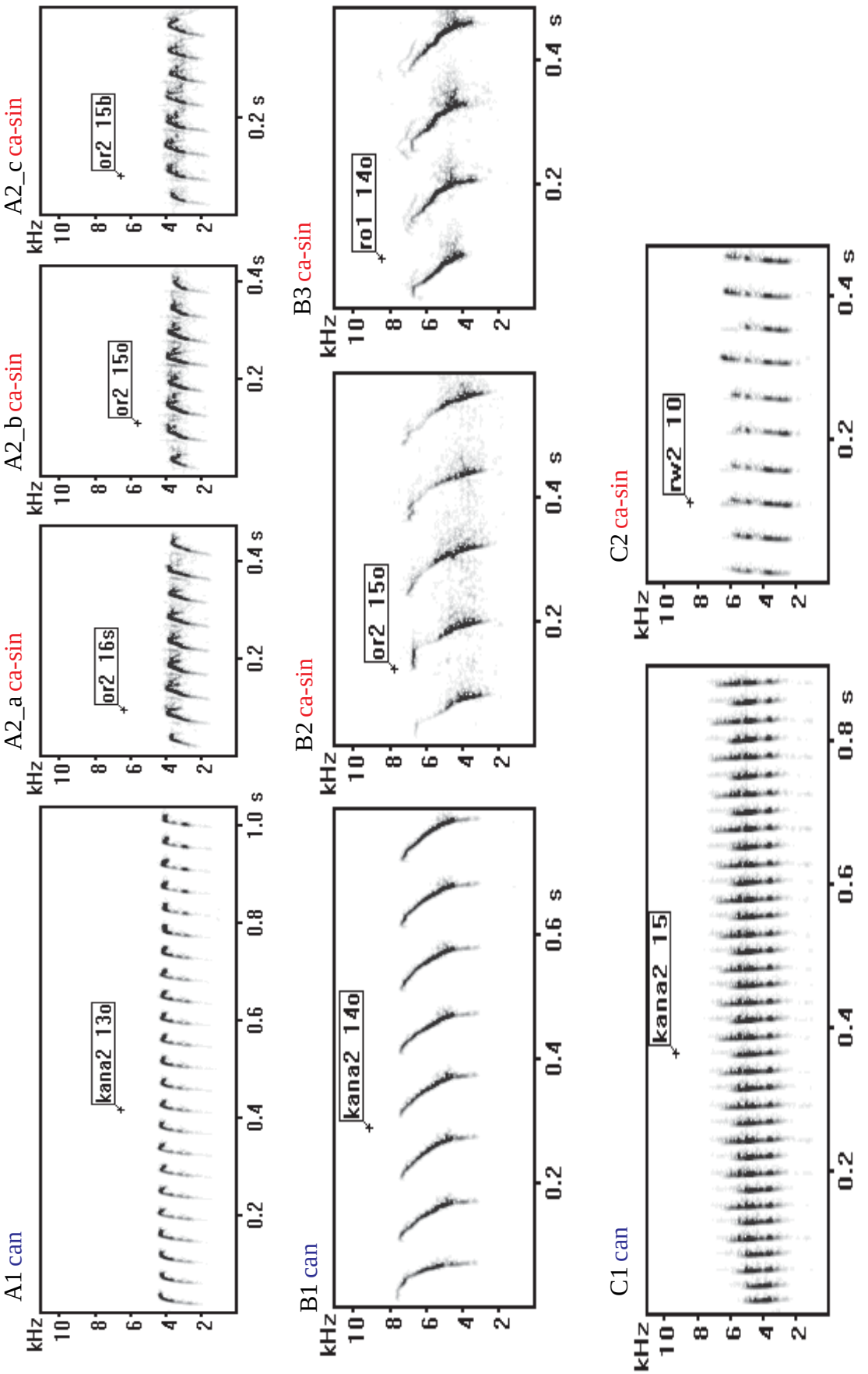
Furthermore tours were produced by ca-sin with a constant repetition rate (number of syllables per time, Hz) similar to that of their canary tutors (Fig. 3.14AB). However canaries can produce tours with a repetition rate as high as 55 syllables per seconds (see Fig. 3.15), while sparrows 'imitated' such a tour much slower (Fig. 3.14C).

Fig. 3.14: Tours sung by three ca-sin males compared to their can (kana2) tutor's tours. Data are given as mean ± sem.

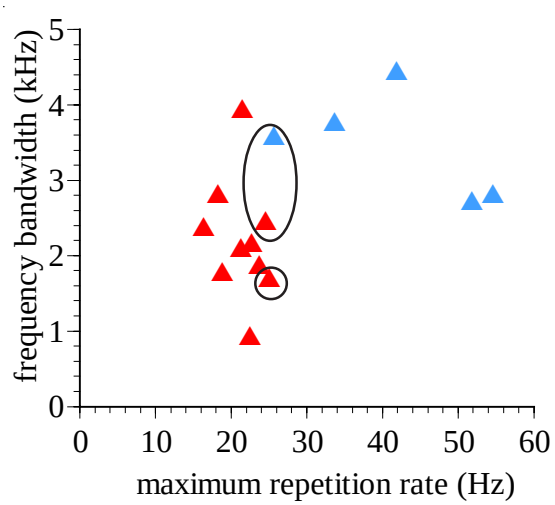
A) Example of a tour with a relatively 'high' repetition rate (in Hz).
A1) canary: 22.5 ± 0.07 Hz;
A2_a - A2_c) ca-sin orange left+right: 20.1 ± 0.13 Hz.

B) Example of a tour with a relatively low repetition rate:
B1) canary: 10.00 ± 0.16 Hz,
B2) ca-sin orange left+right: 10.10 ± 0.35, B3) ca-sin red left+right: 9.20 ± 0.09 Hz.

C) Example of a canary tour with a relatively high repetition rate; the sparrow produced a tour composed with a similar, learned syllable, but with a much lower repetition rate (however, for a sparrow this was the second highest repetition rate I found; see Fig. 3.15):
C1) canary: 42.1 ± 0.27 Hz,
C2) ca-sin red-white: 24.4 ± 0.14 Hz.


A1 can
A2_a ca-sin
A2_b ca-sin
A2_c ca-sin
B1 can
B2 ca-sin
B3 ca-sin
C1 can
C2 ca-sin
kana2 13o
or2 16s
or2 15o
or2 15b
kana2 14o
or2 15o
ro1 14o
kana2 15
rw2 10
kHz
s

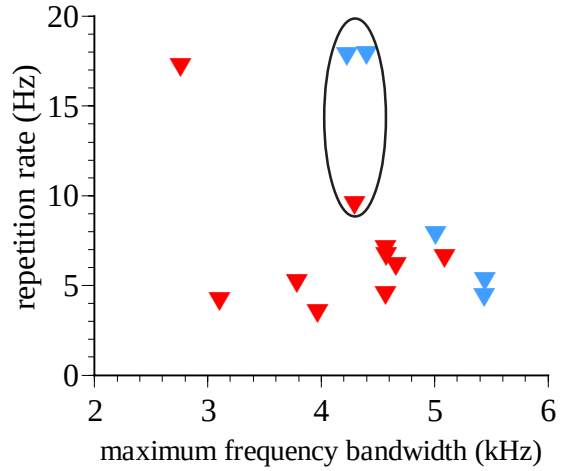
Canaries reached larger *maximum repetition rates* than sparrows did (separate variance t = 3.69, df = 4.2, p = 0.019). It is also obvious from Fig. 3.15, that the same repetition rate in house sparrows resulted in a smaller frequency bandwidth of the syllables than in canaries (circled symbols in Fig. 3.15).



sparrow		canary	
mrrate	**fre**	**mrrate**	**fre**
24.41	2.49	25.57	3.61
23.70	1.90	33.63	3.79
21.41	3.96	51.72	2.75
24.97	1.72	41.83	4.48
18.73	1.81	54.55	2.84
18.18	2.84		
22.42	0.95		
16.29	2.41		
21.23	2.12		
22.64	2.20		

Fig. 3.15: Relationship between maximum repetition rate (mrrate) and its corresponding frequency bandwidth (frequ) of ca-sin (n = 10) and canary tutors (n = 5). Data values are shown in the integrated table. Marked value and black arrow: highest maximum repetition rate found. For statistical details and circled symbols, see text.

Domestic canaries produced a significantly larger *maximum frequency bandwidth* than sparrows did (separate variance t = 2.52, df = 10.7, p = 0.029)(Fig. 3.16). Fig. 3.16 also reveals, that sparrows displayed a slower repetition rate at the same frequency bandwidth than canaries did (circled symbols in Fig. 3.16).



sparrow		canary	
mfre	**rrate**	**mfre**	**rrate**
5.08	6.55	4.40	17.91
4.56	4.54	5.00	7.96
4.65	6.12	4.22	17.82
3.96	3.48	5.44	5.30
4.56	7.04	5.43	
4.57	6.68		
4.29	9.52		
2.75	17.24		
3.10	4.18		
3.78	5.19		

Fig. 3.16: Relationship between maximum frequency bandwidth (mfrequ) and its corresponding repetition rate (rrate) of ca-sin (n = 10) and canary tutors (n = 5). Data values are shown in the integrated table. For statistical details and circled symbols, see text.

3.3.3.2 INTRA-SPECIFIC COMPARISON

A) CA-SIN INTRA-INDIVIDUAL COMPARISONS: SYLLABLES SUNG BETWEEN TOURS AND IN PURE SYLLABLE SEQUENCES

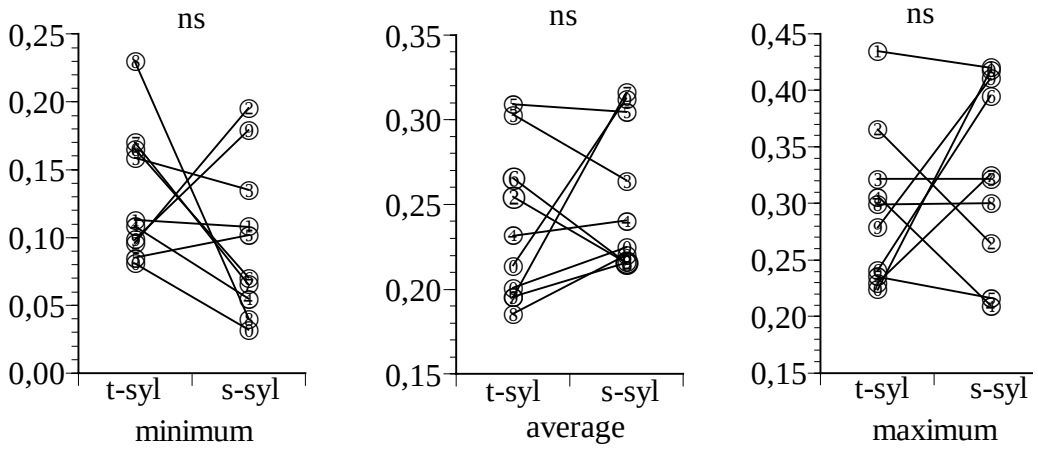
Single syllables sung in tour-comprising sequences are in the following referred to as t-syl while syllables sung in pure syllable sequences are called s-syl (silence intervals were measured as described in 3.2.5, Fig. 3.3).

Silent intervals were significantly longer between two t-syl, or between t-syl and the following tour than between two s-syl (paired sample t test, t = 3.438, df = 9, p = 0.007). However, average (paired sample t test, t = -0.527, df = 9, p = 0.611) and minimum (paired sample t test, t = -0.997, df = 9, p = 0.345) *silence intervals* did not differ significantly. There was no significant difference between t-syl and s-syl neither in average (paired sample t test, t = -0.961, df = 9, p = 0.362), minimum (paired sample t test, t = 0.135, df = 9, p = 0.896) or maximum (paired sample t test, t = -1.562, df = 9, p = 0.153) *frequency range*, nor in average (paired sample t test, t = -0.970, df = 9, p = 0.357), minimum (paired sample t test, t = 1.174, df = 9, p = 0.270) or maximum (paired sample t test, t = -1.060, df = 9, p = 0.317) *syllable duration* (Fig. 3.17).

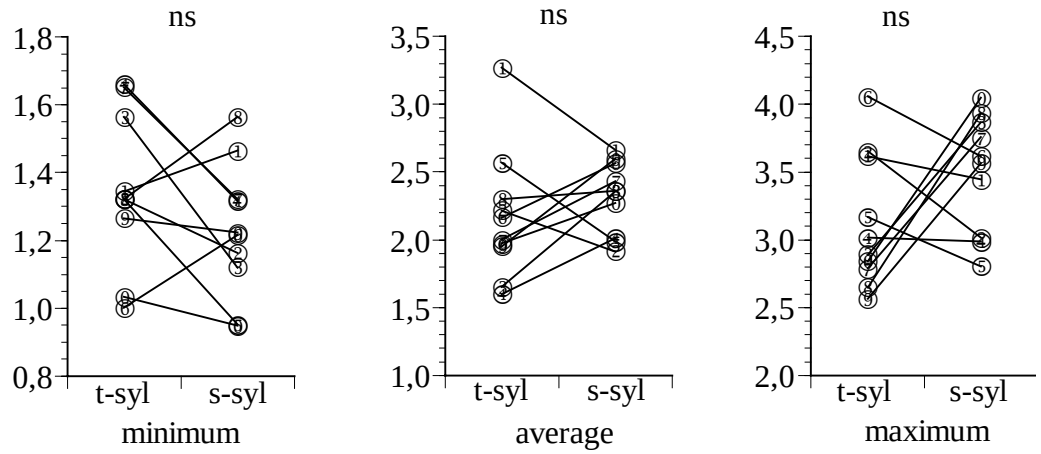
Comparisons of Fig. 3.12 and 3.13 with Fig 3.17 reveals that s-syl and t-syl are quite different from syllables sung within tours. Most obvious is the shorter silence interval between tour syllables (mean 0.025 seconds) relative to silence intervals between s-syl and t-syl respectively (mean 'average interval': 1.4 seconds), and the shorter duration of tour syllables (mean: 0.06 seconds) relative to other syllables (mean 'average duration': 0.25 seconds). The covered frequency range of a tour syllable was slightly smaller (mean frequency range: 1.8 kHz) than in s-syl and t-syl (mean 'average frequency range': 2.3 kHz).

Fig. 3.17: Comparisons of the indicated syllable characteristics (headings also apply to y-achses). The syllables came from ca-sin (n = 10) who could also sing canary-like tours. P-values of the respective statistical tests are presented in the graphs, ns = not significant. For details about statistics see text. t-syl: syllable from a tour comprising sequence; s-syl: syllable from a pure syllable sequence.

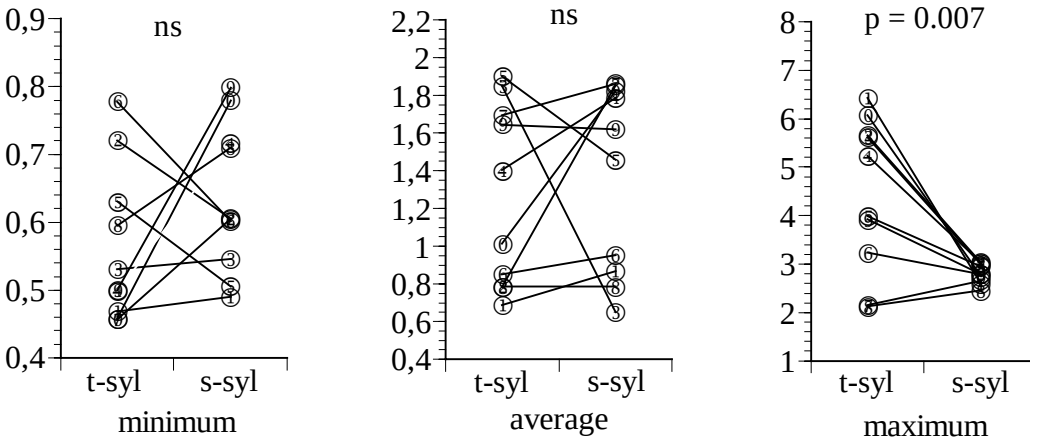
A) DURATION (seconds)



B) FREQUENCY RANGE (kHz)



C) INTERVAL BETWEEN SYLLABLES (seconds)

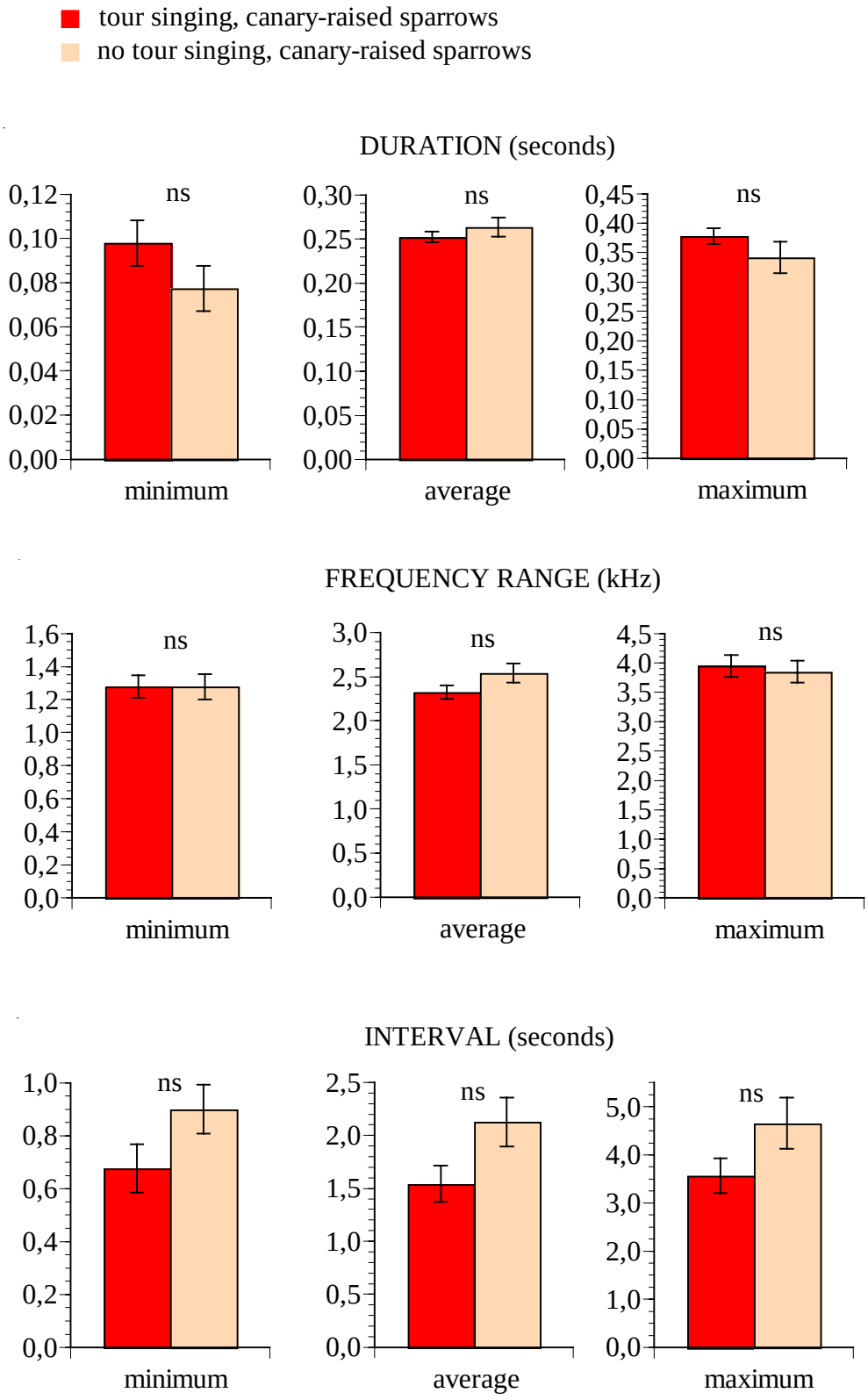


B) CA-SIN vs CA-NOSIN: SYLLABLES OF PURE SYLLABLE SEQUENCES

Ca-sin and ca-nosin were different in whether or not they produced tours and in the percentage of copied and „free“ syllables (see Fig. 3.5). In all other measures they were very similar (including repertoire size)(Fig. 3.18).

There was no significant difference between syllables of ca-sin and ca-nosin neither in average (students t-test, separate variance t = 1.197, df = 15.9, p = 0.249), minimum (students t-test, separate variance t = -1.014, df = 14.4, p = 0.327) or maximum (students t-test, separate variance t = -1.225, df = 14.4, p = 0.240) *syllable duration*. Nor did a comparison of *frequency range* reveal any significant difference, neither in average (students t-test, separate variance t = 1.553, df = 17.4, p = 0.138), minimum (students t-test, pooled variance t = -0.015, df = 19, p = 0.988), or maximum (students t-test, pooled variance t = -0.092, df = 19, p = 0.928) measures. The *interval between single syllables* was always shorter in ca-sin than in ca-nosin, though differences did not become significant, neither in average (students t-test, separate variance t = 1.632, df = 15.3, p = 0.123), minimum (students t-test, separate variance t = 0.880, df = 16.1, p = 0.392) or maximum (students t-test, separate variance t = 1.703, df = 17.3, p = 0.106) measures.

Fig. 3.18: Comparisons of the indicated syllable characteristics (headings also apply to y-achses). The syllables were sung in pure syllables sequences by canary-reared house sparrows, singing tours (ca-sin; n = 10) or not (ca-nosin; n = 11). In all graphs means ± sem are given, ns = not significant. For details about statistics see text.


tour singing, canary-raised sparrows
no tour singing, canary-raised sparrows
DURATION (seconds)
0,12
0,10
0,08
0,06
0,04
0,02
0,00
ns
minimum
0,30
0,25
0,20
0,15
0,10
0,05
0,00
ns
average
0,45
0,40
0,35
0,30
0,25
0,20
0,15
0,10
0,05
0,00
ns
maximum
FREQUENCY RANGE (kHz)
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0,0
ns
minimum
3,0
2,5
2,0
1,5
1,0
0,5
0,0
ns
average
4,5
4,0
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
ns
maximum
INTERVAL (seconds)
1,0
0,8
0,6
0,4
0,2
0,0
ns
minimum
2,5
2,0
1,5
1,0
0,5
0,0
ns
average
5,0
4,0
3,0
2,0
1,0
0,0
ns
maximum

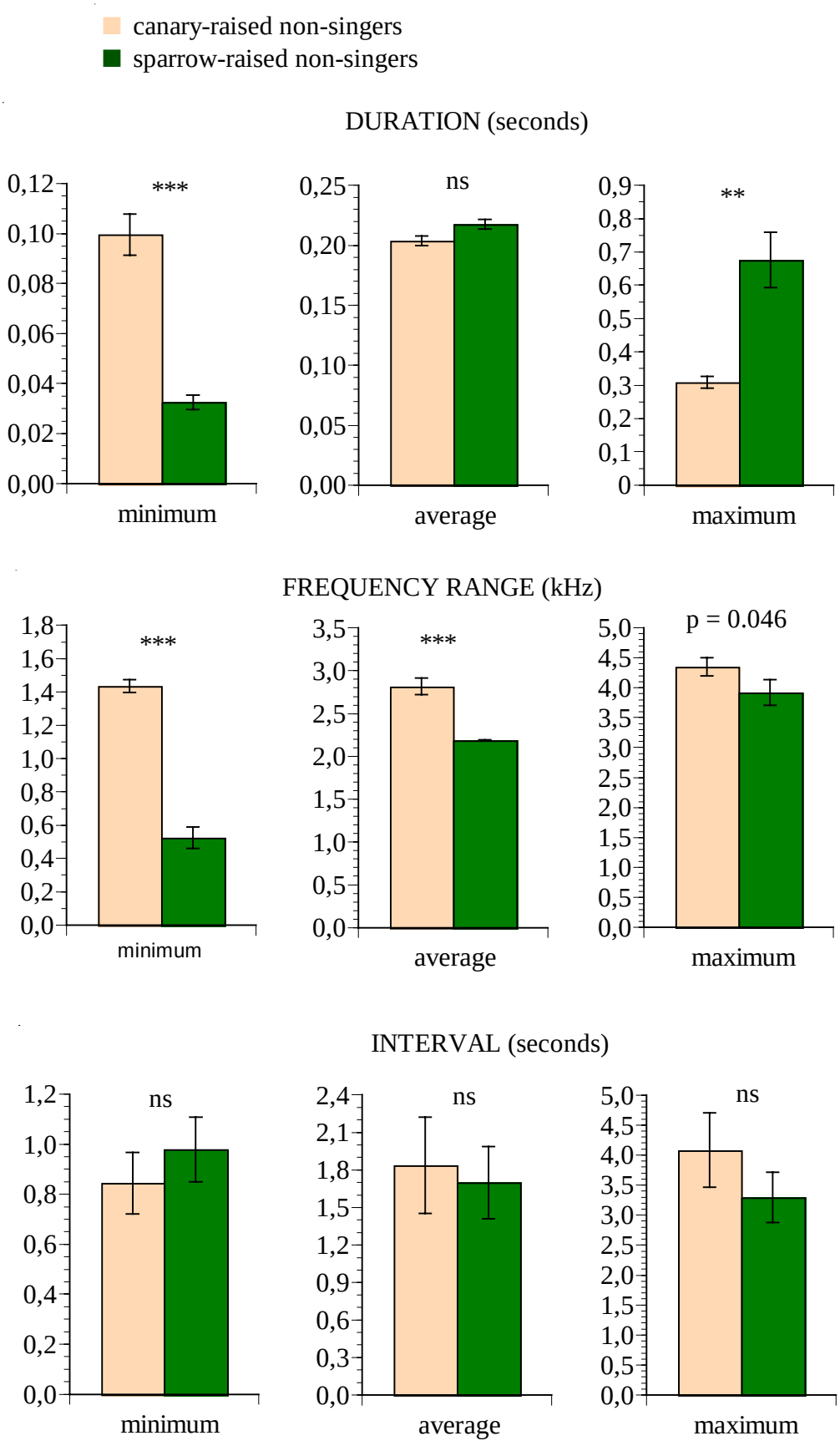
C) CA-NOSIN vs SP-NOSIN: SYLLABLES FROM PURE SYLLABLE SEQUENCES

The shortest syllables of sparrow-raised birds were significantly shorter than syllables of canary-raised individuals (pooled variance $t = 7.728$, $df = 11.3$, $p << 0.001$, $\alpha = 0.016$) and the longest syllables of ca-nosin were significantly longer than syllables produced by sp-nosin (separate variance $t = -4.278$, $df = 8.7$, $p = 0.002$, $\alpha = 0.025$). The average duration of syllables, however, did not differ significantly between the two groups (separate variance $t = -0.3154182$ $df = 8.2$, $p = 0.760$, $\alpha = 0.05$).

Ca-nosin produced on average (separate variance $t = 6.657$, $df = 9.0$, $p << 0.001$, $\alpha = 0.025$) and at minimum (pooled variance $t = 12.558$, $df = 17$, $p << 0.001$, $\alpha = 0.016$) significantly larger *frequency ranges* per syllable than in sp-nosin; however maximum *frequency range* was only weakly significantly larger in ca-nosin than sp-nosin (pooled variance $t = 2.152$, $df = 17$, $p = 0.046$, $\alpha = 0.05$).

Intervals between two syllables did not differ significantly, neither in average (pooled variance $t = 0.281$, $df = 17$, $p = 0.782$), minimum (pooled variance $t = -0.366$, $df = 17$, $p = 0.719$) nor in maximum (pooled variance $t = 1.029$, $df = 17$, $p = 0.318$) measures (Fig. 3.19).

Fig. 3.19: Comparisons of the indicated syllable characteristics (headings also apply to y-achses). The syllables were sung in pure syllable sequences by ca-nosin (n = 10) or sp-nosin (n = 9). P-values of the respective statistical tests are presented in the graphs, *** indicates $p < 0.001$, ** indicates $p < 0.01$, 'ns' stands for not significant differences. In all graphs means ± sem are given; for details about statistics see text.


canary-raised non-singers
sparrow-raised non-singers
DURATION (seconds)
0,12
0,10
0,08
0,06
0,04
0,02
0,00
***
minimum
0,25
0,20
0,15
0,10
0,05
0,00
ns
average
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
**
maximum
FREQUENCY RANGE (kHz)
1,8
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0,0
***
minimum
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
***
average
5,0
4,5
4,0
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
p = 0.046
maximum
INTERVAL (seconds)
1,2
1,0
0,8
0,6
0,4
0,2
0,0
ns
minimum
2,4
2,1
1,8
1,5
1,2
0,9
0,6
0,3
0,0
ns
average
5,0
4,5
4,0
3,5
3,0
2,5
2,0
1,5
1,0
0,5
0,0
ns
maximum

3.3.4 CUMULATIVE CURVE - PRODUCTION OF NEW SYLLABLES WITHIN 150 SECONDS CONTINUOUS VOCALIZATION

As already mentioned one surprising result was, that ca-sin produced sequences comprising tours and syllables, and sequences containing syllables only. The latter sounds like normal house sparrow vocalization. Tour-comprising and pure syllable sequences of an individual were thus compared with canary tutors and sparrow siblings (sp-nosin, ca-nosin) separately.

3.3.4.1 USING COUNTED NUMBERS OF NEW SYLLABLES

Ca-sin, when producing a pure syllables sequence, did not differ significantly from sp-nosin in absolute number of different syllables, but both produced significantly fewer different syllables than canaries did within 150 seconds of continuous vocalization (Kruskal-Wallis-Test with *post hoc* multiple comparisons, H = 11.732, $p < 0.001$, Bonferroni adjustment $\alpha = 0.025$) (Fig. 3.20a). When the same ca-sin individuals, however, produced a sequence comprising tours, they differed significantly from sp-nosin but not from canaries anymore (Kruskal-Wallis-Test with *post hoc* multiple comparisons, H = 18.018 $p < 0.001$, Bonferroni adjustment $\alpha = 0.025$)(Fig. 3.20b).

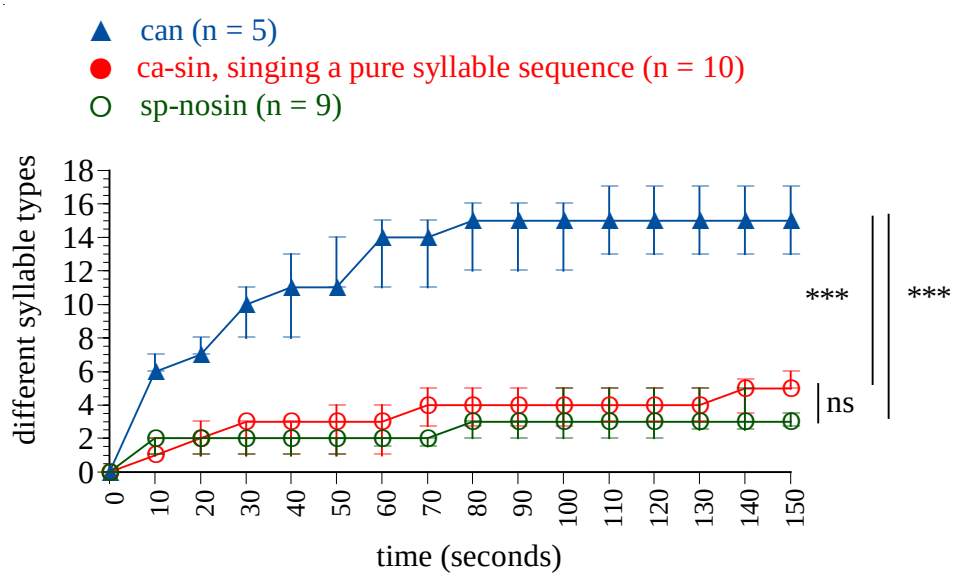


Fig. 3.20a: Counted numbers of new syllable types plotted against the respective time interval of 10 seconds. Data represent median, 1st and 3rd quartiles of groups indicated. P-values are given in the graph, *** indicates $p < 0.001$, ns = not significant. When singing pure syllables sequences ca-sin did not differ from their sp-nosin siblings.

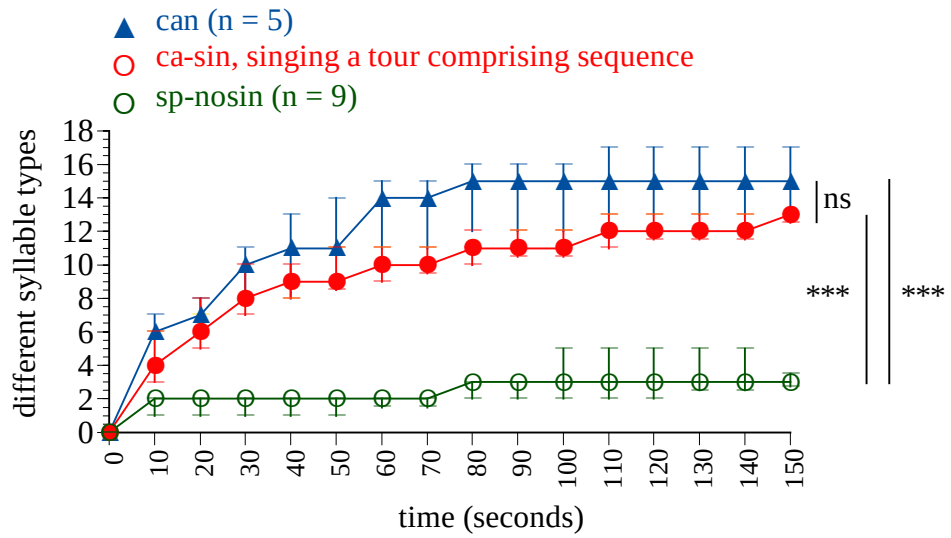


Fig. 3.20b: Counted numbers of new syllable types plotted against the respective time interval of 10 seconds. Data represent median, 1st and 3rd quartiles of groups indicated. P-values are given in the graph, *** indicates $p < 0.001$, ns = not significant. When ca-sin sung a sequence comprising both tours and syllables, then they were more similar to their canary foster fathers than to their sp-nosin siblings.

The higher number of different syllables in tour-comprising sequences did not result from a higher total number of syllables. Indeed the total number of syllables produced in an analysed sequence could be higher in pure syllable sequences (see Fig. 3.21), especially when a bird used 3-4 syllable tours (for examples, see Appendix 5).

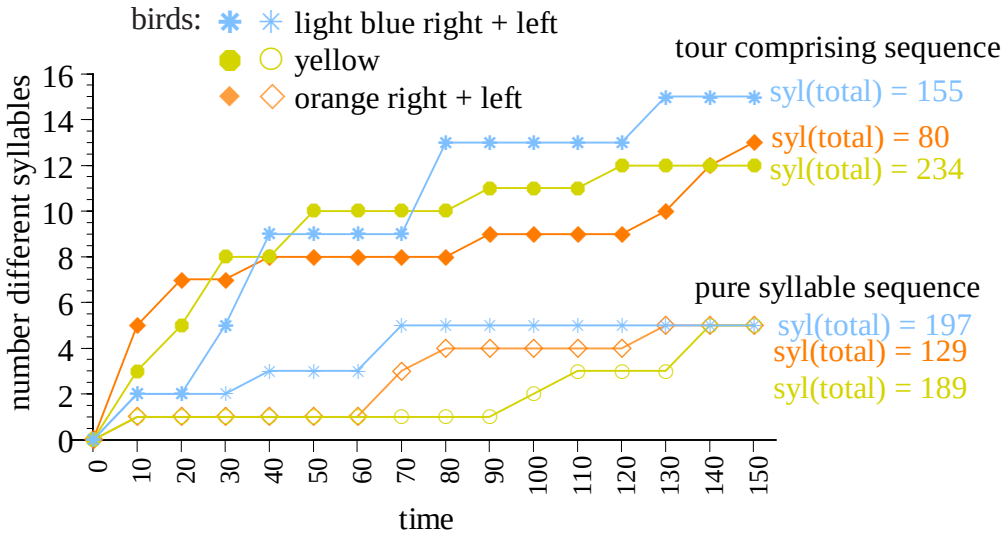


Fig. 3.21: Different syllable types plotted against the respective time interval of 10 seconds. From three ca-sin (light blue right + left, yellow, orange right + left) both a tour comprising and a pure syllable sequence is given. Same colour indicates the same individual. syl(total): total number of syllables produced in the respective sequence. syl(total) may, but need not be higher in one of the sequence types.

3.3.4.2 USING THE COUNTED NUMBER OF SYLLABLES AS PERCENTAGE OF AN INDIVIDUAL'S TOTAL REPERTOIRE

Ca-sin possessed a repertoire size of 32 - 45 syllables. Their canary tutors, however, individually owned only 16 - 22 syllables. Thus when ca-sin individuals produced a sequence comprising tours, they produced within 150 seconds continuous vocalization a significantly higher percentage of their total repertoire than ca-nosin, but a significantly lower percentage than can (Kruskal-Wallis-Test, $H = 19.959$, $p < 0.001$, Bonferroni adjustment $\alpha = 0.025$, Dunn's Test post hoc: p (can, ca-nosin) < 0.001, p (can, ca-sin tour sequence) < 0.001), p (ca-sin, ca-nosin) < 0.001) (Fig.3.22A).

However, when ca-sin produced a pure syllable sequence, they did not differ significantly from ca-nosin in percentage number of different syllables, but both produced significantly less different syllables than can did within 150 seconds continuous vocalization (Kruskal-Wallis-Test, $H = 11.632$, $p < 0.001$, Bonferroni adjustment $\alpha = 0.025$, Dunn's Test post hoc: post hoc: p (can, ca-nosin) < 0.001, p (can, ca-nosin) < 0.001), p (ca-nosin, ca-sin syllable sequence) > 0.05) (Fig. 22B).

(For the canary data the study-specific analysis has to be taken into account: a) in this study 150 seconds of vocalization include silence intervals up to 8 seconds and b) the data are related to a canary's total *vocal* repertoire not to its (smaller) song repertoire, which is usually used).

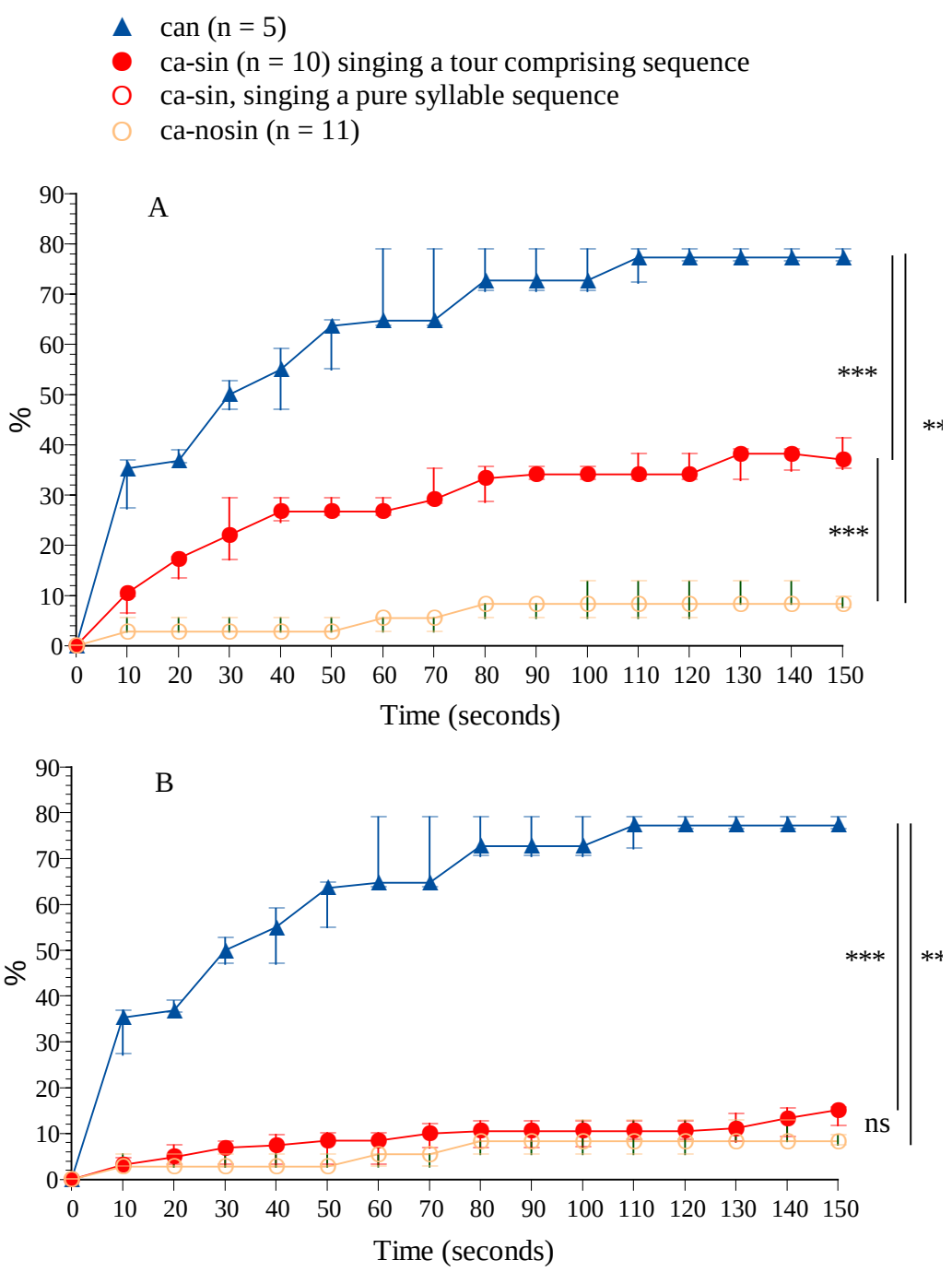


Fig 3.22: Number of syllable types as percentage of the total vocal repertoire plotted against the respective time interval of 10 seconds. Data represent median, 1st and 3rd quartiles of groups indicated. P-values are given in the graph, *** indicates $p < 0.001$, ns = not significant. Again, when singing pure syllable sequences ca-sin, did not differ from their siblings, who never sung a tour (B). But when the same birds sung tour-containing sequences they differed from their siblings, though they did not reach their canary foster fathers' values (A).

3.3.4.3 THE RECALL RATE K

The recall rate K stands for the time a bird needs to produce 63% of its individual final niveau of different syllables (graphically shown in a repertoire curve, see 3.3.4; for detailed explanation see 3.2.5.4).

I calculated the recall rate only for curves to which the Brody function fits to 98%, thus pure syllable sequences could not be used for this analysis. In addition to can and ca-sin the recall rate K for some wild canaries *Serinus canaria* (n = 4) and white-browed sparrowweavers *Plocepasser mahali* (n = 4) were calculated; unpublished data sets were kindly offered by Conny Voigt and Dr. Stefan Leitner.

A first statistical analysis with these very few data reveals that domestic canaries (dcan) and their sparrow pupils (ca-sin) had a comparable recall rate. K of wild canaries (wcan) did not differ significantly from dcan, and ca-sin did not differ significantly from white-browed sparrowweavers (weav). Wild canaries and white-browed sparrowweavers, however differ significantly in their recall rate (Fig. 3.23).

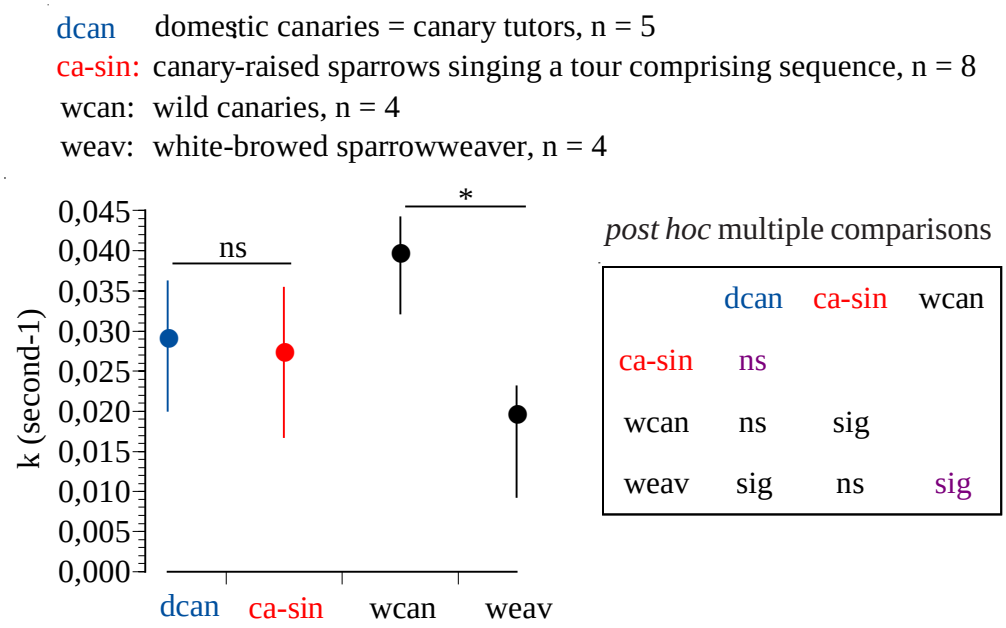


Fig 3.23: The recall rate K of four species. K was calculated using the Brody equation (for details see 3.2.5.4). Data represent minimum, median and maximum of groups indicated. Results of Kruskal-Wallis-Test with *post hoc* multiple comparisons following Conover 1980 are given in the table as ns = not significant and sig = $p < 0.05$. Only the two most important statistical results of Kruskal-Wallis-Test with *post hoc* multiple comparisons are given in the figure as ns = not significant, * = $p < 0.05$.

3.3.5 A SPECIAL CASE: RAMSES

In 1999 I obtained a canary singing house sparrow male of about 4 months of age. He was raised together with a female sibling in the neighbourhood of a caged canary pair. The young sparrow had social contact to its sibling and to the caregiving humans. He could hear sparrows through the open window and the canaries in the room, but he did not interact with any of them. Thus Ramses stands between my sparrow-raised (a) and canary-raised (b) birds: he had (a) social contact to a conspecific sibling, only saw and heard a canary from a distance, and (b) he was fed by a human and had no social contact to adult house sparrows.

By curiosity first tape recordings were taken in autumn of the same year when Ramses arrived in our institute. This tape was not analysed in detail, because brains of all ca-sin were only available from summer, and for analyses I used only tapes from the equivalent season. Furthermore this tape did not meet the rules for the other tape recordings because no sound-proof room was available and in the beginning his sister sibling was in the room (though separately caged) to habituate him. Ramses was my first canary-like singing sparrow male, thus I nevertheless looked through the tape. He sung canary-like tours not only during the breeding season, but also in autumn (I also heard other sparrow males doing this but could not tape record them). The temporal and spectral patterns of some tours seemed to be very similar in both seasons (Fig. 3.24, red arrow). Also some syllables looked stable in both seasons (Fig. 3.24, C), while others had become variable (Fig. 3.24 B, blue arrow) in autumn. Also in summer Ramses varied a given syllable by singing it at different frequencies or/and by adding a second (or even a third) note (Fig. 3.24, green arrow). The given variations did not occur just occasionally, but were repeated consistently at different frequencies and in the one-note or two-note version respectively (Fig. 3.24, green arrow lower row).

This one tape taken in autumn does not provide enough data to conclude whether syllables might occur throughout the year while others are seasonal, nor which tours are produced identical in both seasons and which not.

Beginning with his first spring, Ramses was kept and tape-recorded like all birds I raised myself, and also all measurements of his song were taken as described above (sound

reduced rooms, separated from conspecifics of both sexes, a caged domestic canary male in the room, tape recordings on two successive days).

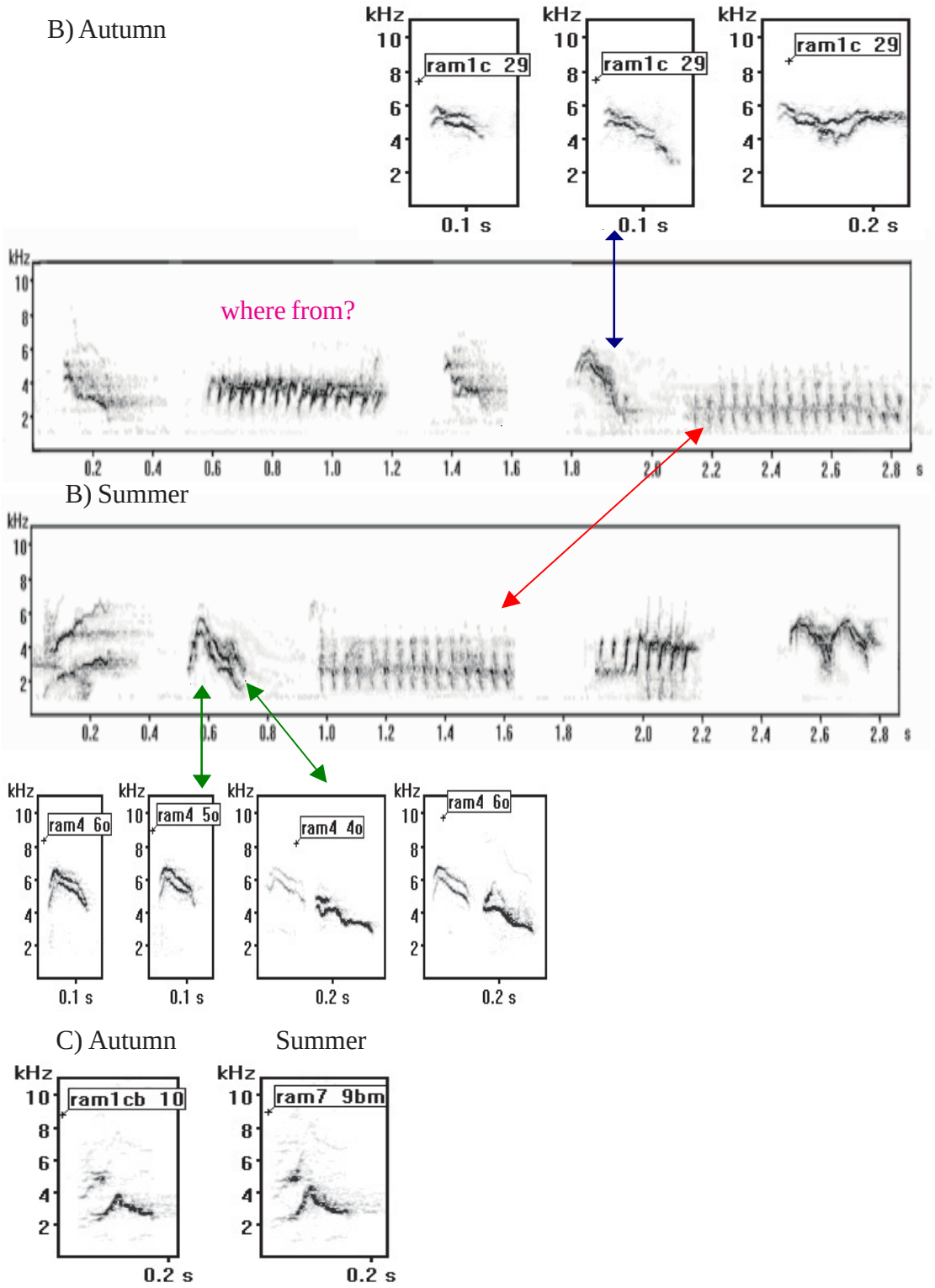


Fig. 3.24: Digital spectrograms of a canary-like singing house sparrow (Ramses) from breeding (summer) and non-breeding season (autumn). Details (arrows, „Where from?“) are explained in the text. Please note the slightly different time scales of some of the digital spectrograms.

Ramses had a total repertoire of 45 different syllables. Repertoire composition was similar to my canary-raised sparrows: he owned 10 of the 12 „common“ syllables as well as two voice syllables, and varied syllables by changing the position and portion of vibratos within a given syllable. Syllables used in tours mostly lacked overtones, as is typical for canaries. Some tours looked similar to those of the domestic canary who was in his room the first 6 months after he arrived in the institute (one example is given in Fig. 3.24 marked with „Where from?“). In the following year I used this canary male as a tutor for my ca-sin orange right+left - and he also copied this tour (see Fig. 3.4B). It may be that Ramses learned this tour after his arrival in the institute (with a minimum age of 6 months), but I cannot show this conclusively.

Ramses also produced both types of sequences. His vocalizations of tour comprising and pure syllable sequences did not differ from my ca-sin in most of the parameters measured (results 3.3.2 and 3.3.3). The only detectable difference was found when plotting the repertoire curve (vgl. Fig. 3.20ab). The repertoire curves of ca-sin revealed that they produced more different syllables in a defined time window when singing a sequence including tours than when singing a pure syllable sequence (see results 3.3.4.1 und 3.3.4.2). In Ramses, however, this difference was lacking: the cumulative curve was always the same whether singing sequences with or without canary-like tours (Fig. 3.25).

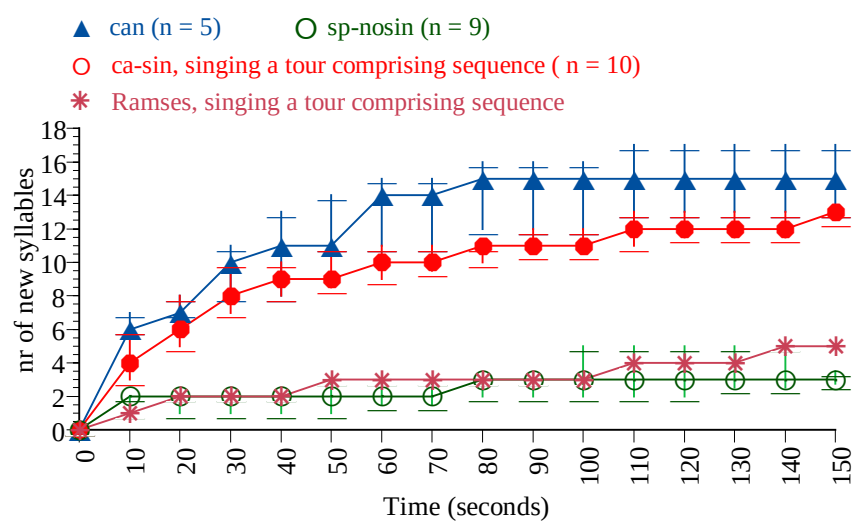


Fig. 3.25: Repertoire curve visualizing the production of new syllables within 150 seconds continuous vocalization. Data represent median, 1st and 3rd quartiles of groups indicated. For comparison data of can, ca-sin and sp-nosin were taken from Fig. 3.20. Ramses clearly did not increase the recall of new syllables when singing a tour-comprising sequences as ca-sin did (for comparison see Fig. 3.20b).

3.4. DISCUSSION

The range of acoustic stimuli that may be imitated by young songbirds includes not only widely divergent variants of conspecific song (e.g. Marler 1970; Podos et al. 1999) but under certain rearing conditions even heterospecific songs (e.g. Baptista & Petrinovich 1984; Marler & Peters 1989). Canary-reared house sparrows who copied canary tours reveal an unexpectedly wide learning system, in that they can be induced to memorize also a hetero-specific model.

Syllables

My canary-raised sparrows' total repertoire seemed to be limited to about 32 to 41 different syllables; this number is much larger than expected from wild sparrows. The repertoire of canary-raised sparrows consisted of three syllable types: a) not learned but developed by all sparrows, independent of their tutors; b) clearly copied from their canary tutor; and c) individual-specific „free" syllables which were never sung by one of the other birds and were characterized by a very high portion of vibratos (rapid frequency modulations). Both ca-sin and ca-nosin learned syllables from their canary tutors, but while ca-sin used them nearly exclusively for their tours or at least in tour-comprising sequences, ca-nosin sung the learned syllables „separately" but not as tours. In parallel, ca-sin had a tendency to pause for shorter intervals between syllables than ca-nosin. Thus ca-sin seemed to learn more syllables (tours) and a slightly „better" (shorter interval) sequential arrangement. One could be tempted to interpret the „free" syllables with the very (unusually) high portion of vibratos as an attempt to produce tours. But we judge the effort as „not-successful" because the rapid frequency modulations were not separated and thus not identified as separate syllables by human analysers. However Wickler (1982) argued that the brief, noise-like vocalizations might be „compressed melodies". Maybe at least some of these 'free' syllables' represent „compressed tours". Both groups (ca-sin, ca-nosin) learned canary syllables lacking harmonics. Harmonics, however, are typical for house sparrow calls and important in their social life (Nivison 1978). All clearly not learned „common" syllables contained at least one overtone.

While both canary-reared groups produced syllables similar with respect to duration and frequency range, they were significantly different from their sparrow-reared siblings.

Canary-raised individuals learned syllables with a larger frequency range than normally used by sparrows. However maximum frequency range did not differ between canaries, canary-raised and sparrow-raised sparrows. The question arising is: why do house sparrow males on average not produce more often syllables with large frequency ranges? The difference in the average usage of large frequency ranges might be explained by canary and sparrow females preferences. In canaries, song is most important for female choice (e.g. Halle et al. 2003). Thus the excellence of a singer is (besides others) identified by his production of a rapid succession of syllables with large frequency ranges. Although sparrows were able to sing the same syllables (though not as fast as canaries), the key to pair formation in sparrows is thought to be the males' ownership of a suitable nest site (Summers-Smith 1988). Furthermore both intra- and extra-pair mate choice is influenced by the size of the male's black bib which may be indicative of male quality (Cordero et al. 1999). Thus my results indicate what sparrows *can* learn under certain circumstances, but *not* what is *important* for their 'natural' vocal communication. Nevertheless it offers an instrument to test the hypothesis that song plays a minor role in female choice though is highly important for sparrows' social life.

Tours and temporal organisation of song

Sparrows' singing is known to be monotonous in that they repeat one syllable many times (Nivison 1978); however the silence intervals between these syllables are much longer than intervals within tours. Nevertheless in an agonistic context house sparrows naturally produce a tour-resembling vocalization (called scolding sequence) based on the definition „fast repetition of one syllable type". These scolding sequences never occurred when my birds were tape recorded as described, but e.g. when being handled by humans to take blood, though a given syllable might occur separately. It seems as if the decrease of silence intervals between the syllables results from excitation but not from a structural concept. For a scolding sequence sparrows used syllables which contained many harmonics. Thus these syllables and in turn the scolding sequences sound very harsh and very different from canary tours.

On the other hand house sparrows did learn to produce canary-like tours: a fast repetition of syllables poor in overtones or *lacking them altogether*. Taking a tour as a unit,

comparisons revealed differences in the two species. The sparrows produced each tour-type with a constant repetition rate, similar to that of their canary tutors, but only up to 25 Hz; sparrows never went beyond this point, while canaries may go much faster (up to 70 Hz; Suthers 1997). Besides a seemingly limited repetition rate sparrow were obviously limited in singing rapid successions of large frequency ranged syllables: Either they sang the same repetition rate like their canary tutors, but then syllables covered smaller frequency ranges, or they sang syllables with an equally large frequency range, but slower. This points to morphological constraints (discussed in more details in chapter 6). While canaries varied the number of syllables within a given tour, sparrows varied the number of syllables only very little, if at all. And they separate tours by an interval larger than the interval between syllables within the tours. Taken together these facts - constant repetition rate, constant number of syllables, separating tours by a larger pause - may lead to the conclusion that sparrows treat tours as „multi-note“ syllables, each of which is about the same length as a long sparrow syllable.

The sparrow’s temporal organization of song sequences (length of song units, i.e. syllables or tours, combined with duration of pauses between the respective units) turned out to be species-specifically determined: pure syllable sequences and tour-containing sequences (seeing tours equivalent to syllables) did not differ in their temporal structure. Constraints for learning the temporal song structure seem to exist in many bird species. Examples are the chaffinch (*Fringilla coelebs*) which will learn a greenfinch (*Chloris chloris*) or canary (*Serinus canaria*) song, but will utter them in chaffinch phrases (Conrads 1977; Slater 1983a); the marsh warbler (*Acrocephalus palustris*) copies songs from as many as 76 different species, but the species-specific qualities of marsh warbler song are retained in the temporal and sequential patterning of these syllables (Lemaire 1978); zebra finches (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata*) also show the tendency to organize foreign song syllables into their own species-specific phrases (Clayton 1989). Güttinger (1979) suggested that the learning of single syllables (or notes) and the species-specific temporal song program are two relatively independently operating principles which become bound together at a certain time.

Further peculiarities have to be taken into account. Birds who sing continuously at a rapid tempo for long periods without pausing for a normal inspiration use - depending on the syllable repetition rate - two different respiratory patterns (Suthers 1999; for details see chapter 1: 1.5.2 respiration during singing). The limit, forcing an individual to switch from one respiratory pattern to the other, is probably determined by mechanical properties, like mass and compliance of the thoracic and abdominal structures that must oscillate at the frequency of ventilation. Thus the syllable-like temporal organisation of tour comprising song in the house sparrow could result from morphological constraints rather than from a pre-determined song program (the question of morphological constraints on vocal performance is addressed in chapter 6).

Ecological (social and environmental) constraints

In house sparrows perceptual constraints might be coming from the social partner: the closer their interaction with the tutor the more young sparrows imitate. Sparrow-raised young, who could see and hear neighbouring canaries, learned only the vocalization of conspecifics who fed them. The hand-raised sparrow Ramses, fostered by humans, learned the song of a canary male without any social interaction; the young bird may have combined the „silent“ human foster parent with the nearest available adult avian vocalization.

Canaries as foster parents can override sparrows ‘innate’ predisposition of the recall rate of different syllable types, i.e. canary-raised sparrows produced more different syllables in shorter time intervals when singing canary-like sequences. This points to the possibility that the acquisition of the vocalizations of social partners is important in the normal life of a sparrow (Wickler 1982); it goes in line with other social learners like swamp and white-crowned sparrows (e.g. Marler & Peters 1977; Baptista & Petrinovich 1984, 1986). Nevertheless it remains unclear, how and why canary-like singing house sparrows make a difference in the recall of new syllables between sequences consisting of syllables only and sequences that contain tours. It may be that the complete sequences are stored as separate units, or that tours are linked to a special function and thus alter the sequence’s syntax.

It seems that the physical environment is also important during ontogeny (indeed it has already been shown that this is true for adult birds; Nivison 1978). Sparrows raised and

kept in sound proof chambers - even together with canaries - vocalized only rarely. When transferred to laboratory rooms they were sized with panic (pers. observation). They remained panicky though they eventually got used to the 'echoes' in the room; nevertheless vocalization frequency did not increase. The picture arising from that is that the social environment might be important for „singing concepts" while the physical environment could be important for „singing activity".

Recall rate K - a new research tool?

Males of a given species produced 63% of their total repertoire within a definite time range irrespective of the size of their repertoire. This turned out to be true not only for the house sparrows and domestic canaries of the present study, but also for males of the white-browed sparrowweaver *Plocepasser mahali* (unpubl. data Conny Voigt) and wild canary *Serinus canaria* (unpubl. data Dr. S. Leitner). Evolutionarily this may be due to a sender-receiver compromise: environmental factors and receiver-characteristics may define a specific attention time that can be used for communication, whereas sender-specific properties (e.g. neuronal or morphological limitations/constraints?) may limit a higher recall rate, to the effect that a listener „knows" that within their attention time they hear a definite proportion of a given sender's vocabulary. In research the recall rate K might be a useful standard for comparing singers of a) the same species with respect to singers' quality (how fast a male reproduces his song), and b) of different species with respect to possible constraints in song production (including receiver specificities).

My sample size is too small for a thorough cross-species comparison; it shows, however, that K tended to be species-specific and that canary-like singing house sparrows surprisingly adjusted their recall rate to that of their tutor species when they sang sequences that include copied features.

Nivison's results revisited

There exist many records through hundreds of years about the imitative abilities of house sparrows especially concerning the production of canary-like song (reviewed in chapter 1). Nivison (1978) failed to get canary-singing house sparrows by raising sparrow chicks in canary nests. This might be mainly due to two reasons. First Nivison only reared 2 individuals in canary nests. In my study only about 1/5 of my canary-raised, morphological

not conspicuous house sparrows (10 out of 54) produced canary-like tours. Second Nivison did not add protein to the food provisioning of canary foster parents. This led to morphological abnormalities of his canary-reared sparrows. In European starlings, *Sturnus vulgaris*, it has been shown that quantitative and qualitative food shortage of fledglings influenced singing behaviour of yearlings (Buchanan et al. 2003). Thus Nivison's sparrows might not have produced - or learned? - canary-like tours due to food restriction during development. In contrast, my canary-raised birds were provided with food equivalent to sparrow-raised individuals and did not suffer from being cross-fostered (using morning weight; see chapter 2).

Nivison (1978) who studied mainly wild sparrows concluded that they have only a small repertoire but a highly complex acoustic communication. This conclusion resulted mainly from two aspects: house sparrows may change the meaning of a call by a) controlled variation of harmonics and b) using a given syllable in different contexts. The different results of Nivison's and my studies may be based especially on the very different rearing conditions, tape recordings and methods of analysis.

Shortcomings

Some of my results might be due to very particular tape recording and analyses conditions in this study. Sparrows are highly social birds year round (Summer-Smith 1988). They may tolerate other species, i.e. while feeding (Katzi 1969 in Glutz von Blotzheim 1997) if there is enough space and food. Most often, however, they act aggressively towards other species (e.g. Butterfield 1952; Harrison 1947, 1949; further references in Glutz von Blotzheim 1997). Indeed there are several observations of inter-specific agonistic behaviour, though explanations are still missing (Bell 1949; Nowak 1974; Marchant 1982). Own observations are consistent with that: sparrow young left in aviaries beyond independence (4 with crippled feet; excluded from this study) did not interact with the canaries except when they chased away the smaller canaries from food dishes. In spring we had to separate the sparrow males because they injured especially the canary females suggesting that they tried to copulate with them. For this study I had to keep canary-raised sparrows separated from conspecifics, with only a hetero-specific - a canary - companion in the room (though in an own cage) with whom they might not directly

communicate. Taken this together the individuals could freely play with their own acoustics.

It may turn out that in intra-specific interactions also canary-like singing sparrows will only make use of a small part of their vocal repertoire or be more stereotypic in sequence structure. Also the large differences between tapes from two successive days might disappear, although Nivison (1978), too, showed slight changes in utterance of certain calls depending on day time. All these details can be clarified - now as it is proven that sparrows indeed can learn canary-like tours - by raising young sparrows in canary nests (improving canaries food provisioning) and tape recording the yearlings several weeks on several days at different times of the day in different contextual situations (alone, opposed to sparrow male or/and females, etc). From this also a more precise syllable catalogue might be developed, taking into consideration that the meaning of a syllable may depend on the context (my syllable catalogue does not include function!). Moreover by boiling down the vast sound productions I may have excluded meaningful syllables because they were produced only rarely due to missing situations. This might be especially true for two-voice syllables.

However, besides peculiarities and unexplained differences this pilot study is the first to present digital spectrograms of canary-like singing house sparrows and may give an impression of house sparrow's learning abilities.

Questions arising

As selection acts on individuals, it will be to the advantage of them to behave in one way rather than in another (Slater 1989). Thus the important question is to identify the consequences through which natural and/or sexual selection acts. In house sparrows extensive studies have been done on the importance of the males' black bib (e.g. Veiga 1993; Kimball 1996; Cordero et al. 1999; Buchanan et al. 2001; Gonzalez et al. 2001; Schwagmeyer et al. 2002); but nothing is known about the importance of learned song features (foreign or conspecific) for their social life. In different species females show unlearned as well as imprinted preferences when choosing their mates. For example female zebra finches prefer males with songs four standard deviations longer than normal songs (Neubauer 1999), female cowbirds guide a male to sing their preferred subspecies'

song (West & King 1985), and female parasitic widow birds choose a male who includes in his song certain finch-species-specific phrases that he has learned from his foster parents, provided that these phrases are the same that the female heard in her foster parent nest (Nicolai 1964, 1974)[5].

My cross-fostering experiments show that sparrows to a certain extent make use of their song learning ability. Future studies will have to reveal the social function of learned features in general, which could not be analysed in this study, and for attracting females in particular: would sparrow males use tours to attract females? And would female house sparrows prefer tour-singing males over 'normal' singing ones? Further studies should clarify what house sparrows normally learn instead of the tours, in which context males use the learned hetero- or conspecific syllables and whether young sparrows will learn tours from their canary-like singing fathers, similar to foreign-song traditions established in bullfinches (Nicolai 1959).

[5] Besides song, passerine females prefer morphological features; e.g. female widow birds *Euplectes progne* prefer males with extremely extended tails (Andersson 1982) and females of the monomorphic long-tailed finch *Poephila acuticauda* strongly preferred males with an artificially applied white crest (Burley & Symanski 1998).

4 THE SONGBRAIN OF CANARY-LIKE SINGING HOUSE SPARROWS

4.1 INTRODUCTION

Oscine songbirds learn their song by modifying their vocal output until it matches an auditory model memorized during a sensitive phase (Thorpe 1958; Marler 1997). This learned behaviour is regulated by a discrete, songbird specific network of forebrain nuclei (for details see chapter 1, 1.3 the songbird brain). The two major nuclei controlling learned song patterns are HVc and RA. Single HVc neurons unambiguously code for syllable identity but not for smaller motor units such as intra-syllable features as note or motif identity (Yu & Margoliash 1996; Margoliash 1997); RA neurones encode notes and are involved in motor control of the syrinx (Yu & Margoliash 1996). In the following chapter I searched for relations between the vocal proficiency found (i.e. singing, or not singing, canary-like tours) and brain structure in canary- and sparrow-raised house sparrows. I controlled for rearing conditions, seasons, and possible influences of captivity on the studied brain structures.

In several species it has been shown that differences in volume of the telencephalic song control nuclei like HVc are predicative of differences for example in repertoire size and phrase duration (Airey & DeVoogd 2000). The size of song nuclei appeared to reflect differences in neuronal number, cell size, spacing and dendritic spine density within the song nuclei (e.g. Airey et al. 2000). However, the correlation between song complexity and size of song nuclei found for several bird species does not seem to be primarily the outcome of differential song learning experiences early in life (Brenowitz et al. 1995). The size of song nuclei may rather set an upper limit to the number of songs (or song types, etc.) that a bird can learn (see Brenowitz & Kroodsma 1996). Thus whether or not song learning can have an effect on the development of the song nuclei could be tested if one were to tutor birds with extremely large repertoires and so induce them to function at their maximum learning capacity (Brenowitz et al. 1995).

My study will be an extension of this, transgressing species borders: house sparrows, thought to be poor singers with a small repertoire size, can learn to some extent the song of domestic canaries, known for their comparably large repertoire and complex songs. Furthermore in chapter three I argued that house sparrows' canary-like tours are different from scolding sequences which might result from excitement, but not from learning. If this is true, I would expect that tour-singing sparrows differ in song nuclei size from others independent of rearing

parents. Therefore I analysed whether differential vocal skills (tour-singing or not) or early rearing experiences (sparrow- or canary-raised) might have influenced the brain anatomy of my house sparrows, or whether the size of song nuclei sets an upper limit to the extent that house sparrows can learn the canary song.

The study was only possible under laboratory conditions. This, however, raises questions about comparability with, and relevance for, wild sparrows. Animals in the wild are confronted with environmental demands that are lacking in captivity, for example climatic conditions, motility, searching for food, avoiding or escaping predators. Numerous comparative studies have demonstrated a reduction in brain size and changes in the allometric relations between different brain parts when wild species reach the domestic[1] state (Kruska 1980; Röhrs 1985; Ebinger et al. 1984). But even human commensals[2] have been shown to reduce several brain parameters. For example, total telencephalon volume is reduced by 3% and the hyperstriatum ventrale (a region within the telencephalon!) by 11% in free living urban pigeons compared to the brain of their wild ancestor, the rock dove (Ebinger & Loehmer 1984). Thus to control for effects of breeding house sparrows in captivity for several generations I compared wild-caught with laboratory sparrow-raised sparrows.

The observation that Ramses produced summer-like tours during autumn when the song nuclei should have been regressed was surprising. Taking into account that house sparrows form pairs already in autmn a further control was recommended. A photoperiodically and/or hormonally induced shrinkage of forebrain nuclei occurs in many temperate-zone species during the non-breeding season and has also been shown for wild house sparrows (Whitfield-Rucker & Cassone 2000); nuclei size is restored in spring by an addition of naïve neurons (for review see Ball & Balthazart 2002; Schlinger & Brenowitz 2002). Such seasonal changes in nuclei size are paralleled by changes in temporal and structural song features. Tours in canary-raised house sparrows should not occur in autumn or at least differ from tours produced in spring. Therefore I compared the song nuclei HVc and RA of canary-raised sparrow males from different seasons.

[1] Domestic animals might be described as „cultivated forms according to the interests of people“ (Encyclopædia Britannica Premium Service 2003).

[2] The commensal (the species that benefits from the association) may obtain nutrients, shelter, support, or locomotion from the host species, which is substantially unaffected.
Urban pigeons are wild, not domesticated birds!

Finally I add a comparison of male and female house sparrows mainly for four reasons:

A) The house sparrow is suggested to be a highly social species (Summers-Smith 1988, Nivison 1978) which might require vocal activity of both sexes. The scolding sequences (see chapter 3, Fig 3.7D) might be an indication thereof.

B) Marek (1979) reported that a female house sparrow, 10-12 day old young, whom he kept until her first breeding season, developed a „song" which included „melodious twittering", „trills" and „downward scales".

C) Ragotzi (1962) mentioned a female sparrow who shpuld have imitated the canary song!

D) And Nivison (1978) described a duet-like display which occurs when a mate returns to the nest.

If it turned out that female song is important for male vocalizations it could strengthen the necessity to analyse songs of male sparrows in different social contexts.

Excursion: As the social context seemed to be very important in house sparrow vocalization I want to give a first glimpse on prospective analyses combining song production and song recognition. This has been done using the immediate early gene ZENK. The acronym 'ZENK' (Mello et al. 1992) belongs to homologous genes cloned in several species, named zif-268 (Christy et al. 1988, Christy & Nathans 1989), egr-1 (Sukhatme et al. 1988), NGFI-A (Milbrandt 1987), and Krox-24 (Lemaire et al. 1988) as well as c-jun gene (Nishimura & Vogt 1988). The ZENK protein is a DNA-binding transcription factor implicated in the regulation of neuronal growth-related genes and induced in the adult songbird brain in response to a variety of stimuli (Ball & Gentner 1998) within minutes: an increase above control levels in ZENK-labelled nuclei was apparent as early as 15 minutes after start of the stimulus. Expression peaked between 1 and 2 hours after stimulation onset and declined thereafter (Mello & Ribeiro 1998). In quiescent adults basal levels of ZENK mRNA in the brains proved to be very low (Ball & Gentner 1998), and in deafened birds a response was specifically absent (Clayton 1997). The locations of ZENK expression show a clear separation into two sets of areas, one where ZENK expression is triggered by song as a motor act (song control nuclei) and another in which expression is triggered by song as an auditory stimulus (different from song nuclei). In males ZENK response to song depends on early experience. Zebra finches, for example, raised in social isolation do not exhibit this response (Jin & Clayton 1997). In birds, raised by their parents, ZENK activation pattern was dramatically different depending on the social

context in which singing occurred (Jarvis et al. 1998; Ball et al. 1997; Mello et al. 1992): it was low when males sang in the presence of females (female context), high when they sang in the presence of other males (male context), and for some animals even higher when they sang by themselves (solo context) (Jarvis et al. 1998). In male countersinging (simulated by playbacks) novel conspecific song elicited the highest response in NCM (Mello et al. 1995; Jarvis & Nottebohm 1997; see chapter 1, Fig. 1.1). But when a particular conspecific song was presented repeatedly, i.e. several times per minute for several hours, it no longer gave any measurable response when presented again some time later (Ball & Gentner 1998). In adult male canaries and zebra finches, unknown conspecific song induced twice the amount of ZENK mRNA as did heterospecific song, while neutral tone bursts within the same range of frequencies proved ineffective (Mello et al. 1992).

Because in this thesis the focus lays on song production not on song perception, I could not analyse the ZENK-stained slides in details up to now. However, the overall distribution of ZENK expression might enlighten some results.

In sum the present chapter encompasses four main complexes:

A) Are there differences in brain morphology between males that produce tours and those that do not? Do cross-fostered sparrows in general differ from sparrow-raised sparrows?

B) Has breeding in captivity for three generations caused a detectable brain reduction?

C) Do forebrain nuclei of canary-raised birds undergo seasonal changes as reported for wild-caught house sparrows?

D) Are there differences in brain morphology between male and female house sparrows?

Excursion: Does ZENK expression pattern differ in relation to sparrow- or canary- song?

4.2 METHODS

4.2.1 ABBREVIATIONS IDENTIFYING THE DIFFERENT GROUPS

Abbreviations for captivity-reared sparrows are the same as used in chapter 3.

- ca-sin: canary-raised sparrow males, producing canary-like tours (n = 10);
- ca-nosin: canary-raised sparrow males, who have never been heard or tape recorded to produce canary-like tours (n = 28);

- sp-nosin: sparrow-raised sparrow males, who have never been heard or tape recorded to produce canary-like tours (n = 28);
- wild: sparrow males caught in the villages around the institute (n = 7);
- sp-fem: sparrow-raised sparrow females, who have never been heard to produce canary-like tours (n = 8).

4.2.2 ANIMAL SUBJECTS

For the different brain comparisons the 38 canary-raised and 28 sparrow-raised males from chapter 3 were used. In addition we had to catch wild house sparrow males from the villages around our institute. And sparrow females originated from the first two years when I could not sex hatchlings; they all stayed after independence in one large aviary. Ca-nosin and sp-nosin were randomly assigned to always 3 subgroups (I, II, III) for the following comparisons:

A) Comparison of ca-sin (n = 10), ca-nosin (n = 11) and sp-nosin (n = 9). Ca-sin-I and sp-nosin-I were randomly chosen out of the total number of ca-nosin and sp-nosin (see abbreviations). All birds were perfused within 8 days in May.

B) Comparison of wild (n = 7) and sp-nosin-II (n = 9). The 9 sparrow-raised males were randomly chosen out of the remaining 19 birds. All birds were perfused within 4 days in May.

C) Comparison of ca-nosin-II (= summer males, n = 10) and ca-nosin-III (winter males, n = 7). The two groups differ only in time of perfusion: ca-nosin-III were perfused within two days in January while ca-nosin-II within 3 days in the end of May.

D) Comparison of sp-nosin-III (n = 10) and sp-fem (n = 8). All birds were perfused within 3 days in the beginning of May.

Before perfusion the birds (ca-sin, ca-nosin-I & II, sp-nosin-I, wild) were housed in cages (55cm x 29cm x 38 cm) which were placed in a sound-proof chamber (65cm x 60cm x 40cm) to reduce ZENK expression to minimum. Birds, all in reproductive conditions, were kept under 16L : 8D conditions (L = light, D= dark). Food consisted of seeds, insects, salad and fruits. Food and water were available ad libitum until playback . Fresh air was provided by a ventilation system. After 24 hours one half of a group indicated above (chosen by chance) heard a playback (à 45 minutes) with canary song, while the other half heard a sparrow song playback respectively. From ca-nosin and sp-nosin always 4 individuals were randomly chosen

as controls hearing „silence“ or a mixture of guitar music and noise of running water. All birds were video taped from 20 minutes before the tape started until 20 minutes after the tape finished. Then the birds were weighed, bled (see chapter 5: hormones) and sacrificed with Diethylether (Merck) followed by an immediate transcardiac perfusion (see below). This was done between 6.00 and 12.00 am.

4.2.3 PERFUSION OF THE BRAINS

The birds were killed with ether within 30 seconds and then perfused immediately transcardially with an isotonic solution of sodium saline (to preserve the tissue). The exchange of blood is indicated for several reasons. First, veins still containing blood can spoil microscopic measurements, in particular when counting cells, because some may be obscured. Second, the in situ-hybridisation requires RNAse free sections; blood however contains amounts of these enzymes which are active even after freezing for the microtome.

The brains were removed from the skulls and stored in fixative solution (FPBS) until use.

4.2.4 CUTTING THE BRAINS

Glassware was sterilised at 180°C for 4 hours. Brains were taken out of the fixative solution and divided in two equal parts along the corpus callosum. The right half was stored back in the fixative solution in the fridge, the left half was cryoprotected by equilibration, first overnight in 10%, followed by 48 hours in 30% sucrose phosphate buffered (pH 7.6) saline (prepared with DEPC). Serial sections in sagittal orientation, each 30 µm thick, were obtained with a freezing microtome (Leica CM 1325) and collected in PBS made with DEPC water. With a thin brush sections were mounted onto different slides (Superfrost plus, Roth, Germany). I obtained five series from adjacent sections to be stained for Nissl, androgen receptor expression, neuron number, and two series for further studies. Before staining slides were air dried at room temperature for two days and then stored in the fridge until use.

4.2.5 NISSL STAINING

Slides passed through 100%, 90%, 70%, 20% ethanol, stained in Thionin solution for 10-20 seconds and dehydrated after cleaning in aqua bidest. by passing through 20%, 70%, 90% and 100% ethanol and finally xylol. After air drying, slides were coverslipped and embedded in Roth-Histokitt.

4.2.6 NEURON-SPECIFIC STAINING

The procedure follows the protocol of Dr. Ute Abraham (2002) which is based on the original paper of Mullen et al. (1992). All steps were done at room temperature, just without the pre-treatment with acid solution (solutions: see Appendix 1), and followed by washing steps in 0.1M PBS. Slides were soaked for 10 min in PBS and pre-treated for 20 min with 0.01M citric acid solution in a microwave (MCL 1825 DUO, Bauknecht, Germany). After cooling down, slides were incubated with 4% normal goat serum (1ml per slide) at room temperature for 45 min followed by an incubation with the (1:100 diluted) primary antibody solution against neuron-specific nuclear protein (mouse anti-NeuN, Chemicon, USA); for later incubation the plates were stored in the refrigerator in the dark overnight.

After having reacted with biotinylated secondary antibody (anti-mouse IgG, Vector Laboratories) for 60 minutes, the slides were incubated with a freshly prepared avidin-biotin-horseradish peroxidase complex (ABC) reagent. Finally the slides were developed by a 10 min incubation in a freshly prepared DAB- H_2O_2 solution. After air drying the slides went through a series of increasing alcohol concentrations ending in xylol. Finally the slides were coverslipped in Histokitt (Roth).

4.2.7 ZENK STAINING

Sections were processed free-floating using the avidin–biotin– peroxidase method (Vectastain ABC kit, Vector Labs). All steps a) required shaking, b) were done at room temperature, just without the incubation of the first antibody which required 4°C, and c) are followed by three washing steps before ABC solution in 0.1 M PB, afterwards in Tris-buffer. To use wash plates in bathes was much more caring for slides than transferring them from plates to plates, but required more solution. Thus bathes (90ml) were used for cheap, and culture plates (à 480µl per chamber) for expensive solutions. The slides were transferred with a very thin brush, if necessary with additional help of a glass pipette with the thin end bent into a small hook. One

Fig. 4.1: Examples for Nissl- and NeuN-stained sections of song nuclei HVc and RA (marked by black arrows) of male and female house sparrows. All birds were raised by house sparrows and killed in the breeding season. Details about sex, song nucleus, staining technique and objective are given below the respective picture. The two staining techniques revealed no different results concerning song nucleus size. Statistical results of sex comparison are given in 4.3.4. Black bars between the pictures represents 50µm. (Varying colouration within a given staining technique is caused to some extent by the used printer).

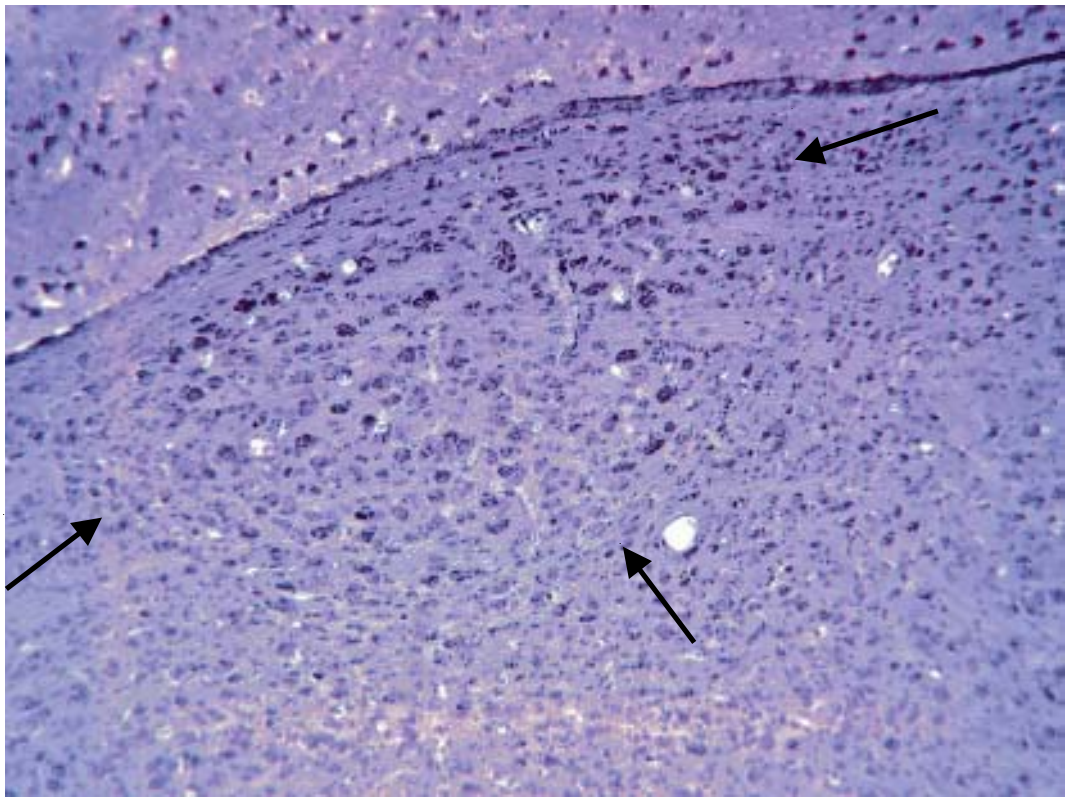


Fig 4.1A) sex: male, song nucleus: HVc, staining technique: Nissl-staining, objective: 10fold.

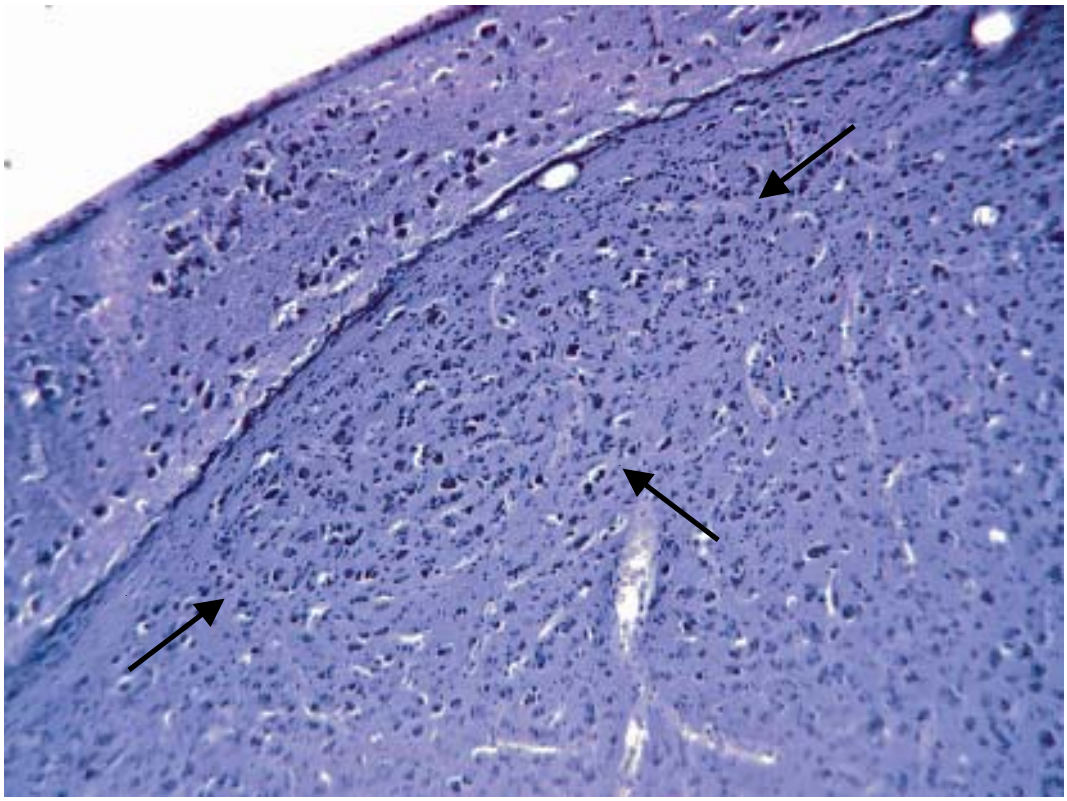


Fig 4.1B) sex: female; song nucleus: HVc, technique: Nissl-staining, objective: 10fold.

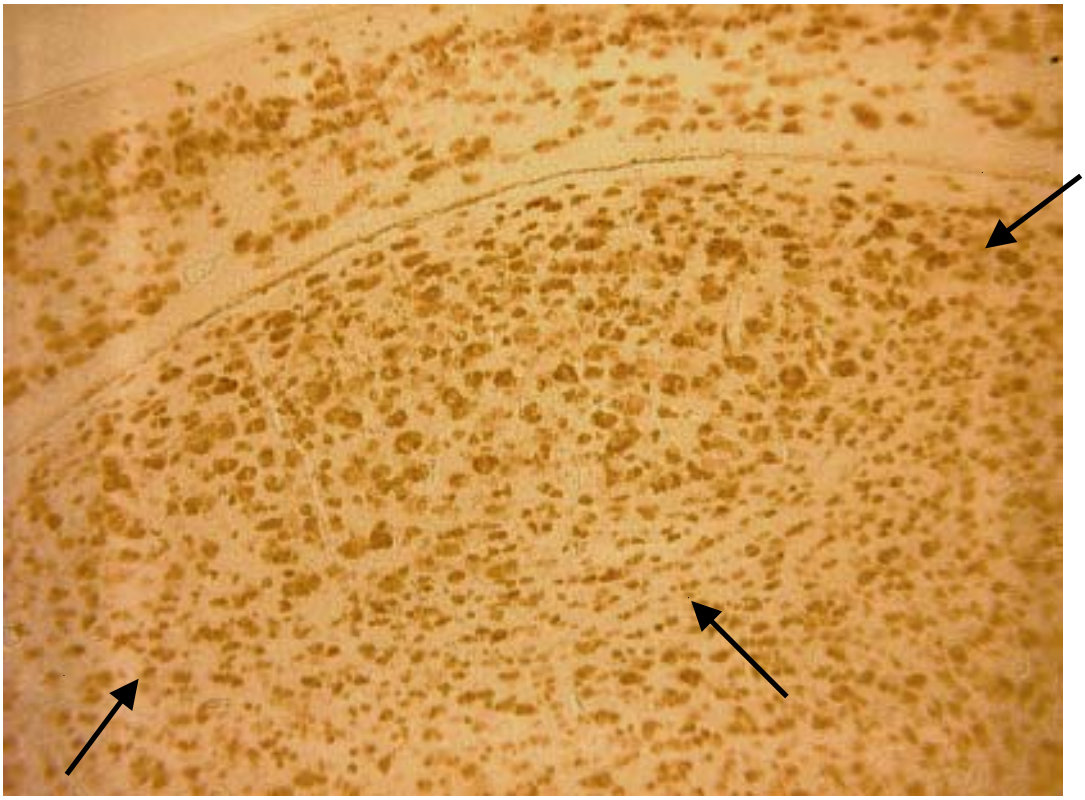


Fig 4.1C) sex: male; song nucleus: HVc, technique: NeuN-staining, objective: 10fold.

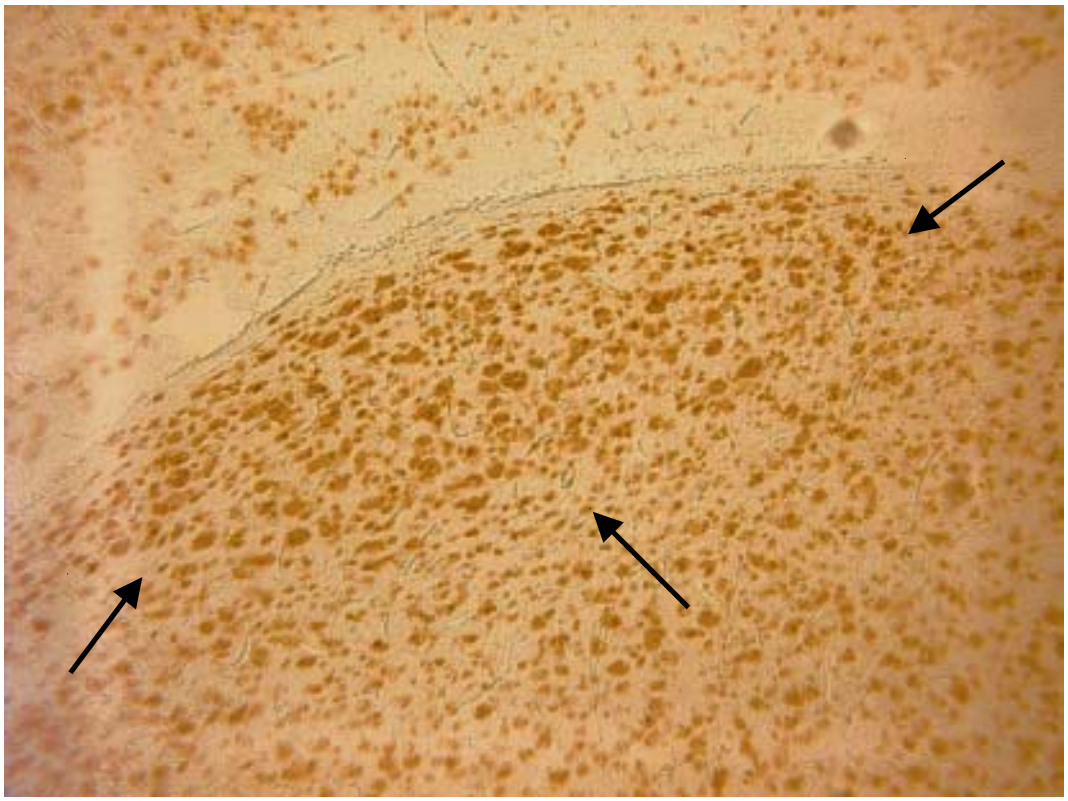


Fig 4.1D) sex: female, song nucleus: HVc, technique: NeuN-staining, objective: 10fold.

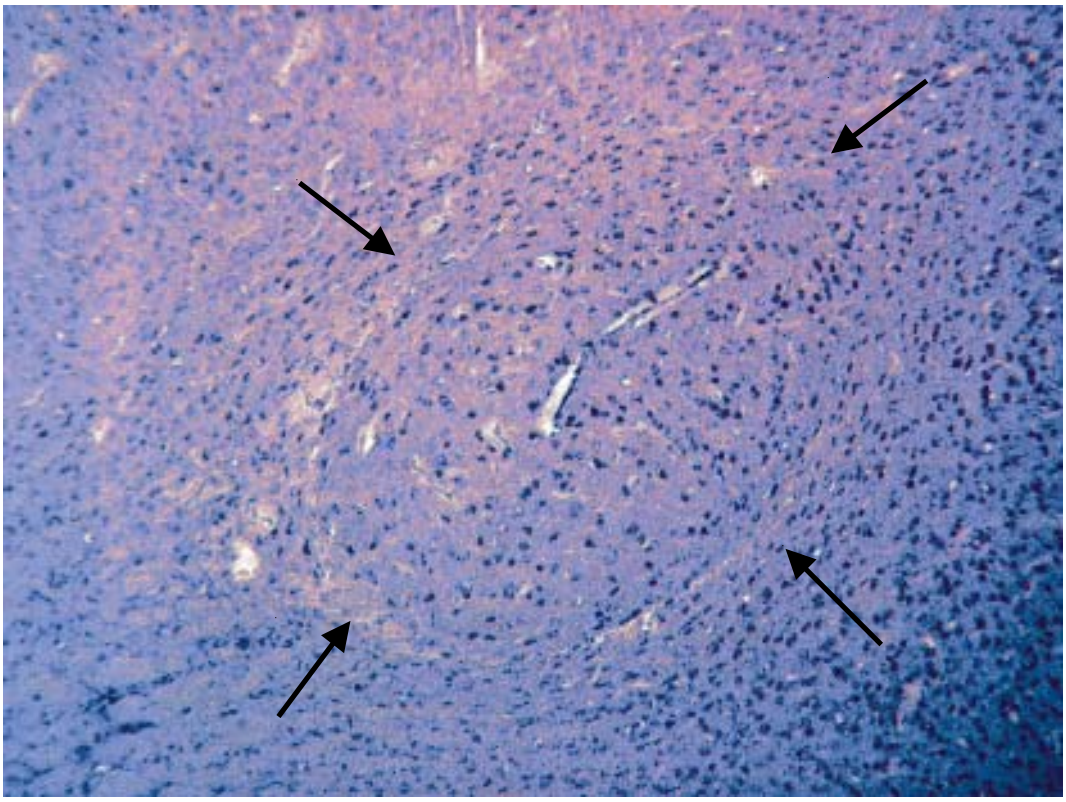


Fig 4.1G) sex: male, song nucleus: RA, technique: Nissl-staining, objective: 6,3fold.

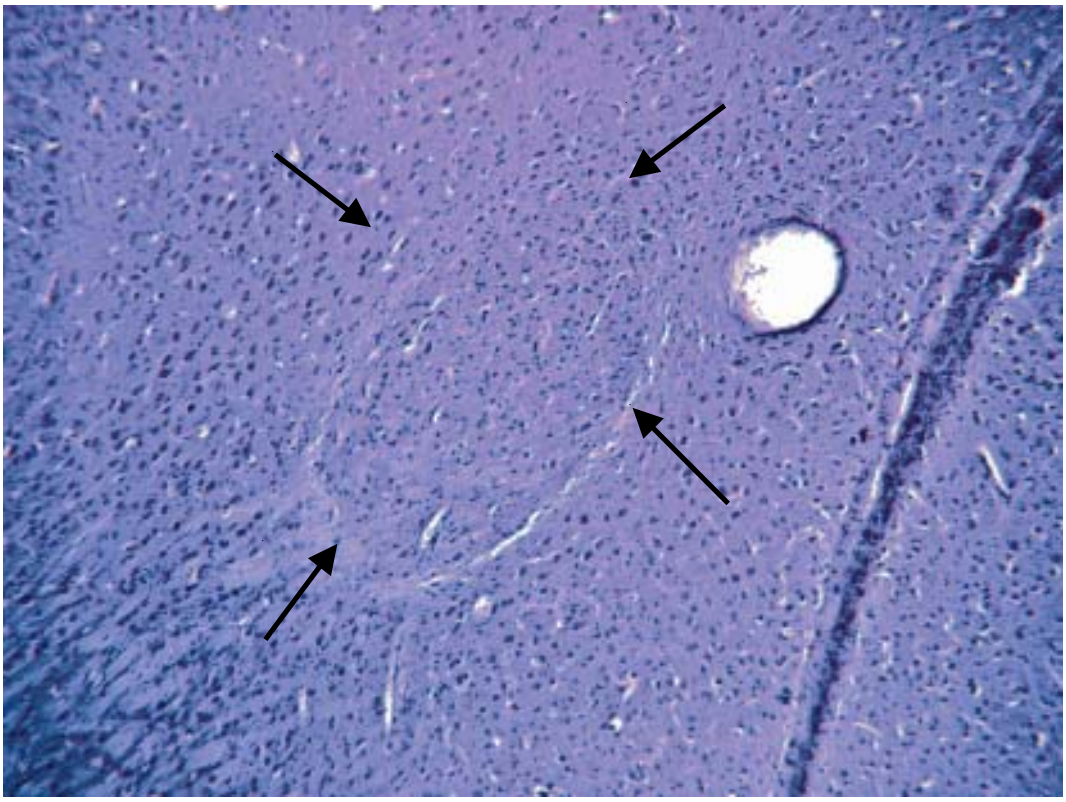


Fig 4.1H) sex: female, song nucleus: RA, technique: Nissl-staining, objective: 6,3fold.

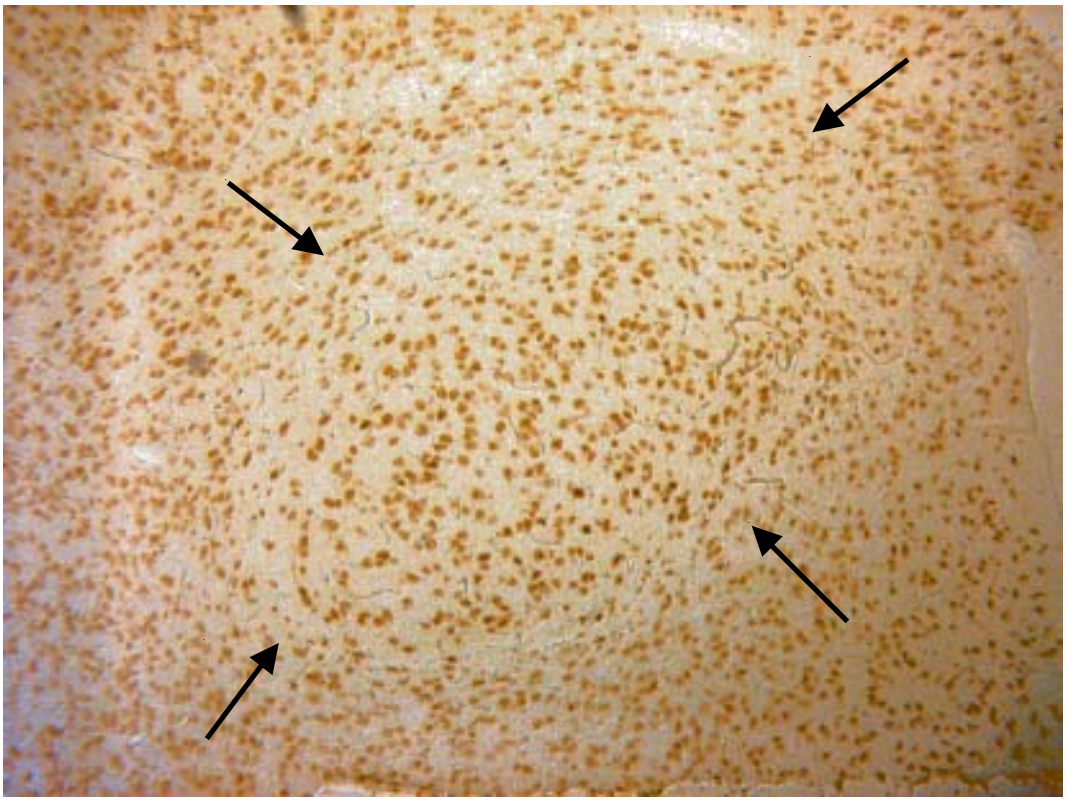


Fig 4.1E) sex: male; song nucleus: RA, technique: NeuN-staining, objective: 6,3fold.

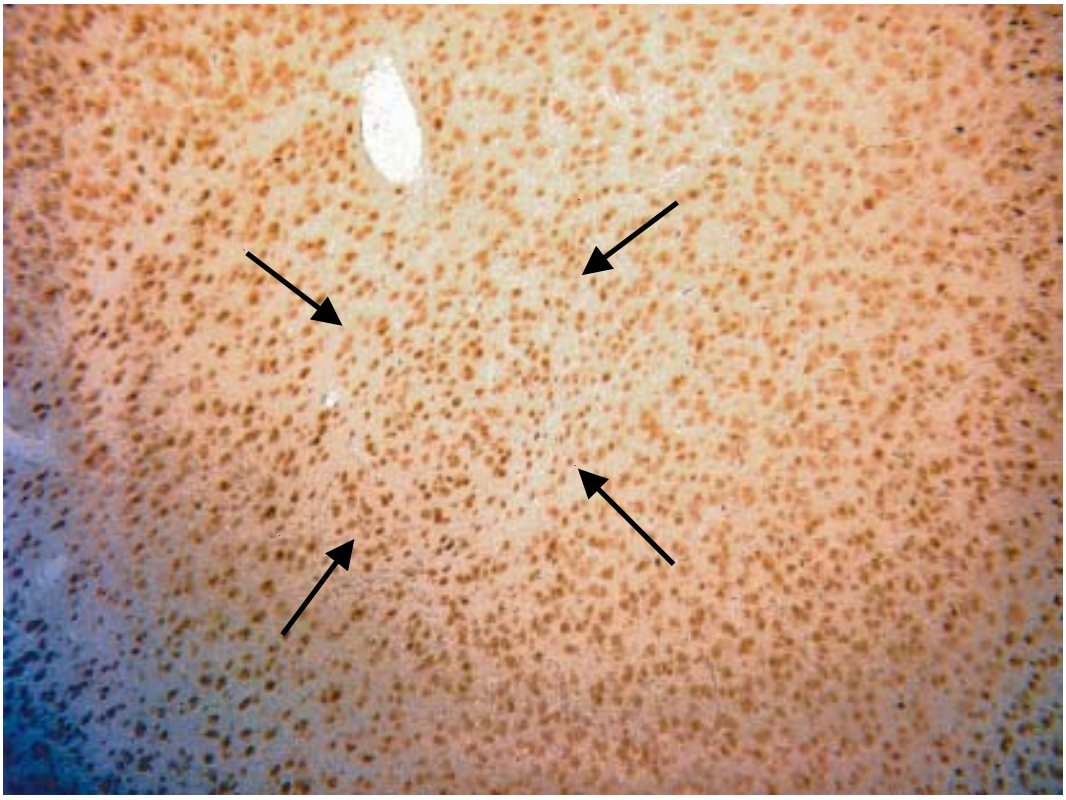


Fig 4.1F) sex: female, song nucleus: RA, technique: Nissl-staining, objective: 6,3fold.

plate (Nunc™ Brand Products, Cat. No. 143982) was used for the slides of one brain, thus some chambers contained two slides of different size.

The free floating staining procedure started with three blocking steps: a) 20 minutes in 1% H_2O_2 in 0,1M PP. b) 3 x 10 minutes in Triton X-100 in 0,1M PP followed by 60 minutes in NGS in 0.1M PP with Triton x 100 and c) 15 minutes in Avidin solution. Then the slides were incubated in the primary antibody (1:15 000, 200µg/ml Santa Cruz C 19, Biotechnology) for 36 h, the only step at 4°C (fridge). After reaction with biotinylated secondary antibody (goat anti-rabbit IG, Vector Laboratories) for 70 minutes slides were transferred into an avidin-biotin-horsredish peroxidase complex (ABC) reagent to stay for 70 minutes (Vector Laboratories). Last the slides were developed by incubation in a nickel sulphate enhanced DAB- H_2O_2 solution. The specificity of the immunoreaction was tested by omitting either the primary antibody, or the secondary antibody, or the ABC-complex or by replacing it by an equivalent concentration of non-specific IgG. No immunostaining was observed in these sections. Stained brain slides were mounted with aqua dest. After air drying the slides were dehydrated by passing through 50%, 70%, 90%,100% ethanol and finally xylol. Finally the slides were coverslipping using Histokitt (Roth).

4.2.8 IN-SITU HYBRIDISATION PROCEDURE

4.2.8.1 CLONING

The cloning of a partial zebra finch AR cDNA (759 bp) has been described previously (Gahr & Metzdorf 1997). The AR fragment has a 96.4% homology with the AR of the canary, a 92% homology with an AR-PCR fragment of the ring dove *(Streptopelia risoria*) (Cao & Gahr, unpublished data), and an 80.1% homology with the human AR. The high homology of the zebra finch AR-PCR product with the AR sequence of my house sparrows allows the use of this fragment for the localisation of AR mRNA in the house sparrow.

4.2.8.2 PREPARATION OF cRNA PROBES

Probes were prepared using sequences for zebra finch androgen receptor (AR) cloned by Dr. R. Metzdorf. For transcription of the antisense or sense probes, the plasmids containing AR sequence were linearised with Nsil or XhoI and transcribed from the T7 or SP6 promoter, respectively. Antisense or sense RNA probes labeled with ^{35}S-CTP (1250 Ci / mmol, NEN) were generated by transcription of the linearised plasmid DNA using the riboprobe system (Promega).

4.2.8.3 IN-SITU HYBRIDISATION

The in situ-hybridisation procedure previously described by Whitfield et al. (1990) was slightly modified as described in details by Gahr & Metzdorf (1997). Briefly, sections were hybridised under coverslips for 15 h at 55°C, using ^{35}S-labeled sense or antisense probe (8 x 10^6 cpm / ml) in (50µl per slide) hybridisation buffer (50% formamide, 600 mM NaCl, 10 mM Tris-Hcl (pH 7.5), 0.02 Ficoll, 0.02% BSA, 0.02% polyvinylpyrrolidone, 1mM EDTA, 0.01% salmon testicular DNA, 0.05% total yeast RNA, 0.005% yeast transfer RNA, 10% dextran sulphate, 0.1% sodium dodecyl sulphate, 0.1% sodium thiosulphate, and 100mM Dithiothreitol). After hybridisation, the slides were immersed in 2 x SSC for 20 min at 25°C to float off the coverslips. The slides were first treated with RNAse A (20 µg /ml) in RNAse buffer (0.5 M NaCl, 10 mM Tris-HCL (pH 8.0), 1 mM EDTA) for 30 min at 37 °C and incubated in the same buffer for 30 min at 37°C. The slides were then washed in 2 x SSC for 30 min at 50°C, in 0.2 x SSC for 30 min at 55°C and in 0.2 x SSC for 30 min at 60°C, then dehydrated sequentially in ascending concentrations of ethanol before being air dried. Sections were counterstained with the Nissl stain thionin.

4.2.8.4 **AUTORADIOGRAPHY** (Herkenham & Pert 1982)

To detect autoradiography silver grains, slide-mounted sections were dipped in the darkroom under safelight conditions into Kodak NTB-2 nuclear track emulsion diluted 1:1 with 0.1 Aerosol 22 (Sigma) in a water bath at 42°C and stored in light-tight boxes at 25°C for 7-14 days. Thereafter the slides are developed in Kodak D19 for 2 min at 16°C, rinsed in deionised water for 30 sec, fixed in Kodak fixer for 5 min, and washed in deionised water. Sections are then counterstained with 0.1% Thionin and coverslipped with Histokitt (Roth).

4.2.9 DATA ANALYSES

4.2.9.1 NISSL- AND NEUN-STAINING

Brain slices were visualized using a light microscope (Leitz Aristoplan) combined with a video camera (spot insight, visitron systems). Measurements were done by using an image analysis system (Metamorph 4.6, Visitron, Germany). Data were automatically exported into a prepared sheet of Excel 2000 (PC, Microsoft office). For volume measurements the periphery of each brain nucleus (identified as association of intensive coloured cells) was drawn on

digitized images and the area was calculated by a built-in function of the software (Metamorph). The volume of both brain nuclei was then calculated following Gahr & Garcia-Segura (1996): Σ'measured areas' x slice thickness (30 µm) x interval between section (12 µm). This simple formula yields reliable results for this measurements.

4.2.9. 2 IN SITU-HYBRIDIZATION

Areas of labelling were compared with the brain map for the zebra finch (Stokes et al. 1974; Nottebohm et al. 1976; Nixdorf & Bischof, unpubl. manuscript). The analysis consisted of quantifying the mean relative amount of mRNA per cell within the HVc. The relative amount of mRNA per cell (grains/cell) was measured under high power (4003) with the help of an image analysis system (Metamorph) on a video screen. A cell was counted as an AR- expressing cell if the number of grains over the cell exceeded five times the background number. The background number was defined as the mean number of grains over three to five cell-sized areas of neuropil across the field of analysis for each region. Areas defined in lightfield illumination (Nissl-staining) were analysed in every sixth section of the HVc and RA of each animal.

4.2.10 STATISTICAL ANALYSES

Statistical analyses were performed with Systat 9.2 (Systat Software Inc., Richmond, CA.) following Lamprecht (1999). All data were first tested for normal distribution (Kolgomorov-Smirnov Lilliefors test) and equality of variances (Levine test). Several authors do not use the measured brain nuclei data, but standardise them in relation to body size (tarsus length or body weight), or to brain size represented by telencephalon volume, respectively. Body weight, however, might be an unsuitable reference in several respects as it varies within individuals, for example between seasons (Harvey & Krebs 1990). Brain data have been shown to highly correlate with morphological, life history or environmental variables (Sacher 1959), but not with temporary physiological conditions such as body weight (Leitner 1999). Thus I conducted General Linear Models (GLM) with telencephalon volume (V(telencephalon)) or tarsus length as covariates.

All results refer to two-tailed tests. In most cases tarsus length and telencephalon volume as covariate gave similar results. I therefore present only the results with telencephalon volume as covariate, except when the results of the two covariates differed.

4.3 RESULTS

4.3.1 DO RAISING CONDITIONS INFLUENCE BRAIN MORPHOLOGY? ARE THERE DETECTABLE DIFFERENCES IN BRAIN NUCLEI IN RELATION TO SINGING ABILITY?

'Raising conditions' refer to 'rearing parents' being either domestic song canaries or house sparrows respectively. 'Singing ability' is related to an individuals ability of producing canary-like tours or not, irrespective of their rearing parents.

Ramses, the canary-like singing house sparrow I received, did not differ from ca-sin in any of the measurements (see Table 4.1), thus I included him in the group of ca-sin for brain- and statistical analyses.

Table 4.1 Comparison of ca-sin (n = 10) and Ramses in the parameters analysed in this chapter. In all measurements Ramses data fell in the range of ca-sin.

measures		**ca-sin (min-max)**	**Ramses**
tarsus	[mm]	17.89 - 19.79	19.18
V(HVC-Nissl)	[mm³]	0.30 - 0.60	0.43
V(HVC-NeuN)	[mm³]	0.32 - 0.55	0.42
V(RA-Nissl)	[mm³]	0.12 - 0.34	0.26
V(RA- NeuN)	[mm³]	0.16 - 0.32	0.26
V(TeV)	[mm³]	241.70 - 290.50	248.30

4.3.1.1 HVc VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

Table 4.2 GLM of factors influencing the volume of HVc (calculated from Nissl-stained sections) in male house sparrows ($r^2 = 0.358$, n = 31).

Factor	**Mean-Square**	**df**	**F-ratio**	**p**
rearing parents	0.005	1	0.900	0.351
singing ability	0.056	1	9.890	**0.004**
V(telencephalon)	0.009	1	1.552	0.224
Error	0.006	27		
Model coefficients				
CONSTANT	0.163			
rearing parents	-0.016			
singing ability	-0.052			
V(telencephalon)	0.001			

HVc volume was not significantly affected by rearing parents (Fig.4.2A), but correlated significantly with singing ability: HVc volume of ca-sin was significantly larger than that of ca-nosin and sp-nosin (Fig.4.2B). Neither telencephalon volume nor tarsus length correlated with HVc volume of any group.

4.3.1.2 HVc VOLUME CALUCATED FROM NeuN-STAINED SECTIONS

Table 4.3. GLM of factors influencing the volume of HVc (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.331$, n = 31).

Factor	Mean-Square	df	F-ratio	p
rearing parents	0.0002	1	0.019	0.891
singing ability	0.070	1	8.274	**0.008**
V(telencephalon)	0.006	1	0.718	0.404
Error	0.009	27		
Model coefficients				
CONSTANT	0.171			
rearing parents	-0.003			
singing ability	-0.058			
V(telencephalon)	0.001			

Again, HVc volume was not significantly affected by rearing parents (Fig.4.2A), but correlated significantly with singing ability: HVc volume of ca-sin was significantly larger than that of ca-nosin and sp-nosin (Fig.4.2B). Neither telencephalon volume nor tarsus length correlated with HVc volume of any group.

4.3.1.3 ANDROGEN RECEPTOR EXPRESSION IN HVc

Table 4.4.: GLM of factors influencing the androgen receptor expression in HVc in male house sparrows ($r^2 = 0.041$, n = 31).

Factor	Mean-Square	df	F-ratio	p
singing ability	0.035	1	0.091	0.766
V(telencephalon)	0.248	1	0.648	0.433
Error	0.383	16		
Model coefficients				
CONSTANT	5.264			
Singing ability	-0.054			
V(telencephalon)	-0.008			

In contrast to brain morphology, the androgen receptor expression in HVc was not significantly influences by singing ability (Fig.4.2B). Again there was no detectable correlation with telencephalon volume or tarsus length .

4.3.1.4. RA VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

Table 4.5. GLM of factors influencing the volume of RA (calculated from Nissl-stained sections) in male house sparrows ($r^2 = 0.058$, n = 31).

Factor	Mean-Square	df	F-ratio	p
rearing parents	0.009	1	1.496	0.232
singing ability	0.001	1	10.250	0.621
V(telencephalon)	0.001	1	0.171	0.683
Error	0.006	27		
Model coefficients				
CONSTANT	0.157			
rearing parents	-0.021			
singing ability	-0.008			
V(telencephalon)	0.0003			

RA volume was not significantly affected by singing ability (Fig.4.2B) or rearing parents (Fig.4.2A). And it did not correlate with telencephalon volume or tarsus length .

4.3.1.5 RA VOLUME CALCULATED FROM NeuN-STAINED SECTIONS

Table 4.6. GLM of factors influencing RA volume (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.132$, n = 31).

Factor	Mean-Square	df	F-ratio	p
rearing parents	0.006	1	1.376	0.251
singing ability	0.001	1	0.274	0.605
V(telencephalon)	0.011	1	2.559	0.121
Error	0.004	27		
Model coefficients				
CONSTANT	-0.046			
rearing parents	-0.017			
singing ability	-0.008			
V(telencephalon)	0.001			

RA volume was not significantly affected by singing ability (Fig.4.2B) or rearing parents (Fig.4.2A). And again it did not correlate with telencephalon volume or tarsus length.

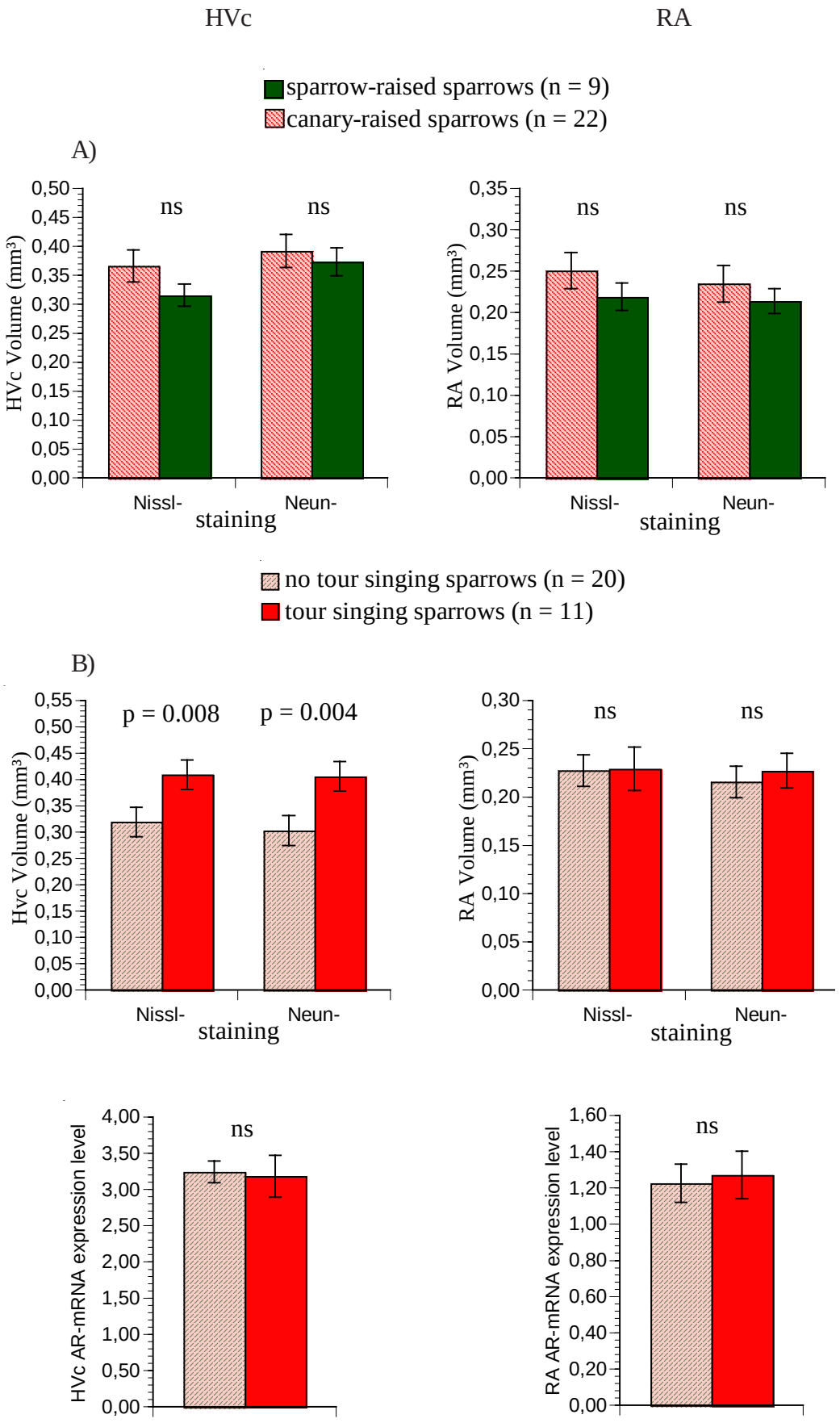
4.3.1.6 ANDROGEN RECEPTOR EXPRESSION IN RA

Table 4.6 GLM of factors influencing androgen receptor expression in RA in male house sparrows ($r^2 = 0.017$, n = 18).

Factor	Mean-Square	df	F-ratio	p
singing	0.031	1	0.232	0.637
V(telencephalon)	0.029	1	0.214	0.650
Error	0.135	16		
Model coefficients				
CONSTANT	1.949			
singing	-0.051			
V(telencephalon)	-0.003			

Also androgen receptor expression was not significantly influenced by singing ability (Fig. 4.2B), nor did it correlate with telencephalon volume or tarsus length.

Fig. 4.2: Comparison of different measures of HVc (left side) and RA (right side) of male house sparrows (n = 31) who were grouped together either A) according to their rearing parents (canaries or sparrows) or B) according to their singing abilities (tour-singing or not). Numbers of sparrow individuals in the respective groups according to studied factors are given in the legends. Data are presented as means ± sem; p-values of the respective statistical tests are given in the graph, ns = not significant. For details about statistics see Tables 4.1 – 4.6. A comparison between the canary-raised and sparrow-raised group for androgen receptor (AR) expression was not possible.


HVc
RA
sparrow-raised sparrows (n = 9)
canary-raised sparrows (n = 22)
A)
HVc Volume (mm³)
RA Volume (mm³)
ns
Nissl-staining
Neun-staining
no tour singing sparrows (n = 20)
tour singing sparrows (n = 11)
B)
Hvc Volume (mm³)
p = 0.008
p = 0.004
HVc AR-mRNA expression level
RA AR-mRNA expression level

4.3.2 DOES CAPTIVITY INFLUENCE BRAIN MORPHOLOGY?

In the following General Linear Models (GLM) the term „origin“ refers to the groups wild and sp-nosin-II (for abbreviations see 4.2.1).

4.3.2.1 HVc VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

HVc volume did not differ significantly between wild and captivity-bred sparrows (Fig.4.3A), nor did it correlate with telencephalon volume or tarsus length.

Table 4.7. GLM of factors influencing HVc volume (calculated from Nissl-stained sections) in male house sparrows ($r^2 = 0.124$, n = 16).

Factor	Mean-Square	df	F-ratio	p
origin	0.002	1	0.171	0.686
V(telencephalon)	0.013	1	1.471	0.247
Error	0.009	13		
Model coefficients				
CONSTANT	0.107			
origin	0.010			
V(telencephalon)	0.001			

4.3.2.2 HVc VOLUME CALCULATED FROM NeuN-STAINED SECTIONS

HVc volume again did not differ significantly between wild and captivity-bred sparrows (Fig.4.3A), nor did it correlate with telencephalon volume or tarsus length.

Table 4.8. GLM of factors influencing HVc volume (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.022$, n = 16).

Factor	Mean-Square	df	F-ratio	p
origin	0.002	1	0.241	0.632
V(telencephalon)	0.0002	1	0.026	0.873
Error	0.008	13		
Model coefficients				
CONSTANT	0.293			
origin	0.011			
V(telencephalon)	0.0001			

4.3.2.3 RA VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

RA volume was not significantly different between wild and captivity-bred sparrows (Fig. 4.3A), but it correlated significantly with telencephalon volume: the Pearson correlation factor in wild birds was 0.720 (Bartlett Chi-square statistic: 3.291, df = 1, p = 0.070) and in captive birds 0.780 (Bartlett Chi-square statistic: 6.100, df = 1, p = 0.014, $\alpha = 0.025$). Tarsus length as covariate, however, did not correlate with RA volume (Fig.4.3B).

Table 4.9. GLM of factors influencing RA volume (calculated from Nissl-stained sections) in male house sparrows ($r^2 = 0.576$, n = 16).

Factor	Mean-Square	df	F-ratio	p
origin	0.0004	1	0.289	0.600
V(telencephalon)	0.024	1	16.303	**0.001**
Error	0.001	13		
Model coefficients				
CONSTANT	-0.139			
origin	0.005			
V(telencephalon)	0.001			

4.3.2.4 RA VOLUME CALcULATED FROM NeuN-STAINED SECTIONS

RA volume was not significantly different between wild and captivity-bred sparrows (Fig. 4.3A), but it correlated significantly with telencephalon volume: the Pearson correlation factor in wild birds was 0.626 (Bartlett Chi-square statistic: 2.236, df = 1, p = 0.135) and in captive birds 0.758 (Bartlett Chi-square statistic: 5.548, df = 1, p = 0.019, $\alpha = 0.025$). Again tarsus length as covariate did not correlate with RA volume (Fig.4.3B).

Table 4.10. GLM of factors influencing RA volume (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.524$, n = 16).

Factor	Mean-Square	df	F-ratio	p
origin	0.001	1	0.780	0.393
V(telencephalon)	0.020	1	12.306	**0.004**
Error	0.002	13		
Model coefficients				
CONSTANT	-0.109			
origin	0.009			
V(telencephalon)	0.001			

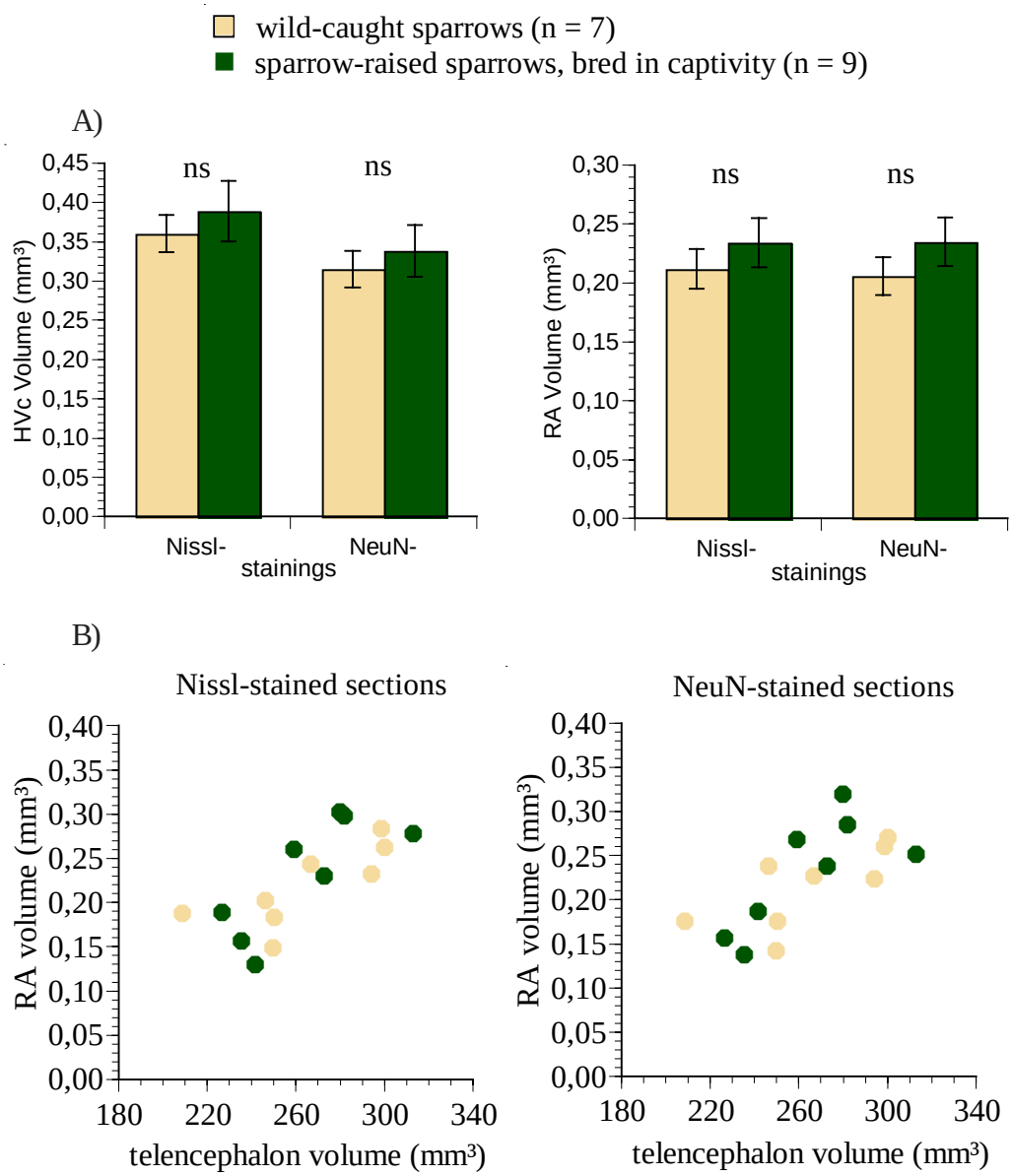


Fig. 4.3A: Comparisons of HVc and RA volume. Data are presented as means ± sem; ns = not significant. For details about statistics see Tables 4.7 – 4.10. Both staining techniques revealed the same results: the volumes of brain nuclei did not differ between captivity-reared and wild house sparrows.

Fig. 4.3B: RA volume (Nissl-stained and NeuN-stained sections) plottet against telencephalon volume. For Pearson correlation factor and the respective p-values see text. RA volume of captivity-hatched birds correlated significantly with telencephalon volume in both staining techniques, but no significant correlation was found in wild birds.

4.3.3 DO MALE SPARROWS' BRAIN NUCLEI UNDERGO SEASONAL CHANGES?

4.3.3.1 OVERALL BRAIN SIZE

Neither brain weight (pooled variance t = 0.579, df = 15, p = 0.571) nor telencephalon size (pooled variance t = 1.377, df = 15, p = 0.189) differed significantly between seasons.

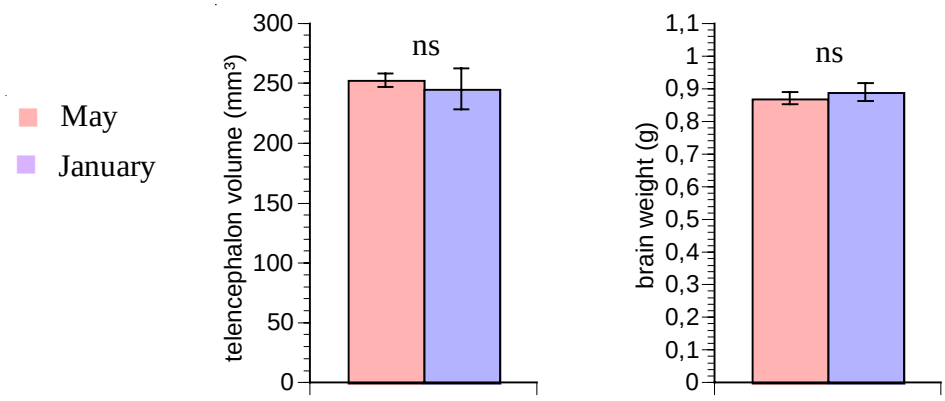


Fig. 4.4. Brain weight (after perfusion) and telencephalon size (Nissl-stained and NeuN-stained sections) of house sparrows perfused in January or May. Data are presented as means ± sem; ns = not significant. For details about statistics see text. Both staining techniques revealed the same results: there was no seasonal effect on either of the measurements.

4.3.3.2 HVc VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

Table 4.11. GLM of factors influencing HVc volume (calculated from Nissl-stained sections) in male house sparrows (r^2 = 0.450, n = 17).

Factor	Mean-Square	df	F-ratio	p
season	0.346	1	9.408	**0.008**
V(telencephalon)	0.032	1	0.858	0.370
Error	0.037	14		
Model coefficients				
CONSTANT	-2.648			
Season	-0.147			
V(telencephalon)	0.312			

HVc volume calculated from Nissl-stained sections differed between seasons: males had significantly larger HVc volumes in summer than in winter (Fig. 4.5A). HVc volume did not correlate with telencephalon volume or tarsus length.

4.3.3.3 HVc VOLUME CALCULATED FROM NeuN-STAINED SECTIONS

Table 4.12. GLM of factors influencing HVc volume (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.411$, n = 17).

Factor	Mean-Square	df	F-ratio	p
season	0.413	1	9.497	**0.008**
V(telencephalon)	0.013	1	0.292	0.598
Error	0.044	14		
Model coefficients				
CONSTANT	-3.072			
season	-0.168			
V(telencephalon)	0.378			

HVc volume calculated from NeuN-stained sections differed between seasons: males had significantly larger HVc volumes in summer than in winter (Fig. 4.5A). HVc volume did not correlate with telencephalon volume or tarsus length .

4.3.3.4 RA VOLUME CALCULATED FROM NISSL-STAINED SECTIONS

Table 4.13. GLM of factors influencing RA volume (calculated from Nissl-stained sections) in male house sparrows ($r^2 = 0.630$, n = 17).

Factor	Mean-Square	df	F-ratio	p
season	0.372	1	19.926	**0.001**
V(telencephalon)	0.210	1	11.244	**0.005**
Error	0.019	14		
Model coefficients				
CONSTANT	-9.693			
season	-0.159			
V(telencephalon)	1.538			

RA volume differed between seasons: males had significantly larger RA volumes in summer than in winter (Fig. 4.5B). And RA volume correlated significantly with telencephalon volume, i.e. the larger the telencephalon volume the larger the HVc volume. The Pearson correlation factor in winter was 0.621 (Bartlett Chi-square statistic: 2.194, df = 1, p = 0.139) and in summer 0.708 (Bartlett Chi-square statistic: 5.210, df = 1, p = 0.022) (Fig. 4.5C). With tarsus length as covariate the seasonal difference remains significant, but tarsus length did not correlate with RA volume.

4.3.3.5 RA VOLUME CALCULATED FROM NeuN-STAINED SECTIONS

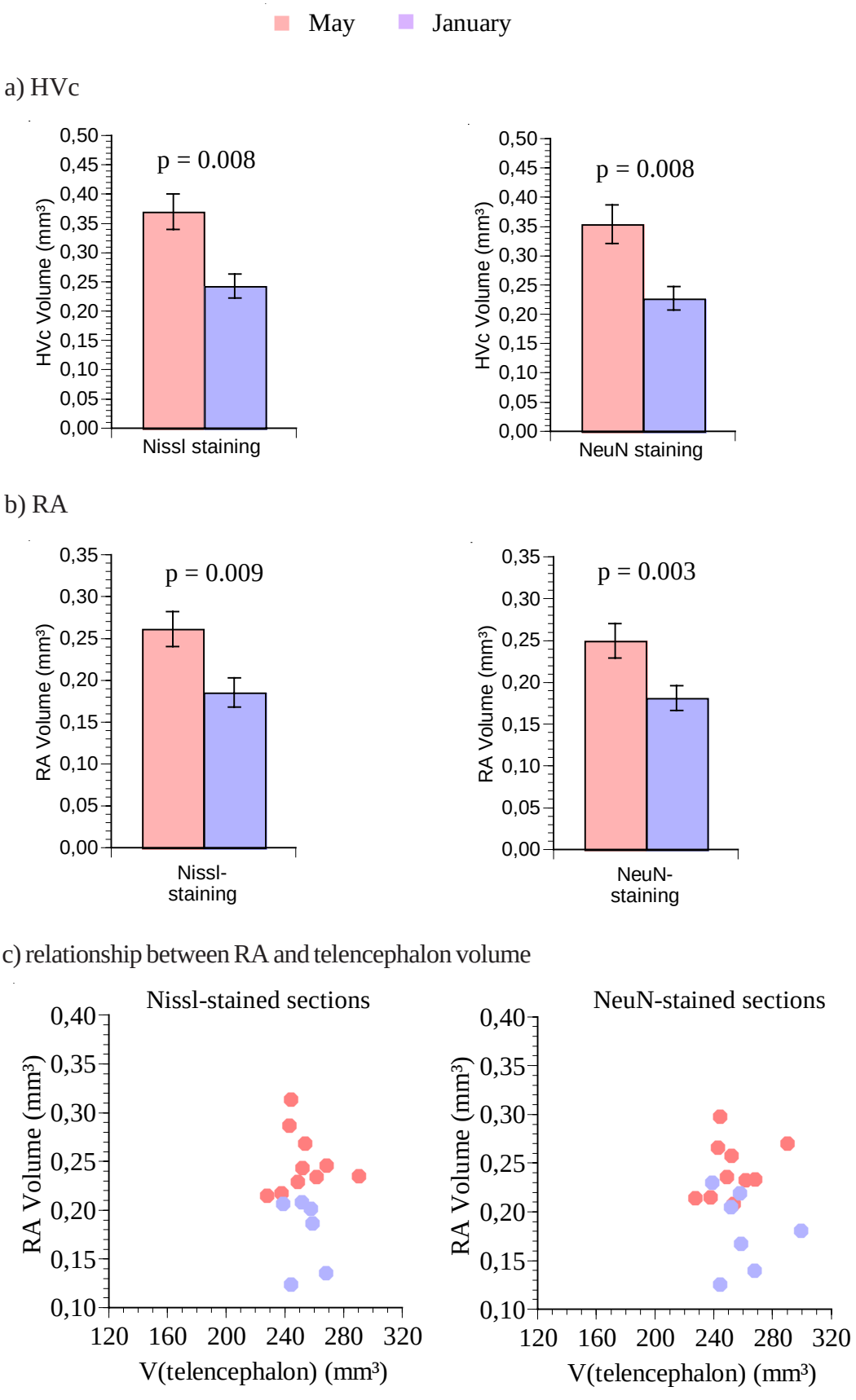
Table 4.14. GLM of factors influencing RA volume (calculated from NeuN-stained sections) in male house sparrows ($r^2 = 0.569$, n = 17).

Factor	Mean-Square	df	F-ratio	p
season	0.260	1	12.682	**0.003**
V(telencephalon)	0.246	1	12.023	**0.004**
Error	0.020	14		
Model coefficients				
CONSTANT	-10.429			
season	-0.133			
V(telencephalon)	1.666			

RA volume differed between seasons: males had significantly larger RA volumes in summer than in winter (Fig. 4.5B). And RA volume correlated significantly with telencephalon volume, i.e. the larger telencephalon volume the larger the HVc volume. The Pearson correlation factor in winter was 0.645 (Bartlett Chi-square statistic: 4.039, df = 1, p = 0.044) and in summer 0.834 (Bartlett Chi-square statistic: 5.341, df = 1, p = 0.021) (Fig. 4.5C). With tarsus length as covariate the seasonal difference remains significant, but tarsus length did not correlate with RA volume.

Fig. 4.5AB: Comparison of ca-sins' song nuclei HVc and RA in January (n = 7) or May (n = 10). Data are presented as means ± sem; p-values of the respective statistical test are given in the graph. For details about statistics see Tables 4.11 – 4.14.

Fig 4.5C: RA volume from Nissl-stained and NeuN-stained sections plottet against telencephalon volume. For the Pearson correlation factors and the respective p-values see text.


May
January
a) HVc
p = 0.008
HVc Volume (mm³)
Nissl staining
p = 0.008
HVc Volume (mm³)
NeuN staining
b) RA
p = 0.009
RA Volume (mm³)
Nissl-staining
p = 0.003
RA Volume (mm³)
NeuN-staining
c) relationship between RA and telencephalon volume
Nissl-stained sections
RA Volume (mm³)
V(telencephalon) (mm³)
NeuN-stained sections
RA Volume (mm³)
V(telencephalon) (mm³)

4.3.4 DO FEMALES DIFFER FROM MALES IN VOLUME SIZE OF SONG NUCLEI?

Pictures of male and female song nuclei were already presented in Fig. 4.1 as examples for Nissl- and NeuN-staining techniques.

4.3.4.1 Overall brain size and tarsus length

Neither tarsus length (pooled variance t = -0.945, df = 16, p = 0.359) nor telencephalon volume (pooled variance t = 1.072, df = 16, p = 0.300) nor brain weight after perfusion (pooled Variance t = -1.228, df = 16, p = 0.237) differed significantly between sexes.

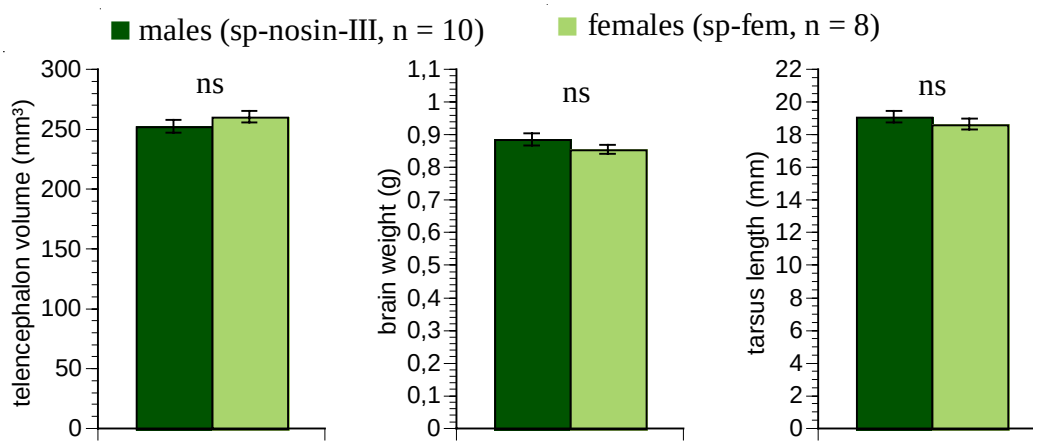


Fig. 4.6. Comparison of male and female house sparrows, both raised in captivity. Data are presented as means ± sem; ns = not significant. For details about statistics see text. In overall measurements sexes did not differ significantly.

4.3.4.2 HVc volume calculated from Nissl-stained sections

Table 4.15: GLM of factors influencing HVc volume (calculated from Nissl-stained sections) in male and female house sparrows ($r^2 = 0.838$, N =18).

Factor	df	Mean-Square	F-ratio	P
sex	1	0.349	77.352	< **0.001**
V (telencephalon)	1	0.016	3.572	0.078
Error	15	0.0045		
Model coefficients				
CONSTANT		-0.280		
sex	f	-0.145		
V (telencephalon)		0.002		

Males had a significantly larger HVc volume than females, tarsus length as covariate gives the same results (Fig. 4.7A). Neither telencephalon volume nor tarsus length correlated with HVc volume calculated from Nissl-stained sections.

4.3.4.3 HVc volume calculated from NeuN-stained sections

Table 4.16.: GLM of factors influencing HVc volume (calculated from NeuN-stained sections) in male and female house sparrows ($r^2 = 0.803$, N =18)

Factor	df	Mean-Square	F-ratio	P
sex	1	0.317	61.280	< **0.001**
V(telencephalon)	1	0.021	4.136	0.060
Error	15	0.005		
Model coefficients				
CONSTANT		-0.366		
sex	f	-0.138		
V (telencephalon)		0.002		

Males had a significantly larger HVc volume than females, tarsus length as covariate gave the same results (Fig. 4.7.A). Neither telencephalon volume nor tarsus length correlated with HVc volume calculated from NeuN-stained sections.

4.3.4.4 RA volume calculated from Nissl-stained sections

Table 4.17: GLM of factors influencing RA volume (calculated from Nissl-stained sections) in male and female house sparrows ($r^2 = 0.837$, N =18).

Factor	df	Mean-Square	F-ratio	P
sex	1	0.172	76.633	<< **0.001**
V (telencephalon)	1	0.006	2.885	0.110
Error	15	0.002		
Model coefficients				
CONSTANT		-0.160		
sex	f	-0.102		
V (telencephalon)		0.001		

RA volumes were significantly smaller in females than in males (Fig. 4.7.B). Neither telencephalon volume nor tarsus length correlated with RA volumes.

4.3.4.5 RA volume calculated from NeuN-stained sections

Table 4.18: GLM of factors influencing RA volume (calculated from NeuN-stained sections) in male and female house sparrows ($r^2 = 0.804$, N =18).

Factor	df	Mean-Square	F-ratio	P
sex	1	0.147	61.192	< **0.001**
V (telencephalon)	1	0.004	1.822	0.197
Error	15	0.002		
Model coefficients				
CONSTANT		-0.107		
sex	f	-0.094		
V (telencephalon)		0.001		

RA volumes were significantly smaller in females than in males (Fig. 4.7.B). Neither telencephalon volume nor tarsus length correlated with RA volumes.

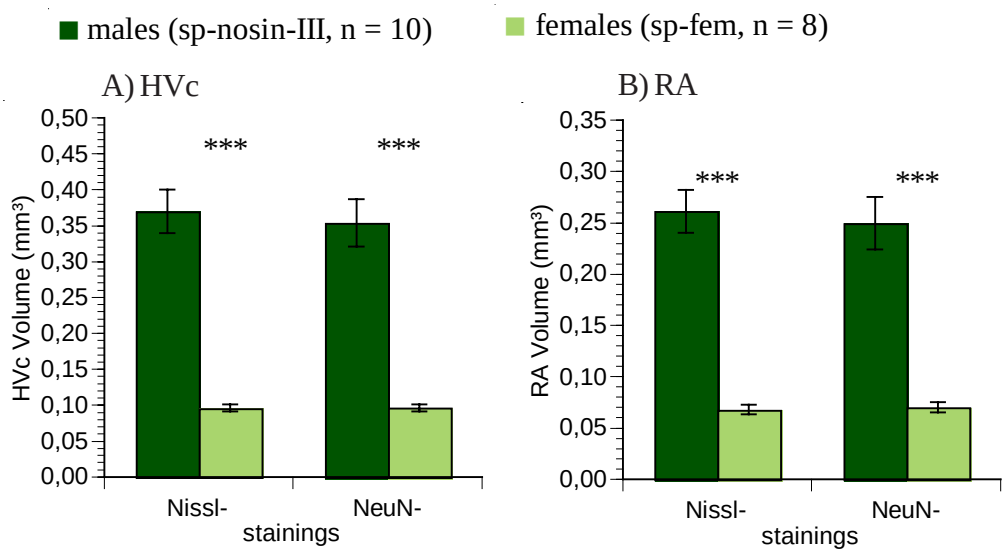


Fig. 4.7A-B: Comparison of HVc and RA of male and female house sparrows, both raised in captivity by sparrows. Data are presented as means ± sem; p-values of the respective statistical test are given in the graph, *** = $p < 0.001$. For details about statistics see Tables 4.15 – 4.18. Males obviously possessed about 4 times larger song nuclei than females.

4.3.5 EXCURSION: PROSPECTS FOR STUDYING SONG PRODUCTION AND SONG RECOGNITION WITH THE IEG ZENK

The following image sequence gives a first impression of sparrows' reactions to sparrow- or canary-playback, respectively. My focus lays on the song nuclei HVc and RA; for general pattern of ZENK expression throughout the brain see e.g. Wronski (1995) and Ball & Gentner (1998).

House sparrow males did not (or only rarely) sing without any stimulation. With reduced song activity and song perception basal ZENK expression occurred only in single cells if at all. Brain images of control birds being either silence or a mixture of music and noise of running water looked very similar. This is true for both nuclei (Fig. 4.8 A, B, I, J).

If wild sparrows listened to conspecific (sparrow) song, ZENK-labelled cells can be found in the HVc-shelf, while canary playback did not induce much ZENK expression in wild sparrows (Fig.4.8 C, D). This is exactly in line with the findings in other species. If a canary-raised individual listened to a canary playback, a clear ZENK expression was found in the surrounding of HVc, while in canary-raised sparrows listening to sparrow playback only a small ZENK response was induced (Fig. 4.8 E, F). In all listening, but not singing, individual the HVc itself

was free from ZENK-labelled cells (Fig. 4.8 C-F). This was different when individuals sang themselves: there was a strong ZENK response within HVc when canary-reared sparrows sang, irrespective of whether they heard canary or sparrow playback (Fig. 4.8 G, H). A direkt comparison of pictures Fig. 4.11G and Fig. 4.11H might give the impression that in canary-reared sparrows singing with a sparrow playback induced a stronger ZENK expression than singing in front of a canary playback; however the intensity of ZENK-labelling as well as the amount of ZENK expression is influenced by the amount of singing as well as by locomotion (see Wronski 1995). Therefore a comparison will have to include an analysis of the respective video tapes.

The ZENK expression patterns in HVc and HVc-shelf were very similar in RA and RA-cup concerning both control tapes (Fig. 4.8 I, J) as well as singing versus listening (Fig. K-N). Interestingly ZENK expression in RA-cup seemed to be different from HVc-shelf according to the presented stimuli: in canary-reared birds ZENK-labelled cells could be found in birds after listening to sparrow tapes, while only few immunoreactive cells were seen in canary-reared birds after listening to canary-tapes.

Fig. 4.8: ZENK expression in HVc & HVc-shelf (A-H) and RA & RA-cup (I-N) of male house sparrows killed in May. The sparrows of the different groups were kept in sound-proof chambers for 24 hours before listening to a playback of conspecific or heterospecific song (à 45 minutes). Details about the individual (wild or canary-reared), tape, nucleus and ZENK expression pattern are given below the respective image. Pictures of HVc and HVc-shelf were always taken with a 10fold objective, RA and RA-cup with a 6.3fold objective of a light microscope. However for thorough quantification much higher enlargements will be necessary. Black arrows indicate the boundary of the respective song nucleus, white arrows indicate examples of ZENK-immunopositive cells. Black bars between the pictures represents 50µm. (The slightly varying colouration of the pictures are mainly the result of colour management of the printer).

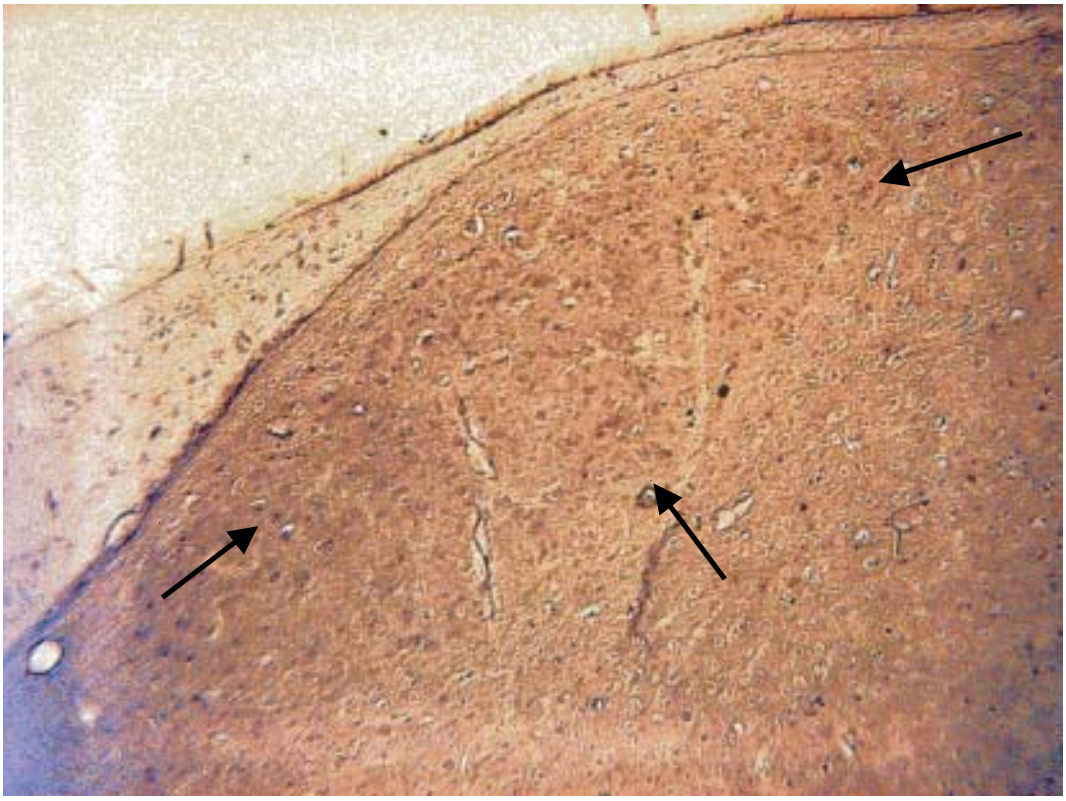


Fig. 4.8A) bird: canary-raised sparrow, tape: silence, area: HVc and HVc-shelf; the bird did not sing, only very basal ZENK-expression can be found. —

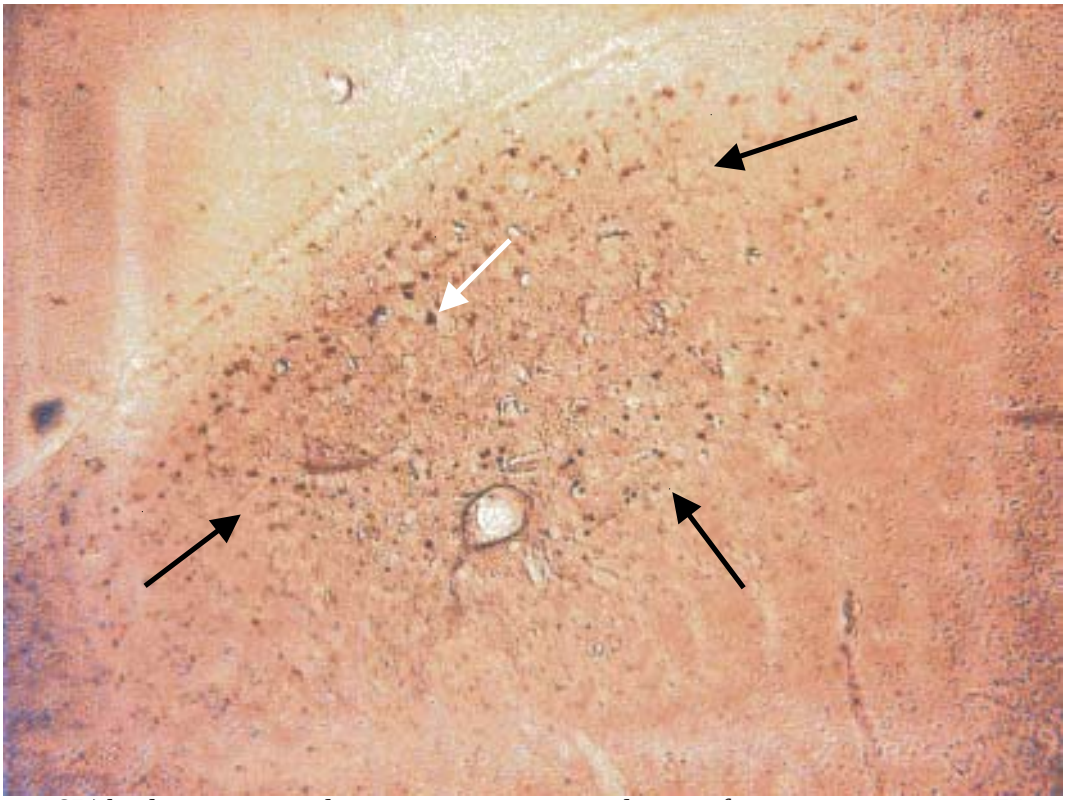


Fig. 4.8B) bird: canary-raised sparrow, tape: music and noise of running water, area: HVc and HVc-shelf, the individual sang a little bit, but not intensive thus some immunopositive cells can be seen within the nucleus, but only basal ZENK expression in the shelf.

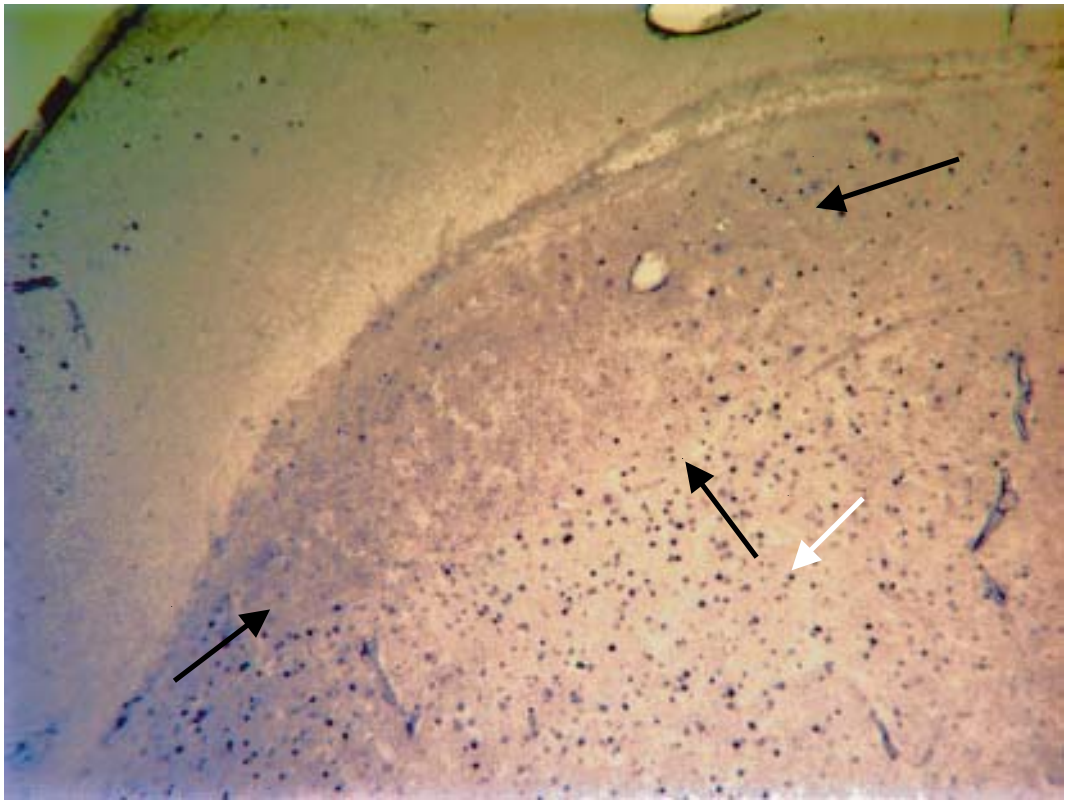


Fig. 4.8C) bird: wild caught sparrow, tape: sparrow, area: HVc and HVc-shelf. The bird is only listening but not singing thus a intensive ZENK response can be found in HVc-shelf.

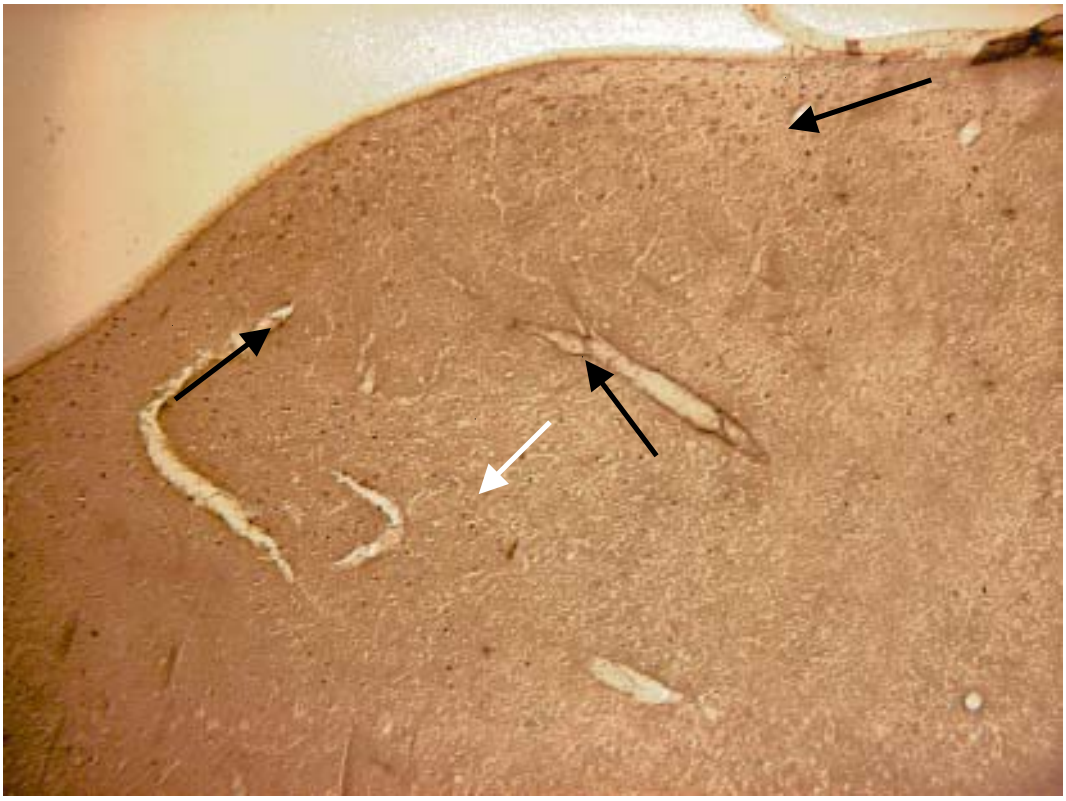


Fig. 4.8D) bird: wild caught sparrow, tape: canary, area: HVc and HVc-shelf. The bird is only listening but not singing. The heterospecific stimuli induced only low ZENK response.

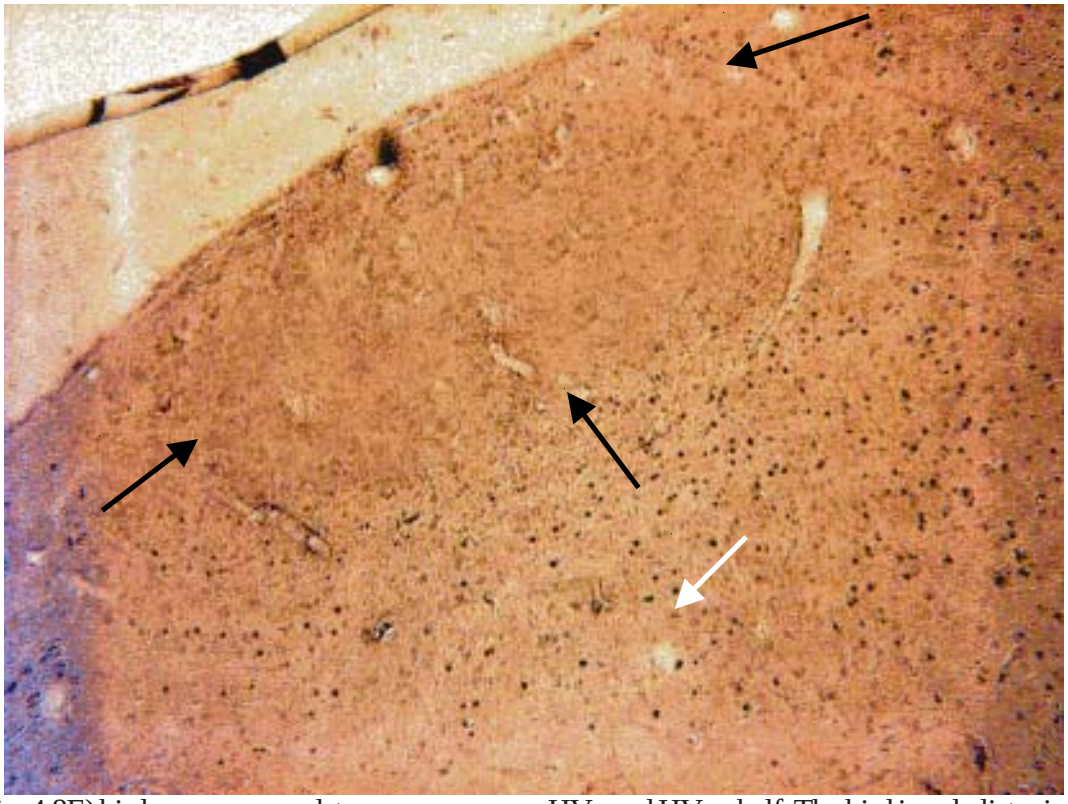


Fig. 4.8E) bird: canary-reared, tape: canary, area: HVc and HVc-shelf. The bird is only listening but not singing thus an intensive ZENK response can be found in HVc-shelf.

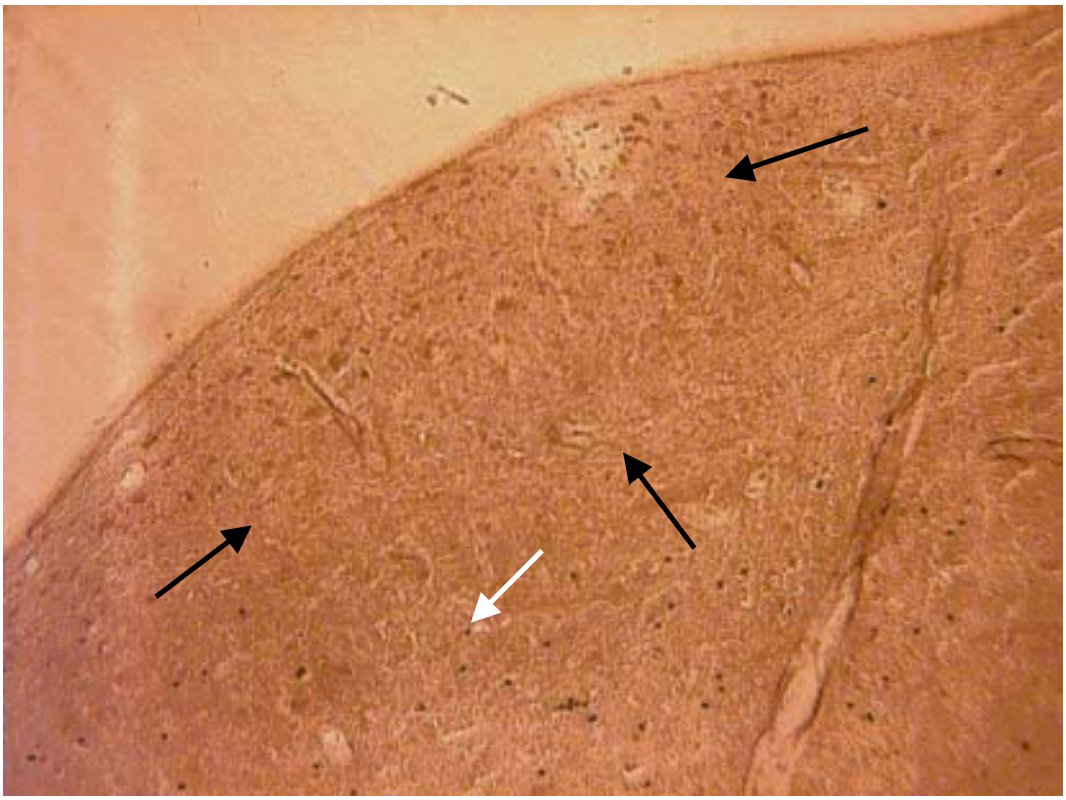


Fig. 4.8F) bird: canary-reared, tape: sparrow, area: HVc and HVc-shelf. The bird is only listening but not singing thus a ZENK expression can be found in HVc-shelf. Listening to sparrow song seemed to induce a lower ZENK response than canary song (Fig. 4.8E)

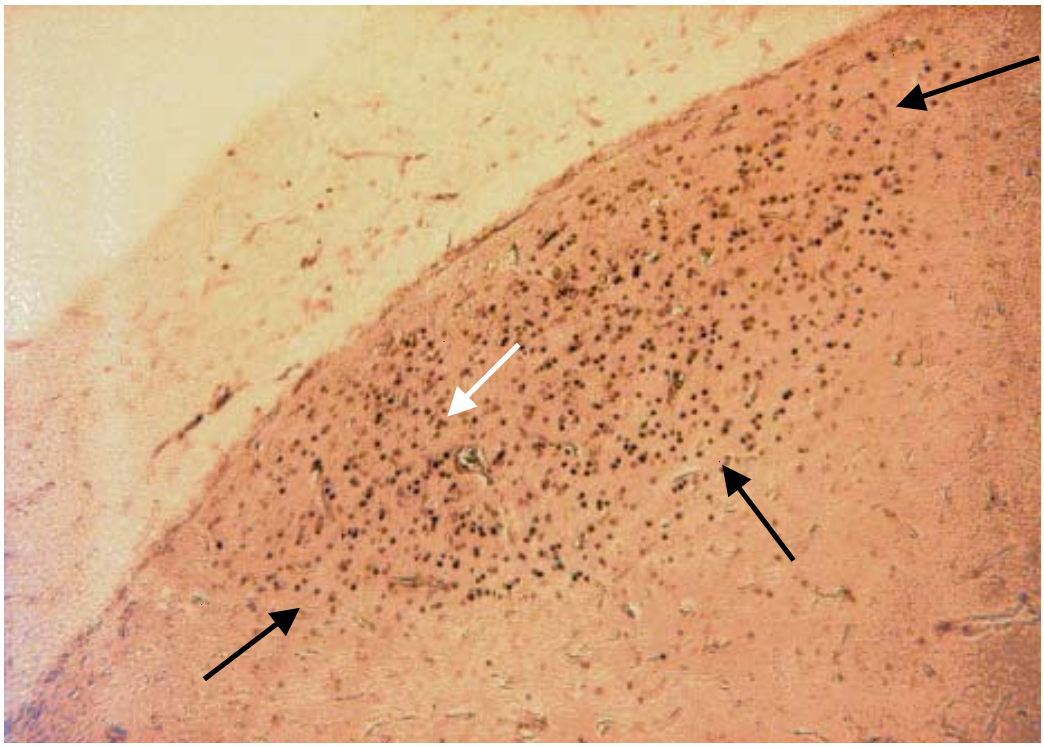


Fig. 4.8G) bird: canary-reared, tape: canary, area: HVc and HVc-shelf. The bird is singing, thus an intensive ZENK expression can be found within HVc. ——

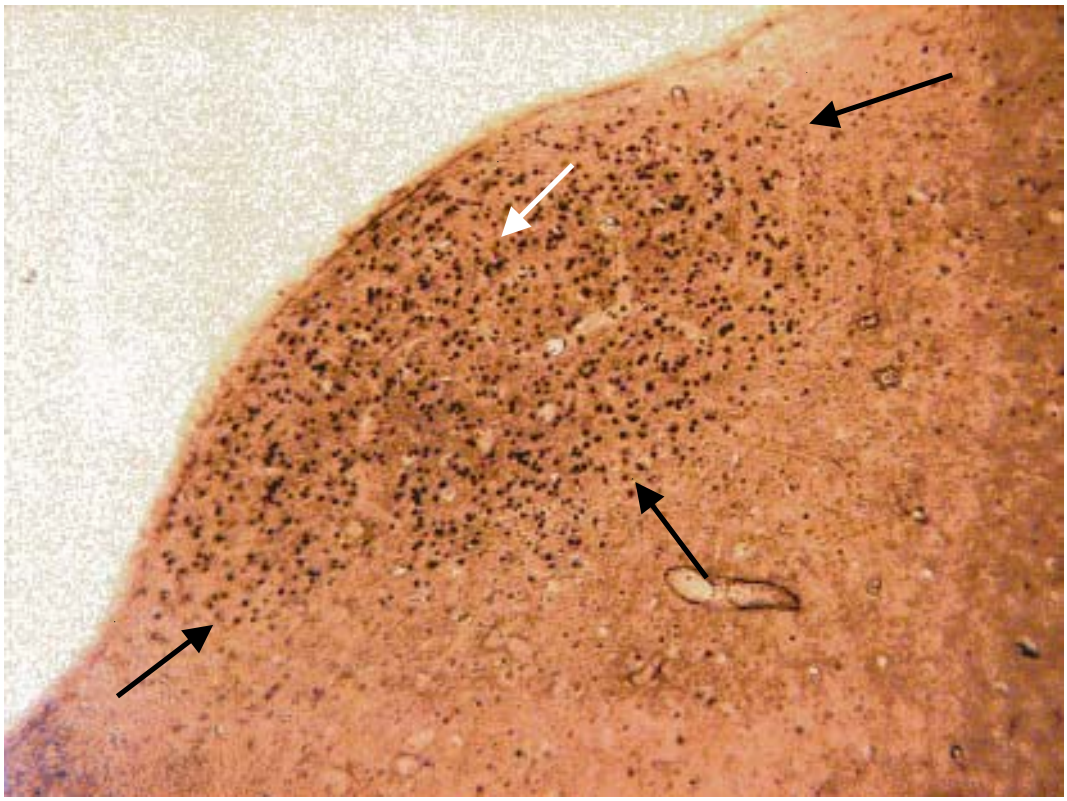


Fig. 4.8H) bird: canary-reared, tape: sparrow, area: HVc and HVc-shelf. The bird is singing, thus an intensive ZENK expression can be found within HVc.

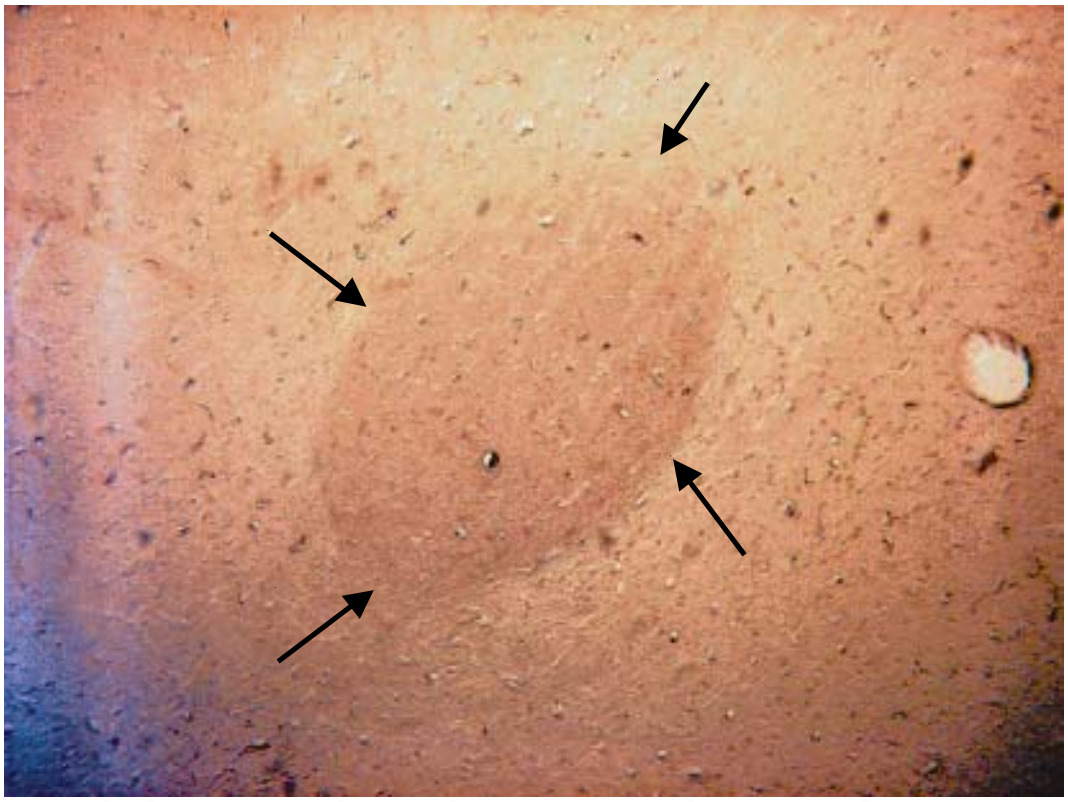


Fig. 4.8I) bird: canary-reared, tape: silence, area: RA and RA-cup. Without any acoustic stimulus ZENK expression is very low.

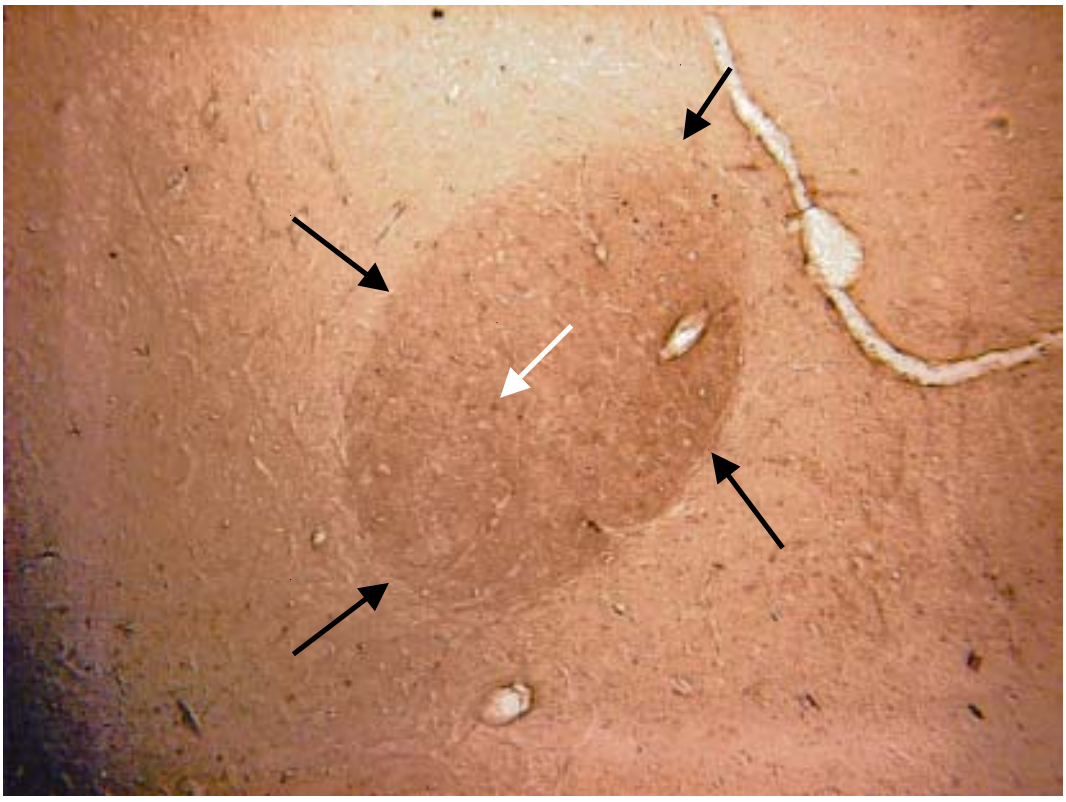


Fig. 4.8J) bird: canary-reared, tape: music and noise of running water, area: RA and RA-cup. Noise did not increase ZENK expression above the basal level.

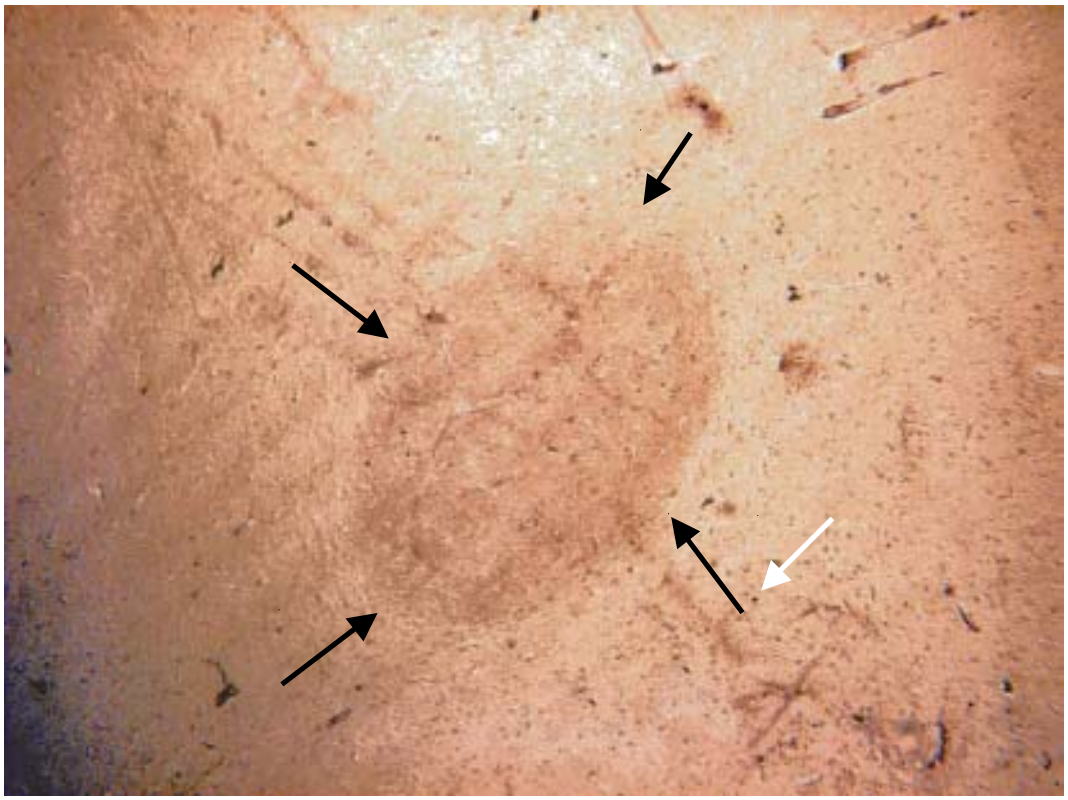


Fig. 4.8K) bird: canary-reared, tape: canary, area: RA and RA-cup. The bird was not singing, only basal ZENK expression can be seen.

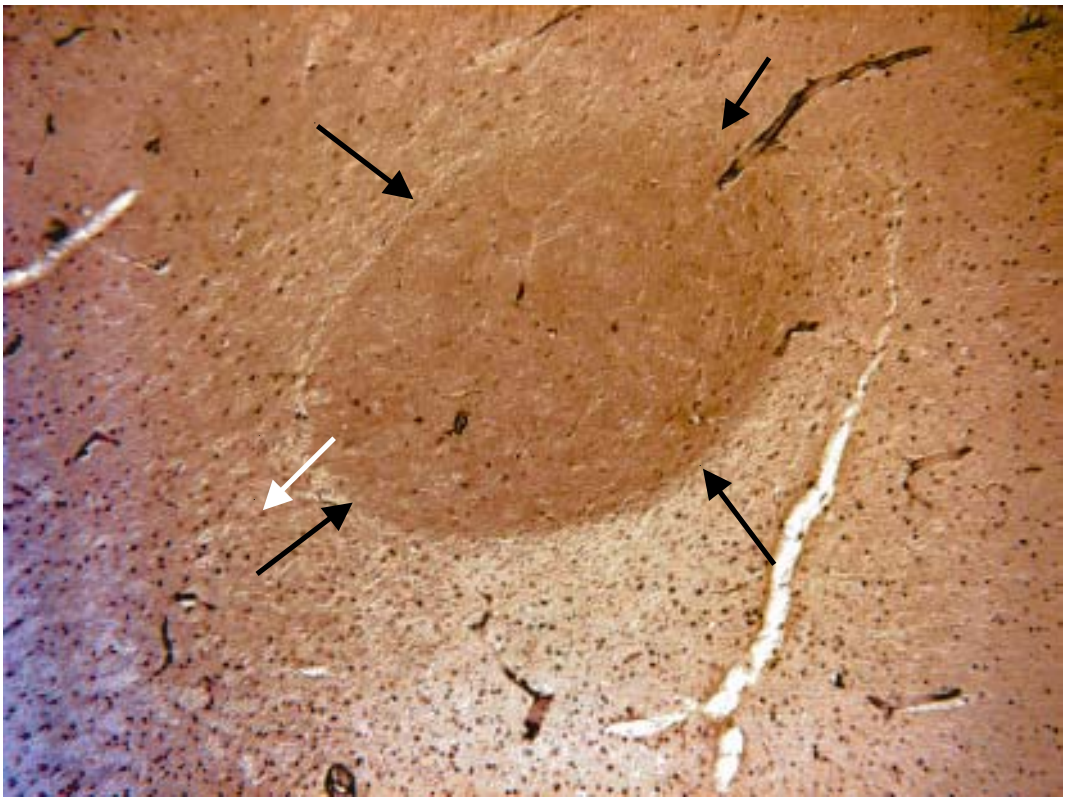


Fig. 4.8L) bird: canary-reared, tape: sparrow, area: RA and RA-cup. The bird was not singing, thus the intensive ZENK-immunopositive reaction occurred in the RA-cup.

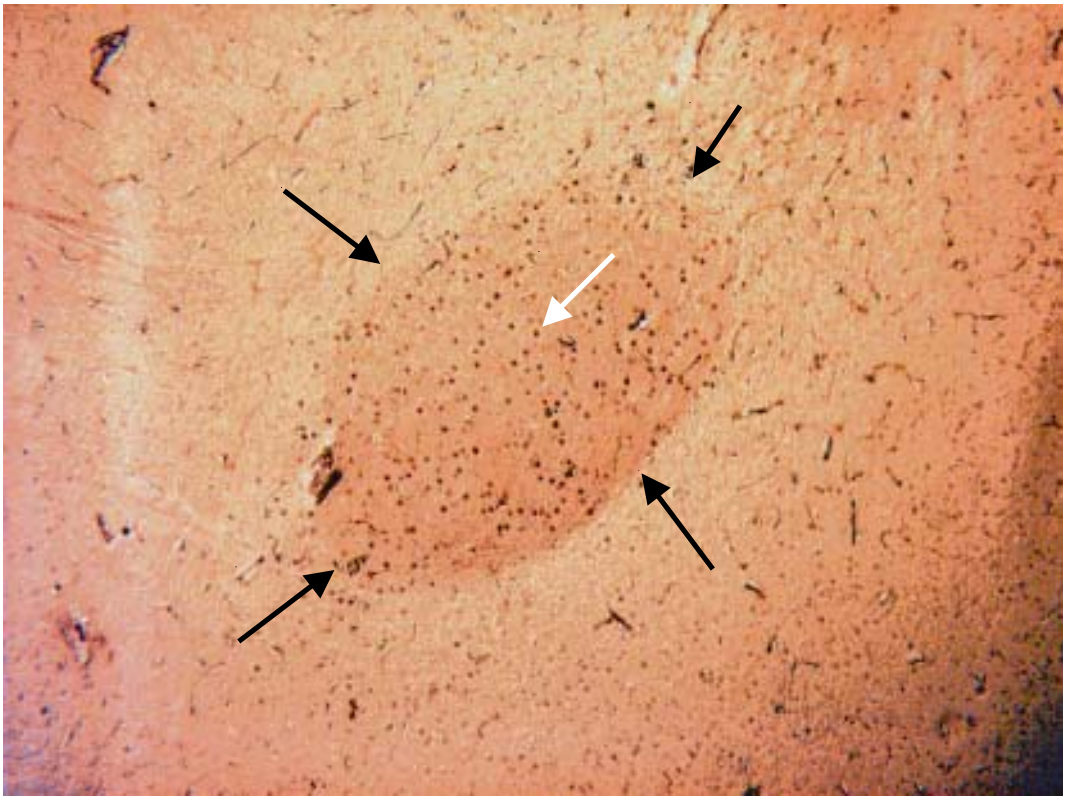


Fig. 4.8M) bird: canary-reared, tape: canary, area: RA and RA-cup. The bird was singing, thus ZENK expression can be seen within the nucleus. —

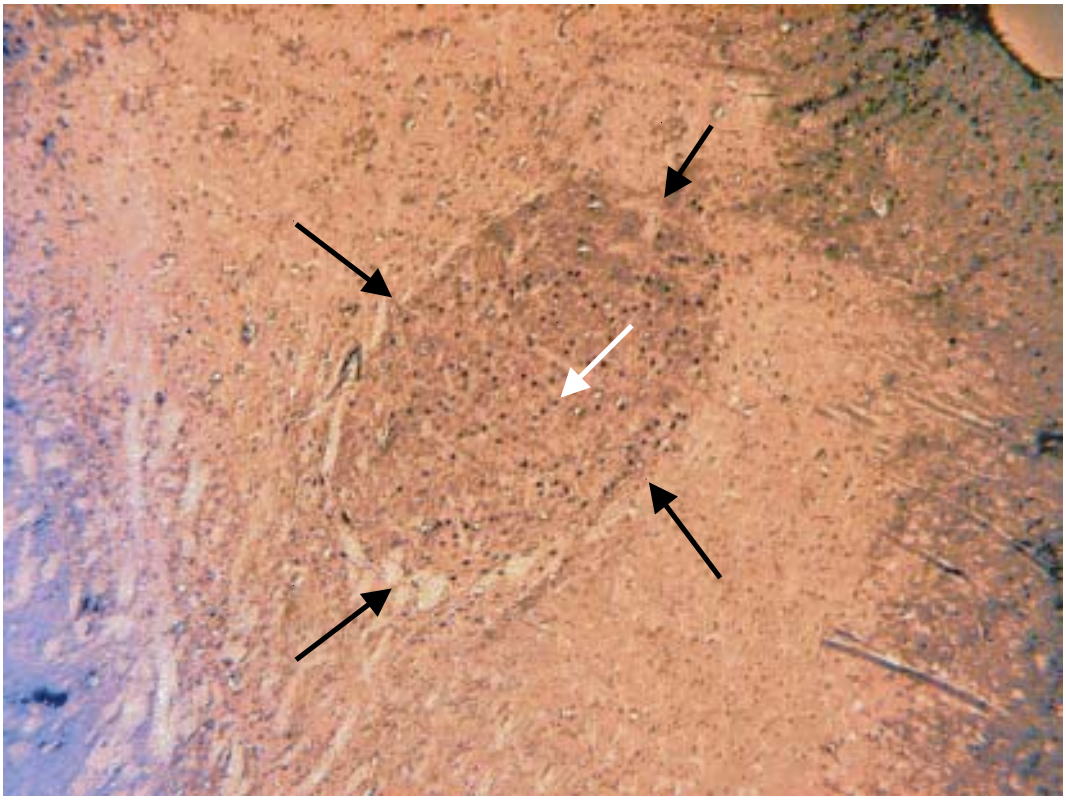


Fig. 4.8N) bird: canary-reared, tape: sparrow, area: RA and RA-cup. The bird was singing, thus ZENK expression can be seen within the nucleus.

4.4 DISCUSSION

4.4.1 Differences in nuclei size according to vocal skills and/or rearing conditions?

HVc volume of tour singing males was significantly larger than that of non-singers, although both produced about same sized repertoires (sum of learned an un-learned syllables). However RA volume (Nissl-stained or NeuN-stained) did not differ. Two main conclusions can be drawn from this:

A) the repertoire learning capacity faces an upper limit. All individuals fully utilize this learning capacity, but cannot surpass its limit;

B) within a determined range of learning abilities, HVc volume seems to show a relation to singing complexity but not to repertoire size (number of syllables).

In the discussion in chapter 3, I already mentioned that the syllable catalogue is based on particular tape-recording and analyses conditions in this study. Although syllable usage seemed to vary between days, all individuals of a given group produced within the same analyzed time span a comparable number of syllables. I take this as an indication that the sparrow repertoire size as suggested in chapter 3 is representative of the total repertoire.

RA neurons encode single notes (Yu & Margoliash 1996), while HVc functions as a sensory motor integration area coding for syllables, motifs and higher-order patterns (Yu & Margoliash 1996; Margoliash 1997). Thus, as canary-like singing sparrow males have an increased HVc, but similar-sized RA volume compared to ca-nosin and sp-nosin, this might strengthen the idea that ca-sin memorized canary-like tours as a unit (i.e. 'multi-note syllables' as suggested in chapter 3) rather than a series of separate notes.

The tour-resembling scolding sequence was produced by individuals of all groups and therefore did not seem to be learned. The fact that only 'tour'-like singing males have an increased HVc denies the hypotheses that tours and scolding sequence might be conceptionally similar and emphasises that canary-like tours were indeed learned.

Canary-like tours are different from normal sparrow syllables for two main reasons: natural sparrow syllables a) are mainly one-note[3] syllables; b) possess at least one harmonic, except

[3] Some authors wrote about „disyllabic elements" (e.g. Glutz von Blotzheim 1987) like the two-folded sparrow chirp (see chapter 3, Fig. 3.1C). Because sparrows combine the two frequency sweeps without a break, it can be called an „one-note syllable"; a note has been defined as the shortest, uninterupted structure in a sonagram (see chapter 3, 3.2.3.1 terminology for song analyses).

for three calls (Nivison 1978). Sparrows' canary-like tours, however, were combinations of several identical notes mainly lacking harmonics and sung with a constant (probably learned) repetition rate. Ca-nosin also produced syllables which might have been learned from canaries and lack overtones, nevertheless ca-nosin did not differ in any of the brain measures from sp-nosin who did not learn from canaries, but owned smaller sized HVc volumes than ca-sin who not only sang syllables lacking overtones, but produced the canary-like tours. It seemed that combining several notes with a precise temporal pattern is more demanding and needs more brain space (i.e. larger HVc volume) than learning only syllables - be they con- or heterospecific - or 'just' filtering harmonics.

All canary-reared birds (ca-sin, ca-nosin) had the same opportunity to learn from their respective canary tutors or at least from the tapes with canary songs played each day in addition to their canary tutors. However only some individuals (ca-sin) learned to produce canary-like tours and these were the individuals with significantly larger HVc volumes. Thus one might conclude that ca-sin were privileged in their (inherited?) brain capacity and in turn in song learning. It is less probable that ca-sin were also endowed with better neuronal motor control, because RA, which is suggested to play an important role in the coordination of respiration, syrinx, and larynx activities (Margoliash 1997), did not differ between ca-sin and all other tested sparrows. However, support for this conclusion will require further studies of other song nuclei involved in motor coordination (e.g. nXIIts, ICo, DM, RAm, Am; for explanations see chapter 1, 1.3.2 Anatomy and function of the song control system).

The difference in HVc volume requires to study the underlying mechanisms. One explanation for the volume differences between singers and non-singers could be an increased number of glia cells. Glia cells are known to interact extensively with neuronal elements in the brain, influencing their activity. They participate in formation and rebuilding of synapses, are generally accepted to be the major site for neurosteroid formation, and play a prominent role in protection and repair of nervous tissue (Hansson & Ronneback 2003; Tsutsui et al. 2000). Thus glia cells or the ratio of neuron to glia cells may be a critical determinant for the degree of behavioural versatility (Nealen & Perkel 2000); this question will be answered after counting cells in Nissl-stained sections (colouration of glia cells and neurons) and NeuN-stained sections (only colouration of neurons) followed by a comparison of both. Another explanation for an increased volume of HVc might be an increase in synaptical connectivity. Several experimental learning

paradigms in vertebrates demonstrate that the number of dendritic spines, a major class of synapses, positively correlated with memory formation; indeed this is also true for songbirds (Airey et al. 2000). I therefore kept the second half of each brain used for this study in store for later quantification of dendritic spine density on Goldi-stained neurons.

4.4.2. Effects of captivity on brain morphology?

Though my house sparrow breeding pairs were already hatched in captivity and lived up to 3 years in our aviaries or cages, neither they nor their young differed from wild-caught males in any of the measured brain features. Also the correlation between RA volume (Nissl, NeuN) and telencephalon volume is of comparable magnitude in both groups. Thus it has to be assumed that captivity per se does not cause changes in volumes of total telencephalon or forebrain song nuclei. This is in fact also true for other telencephalic regions like the hippocampus (Healy et al. 1996).

4.4.3 Effects of seasons on brain morphology?

In different seasons (winter, summer) males showed dramatic differences in the size of both nuclei studied, RA and HVc. The magnitude of these differences was comparable to that reported for wild-caught house sparrows in the lab (Whitfield-Rucker & Cassone 2000) and domestic canaries during different seasons (Nottebohm 1981).

Overall brain size of my house sparrows, i.e. brain weight or telencephalon size, did not differ seasonally. Seasonal variations in brain weight seem to be species-specific. While total brain weight of Towhees, for example, also did not change in relation to photoperiod (Brenowitz et al. 1991), individual brain weight increased for up to 15% in laboratory-reared canaries and in blackbirds during the breeding season (Nottebohm 1981; Kirn et al. 1989). The observed differences in the sizes of house sparrows' song nuclei between seasons must result from anatomical changes specifically within HVc and RA, as they cannot be attributed to differences in overall brain size.

Both volume measurements (Nissl-stained and NeuN-stained) revealed the same volume differences between seasons. These volumetric differences probably resulted from differences in neuron number. However I did not distinguish between the three cytoarchitectonic regions (Kirn et al. 1989; Fortune & Margoliash 1995), thus I cannot speculate whether volumetric differences resulted from neurogenesis in the ependymal zone along the lateral ventricles, or

from cell migration or from still other factors (Goldman & Nottebohm 1983; Alvarez-Buylla & Nottebohm 1988).

The differences in brain size in relation to singing behaviour need further studies. Some syllables became more variable in the non-breeding season while others remained stable. Occasional observations on one sparrow (Ramses) suggested that also the temporal pattern could remain precise to some extent (see chapter 3). That also in autumn 'elaborate' singing skills might be necessary and should not vary in essential features is probable when taking into account the sparrow's social life, because:

a) house sparrows form pairs already during autumn and winter. Although the ownership of a suitable nest site might be the key feature for pair formation (e.g. Summers-Smith 1988), copulations occur after males show a sexual display including body movements combined with singing (Summers-Smith 1988; personal oberservations);

b) furthermore sparrows form action societies of about 50 and up to 200 birds (Fallet 1958) with a relative stable flight composition (Summers-Smith 1954); the coherence is fairly strong throughout the year, with single individuals rarely moving between different flocks (Fallet 1958). The social life of house sparrows is based besides others on a complex vocal communication system (Nivison 1978); this makes it reasonable to assume that some vocalizations remain stable in all seasons.

A challenge for further research is to study the underlying mechanism how sparrows face social requirements of vocal skills in the time of decreased song nuclei.

4.4.4 Sex differences in brain size?

Female house sparrows owned a significantly smaller HVc and RA than males. A literature analysis of Gahr et. al. (1998) revealed that sex differences in song nuclei size tend to be larger in species in which only males sing than in species where females sing too (see Table 4.19).

Table 4.19: Sex differences in the size of song nuclei HVc and RA (given as ratio of male to female) grouped by singing ability of females. Modified from Gahr et al. 1998.

Species	**HVc**	**RA**
I. Only males sing		
zebra finch	13.6-5.0	11.9-5.5
orange bishop	> 29	29
II. females sing, sexes posses different repertoire size		
canary	4.3-2.7	3.0-2.7
red-winged blackbird	3.2	4.7
III. females sing, sexes possess similar repertoire size		
white-crowned sparrow	2.4	3.7
bush shrike	1.8	2.0

Gahr et al. (1998) concluded that HVc and RA need to obtain an adequate size to allow song production. In my house sparrows HVc is about 3.8 times and RA 4.3-3.6 (Nissl-NeuN-staining) times larger than in females and thus sex differences were similar to canaries and red-winged blackbirds. In turn this suggests that the house sparrow belongs to the species in which both sexes sing. That both sexes sing is supported by behavioural observations. Sparrow females produced scolding sequences in aggressive situations (see chapter 3). Marek (1979) reported about a sparrow female who developed an elaborate song without a tutor, and Ragotzi (1962) about a sparrow female who should have copied the canary song. Nivison (1978) described an elaborate system of calls that are uttered with some precision and coordination resembling duetting; it occurs when there are chicks in the nest and a mate is very determined to enter. This display seems to parallel that of the Boubou shrike (*Laniarius aethiopicus*), where duetting occurs during nest-relief (Hooker & Hooker 1969) and the duet also may be initiated by either mate.

Besides the fact that it seems worthwhile to study vocalizations of sparrow females in more detail, these findings strengthen my concerns in chapter 3, that the male repertoire I described can only give a first impression about a sparrow male's singing ability. It supports the need to have males tape-recorded in social context to get a realistic view on the actually used repertoire. And this also may enlighten the understanding of the term „song complexity" in house sparrows, as this might not be basically determined by the number of syllables produced but by the ability to use and understand the factual meaning of given syllables in different situations. This, however, might be important for both sexes, thus complexity could be similar though the syllable repertoire seems to be different (Nivison 1978).

4.4.5 Excursion: Zenk-expression in house sparrow's song brain

ZENK protein is expressed at high levels as early as 15 minutes after a conspecific song stimulus started (Mello et al. 1992, Mello & Ribeiro 1998). The expression was especially high in areas of the auditory telencephalon such as the caudal and medial neostriatum (NCM), but it also occurred in the HVc-`shelf´ and the RA-`cup´ (Ball & Balthazart 2001). ZENK expression is basal in response to simple tones, but it is several times higher in response to conspecific as opposed to heterospecific song (Mello et. al. 1992). The ZENK response to song is dependent on early experience, e.g. zebra finches raised in social isolation do not exhibit this response (Jin &Clayton 1997). However, I found no reference in literature studying ZENK response in birds cross-fostered by a foreign species.

The ZENK labelled cells in RA-cup occurring in sparrow-, but not in canary-tape listening canary-reared birds suggests, that they recognise the different syllables although they never heard sparrow vocalization before. It will be interesting to compare the syllables of the sparrow tapes (tape recordings were taken in the wild) with the syllable catalogue of the canary-raised birds to see whether the presented syllables are similar (or identical?) to the unlearned syllables which all canary-reared as well as some sparrow-reared sparrows produced (see chapter 3).

In the HVc- shelf less immunopositve cells seemed to be found in canary-reared birds listening to canary playback than in wild sparrows listening to sparrow playback. However there were clearly more ZENK-labelled cells than in canary-reared birds listening to sparrow playback. Indeed canary-reared birds listening to sparrow playback seemed to react like wild sparrows listening to canary playback. Influenced by early learning experiences, canary-reared sparrows seemed to be more familiar with the structure of canary song than with the simple sparrow vocalization; the reaction seemed not to reach the level of conspecific song recognition. This favours the idea that the canary-like structure in ca-sin is indeed learned.

The ZENK expression pattern in/around HVc and RA seems to go in line with the findings that HVc but not RA was influenced by canary song complexity (see results of this chapter) and that canary-reared sparrows also produced unlearned, sparrow-typical syllables (see chapter 3). But all this has to be read with the reservation that for concrete results detailed studies of other regions, especially NCM, are necessary, as are video tape analyses.

4.4.6 SUMMARY OF THE MOST IMPORTANT RESULTS

House sparrows can be induced to memorize a relatively wide range of model sounds. Nevertheless the repertoire learning capacity faces an upper limit which individuals fully utilise, but cannot go beyond. Within a determined range of learning abilities, HVc and RA morphology seems to show a relation to singing complexity (production of canary-like tours) but not to total repertoire size (number of syllables). Furthermore in males HVc and RA morphology showed dramatic differences in different seasons (winter, summer), while captivity per se did not cause changes in overall brain size (i.e. telencephalon volume, brain weight) or any of the measured features of forebrain song nuclei. Males owned significantly larger song nuclei than females. The sex differences in brain size fall into the range of species with singing females who possess a repertoire size different from males. ZENK response in HVc-shelf respectively seemed to underline the result that the canary-like sequences in canary-reared house sparrow vocalizations were indeed learned, while several sparrow typical syllables did not have to be learned.

The result of increased HVc volume in tour-singing sparrow males recommend further detailed studies about learned vocal skills and brain anatomy on the cellular level (e.g. neuron number, neuron density, spine density, etc). However, the cross-fostering procedure and moreover the comparison of two not closely related species first demand further controls: cross-fostering might influence hormonal states of an individual (details see chapter 5) and in turn song nuclei volumes; and vocal skills, here related to brain size, could be constrained to some extent also by morphology (details see chapter 6).

5 INLFUENCE OF STEROID HORMONES ON THE VOCALISATION OF MALE HOUSE SPARROWS

5.1 INTRODUCTION

Steroid hormones represent a major class of regulatory influences on neural growth and behaviour. Estrogen or testosterone treatment promotes the migration and/or survival of new HVc neurons in both developing and adult birds (e.g. Rasika et al. 1994; Burek et al. 1995; Hildago et al. 1995). Sex steroids have also been shown to drive significant increases in somal size, spacing between cell somata, dendritic growth, and number of synapses within various song regions (Bottjer & Johnson 1997). The correlation of vocal skills (singing canary-like tours or not) and augmented song system anatomy of chapter 4, however, based on the assumption that canary-like tours produced by canary-raised house sparrows resulted from song learning and memory. The present chapter controls for possible objections from the field of endocrinology.

Many song control nuclei contain a large number of cells with receptors for androgenic hormones, including HVc and RA (e.g. Arnold et al. 1976; Gahr 1990b; Balthazart et al. 1992). For example, testosterone treatment stimulates pronounced growth of HVc in adult canaries as well as in juvenile female zebra finches, and leads to stereotyped song production. The mechanisms by which hormones induce neural growth and learned song behaviour are poorly understood.

Male singing activity is correlated with circulating levels of plasma testosterone (details see chapter 1, 1.3.3 testosterone and song), i.e. song rate increases with elevated plasma T level (Table 5.1).

In the wild, house sparrows show maximum singing activity when testosterone plasma level is highest (Hegner & Wingfield 1986a). Thus an elevated plasma testosterone level via increased song rate may accidentally lead to tour-like structures in the song of house sparrows. The native song of house sparrows comprises sequences of repeating one type of syllables separated by silence intervals longer than 0.5 seconds. These sequences differ from tours only in their temporal structure as intervals between tour syllables are below 0.4 seconds (details see chapter 3). With increased singing activity and more rapid singing there is also an increased probability for spontaneous occurrence of short tours. Furthermore, testosterone treatment of

Table 5.1. Overview of experimental studies testing the effect of testosterone (T) on male behaviour in birds. In these studies, control males had T levels below the breeding baseline (as during chick feeding) (adapted from Foerster 2002).

behavioural trait	effect of elevated T	species	Selected reference
song rate	increase	pied flycatcher	Silverin 1980
		reed warbler	Dittami et al. 1991
		dark-eyed junco	Ketterson et al. 1992; Casto et al. 2001
		Lapland longspur	Hunt et al. 1997
		European starling	De Ridder et al. 2000
		spotted sandpiper	Oring et al. 1989
		great tits	Van Duyse et al. 2002
	no effect	red-winged blackbird	Beletsky et al. 1995

female starlings, for example, who normally do not sing complex songs, clearly stimulated singing behaviour in isolation and revealed their ability to sing memorized, quite complex songs (Hausberger et al. 1995). This raises the question whether house sparrows with elevated testosterone levels produce syllables with tour-like structures without learning experience.

Dehydroepiandrosterone (DHEA) can act as a precursor of testosterone (Baulieu & Robel 1996; Longcope 1996). DHEA, though it has been studied intensively (especially in mammals), remains an enigmatic steroid (Lieberman 1986). It is known to have a wide variety of physiological effects including major regulatory effects upon the immune system (e.g. Robel & Baulieu 1995; Shealy 1995; Loria et al. 1996; Kroboth et al. 1999) and neuro-anatomical effects in adult animals (Soma et al. 2001). Thus it has to be ruled out that tour singing in canary-raised house sparrows is at least partially the result of testosterone via DHEA.

First I tested whether wild-caught house sparrows with experimentally elevated or lowered androgen plasma levels differ in their singing behaviour and vocal skills from control individuals with natural plasma levels during breeding season. Then I compared hormone data from the experimental groups with androgen plasma levels of my captivity-bred house sparrows to find out whether captivity in general, and canary-rearing in particular, may induce complex songs by raising androgen levels.

5.2 METHODS

5.2.1 ANIMAL SUBJECTS

5.2.1.1 EXPERIMENTAL ALTERATION OF PLASMA STEROID LEVELS IN WILD-CAUGHT HOUSE SPARROWS

I caught 30 wild house sparrows in the Fünfseenland [Five Lakes Region]**,** Bavaria, using mistnets in April 2001. Three birds were kept in an aviary in reserve. 27 birds were housed in individual cages (Joko, Bramstedt/Bassum; 122cm x 50cm x 50 cm) in groups of 6-7 (2-3 individuals per experimental group) in ventilated rooms. Birds were spaced to allow tape recording of individuals. Birds were kept under L/D 16h/8h light regime to simulate breeding conditions. All animals were in reproductive state indicated by the completely black bill (see Appendix 2, Fig. A2.1). Food (seeds, insects, salad and fruits) and water were available ad libitum during the whole experiment.

After two weeks of habituation individual birds were randomly assigned to three experimental groups defined by implants (see 5.2.2 implantation of pellets)

5.2.1.2 COMPARISON OF STEROID HORMONE LEVELS OF CANARY-RAISED AND WILD HOUSE SPARROWS

Steroid hormone levels of my canary-raised house sparrows, singing canary-like tours (ca-sin) or not (ca-nosin), were compared to the testosterone- and placebo-group of the experiment of part 5.2.1.1 and an untreated group of wild-caught birds. The control group of untreated wild house sparrows were already used in chapter 4 to study possible influences of captivity on song nuclei size. To study song recognition in canary-raised house sparrows via ZENK expression, I performed an experiment in sound-proof chambers 2.5 days before birds were perfused. Food and light regime were identical for all birds (for details about the procedure during the ZENK experiment, see chapter 4).

5.2.2 IMPLANTATION OF PELLETS

The implantation was done between 8.00 and 9.00 am. For hormonal treatment I used time release pellets (Innovative Research of America, USA), which offer a regular release of drugs. The required dosage was calculated following Fusani (1999). The testosterone-group was implanted with one pellet containing 1mg testosterone (21-day release pellets, 35µl / day); the

"blocker-group" was implanted with two pellets, one pellet containing 1mg Flutamide (21-day release pellets, 35µl / day) and one pellet containing Fadrazole (30-day release pellets, 35µl / day); control birds were implanted with an empty placebo pellet, called placebo-group. All pellets were implanted subcutaneously on the bird's back; the incision was closed with Histoacryl® (Braun, Aesculap, Germany).

5.2.3 SONG BEHAVIOUR AND ANALYSES OF THE IMPLANTATION GROUP

Before implantation each bird was tape recorded twice a week (between 9.30 to 12.00 am and 3.30 to 6.00 pm) for 20 minutes. From day 1 to 8 after implantation the birds were tape recorded each day alternatively in the morning or afternoon. The Sennheiser microphone (ME66, Version K6), connected with an Uher M517 tape recorder**,** was partly shielded to improve separation of the test bird's vocalisation from background noise by the other birds.

Tape recordings were digitised at 22.050 kHz (= sampling rate) using a Hamming window. The recordings and the analyses were carried out with digital sound analysis system Avisoft SaslabPro (Specht 2000, Avisoft Bioacoustic, Germany) using a Dell computer (Dell OPTILEX GX 150) and Microsoft Windows 2000. Spectograms of songs were generated using a Fast Fourier Transform (FFT) of 256 points, a Filter Bandwidth of 300 Hz and time resolution of 8,931 msec (Frame). For quantification spectrograms of Saslab32 were used (for details see chapter 3.2 song, methods).

To evaluate whether spontaneous trills or tours occurred, I checked all spectrograms of all 20-min tape recordings. When the singing rate (number of syllables) increases, intervals decrease and in turn, the probability to produce trill-like structures increases. Thus to assess the probability of spontaneous trills or tours, respectively, in relation to experimental alteration of plasma steroid levels I counted each syllable within each 20-min session.

For canary-raised sparrows tours were catalogued according to visual spectrogram-morphology in Powerpoint (Microsoft Office 2000). To assess syllable similarities in cases of doubt I superimposed spectrogram copies using Adobe Photoshop (details see chapter 3).

5.2.4 BLOOD SAMPLING

Blood was taken once a week before implantation and at day 8 after implantation before killing the birds. As hormonal state changes during the day all birds were bled within one hour (8.00 – 9.00 am) to reduce variability of hormonal levels. With a needle (0,5 x 16, Terumo, Neolus) the wing vein was pricked and 150-200µl blood samples were collected in heparinized microcapillaries (Length 75 ± 100 mm, Brand, Cat. No 7493 11). After centrifugation (2500rpm, 5 min) plasma (50-100µl) was collected and subsequently treated with 10 microliters β-propiolactone solution according to US import regulations for avian blood. Samples were then stored at -80°C until transport on dry ice to Princeton under permission of German and US authorities.

5.2.5 PERFUSION

After the last tape recording the birds were bled, weighed and then killed with Diethylether (Merck) between 8.00 and 12.00 am, followed by an immediate transcardiac perfusion first with 0.9% sodium chlorid (200ml) and then with a 4% formaldehyde solution in PBS-buffer (= FPBS). From the dead bird weight of organs (gonads) and skeletal measures (tarsus, bill) were taken. Total brains were weighed and stored in 4% FPBS in the fridge until further analysis.

5.2.6 STEROID HORMONE MEASUREMENT

Plasma concentrations of the androgens testosterone (T) and dehydroepiandrosterone (DHEA), and the oestrogen estradiol (E_2) were measured by an indirect radioimmunoassay (RIA) after chromatography using a modification (Hau et al. 2000) of the method described by Wingfield and Farner (1975).

5.2.6.1 REAGENTS

Antisera were obtained from Wien Laboratories, Succasunna, New Jersey (T, DHEA) and Biogenesis Inc, Brentwood, NH, USA (E2) with cross reactivities given in Table 5.2. Cross-reactivities, however, only play a minor role as steroids elute in different fractions with minimal overlap. Thus, since these fractions are analysed separately with the respective antisera, cross-reactivities can be neglected (see Goymann 1999).

Standard steroids were purchased from Sigma and steroids labelled with tritium from NEN Life Science Products, Boston, USA (now: Perkin-Elmer, Boston, USA). All chemicals used were of analytical grade (Appendix 1). The assay buffer for sex steroids was a 1.0 M phosphate buffered NaCl solution with 1% gelatine and 1% sodium azide (PBSG), pH 7.0.

Table 5.2: Percent cross-reactivities of androgen and estrogen antisera with other steroid compounds.

	% cross reactivity		
Compound	**T**	**DHEA**	**E_2**
5á-Dihydrotestosterone	63.20	0.07	
Δ-1-Testosterone	46.50		
5á-Androstan-3α,17β-diol	17.70		
Δ5-Androsten-3β,17β-diol	14.00		
5á-Androstan-3,17-dione	3.20		
Epi-Testosterone	<2.20		
Aldosterone	4.50	2.5	<0.01
Hydrocortisone	<0.20		
Progesterone	<0.20		<0.01
17-OH-Progesterone			<0.01
Prognenolone			<0.01
Estradiol	<2.20		
Epiandrosterone		7.5	
Dehydroepiandrosterone (DHEA)	<0.02	100	<0.01
Androstenedione	<0.03		
Danazol	<0.08		
Estradiol-17β (E_2)			100
Estrone			14.00
Estriol			5.00
Cortisol			0.01
Deoxycorticosterone			<0.01
Corticosterone			<0.01
Cortisone			<0.01
Testosterone (T)	100	0.08	<0.01

5.2.6.2 SOLVENT DESTILLATION

ACS reagent quality dichloromethane (Methylene-chloride) and ethyl acetate was distilled within 24 hours of use, using a standard distillation apparatus (distillation flask, condenser, heater, collection vessel). The first and the last 50mls were discarded. For dichloromethane, a Variac controlling the heater was set at 45°C. For ethyl acetate it was set at 70-75°C. Iso-octane (2,2,4 trimethylpentane) and chloroform can not be distilled due to extreme

inflammability, so I used nanograde quality only (Mallinckrodt). Distilled solvents were stored in the dark until use to avoid peroxide formation.

5.2.6.3 PREPARATION OF PLASMA SAMPLES AND EXTRACTION OF STEROIDS

Plasma samples were defrosted and transferred to glass centrifugation vials, after the exact amount of plasma had been measured (ranging between 50-100µl). All samples were brought to the same volume (400µl) and refrigerated overnight at 4°C with 20µl of each tritiated steroid (T, DHEA, E_2) to allow hot steroids to equilibrate with plasma lipids and binding proteins. Two aliquotes of each labelled steroid were pipetted into scintillation vials directly, scintillation fluid was added and stored in the dark until counting to determine the total amount of radioactivity added to the extraction tubes.

Samples were extracted once with redistilled dichloromethane in fridge overnight. The organic phase was decanted in a new vial and dried under a stream of nitrogen at 40°C.

5.2.6.4 CHROMATOGRAPHY ON CELITE COLUMNS

For columns only a doublewater trap and pure propyleneglycol in glycol phase (no ethylene glycol) were used. Extracted steriods were separated with diatomaceous earth (celite) short columns following Soma & Wingfield (2001) modified by Hau et al. (in press). The columns were prepared the preceding day by packing 5ml serological pipettes first with a 0.8 ml 'water trap' made of a water-celite-mixture (1:3, volume : weight [v:w]) and then with a 0.6 ml pure glycol phase consisting of a propylene glycol*-celite mixture (3:6, v:w). Before packing, a glass bead was placed at the bottom of each column to avoid leaking of the celite from the columns. The water trap prevents glycols from leaving the columns when using high concentrations of polar solvents. Finally the columns were wetted once with 4ml of isooctane.

The dried extracts were re-dissolved with 0.5 ml of 10% freshly redistilled ethyl acetate in isooctane and loaded onto columns. Then the columns were washed again with 2.5 ml 10% ethyl acetate in isooctane. Now the steroids were separated on the basis of their polarity by eluting columns with 2.0 resp. 2.5 ml increasing concentrations of ethyl acetate (EA) in isooctane. The sequence of steroids in the fractions was: DHEA (20% EA), T (40% EA) and E_2 (50%

*[propylene glycol: 1,2 propanediol]

EA). All fractions were dried under a stream of nitrogen at 40°C and re-dissolved in 550µl PBSG.

5.2.6.5 RADIOIMMUNOASSAY

A standard curve was established by serial dilution of a stock standard solution with a concentration range of standard hormone duplicate. Three triplicate assay control vials were set up. (A) The total count comprised 200µl assay buffer, 100µl tritiated steroid and 100µl of the respective antibody. These tubes represent the total counts added to the assay system (no dextran-coated charcoal was later added to these tubes). (B) The non-specific binding control consists of 200µl assay buffer and 100µl of the respective tritiated steroid. It represented the residual free counts not absorbed by charcoal. (C) Maximum binding was the same as total count, except that charcoal was later added.

Aliquots (100µl) of the corresponding sample fraction were transferred to glass vials. First the respective antiserum (100 µl) was added to the standard curve, to controls (except non-specific binding) and to aliquots of samples. After 30 min 5000dpm of the respective tritiated hormone label was added and samples incubated overnight at 4°C.

Free steroids were separated from the bound fraction by adding 550µl dextran-coated charcoal to all tubes, except for total count, to which 550µl assay buffer was added. After12 minutes incubation with charcoal samples were spun (10 minutes, 4°C, 2000ppm). The aqueous part was decanted in scintillation vials, vortexed and counted (Counter: Packard Tri-Carb 2100 TR) to an accuracy of 2% to estimate individual extraction recoveries.

5.2.6.6 DATA CALCULATION

Standard curves and samples concentrations were calculated with a personally (Prof. Dr. Martin Wikelski) prepared Excel 2000 spreadsheet, comparable to the commonly used Immunofit 3.0 (Beckman Inc.), using a four parameter logistic curve fit **$(y=[a-d]/[1+\{x/c\}^b]+d)$**. The lower detection limit of the standard curves was determined as the first value outside the 95 confidence interval for the zero standard (B_{max}). Lower detection limits for androgens and oestrogen ranged from 0.025 to 0.043 ng/ml. For all statistical analyses, non-detectable values were assumed to be equivalent to these minimum detectable values, thus giving a conservative estimate of hormone levels.

Water blanks were always below the lower detection limit. The inacurracy of the assays was below 5 %. Intra-assay variation is typically below 8% for all assays. Inter-assay variation for all hormonal assays ranged between 2.8% and 3.5%.

5.2.7 STATISTICAL ANALYSES AND DATA PRESENTATION

For statistical analyses I used Systat 9.2 (Systat Software Inc., Richmond, CA), additional SSS (Rubisoft Software). E_2 concentrations ranged below the detection limit for nearly all samples, thus E_2 was excluded from all further analyses.

All data were tested for normality (Kolgomorov-Smirnov Lilliefors test) and equality of variances (Levine test). Data that passed these tests were analysed using conventional parametric statistical tests. Data that did not pass these tests were analysed using robust rank order tests following Siegel & Castellan 1988 (see also Lozan & Kausch 1998).

In the analyses of plasma androgen level of canary-raised house sparrows, producing tours (ca-sin) or not (ca-nosin), I included the (transformed) data of control- and testo-implanted birds as baselines and untreated wild birds as a control. In this case the ANOVA was combined with Bonferroni adjusted post hoc comparisons. The significance level was set to $\alpha = 0.05$ and p-values were for two tailed tests. For multiple comparisons (Lamprecht 1999) the significance level α was adjusted following the sequential Bonferroni (sequ. Bonf.) method (Rice 1989).

5.3 RESULTS

5.3.1 EXPERIMENTAL ALTERATION OF PLASMA STEROIDS

5.3.1.1 BODY MEASURES: BODY AND GONAD WEIGHT

Data show, that nearly all birds lost weight within the first week but regained weight again up to the start of the experiment and remained nearly stable until implantation, which caused a slight decrease in all birds. Birds of different groups did not differ in their body weight (one-way ANOVA, $F_{2,24} = 0.82$, $p = 0.45$) (Fig. 5.1).

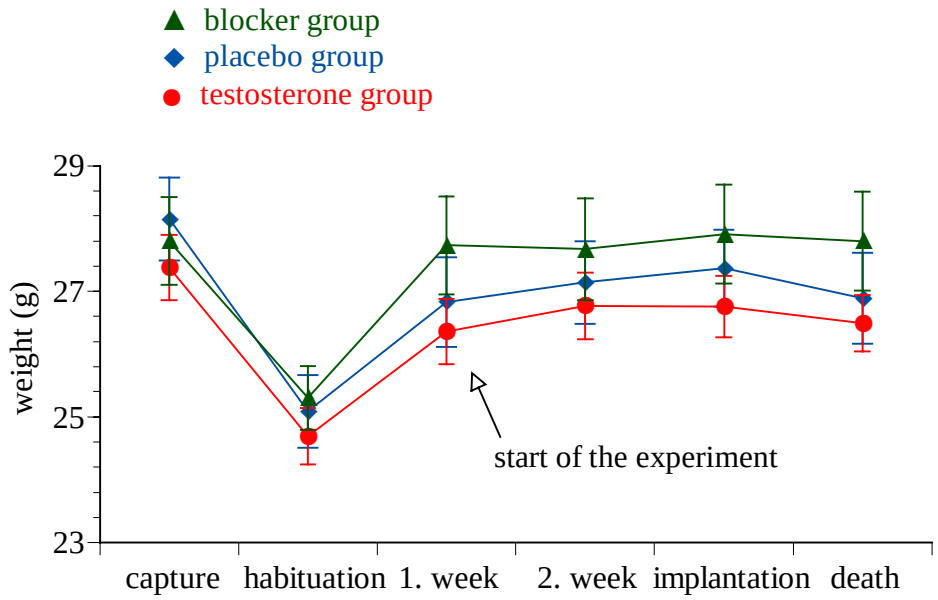


Fig. 5.1: Body weight [g] of wild house sparrows during two weeks of habituation and the experiment (1st week - death). Each symbol indicates mean ± sem for 9 males. Details concerning the groups see 5.2.2 implantation of the pellets.

All birds were in full reproductive state, indicated by a completely black bill and large gonads (see chapter 1). Birds of different groups did not differ in gonad weight (one-way ANOVA, $F_{2,24} = 0.61$, $p = 0.55$) (data are given in Table 5.3).

Table 5.3: Weight (g) of left and right gonads of wild-caught house sparrows after one week of the implantation of placebo-, testosterone or Fadrazole + Flutamide pellets. Each group contains 9 males randomly assigned before the start of the experiment.

Gonad	**Placebo**	**Testosterone**	**Fadrazole+Flutamide**
Left (mean ± sem)	0.22 ± 0.02	0.20 ± 0.02	0.23 ± 0.01
right (mean ± sem)	0.22 ± 0.02	0.21 ± 0.02	0.23 ± 0.02

5.3.1.2 VOCALIZATION OF WILD-CAUGHT MALE HOUSE SPARROWS

There was no canary-like tour in any of the tape recordings. The individuals of the different groups did not differ in their singing rate neither before nor after implantation (repeated measures ANOVA, $F_{2,24} = 0.06$ $p = 0.94$). Despite treatment with different pellets in no group a significant change in singing behaviour could be detected (repeated measures ANOVA, $F_{1,24} = 1.02$, $p = 0.32$). There was also no interaction between groups and time of implantation (before or after) (repeated measures ANOVA, $F_{2,24} = 0.12$, $p = 0.89$) (see Fig. 5.2).

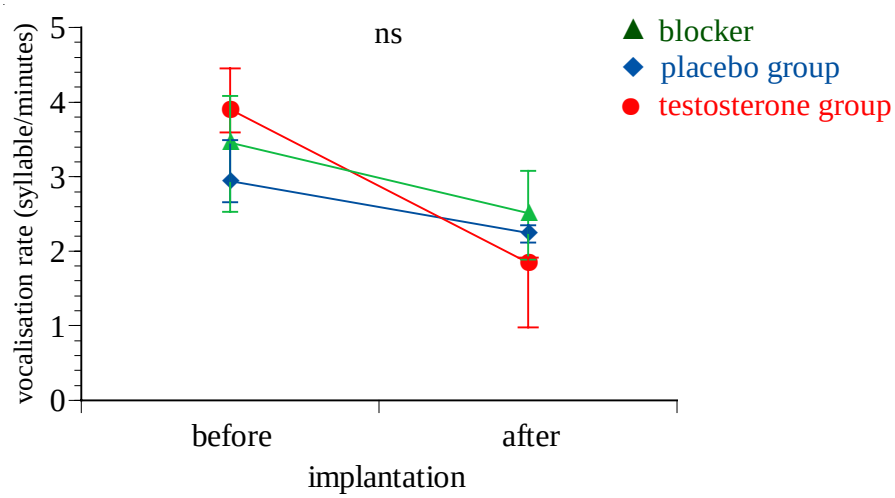


Fig. 5.2: Vocalization rate of wild house sparrows before and after implantation of the placebo, testosterone-, or Flutamide + Fadrazole (blocking) pellets respectively. Each symbol stands for 9 males. Data had been ln-transformed for the statistical analyses (details see text) and are now presented as back-transformed means ± sem; 'ns' stands for not significant differences.

5.3.1.3 STEROID HORMONE LEVEL

The concentrations of plasma testosterone did not differ between first and second week, thus for further analysis I used the mean of both weeks (T12 = before implantation).

Birds with testosterone pellets had significantly higher testosterone-levels after the implantation than before (robust rank test, $U = -3.48$, $p << 0.001$, sequ. Bonf. post hoc $\alpha = 0.016$). There were no significant difference in the placebo group between T12 and treatment (robust rank test, $U = -0.041$, $p > 0.05$, sequ. Bonf. post hoc $\alpha = 0.05$) and in the blocker group between T12 and treatment (robust rank test, $U = -0.087$, $p > 0.05$, sequ. Bonf. post hoc $\alpha = 0.025$) (Fig. 5.3a)

The concentrations of plasma DHEA did not differ between first and second week, thus for further analysis I used the mean of both weeks (DHEA12 = before implantation).

There was no significant difference in the placebo group between DHEA12 and treatment (robust rank test, $U = 1.90$, $p > 0.05$ sequ. Bonf. post hoc $\alpha = 0.05$). Also, DHEA levels did not differ before and after implantation in the blocking group ($U = -0.098$, $p > 0.05$, sequ. Bonf. post hoc $\alpha = 0.016$) or in the testosterone group (robust rank test, $U = 0.25$, $p > 0.05$ sequ. Bonf. post hoc $\alpha = 0.025$) (Fig. 5.4).

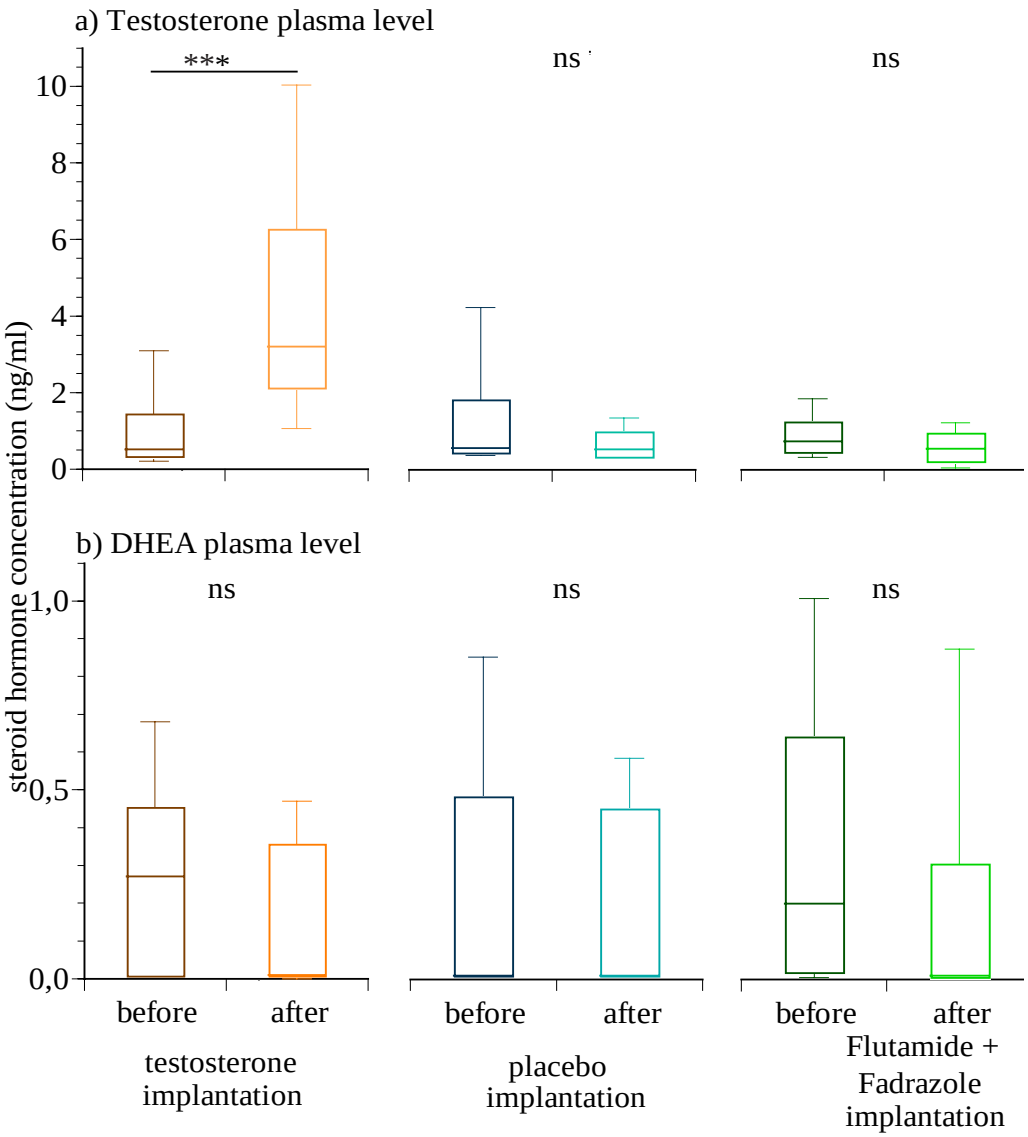


Fig. 5.3: Testosterone (a) and DHEA (b) plasma level of wild-caught male house sparrows before and after implantation of testosterone-, placebo, and Flutamide+Fadrazole pellets. Data are presented as box plots showing median, 1st and 3rd quartiles, minimum and maximum. Data were tested by robust rank test, $p < 0.001$ is indicated by ***, $p > 0.05$ is indicated by 'ns' and represents non-significant differences.

5.3.2 COMPARISON OF STEROID HORMONE LEVELS OF CANARY-REARED AND WILD-CAUGHT HOUSE SPARROWS

The groups differ significantly in plasma testosterone levels (one-way ANOVA, $F_{4,51} = 7.50$, $p << 0.001$). Bonferroni adjusted *post hoc* comparisons (values of *post hoc* probabilities are given in Table 5.5) revealed that testosterone-implanted birds had significantly higher testosterone levels than all other groups, who did not differ significantly from each other (see Fig. 5.4).

Table 5.5: Matrix of pairwise comparison probabilities (Systat output style) for Bonferroni adjusted comparison of testosterone plasma level. For one-way ANOVA analysis I used transformed testosterone (T) data: T_{ln} = ln(sqrt(T))+3.

	placebo	**testosterone**	**ca-nosin**	**ca-sin**	**wild**
placebo	1.000				
testosterone	**0.002**	1.000			
ca-nosin	1.000	**0.001**	1.000		
ca-sin	1.000	**0.012**	1.000	1.000	
wild	1.000	**0.0001**	0.883	0.407	1.000

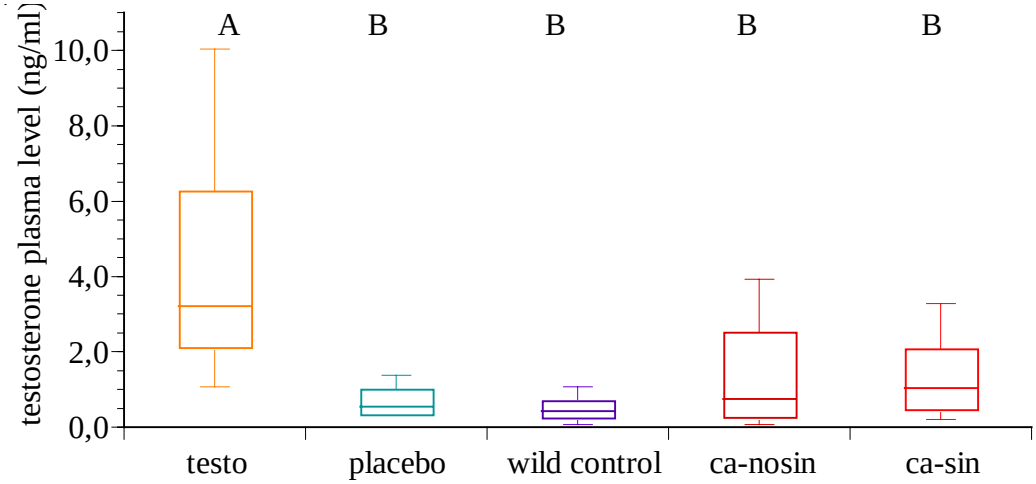


Fig. 5.4 : Testosterone plasma level in male house sparrows. Wild-caught birds were testo- and placebo-group, each with an implant, and the wild control without an implant. Ca-sin and ca-nosin were canary-raised sparrows either singing tours or not. Data are presented as box plots showing median, 1st and 3rd quartiles, minimum and maximum for a better comparison with data of the implantation experiment.
Similar letters above boxes represent non-significant different medians from *post hoc* multiple comparisons (pairwise comparison probabilities see Table 5.5).

Groups differed significantly in plasma DHEA levels (one-way ANOVA, n = 56, $F_{3,52}$ = 14.05, p << 0.001). Bonferroni adjusted *post hoc* comparisons (*post hoc* probabilities see Table 5.6) revealed that there is no significant difference in DHEA plasma levels between placebo and testosterone-implanted birds, nor between wild and both canary-raised groups, i.e. ca-sin and ca-nosin. Both placebo- and testosterone implanted birds had significantly lower DHEA levels than wild and canary-raised birds (see Fig. 5.5).

Table 5.6: Matrix of pairwise comparison probabilities for Bonferroni adjusted comparison of DHEA plasma level. For one-way ANOVA analysis I used transformed DHEA data: $DHEA_{exp}$ = exp(sqrt(DHEA)).

	placebo	**testosterone**	**ca-nosin**	**ca-sin**	**wild**
placebo	1.000				
testosterone	1.000	1.000			
ca-nosin	**0.0000034**	**0.003**	1.000		
ca-sin	**0.0002**	**0.035**	1.000	1.000	
wild	**0.001**	**0.049**	1.000	1.000	1.000

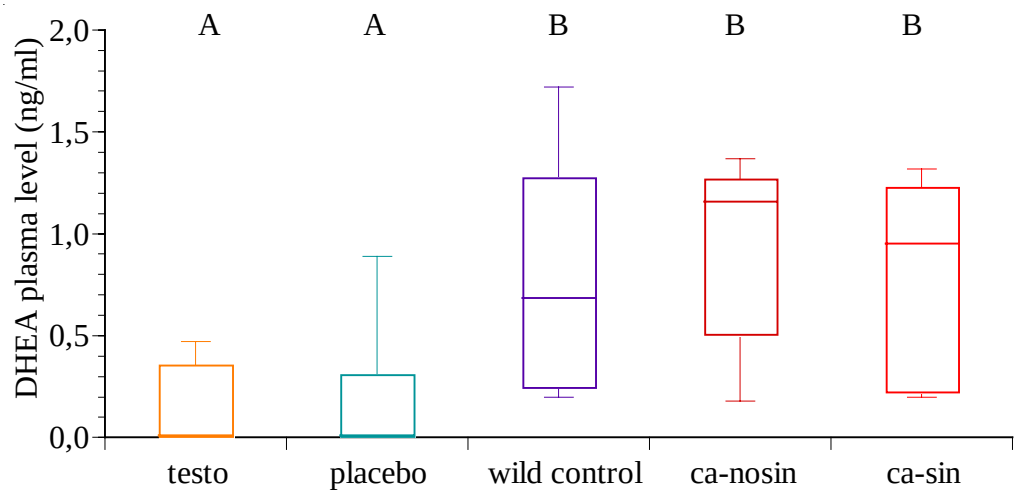


Fig. 5.5: DHEA plasma level in male house sparrows. Wild-caught birds were testo- and placebo-group, each with an implant, and the wild control without an implant. Ca-sin and ca-nosin are canary-raised sparrows either singing tours or not. Data are presented as box plots showing median, 1st and 3rd quartiles, minimum and maximum for a better comparison with data of the implantation experiment. Similar letters above boxes represent non-significant different medians from *post hoc* multiple comparisons (pairwise comparison probabilities see Table 5.6).

5.4 DISCUSSION

5.4.1 TESTOSTERONE

The „blocker group“ is the only one showing at least a short behavioural change in singing activity within the first two days after implantation. The change might result from the fact that these birds received two pellets (instead of one in the other groups) resulting in a longer handling time. Indeed there was no detectable difference in singing activity between birds with testosterone, placebo or blocking implants.

Testosterone-treated house sparrows did not produce ‘spontaneous’ tours as female canaries and starlings do. Even if wild house sparrows may have memorized trills from foreign species

they did not produce them under experimentally elevated testosterone-levels. Whether the sparrows did not memorize foreign songs or whether males differ in mechanisms from females (what might be most probable) can not be decided from this experiment.

Adult male canaries, for example, respond to changing testosterone levels with changes in singing activity and song architecture (Heid et al. 1985). The house sparrows did not react with an increase in singing activity (amount of singing) or song rate (syllables per time) to experimentally elevated plasma testosterone levels only. In European starlings activities like singing were not significantly different between testosterone-implanted and control males (Gwinner & Gwinner 1994) when separated from females, but their singing activity is significantly higher during female presence (Eens et al. 1993). The reason suggested for that is that starlings are hole-nesting songbirds (Pinxten et al. 1989; Pinxten & Eens 1990) in which occupancy of a nest hole is the most important initial step for mating (Eens et al. 1993; Gwinner 1997). In house sparrows, too, holding of a nest site appears to be the key to pair formation. The male announces his ownership of a nest site by regular calling, thereby attracting females. If a female approaches, the calling rate speeds up considerably and the male displays with his wings (Summers-Smith 1988). Given that singing proclaims nest site ownership and attracts mates prior to physical sexual contact, and that female presence increases singing activity and song rate, it can be concluded that song produced in a context unrelated to female courtship is not, but courtship singing is controlled by plasma testosterone (Pinxten et al. 2002). This means that a possible 'accidental' tour production might occur more likely in the presence of females. But I kept my canary-raised males separated from other house sparrows to avoid learning from conspecifics. Thus while tape recording the canary-like singing house sparrows, and consequently also the birds in the hormone experiment, were separated from females. Although ca-sin (canary-like tour singing house sparrows) stayed in a non-courtship situation and had low testosterone levels, they produced canary-like tours. This, together with the findings about plasma testosterone level, makes a purely hormonal explanation of tour singing in canary-raised house sparrows unsatisfying; indeed the hypothesis of neuro-anatomical differences between ca-sin and ca-nosin based on learning (or not) a complex temporal pattern is favoured. In conclusion tours are not suggested to be produced just by elevated plasma testosterone levels, but had to be learned.

5.4.2 DHEA

It is a surprising result that birds of the placebo- and testosterone-group had significantly lower DHEA-levels than the house sparrows of the song study.

DHEA can act either as a precursor for testosterone or offer protective compensatory mechanisms to counteract stress (Kroboth et al. 1999). In humans, for example, serious illness lowered plasma DHEA-level, while acute stress of exercise (e.g. Diamond et al. 1995) and chronic stress (Bernton et al. 1995) resulted in an acute increase in DHEA concentrations. No increase of DHEA was observed in the cerebral cortex of rats accustomed to being handled for 1 min after CO_2 inhalation or a 5-min foot shock (Barbaccia et al. 1994); but 2 days after the heavy stress of adrenalectomy or a corresponding sham-operation DHEA-S[1] increased in the brain (Corpéchot et al. 1981). This leads to the conclusion that the sparrows of the song study faced severe stress for a longer time.

Holding conditions – including temperature, food quality, food availability, day length – were exactly the same for the experimental groups and for the birds of the song study. But sparrows of the hormone study were caged in living rooms, while the birds of the song study were kept for 2.5 days in a sound-proof chamber (see chapter 4) to determine their behavioural and neuronal (IEG[2]) reaction to hetero- and species-specific vocalizations.

Wild caught birds from the sound-proof chamber had significantly higher DHEA-levels than both placebo and T-implanted sparrows. Both canary-raised and wild-caught sparrows showed strong locomotion activities in response to playbacks, but they did not differ in DHEA-levels from silence-, nor noise-controls who mainly did not move in their cages. This suggests that an elevated DHEA level is not caused by high locomotive activities or acoustic presentations, but relates to keeping conditions (reduced echoes, smaller cages, lack of social partners) in sound-proof chambers. Neither in autumn nor in spring birds Soma et al. (2001) found increased DHEA-levels after capture, independent of handling time (10 and 30 minutes); they concluded that stress does not increase plasma DHEA in song sparrows. It may be that their song sparrows only suffered from „low stress“ during capture and handling for a relative short time (30 minutes),

[1] DHEA-S: DHEA with a reversibly conjugated sulfate group (Lavallee et al. 1996; Luu-The et al. 1996)

[2] IEG: immediate early gene. This experiment is a continuation of this thesis. It was done just before the birds were killed to study brain anatomy. Some details are given in chapter 4.

while my house sparrows suffered from a longer lasting (2.5 days) more severe stress. My study seems to provide the first evidence for a bird that differences in stress result in differences in DHEA response.

6 SONG PRODUCTION AND FUNCTIONAL MORPHOLOGY

6.1 INTRODUCTION

Any biological trait may evolve under the influence of a variety of selective forces, and often these selective forces act in opposition; this is especially important in vocal communication systems (Ryan & Brenowitz 1985). While Greenewalt (1968), based on the two-voice theory, argued that the vocal tract plays no role in song production, the importance of the vocal tract became more and more obvious (Nowicki & Marler 1988) during the last decade. Nowicki's (1987) study with song sparrows, *Melospiza melodia*, singing in a helium atmosphere provided a clear demonstration that the vocal tract is involved in song production. Furthermore Westneat et al. (1993) have shown with white-throated sparrows *(Zonotrichia albicollis)* and swamp sparrows *(Melospiza georgiana)* that dynamic changes in beak gape are highly correlated with the acoustic frequency of the sound produced. Sound modification by opening and closing the beak suggests a limiting constraint of body morphology, e.g. beak size and jaw mechanics, on vocal skills, especially when syllables are produced in a rapid sequence like trills and/or include rapid frequency modulations. In Darwin's finches, species with larger beaks and body size have evolved songs with comparatively low rates of syllable repetition and narrow frequency bandwidths while the reverse is true for smaller species (Podos 2001).

Further physiological constraints on the temporal complexity of song arise from respiratory demands. Only a limited volume of air is available for expiration and there is a need for respiratory gas exchange. Abbreviated inspirations similar to canary mini-breaths are prominent song features in all songbird species studied so far, suggesting that the use of mini-breaths is a widespread motor adaptation for singing to replenish the expelled air (Hartley & Suthers 1989; Suthers 1997). Increasing body size most likely limits the maximum possible trill rate, presumably by increasing inertial forces. For example, the highest trill rates for mini-breath syllables are 30/s in canaries, *Serinus canaria* (weight: 18 g) and 16/s in the larger northern cardinal, *Cardinalis cardinalis* (weight 40 g) (Suthers 1997; Suthers & Goller 1997). Above this rate birds use a pulsatile expiration. Thus a conflict between phonetic and temporal complexity is obvious: birds with phonetically complex syllables tend to sing short songs at a moderate pace. Those with temporally complex songs often sing rapid trills that may last many seconds, but often are phonetically less complex. It is also likely that these opposing demands influence the pattern of song organization. Swamp sparrows, *Melospiza georgiana*,

for example, that accurately copied the syllables at the increased rate of the tutor song had to interrupt song in a species-atypical fashion for aspiration (Podos 1996).

The canary song contains sequences comprising rapid repetition of one syllable, called tour (Güttinger 1979); joined tours form song types. House sparrows imitated canary tours, but they did not achieve the length and temporal complexity of song types (details see chapter 3). In this chapter I investigate the possibility that differences in bodily structure may influence the extent to which canary tours and song types can be copied by a sparrow.

6.2 METHODS

6.2.1 ANIMAL SUBJECTS AND TAPE RECORDINGS

All house sparrows and domestic canaries were bred in our institute and kept in cages or aviaries as described in detail in chapter 2. Tape recordings and results are described in chapter 3. All birds were in reproductive state, indicated by a completely black bill and large gonads (gonad weight in captivity-bred sparrow males: n = 59, mean ± sem left side: 0.20 g ± 0.01, mean ± sem right side: 0.20 g ± 0.01). Fresh air was controlled daily.

6.2.2 HISTOLOGY

Fresh syrinxes were weighed immediately after perfusion on a Sartorius balance (Sartorius Basic, BA 110s, Sartorius, Germany, 0.0001g). After perfusion and postfixation (1h) in FPBS, total syrinxes passed through 70%, 80%, 90%, 100% (2x) ethanol, 100% ethanol + amylacetat (1:1), 100% amylacetat (2x), amylacetat + paraffine (1:1) and double embedding in paraffine. After 72 hrs sections of 7 µm were cut in widthwise direction and fixed on the slides with a filtered egg white-glycerine solution. Slides passed through 100%, 90%, 80%, 70%, H_20 (2x), were stained in 'Mayer's haemalum' (Kiernan 1999) solution, washed under running water, overstained with 0.2% eosine in 50% alcohol, and passed though 70%, 80%, 90%, 100% ethanol (2x) and finally xylol (2x). Then slides were coverslipped by embedding in Roth-Histokitt.

6.2.3 MEASUREMENTS

Syrinxes of three canary-raised birds were weighed on a precision balance. All three males had large gonads, indicative of breeding state. Syrinx slices were visualized using a light microscope (Leitz Aristoplan) combined with a video camera (spot insight, visitron systems). Measurements were done by using an image analysis system (Metamorph 4.6, Visitron,

Germany). Data were automatically exported into a prepared sheet of Excel 2000 (PC, Microsoft office). For volume measurements the periphery of each bronchus was drawn on digitised images and the area was calculated by a built-in function of the software (Metamorph). The volume of each bronchus was then calculated parallel to HVc volume (see chapter 4): Σ'measured areas' x slice thickness (7 µm) x interval between section (56 µm) (Gahr & Garcia-Segura 1996).

Birds were weighed alive (Kern 440-33, Germany, max. 120 g, d = 0.01 g), but body measures were taken after perfusion. In this analysis I included the 59 captivity-bred house sparrows (both canary- and sparrow-raised) whom I used for song and brain analyses, except males killed in January.

6.2.4 STATISTICAL ANALYSES

For statistical analyses I used Systat 9.2 (Systat Software Inc., Richmond, CA). First, all data were tested for normal distribution (Kolgomorov-Smirnov Lilliefors test) and equality of variances (Levine test). In normally distributed data sets with equal variances I used the parametric t-test. All tests are two-tailed and the significance level was $p = 0.05$. Usage of statistical tests followed Conover (1980), Sokal & Rohlfs (2000) and Lamprecht (1999). If multiple analyses were conducted with the same data sets (body measures) the significance level α was adjusted following the sequential Bonferroni Method (Rice 1989).

6.3 RESULTS

6.3.1 SYRINX MEASURES

6.3.1.1 SYRINX WEIGHT

The median of house sparrow syrinx weight was 0.025g (n = 3; min: 0.0215g , max: 0.0249g). Comparisons with data from literature (see Table 6.1) show, that syrinx weight of different species is very similar.

Table 6.1: Wet weight (g) of passerine syrinxes from the literature and from my house sparrows.

species	weight (g)	reference
house sparrow	0.025	Salwiczek
domestic canary	0.026 ± 0.005	Johnston & Bottjer 1995
wild canary	0.023 ± 0.006	Leitner 1999
zebra finch	0.026 ± 0.005	Lohmann 1997 cited by Leitner 1999

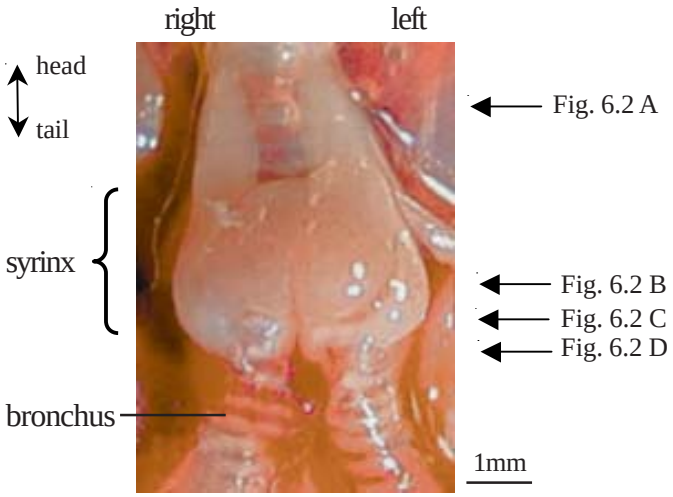


Fig. 6.1: Syrinx of a male house sparrow during the breeding season, ventral view. Arrows on the right side indicate sections presented in Fig. 6.2 (see below). For more details see chapter 1.

6.3.1.2 ASYMMETRY

In my house sparrows the left syrinx was slightly larger than the right one (Fig. 6.2). The syrinx asymmetry, calculated as bronchus volume of the left side divided by volume of the right side, was determined for two sparrows and revealed a median of 1.06. Also canaries (n = 5) possess a slightly larger left than right bronchus (median: 1.12, minimum: 1.08, maximum: 1.21; data were kindly offered by Prof. Dr. Manfred Gahr). Thus syrinx asymmetry in house sparrows tend to be smaller than in canaries.

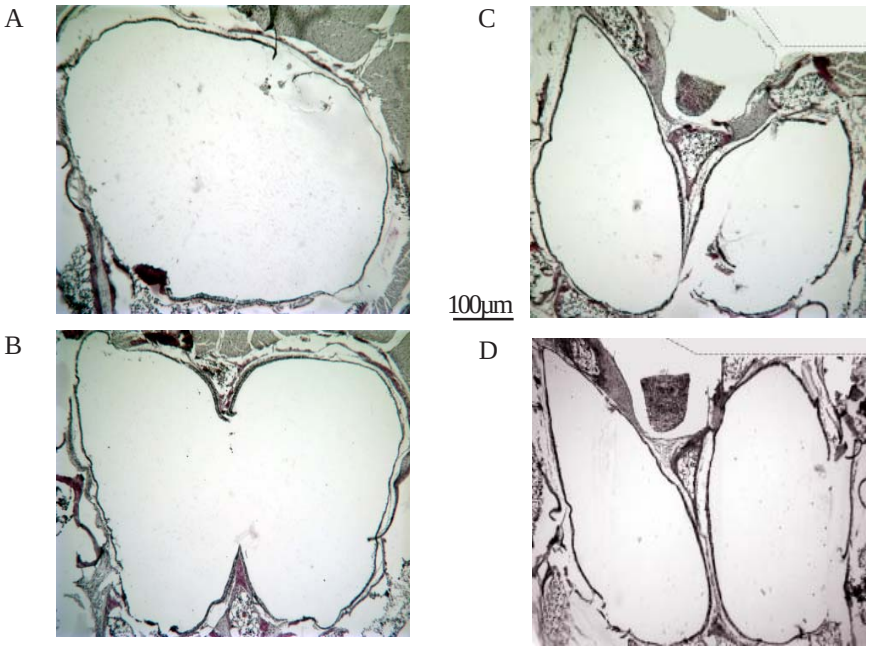


Fig. 6.2: Representative cross sections of a house sparrow syrinx. A) larynx, about 700µm cranial of the syrinx; B) 70 µm cranial, where trachea divides into two separate bronchi; C) first section with completely separated bronchi; D) 70 µm caudal from C. Locations of cross sections are also indicated in Fig. 6.1.

6.3.2 BODY MEASURES

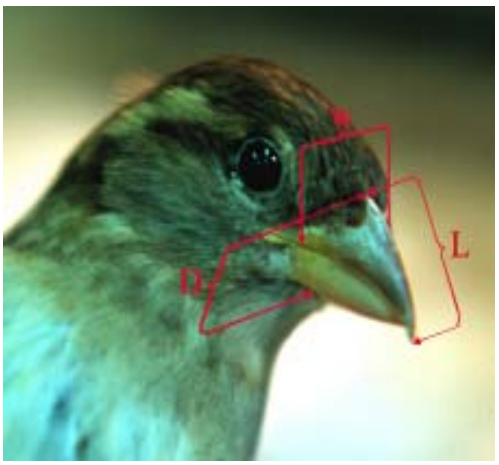


Fig 6.3: Measuring distances following Leisler & Winkler (1991).
L: beak length
D: beak depth
W: beak width

(for this picture I deliberately chose a female, because in males the outline of the black beak fuses with the black bib feathers).

House sparrows did not differ significantly from canaries in tarsus length (separate variance t = 0.80, df = 107, p = 0.43, Bonferroni $\alpha = 0.05$). But house sparrows are significantly heavier than canaries (separate variance t = -1.55, df = 106.6, $p << 0.001$, Bonferroni $\alpha = 0.01$), and they posses larger beaks based on length (separate variance t = -28.55, df = 106.8, $p << 0.001$, Bonferroni $\alpha = 0.013$), depth (pooled variance t = -3.47 df = 107, p = 0.0008, Bonferroni $\alpha = 0.016$) and width (pooled variance t = -8.22 df = 107, $p << 0.001$, Bonferroni $\alpha = 0.025$).

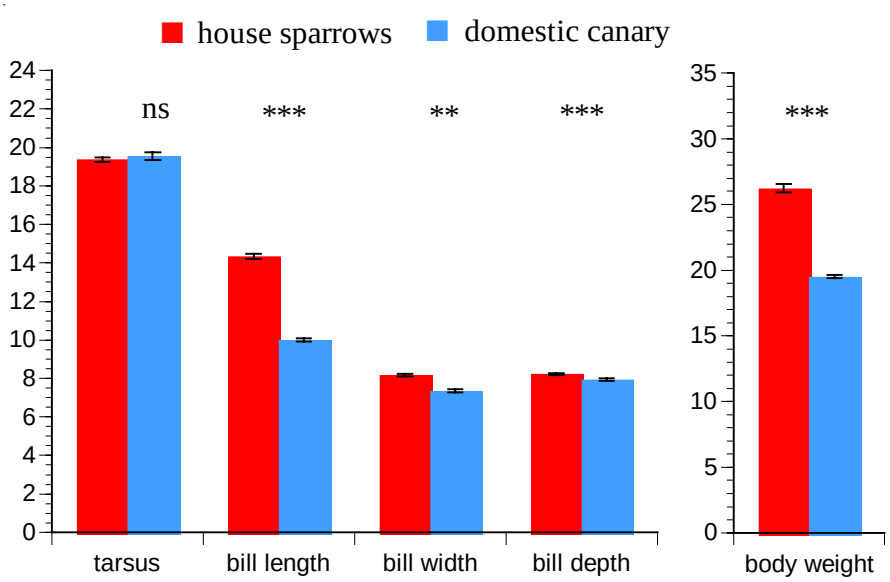


Fig 6.4: Body measures of captivity-reared house sparrows (n = 59) and male canaries (n = 38). The group of house sparrows consists of the birds of the brain study (n = 41). In the graphs $p<0.001$ is indicated as *** and $p<0.01$ as **; 'ns' stands for not significant differences. Data are provided as mean ± sem. Tarsus, beak length, beak width and beak depth are given in 'mm', body weight in 'g'. Details about the statistics are given in the text.

6.3.3 SONG

Chapter 3 gives a detailed description about vocal skills of canary-reared house sparrows in comparison to their canary tutors. Differences between domestic canaries and ca-sin, which might be influenced by body morphology are:

- sparrow tours were significantly shorter than canary tours (see Fig. 3.12);
- sparrows separated tours by a silent interval larger than silent intervals between syllables within a given tour while canaries did not (see Fig. 3.4);
- sparrows displayed a slower repetition rate at the same frequency bandwidth than canaries did (see Fig. 3.15);
- the same repetition rate in house sparrows resulted in a smaller frequency bandwidth of the syllables than in canaries (see Fig. 3.16);
- and canaries reached a larger maximum repetition rate than sparrows did (canary: 55 Hz; ca-sin: 24.95; see Fig 3.15).

6.3.4 CALCULATING THE SWITCHING POINT BETWEEN THE TWO RESPIRATORY PATTERNS

Data of domestic canary and northern cardinal were taken from Suthers (1999). The line between the two species' body weight in relation to its corresponding upper limit for mini-breaths was used as a reference to calculate the theoretical upper limit of repetition rate, where house sparrows (own and from literature) would have to switch from mini-breaths to pulsatile expiration. I used own data (red) and literature data (green); for the latter I calculated a mean value from the mean of each author (data are given in Table 6.1). Fig. 6.7 suggests a limit for house sparrows at a repetition rate between 22.5 - 25 syllables/seconds. The calculated value is very close to the observed maximum repetition rate of tour singing house sparrows as described in chapter 3, 3.3.3.1 (see Fig. 3.15).

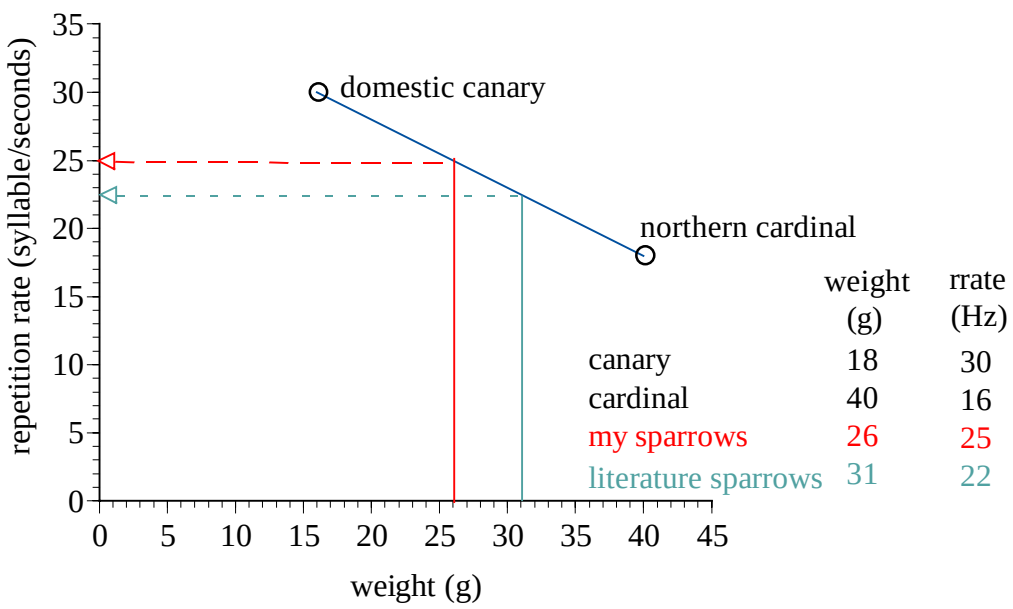


Figure 6.7: Repetition rate, calculated from the data from canaries and cardinals, at which a house sparrow theoretically should switch from mini-breaths to pulsatile expiration. The integrated table gives the data values from Suthers (1999), the mean body weight house sparrows from our aviaries (red) and from literature (green) as well as the respective calculated values for the sparrow's critical repetition rate.

Table 6.1: Body weight (mean - standard error) of house sparrow males from literature.

reference	unit	nr	weight (g)
Baziev 1976	600m	20	28.40 ± 0.32
	1600m	21	28.13 ± 0.37
Folk Et 1970	January	72	30.56 ± 0.28
	February	44	30.48 ± 0.35
	March	67	30.24 ± 0.23
	April	82	31.52 ± 0.21
	May	96	29.37 ± 0.23
	June	39	30.39 ± 0.41
	July	57	29.60 ± 0.34
	August	68	29.81 ± 0.29
	September	60	31.15 ± 0.32
	October	82	30.99 ± 0.20
	November	82	30.39 ± 0.23
	December	69	31.34 ± 0.26
Grimm 1954	Hohenthurm	249	33.68 ± 0.12
	Oppin	69	33.63 ± 0.22
	Passendorf	272	31.81 ± 0.10
	Büschdorf	65	32.68 ± 0.28
Niethammer 1954	Mersch	125	29.51 ± 0.11
	Gereonsweiler	79	28.94 ± 0.94
	Widdendorf	109	30.14 ± 0.10
	Buchholz	95	30.24 ± 0.15
	Schaan	79	30.25 ± 0.17
	Waat	43	29.49 ± 0.14
	Ruhne	35	30.03 ± 0.25
	Eikeloh	85	29.71 ± 0.14

6.4 DISCUSSION

The syrinx weights of house sparrows did not differ from syrinx weights of wild and domestic canaries and of zebra finches. Though syrinx weight allows only a rough estimation of homogeneity of syrinxes - as it does not differentiate between extrinsic and intrinsic muscles (Leitner 1999) - it would suggest that house sparrows are not constrained in sound production by marked muscle deficiencies.

Syrinx weight based largely on muscle mass varies with plasma T-concentration operating within use-disuse changes of muscles (Luine et al. 1980). Castration of adult male zebra finches, for example, is followed by a decrease of syringeal weight to 76% of that of intact animals (Luine et al. 1980). This may be induced by both lower plasma T-level and less singing activity. In contrast to zebra finches, syrinx weight of wild canaries does not vary with changes of gonads - followed by concomitant plasma T-levels during different seasons. In fact wild canary males sing throughout the year except for the short period of moult (Leitner 1999). House

sparrows' pair formation often begins in autumn (Schifferli 1974) which comes along with already increased gonads and increased singing behaviour during late autumn and winter (Hegner & Wingfield 1986a,b). Both autumnal gonads and singing behaviour suggest that house sparrows' syrinx weight would also not differ significantly between breeding season and autumn. This goes in line with my finding that Ramses produced canary-like tours during autumn (see chapter 3). In sum, from the similarity of syrinx morphology between canary tutors and their house sparrow pupils it is reasonable to assume that the observed loss of repetition rate and frequency bandwidth is based on other causes.

Syringeal asymmetries are prominent in some non-passerines (King 1989; Suthers 1994), but are less evident among passerines. In some species the right side is slightly smaller (Luine et al. 1980) and frequency ranges of left and right syrinx differ (Suthers 1999). Also in house sparrows the right bronchus seems to be smaller in volume than the left one, suggesting slightly different frequency ranges. Different dimensions of the bronchi (relative asymmetry) may be taken as an indication for the surface areas available for attachment of muscles (as shown for the skull; Johnston 1976). Thus the relatively high symmetry of house sparrow bronchi may suggests a comparable high symmetry of right and left muscles, and in turn a more bilateral usage of the syrinx instead of the unilateral functional dominance in the canaries.

The song analyses revealed that my house sparrows' songs end up deficient in maximum repetition rate and in frequency bandwidth in relation to a given repetition rate compared to their canary song models. One might assume that other reasons (e.g. acoustics of the room, recording conditions, etc) than brain deficiencies or body morphology might have led to this loss. In chapter 2 and 3 (see e.g. 3.2.1 animal subject) I mentioned that my canary-reared sparrows were caged if possible together with a male canary foster sibling. The song of these canary young were not analysed and described in detail because literature search did not reveal any indication that house sparrows might copy songs from (con- or heterospecific) siblings (for examples about copied tutors see Appendix 2). However, I tape-recorded two of the canary foster siblings and looked through the tapes. There was no indication that they differed from their canary tutors, but seemed to copy them precisely (one example is given in Fig. 6.5). This in turn favours the idea that house sparrows' imitation ability suffers either from their brain- and/or from vocal tract morphology.

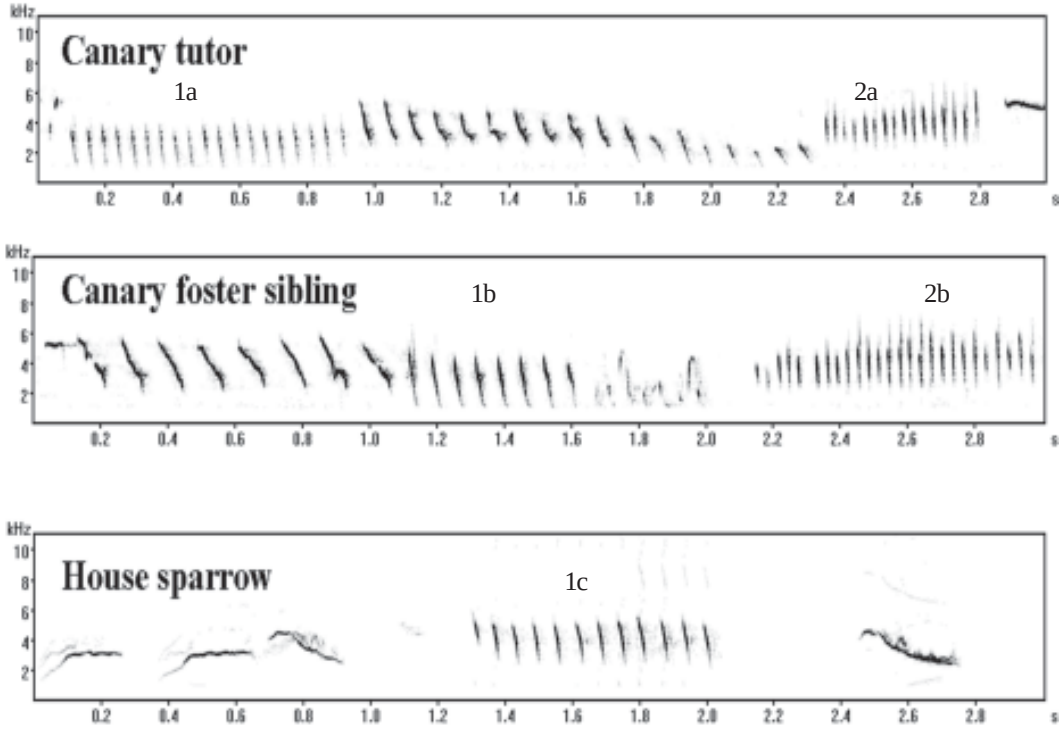


Fig. 6.5: Sonagrams of canary tutor, canary foster sibling and a ca-sin. Presented in the digital spectrogram are song sections of the same length, which contain similar tours. Tours of the following comparisons are indicated by numbers and respective letters:
1a-1c: tour sung by the tutor and both pupils. The house sparrow sang it at a higher sound frequency; the time pattern is imitated accurately.
2a-2b: a tour with a high repetition rate, sung by canary tutor and canary pupil. This tour was produced with a very high repetition rate. The canary foster sibling copied it precisly while the sparrow did not (for details about repetition rates see chapter 3).

The avian jaw apparatus is part of the feeding system (McLalland 1980), thus mechanisms of jaw function and movement patterns as well as functional analysis of beak shape in birds have mostly been correlated to food composition (functional morphology of feeding, Bock 1966; Bairlein & Gwinner 1994; for further references see Hoese & Westneat 1996). Beak length might be one of the most important variables affecting foraging (Johnston 1976). In house sparrows beak length shows seasonal variations as it does in many other birds that are largely granivorous in the winter and insectivorous in the summer; this is due to variation in rate of wear experienced by the constantly growing horny tip (Clancey 1948; Davis 1954; Selander 1958). House sparrow's beak length variation between seasons ranges from 3.5% (Davis 1954) to 12% (Steinbacher 1952) (see Table6.2). However, the length of the canary beak only reaches about 70% (in mean) of the house sparrow beak (see Fig. 6.4). This difference

Table 6.2: Measures of males' beak during different seasons from the literature

reference	unit	nr	beak length (mm)	beak width (mm)
Davis 1954[1]	Winter Berkeley	12	9.29 ± 0.10	
	Summer Berkeley	14	9.69 ± 0.10	
	Winter Pasadena	15	9.41 ± 0.13	
	Summer Pasadena	14	9.97 ± 0.11	
Lack 1940[2]	England	122	9.28 ± 0.37	8.69 ± 0.35
	Germany	35	9.44 ± 0.36	8.86 ± 0.26
	Eastern states	109	9.44 ± 0.44	8.73 ± 0.30
	mid-western states	79	9.51 ± 0.44	8.87 ± 0.28
	Berkely Calif.	91	9.37 ± 0.40	8.74 ± 0.29
	Southern Calif.	70	9.70 ± 0.54	8.93 ± 0.31
	Honolulu	14	9.82 ± 0.30	8.71 ± 0.32
Steinbacher	Janary	14	12.60	
1952[3]	February	8	15.80	
	March	36	12.60	
	April	32	12.60	
	May	33	12.60	
	June	51	13.60	
	July	42	13.80	
	August	33	13.70	
	September	24	13.20	
	October	11	12.60	
	November	15	12.40	
	December	14	12.30	
Packard	August	7	9.44	
1967[4]	October	9	9.04	

[1] beak length: anterior edge of the nostril to the tip, mean - standard error
[2] beak length: the culmen from the nostril to the tip of the beak , mean - standard deviation
[3] in the cited reference data are only available as a figure; beak length: the culmen from the nostril to the tip of the bill
[4] anterior margin of the nostril to the tip of the mandible

in beak length between canaries and house sparrows is larger than the within-house sparrow variation of beak length between seasons. Thus any seasonal changes of beak length in house sparrows seemed to be negligible for song differences between the two species.

Passerines have a conically shaped, horny beak. With increasing dimension (in length, width and/or depth) beak mass and correspondingly the moment of inertia will increase during rapid opening and closing movements. House sparrows beaks were significantly larger in all three dimensions (see. Fig. 6.4.). This suggests that house sparrows did not reach repetition rate and frequency bandwidth at the upper edge of canaries' performances because they own larger beaks (in all dimensions) than canaries. However, theoretically a species can accelerate

a larger mass in comparably short time by using more energy i.e. stronger muscles. An increase of selected muscles has already been demonstrated for columbid species: among the jaw muscles, *M. pterygoideus* plays a profound role in closing the beak. In species that peck seeds and grains from the ground, this muscle is of comparatively simpler structure than it is in species who pluck off large-sized fruits from the lofty tree-branches and grasp them with considerable force before swallowing. The force produced by the muscle during closure of the beak is much greater in the latter than in the former species (Bhattacharyya 1997). In birds with prizing movements (Lorenz 1949; Beecher 1951; Wickler 1961; Neweklowsky 1972) however I would suggest that muscles for jaw opening may be particularly strong (see also Stresemann 1934). Podos (2001) who studied Darwin finches, however suggests an intrinsic trade-off in jaw biomechanics between maximal force and velocity. But whether this intrinsic trade-off also holds true for comparisons between less closely related species, like canaries and house sparrows, remains an open question. Whether house sparrows, having significantly larger bodies than canaries (see Fig. 6.4), also might posses generally stronger jaw muscles, which may eliminate differences in song performance based on different beak dimensions, is not known. This, however, asks for a comparative analysis of sparrow and canary jaw muscles in relation to beak dimension.

Detailed measurements during singing (Calder 1970; Hartley & Suthers 1989; Suthers & Goller 1997) revealed two different respiratory strategies according to repetition rate (for details see chapter 1, 1.5.2). The limit forcing an individual to switch from mini-breaths to pulsatile expiration is probably determined e.g. by body mass (Hartley & Suthers 1989; Hartley 1990; Goller & Suthers 1996a). Ca-sin produced canary-like tours with a repetition rate reaching the theoretical border where sparrows might be forced by their body mass to switch to pulsative expiration. However, I could not find evidence that they went beyond this limit. This raises several questions like: Why did ca-sin not produce canary-like tours with a repetition rate suggesting pulsatile expiration? Do they switch already at a slower repetition rate to pulsatile expiration? Did sparrows' respiratory strategy force ca-sin to increase the silent interval after a canary-like tour, because they need this pause for a larger inhalation?

To summarize, house sparrows owned syrinxes of comparable weight like canaries and other species, suggesting that syrinx muscles might be not limiting in vocal communication. Sparrows had significantly larger beaks relative to domestic canaries by all three dimension measures

(length, width, depth). Literature suggest that this causes severe performance constraints on vocal tract dynamics in that sparrows may be unable to perform the rapid beak movements necessary for high repetition rates and large frequency bandwidth. Furthermore, house sparrows were larger sized (i.e. body weight) and reached maximum repetition rate at the calculated repetition limit, forcing them to switch from mini-breath to pulsatile expiration; however they did not go (far) beyond this point for unknown reasons. My analysis cannot provide evidence that morphological contraints were the main reason that sparrows could not imitate the canary song properly. However, it made wonder about the limits of vocal imitation in a cross-fostered species singing a hetero-specific song. I thus suggest to clarify first in how far bodily structures cause imitation deficiencies, and only then look for possible neuronal shortcomings.

7 GENERAL DISCUSSION

In song bird literature one can find many and detailed studies about song copying in cross-fostered species (e.g. Broughton et al. 1987; Clayton 1987, 1989; Conrads 1989; Güttinger 1979). However, up to now such studies did not include, or have been followed by, a neuro-endocrinological analysis nor have possible ontogenetic and morphological constraints been taken into account.

Imitating house sparrows are a particularly interesting case because it was „difficult to believe that […] the house sparrow *Passer domesticus* could have been taught […] the tune that [has been] recommended for them“ (Thorpe 1955; for an example, see page III) not to speak of such a complex song as that of the well studied domestic canary; therefore I deliberately chose to study canary-like singing house sparrows. Besides peculiarities and open questions this pilot study is the first to present digital spectrograms of canary-like singing house sparrows. Now I can suggest them to be an ideal model for studying inter-specific song learning in relation to brain morphology, with controlling for possible side effects, e.g. a given raising routine, social interactions, potentially modified androgen levels and morphological constraints.

7.1 PIECING TOGETHER

My cross-fostering experiments showed that Thorpe's scepticism was unjustified. House sparrow males showed an unexpected imitative singing ability, learning canary syllables together with a particular temporal pattern resulting in a canary-like tour[1] with a constant syllable repetition rate. Both the ecological and social environment seemed to influence learning. Vocalizations of young reared by canaries in sound-proof chambers were rare and did not comprise canary tours. Sparrow-raised young did not produce canary syllables or tours either, while canary-raised birds did. Moreover the production of new syllables within a definite time seemed to differ between not learned and learned song sequences according to the type of early interaction with the tutor.

In passerines, male song is the acoustic equivalent of the peacock's tail for which Darwin suggested that it was the result of sexual selection by female choice (Catchpole 1987). Elaborate singing is thought to serve as a honest indicator of male attributes important to

[1] Tour = sequence of rapidly repeated notes/syllables of only one type.

female fitness if the displays are costly enough (Searcy & Yasukawa 1996). Available data suggest that learning more as well as more complex songs (or larger repertoires) is associated with augmented brain regions (e.g. Brenowitz & Kroodsma 1996; Airey & DeVoogd 2000; Airey et al. 2000). The cost of brain space for learned tasks, however, is controversially debated (see Gil & Gahr 2002). The „most elaborate“ singers, i.e sparrows singing canary-like tours, owned a significantly increased HVc thus song in sparrows may indeed function as a „peacock tail“ in mate choice. However the function of sparrows' song has been neglected in favour of sparrow males' black bib; elaborated ornaments such as patches of coloured feathers contrasting with the basic coloration have often been explained on the basis that exaggerated sexual traits (influenced by androgens) act as visual cues to male quality. But findings about male bib's functions are contradictory: bib size seems to correlate positively with dominance in flocks during feeding in winter (Møller 1988; Evans et al. 2000) in some populations, but not in others (Kimball 1996, 1997), and small-bibbed males were not cuckolded more frequently than large-bibbed males (Cordero et al. 1999). It seemed to become obvious that sparrow females select males on the basis of multiple indicators of male condition and genetic quality. In house sparrows these indicators of high male quality may in addition to the ownership of a suitable nest site (Summers-Smith 1988) and ornamentation (i.e. male bib, blackened beak) also include a learned elaborate song display.

Neither singing ability nor singing rate per se (i.e. when singing for their own, outside any social context) seemed to be correlated to elevated plasma testosterone levels in males. A house sparrow might sing a complex temporal structure like a tour also outside the breeding season, when their beak was pale-buff or ivory-coloured (see Fig. 1.1) and brain nuclei were decreased. This however does not wonder taking into account that pair formation in house sparrows often occurs during autumn (Summers-Smith 1963, 1988) and important sexually attractive cues like song features and ornamentations, should then be available.

Within taxonomic families there exist no general correlation between song and syringeal complexity or the capacity to learn song (Baptista & Trail 1992). Vast differences in vocal virtuosity occur e.g. in estrildid finches; it ranges from the simple two-note song of the pictorella finch (*Heteromunia pictorella*) to the elaborate, highly complex song of

the Gouldian finch (*Chloebia gouldia*) (Thorpe 1961; Hall 1962; Immelmann et al. 1965, 1977). Syrinx weight, thought to be a rough indicator for syringeal muscle mass, did not differ between house sparrows and elaborate singers like wild and domestic canaries, suggesting that syrinx is not the eye of needle for elaborate singing. The relatively high symmetry of house sparrow bronchi point to a symmetrical use of left and right syrinx halves, as is known for other species that produce many two-voice syllables (Suthers 1999). The neuronal coding for two-voice syllables is still unknown. They may provide another route towards song complexity instead of temporal structure as in canary tours.

The higher the syllable repetition rate and the longer the song, the more challenging it is to meet both the respiratory and phonatory requirements (Suthers & Goller 1997). The house sparrows may be converting a long canary song type consisting of a sequence of several tours into a series of pulsatile trills interrupted periodically by a mini-breath, resulting in tours, which I suggested to be „multi-note syllables“. Motor constraints will normally play little role in vocal development, as long as birds accurately imitate conspecific song models. Offspring should be physically able to produce the song of their parents. House sparrows' natural song comprises many syllables with vibratos, i.e. rapid frequency changes comparable to tours, though with smaller frequency bandwidth and fused sweeps. But sparrows also can sing drawn-out melodies like that of the domestic canary. It seemed to be worth to study first the range of morphological constraints on vocal performance rather than reduce differences in the species-specific acoustic features between model and imitation on possible neuronal deficiencies.

7.2 FUTURE PROSPECTS: FOREIGN-SONG AS A REASEARCH TOOL

Communication involves a signal sender (7.2.1) and a signal receiver (7.2.2), both playing different roles.

7.2.1 Signalling is costly, so the signaller must benefit from sending a signal. And the benefit obviously must come through a recipient's response to that signal. We know much about birds' vocal copying capacity but only very little about its biological relevance. The imitative abilities of house sparrows opens the possibility to study the function of learned features in several social situations.

Most authors argue that elaborate song attracts females or/and rejects rivals (Catchpole & Slater 1995). It might be worth testing whether canary-singing sparrow males use canary-like tours in the presence of females and of other males.

Social tutoring has shown to be important in song learning of house sparrows; this could allow for foreign-song traditions, which may continue for several generations without renewed human intervention as known from bullfinches and marsh tits (Nicolai 1959; Becker 1978; Güttinger et al. 2002). This also makes it possible to identify the tutor(s) from whom young sparrows learned. Up to now the evolutionary consequence of vocal copying is only known for broodparasitic widow birds (Nicolai 1964, 1973), where an exciting case of co-evolution of genetic and traditive characters appeared[2]. Canary singing house sparrows have the potential to become the second one.

Canary singing house sparrows offer a tool to test models of animal signalling, which assume that displays of any kind should be costly if they carry honest information about the quality of the signaller (Zahavi 1975; Clutton-Brock & Albon 1979; Grafen 1990a,b; Godfray 1991):

Sound production is known to require energy for muscle activities during singing (Goller & Larsen 1997a,b; Suthers et al. 1999; Larsen & Goller 2002) and to increase metabolic rate in singing relative to lower or basic metabolic rate (Ward et al. 2003). However, it is still unclear how costly singing itself is. As house sparrows separate pure-syllable sequences from tour-comprising sequences, it might be possible to quantify whether singing of a comparable simple structure (sequence of single syllable) is less or equally energetically costly as singing of a temporally demanding pattern (tours) in a sequence with increased recall rate of different syllable types.

Females of the temperate zone are mostly studied as receivers rather than as sender of song. Thus it was surprising to find reports that a female sparrow also imitated the canary song (Ragotzi 1962) or developed - alone, just by exercise - a song with improvisations including melodious twittering combined with trills (Marek 1979). Video-

[2] Song here serves as a socially acquired marker for the individual's genetically determined mouth colours. As a result, mating only takes place between adult paradise whydahs who have learned the same waxbill song and therefore have to carry identical mouth marking genes.

and tape-recordings of courtship in two pairs of sparrow-raised sparrows showed females, who uttered scolding sequences of rapidly repeated syllables. The behavioural observations were supported by the found male-to-female ratio of nuclei volumes, which is comparable to that reported from species where both sexes sing but differ in repertoire size. Females, who are able to sing like canaries without artificially elevated hormone levels might be interesting subjects to study sex specific neuronal controlling.

7.2.2 Being attentive and responding to a signal is costly, too. The receiver should not react to a signal unless it is also in his interest. It is thus important to find out as what a receiver identifies the heard sounds. Using the „IEG response“ (Sheng & Greenberg 1990) of ZENK, the expression pattern of which depends on early experience (Mello et al. 1992; Jin & Clayton 1997; Ball & Gentner 1998; Jarvis et al. 1998), I found besides behavioural (Salwiczek, in prep.) also neuronal indications that canary-raised house sparrow males recognize canary song at least partially as sparrow-specific. The individual ZENK maps are representations of particular syllables, which could be considered as the outputs of a syllabic code, in its turn understood as the rules by which the brain transforms the physical properties of a set of syllables into a set of representations (Ribeiro et al. 1998). The study of ZENK expression in canary-like singing males may help to understand where and how such birds store and encode learned „tours“ as well as tour-comprising and pure syllable sequences. This in turn could give an answer why sparrows treat both sequences differently.

7.3 IN CONCLUSION

The adoption of foreign song elements does occur under natural conditions in various songbird species including the house sparrow (e.g. Gwinner 1964; Dowsett-Lemaire 1979; Huber 1983; Slater 1983b), though it may go largely unnoticed by us. „Now, if a bird really gets a sound in his mind from hearing it and sets out forthwith to imitate it […], it is a mystery and deserves closest study“ (Thorndike 1911, reprint 1965). Canary singing house sparrows provide a rich tool for an integrative approach (Salwiczek & Wickler 2003), in which neurobiological investigations will be combined with early development, sexual selection vs. natural selection, endocrinology and morphological constraints on song production. It emphasizes that inter-specific comparisons of bird

song and bird brain should include not only correction for phylogeny but also for morphology. This is, because the phenotype of song need not exactly represent the „memetype“ (Salwiczek 2001) as morphology can serve as an interfering factor; thus differences between model and imitation may reflect distorted production rather than copying errors. Furthermore counting syllables or song types to compare different species might not reflect ‘true’ complexity of a song as in some species single syllables might be compressed complex songs (song parts). And rather than search for a „key adaptation“ or single explanation for the imitative ability (song learning ability) in passerines, it is more appropriate to focus on the multiplicity of factors involved in song production that promote their successful adaptation shaped by different selective forces.

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I apologize if I have forgotten somebody – I am almost sure I have.

APPENDIX 1: LIST OF CHEMICALS, SOLUTIONS AND MATERIALS

A1.1 LIST OF CHEMICALS USED FOR ANALYSES (BRAIN, STEROID HORMONES, SYRINX)

CHEMICALS	COMPANY	CAT.NR/LOT
Ac-BSA, 2%	Sigma	B8894
Aerosolsolution	Sigma	
Agarose (low melting, analyt. Grade)	Serva	001140803
Agarose NuSieve GTG	Bio Whittaker	50080
Santa Cruz Egr-1C 19 Rabbit	Santa Cruz	PAK0049
NeuN MAB377	Cemicon	21010288
a-mslgG (H+L)(gt) Biotin*	Alexis	VC-BA-9200
Ammonium Hydroxide	Sigma	A6899
Antielgoseingenin (?)	Roche Diagnostics	1093274
Aqua bidestillata	H. Kerndl	20003
Autoradiography emulsion NTB-2	Integra Biosciences	1654433
Avidin/Biotin Blocking Kit	Alexis	VC-SP-2001
BCIP	Roche Diagnostics	1383221
Blocking solution	Roche Diagnostics	1096176
Bovine Serum Albumin	Sigma	B8894
BSA-solution	Sigma	B-8894
Buffer reference standard	Sigma	B-4895
Citric acid	Sigma	63H 0201
Cytidine 5'-(alpha-Thio)Triphosphare [^{35}S]	NEN Life Sciences	NEG064H25OUC
D(+)Saccharose	Roth	90971
d-^{35}S-CTP (Cytidin 5'alpha-thio)triphosphate	NEN Life Science	L01-026-D
Dextran	Sigma	D-8906
Diethylpyrocarbonate (DEPC)	Sigma	D5758
Dextran Sulfate sodium	Sigma	D8906
Dextran-Sulfate	Sigma	D8906
Diaminobenzidin (DAB)	Sigma	106H-8917
Diethylether reinst stab. mit ETW	Merck	100923
Diethyl pyrocarbonate	Sigma	D5758
di-Sodiumhydrogenphosphat-Dihydrat reinst	Merck	1.06576
Di-Sodiumhydrogenphosphat-heptahydrat	Merck	S9290
Dithiolthreitol	Sigma	D9779
0.1 M Dithiolthreitol-solution	Promega	P1 17B
DNase- solution	Promega	M6IOA
EDTA	Sigma	E5134
Eosine G	Merck	115935
Essigsäureanhydrid	Merck-Schuchardt	822278
Ethanol	Roth	9065.2
HefeRNA	Sigma	R-6750
Ficoll	Sigma	F2637
Filmemulsion	Kodak, Typ NT B2	165 4433

CHEMICALS	COMPANY	CAT.NR/LOT
Formaldehyd, ACS, acid free	Fluka Chemie	47629
Formamid	Sigma	F-7503
Gelatine	Sigma	G-2500
Gel-Blotting-paper	Schleicher & Schuell	CS0589-1
Histokitt	Roth	6638.1
Hydrochloride	Sigma	T3253
Kodak Developer D19	Integra Biosciences	IBO4593
Kodak Fixer	Integra Biosciences	IBO1746
Magnesiumchlorid Hexahydrat	Sigma	63072
Maleic Acid	Sigma	M0375
Methylen Blue	Serva	002919801
Mayers Haemalaunsolution	Merck	109249
NBT 2 Nuclear Track Emulsion	Roche Diagnostics	1383213
Nickel Sulfate Hexahydrate	Sigma	N4882
Nitroblautetrazoliumchl., Solution	Roche Diagnostic	85931627
Normal Serum	Alexis	VC-S-5000
paraffine	Klinipath b.v.	5079a
Paraformaldehyd	Sigma	P6148
Peroxidase VECTASTAIN Elite ABC Kit (rb)	Alexis	VC-PK-6101
Polaroid Black-and-white Print Film	Sigma	F4638-2EA
Polyoxythylensorbitan	Sigma	P9416
Polyvinylpyrolidone (PVP)	Sigma	P5288
Proteinkinase K from Tritirachium Album	Sigma	P2308
rCTP	Promega	P1 14B
Ribonucleic acid type XI	Sigma	R675
RNAse, Pulver 90436524	Roche Diagnostics	109126
RNase	Boehringer	109126
Salmon DNA	Sigma	D7656
Sek. AK (Rabbit IgG) Vectasin Elite ABC Kit	Alexis (D)	PK-6101
Silica Gel Type III	Sigma	S7625
Sodium chloride	Sigma	S9625
Sodium Dihydrogenphosphatedihydrat	Merck	6345
Sodium dodecyl sulfate solution, 10%	Life Technologies	5553UA
Sodium Phosphate Dibasic heptahydrate	Sigma	S9390
Sodium Thiosulfate	Sigma	S1648
$C_6H_50_7Na_3*2H_20$	Sigma	C-8532
Sp6 RNA Polymerase	Promega	P108B
T7 RNA Polymerase	Promega	P207B
Thionine acetate	Serva	07930
Triethanolamine free base	Sigma	T1377
Trizma Base	Sigma	T6066
Trizma hydrochlorid, 1M, pH 7.4	Sigma	T2663
5x TSC-solution	Promega	P1 18B
Xylol	Roth	9713.3

CHEMICALS	COMPANY	CAT.NR/LOT
yeast RNA	Sigma	R6750
Hydrochloride acid, rauchend	Merck	1.00317

PRIMER obtained from Genzentrum, Feodor-Lynen-Str. 25, 81377 Munich, Germany

CHD-2550-F: 5'-GTT ACT GAT TCG TCC ACG AGA-3'
CHD-2718-R: 5'-ATT GAA ATG ATC CAG TGC TTG-3'

3007-F: 5'-TAC ATA CAG GCT CTA CTC CT-3'
3112-R: 5'-CCC CTT CAG GTT CTT TAA AA-3'

A1.2 LIST OF MATERIALS AND MACHINES USED FOR DIFFERENT ANALYTICAL METHODS

Superfrost plus Objektträger	Roth	H867.1
Deckgläser	Merck	631F9419

Sterican® Einmal-Injektions-Kanülen, Dünnwand, 0. x 40mm, 20 G x 11/2" Luer Lock, Gr.1

Sterican® Einmal-Injektions-Kanülen, Dünnwand, 0.40 x 20mm, 27 G x 4/5" Luer-Lock, Gr.20

Blaubrand® Einmal Mikropipetten mit Ringmarke, 100µl in 20°C, Richtigkeit $\leq \pm$ 0.25%, Päzision $\leq$ 0.5%, Cat.No. 7087 44; oder

Brand® Einmal-Kapillarpipetten, 50µl, Richtigkeit $\leq \pm$ 0.5%, Päzision $\leq$1%, NH_4 – heparinisiert, Cat.No. 7086 54

Collection tubes (2ml capless microcentrifuge tubes; Amersham pharmacia biotech)

GMX™ Columns (MircoSpin™ columns pre-packed with a glass fiber matrix; Amersham pharmacia biotech)

Terumo syringe, 50 ml

Perkin Elmer GeneAmp PCR System 2400, and Perkin Elmer GeneAmp PCR System 9600

Elektrophoresis: normal horizontal agarose gel electrophoresis apparatus

Freezing Microtome: Leica CM 1325

precision balance Sartorius Basic BA 110S (max. 110g, < ± 0,0001)

analytical balance Kern 440-33 (max 120g, d=0,01g)

Digital pH Meter, pH525 WTW

magnetic stirrer Heidolph MR 2002, with heat

Microtom HM 335 E

WTC binder D-100 Horo Stuttgart

A1.2 LIST OF SOLUTIONS

A.1.2.1 BLOOD SAMPLING

- Extraction Solution (Buffered solution containing achotrope and detergent; obtained from Amersham pharmacia biotech)
- Wash Solution: this is part of the GFX blood extraction kit which is obtained from amerscham pharmacia biotech inc, order number 27-9603-01
- TE-buffer (10mM Tris HCL, 1 mM EDTA, ph 8.0; 70°C)
- TBE-buffer: 45mM tris-borate, 1mM EDTA, pH 8.0
- Gel: 2.5g NuSieve + 100ml 1xTBE-buffer
- 1% Ethidiumbrom-solution this is approximately 0.5ug/ml
- Queens lysis buffer: 0.1M tris, 0.01M NaCl, 0.01M Na-EDTA, 1% n-lauroylsarcosine, pH 8.0

A.1.2.2 PERFUSION

- 0.9%ige NaCl-Lsg (mind. 100 - 150 ml)

4% FPBS (minimum 150 - 200 ml/brain)

A.1.2.3 NEURON SPECIFIC STAINING

- 25mM physiologicial phosphate buffer saline (PBS)

  50ml 0.4 PB + 750ml dH_20 + 7.2g NaCl; adjust to pH 7.3

- 25mM PBS: 62.5ml 0.4 M PB + 1000ml dH_20 + 9.0g NaCl
- 0.01M citic acid buffer: 2.94g citric acid dissolved in 1.0 L ddH_20; adjust to pH 6
- 4% Normal Goat Serum (NGS): 2ml NGS + 48ml 25mM PBS
- specific antibody: Chemicon NeuN [5µl/1 slide with 1:100]
- 4 slides: 20µl antibody + 1980 µl 25mM PBS
- secondary antibody: Biotinylated anti-*mouse* JgG (SK):

  14µl SK/ 1ml PBS buffer for 1 slide

- ABC reagens: 9µl reagens A + B / 1ml PBS for one slide
- Diaminobenzidin (DAB) solution: 25ml 25mM PBS + 1 pellet (30mg) DAB
- DAB reaction: 3µl H_2O_2 + 1ml DAB

A.1.2.4 ZENK STAINING

- 0,1M phosphate buffer (PP) 2000ml:

  6,24g NaH_2PO_4 x 2 H_2O + 28,46g + Na_2HPO_4 x 2 H_2O + ad 2000ml H_2O_{dest};

  adjust to pH 7,4

- Tris Buffer (mix thoroughly):

  3.305 g Trizma HCl + 0.5 g Trizma base powder + 500 ml dH_2O;

  adjust pH to 7.4 with Tris base solution

- Tris Base Solution (mix thoroughly): 4.84 g Trizma base powder + 10 ml dH_2O

- 0,1% Triton x 100 in 0,1M PP: 270µl Triton x 100 + 300ml 0,1 M PP

- NGS blocking

  5% NGS in 0,1M PP + 0,5% Triton x 100

  + 150µl Triton x 100 ad 30ml 0,1 M PP

  + 5ml NRS ad 29,55ml solution I

- Avidin blocking: 12 drops Avidin-blocking-Reagent ad 30ml 0,1 M PP

- primary antibody:

  1:10 000 dilution Zenk-antibody (Santa Cruz C 19)

  + 9 drops NGS (Elite-Kit) ad 30ml 0,1M PP

  + 12 drops (600µl) Biotin-Blocking-Reagent ad 30ml 0,1M PP

  + 3µl antibody ad 30ml 0.1M PP

- Secondary antibody Goat Anti Rabbit IG, biotiniliert

  75µl stock solution ad 30ml 0,1M PP

- ABC-solution:

  12 drops (600µl) solution A ad 30ml 0,1M PP

  12 drops (600µl) solution B ad 30ml solution I

- colour reaction (0,03% DAB / 1mM $NiSO_4$ / 0,1% H_2O_2)

  + 0,03g DAB (3 Tabs) + 90ml H_2O_{dest} (defrosted at the beginning of the day)

  + 2,63g $NiSO_4(H_2O)_6$

  + 10ml 1M Tris-Buffer

  + 0,3ml 30% H_2O_2 (start of the reaction)

APPENDIX 2: SONG LEARNING EXAMPLES FROM THE LITERATURE

Table A2.1: Examples for social selectivity with selected references

Tutor	Species	Reference
Only live tutor	Short-toed Tree-creepers *Certhia brachydactyla*	Thielcke 1984
	Eurasian Tree-creepers *Certhia familiaris*	Thielcke 1970
	Sedge wren *Cisthothorus platensis*	Kroodsma & Verner 1978
Tape and live tutor	Domestic canary *Serinus canaries*	Waser & Marler 1977
	Common starling *Sturnus vulgaris*	Hausberger 1993; Chaiken et al. 1993
	Chaffinch *Fringilla coelebs*	Thorpe 1958
	White-crowned sparrow *Zonotrichia leucophrys*	Marler 1970
	Swamp sparrow *Melospiza georgiana*	Marler & Peters 1977

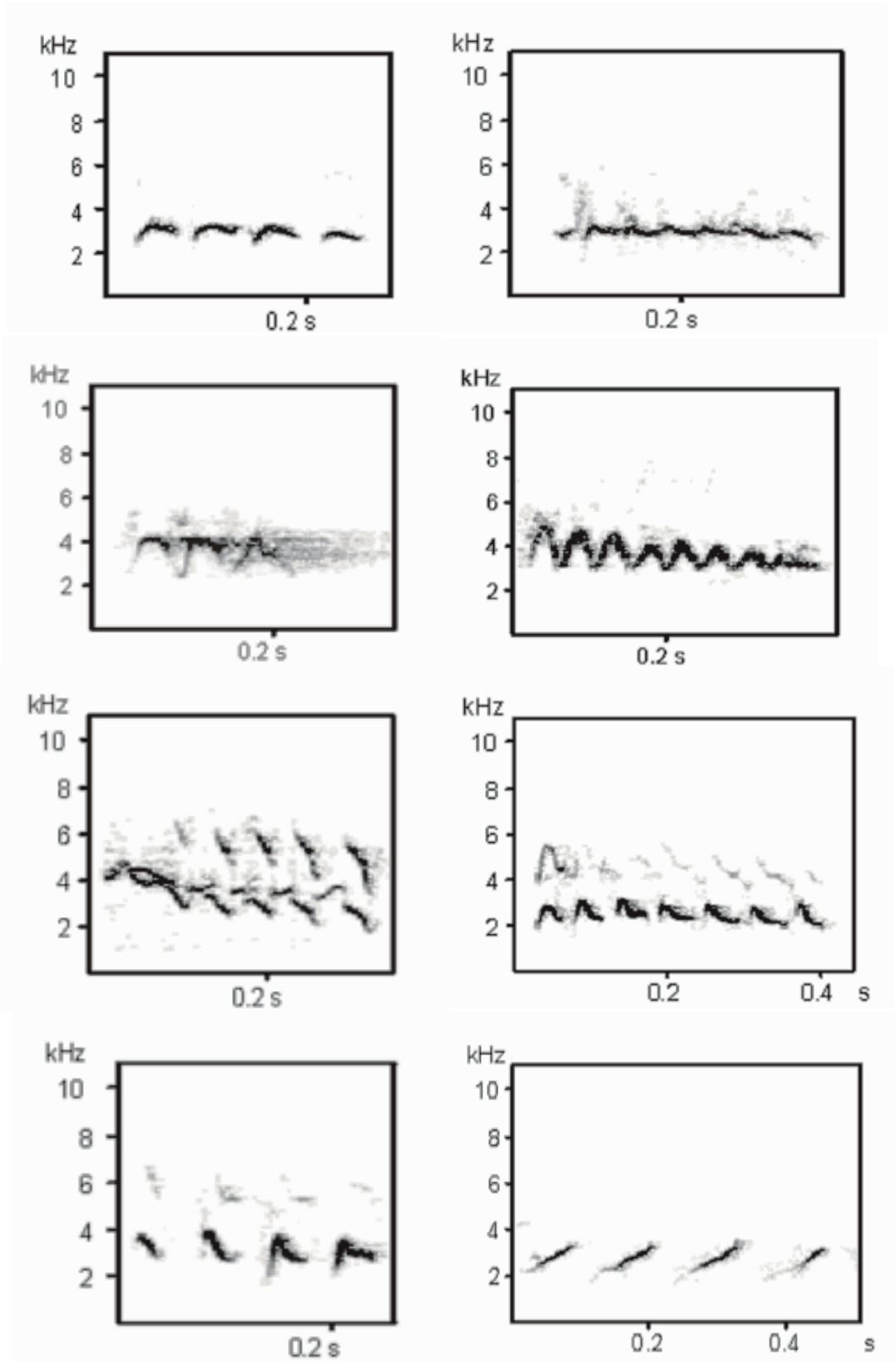
Table A2.2: Choice of tutor in some avian species' vocal development (song and call) with selected publications

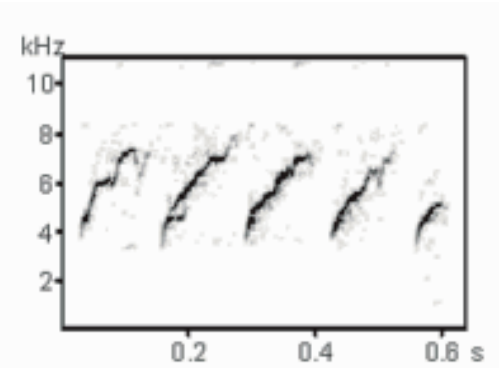
Tutor	Species	Reference
Own or canary foster father; for females: father and mate	Bullfinch *Pyrrhula pyrrhula*	Nicolai 1959
Own or bengalese finch foster father	zebra finch (lab) *Taeniopygia guttata*	Immelmann 1969; Böhner 1983
father: 60% son father: 80% contact call	zebra finch (wild)	Zann 1990; Zann 1993
father	Bengalese finch *Lonchura striata*	Dietrich 1980
Mostly father	Domestic canary *Serinus canaria*	Waser & Marler 1977
	Darwin's finches	Grant 1984; Millington & Price 1985; Gibbs 1990
Adult rivals Territorial neighbour	Song sparrow *Melospiza melodia*	Nice 1943; Beecher et al. 1994
Territorial neighbour	Great tit *Parus major*	McGregor & Avery 1986
	Bewick's wren *Thryomanes bewickii*	Kroodsma 1974
	Marsh wren *Cistothorus palustris*	Verner 1975

Tutor	Species	Reference
	Nuttals's White-crowned sparrow (wild) *Z. l. nutalli*	Baptista 1975; Petrinovich 1988
	Rufous-collared sparrow *Z. capensis*	Nottebohm 1969
	Crested Lark *Galerida cristata*	Tretzel 1965
	Saddleback *Philesturnus carunculatus*	Jenkins 1978
	corn bunting *Emberiza calandra*	McGregor & Thompson 1988
	House finches *Carpodacus mexicanus*	Mundinger 1975; Bitterbaum & Baptista 1979
Territorial neighbour, father	White-crowned sparrow (wild) *Zonotrichia leucophrys*	DeWolfe et al. 1989; Cunningham 1987
Neighbour at settling site	White-crowned sparrow (wild) *Z. l. oriantha*	Baptista & Morton 1988
Same sex conspecific	Indian hill mynah *Gracula religiosa*	Bertram 1970
	Common starling *Sturnus vulgaris*	Hausberger 1993; Chaiken et al. 1993
	Bay wren *Thryothorus nigricapillus*	Levin 1985
	slate-coloured boubou *Laniarius funebris*	Wickler & Sonnenschein 1989
Mate (Parents)	Various cardueline genera e.g. *Carduelis, Carpodacus, Loxia*	Mundinger 1970; Samson 1978; Groth 1993
	African forest weaver *Ploceus bicolor sclateri*	Seibt et al. 2002
Flock members	Black-capped chickadee *Parus atricapillus*	Mammen & Nowicki 1981
Colony members	Yellow-rumped cacique *Cacicus c. cela*	Feekes 1982; Trainer 1988
Alpha male	Village indigobird *Vidua chalyeata*	Payne & Payne 1996
Siblings(father)	Chaffinch (lab) *Fringilla coelebs*	Thorpe 1958
	White-crowned sparrow (lab)	Marler 1970
Estrildid host species	Viduine finches	Nicolai 1964, 1973; Payne 1973

APPENDIX 3: CANARY-LIKE TOURS SUNG BY HOUSE SPARROWS

The following catalogue shows some canary-like tours sung by ca-sin. Each of the selected examples was sung by several sparrow males.

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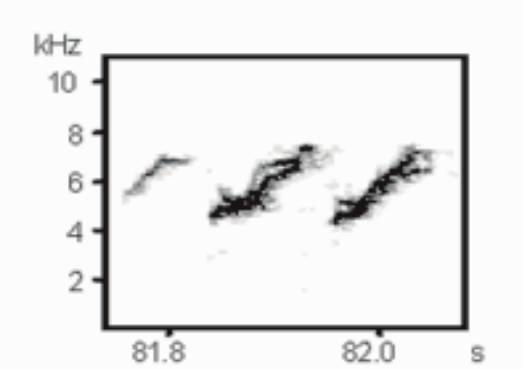
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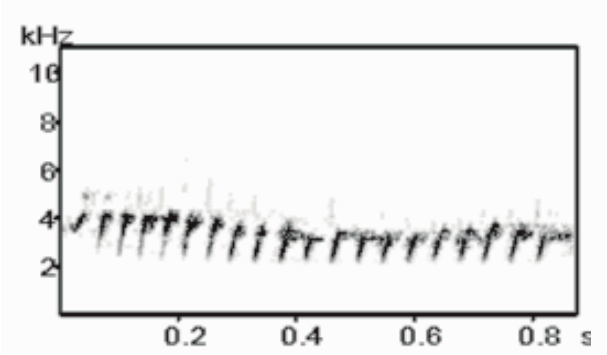
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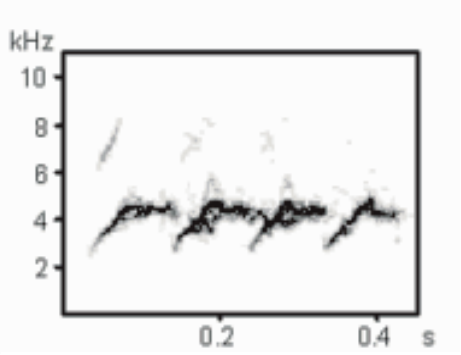
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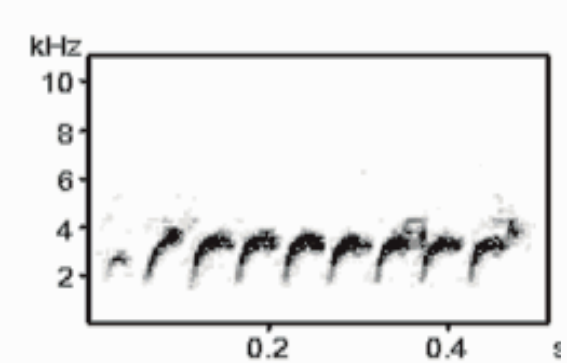
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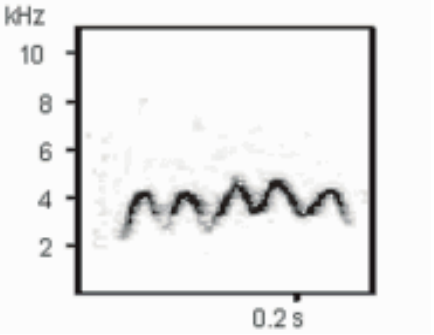
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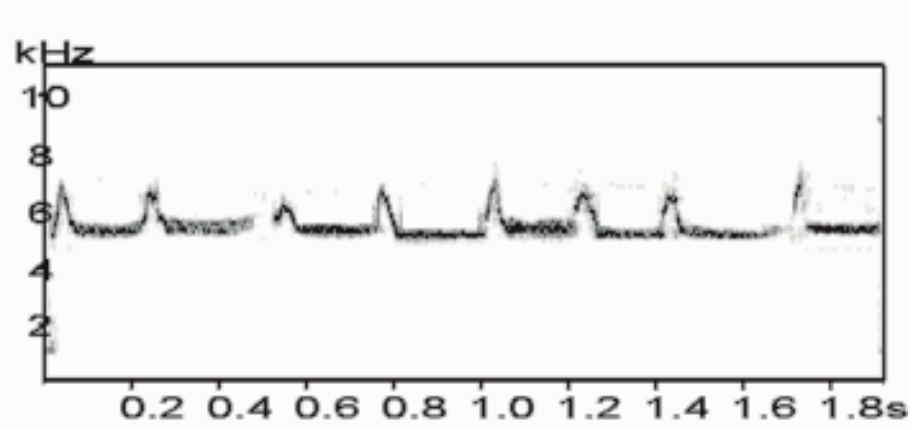
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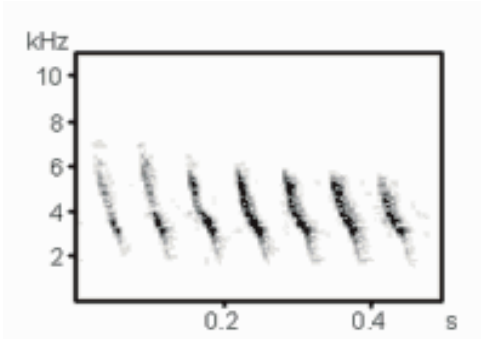
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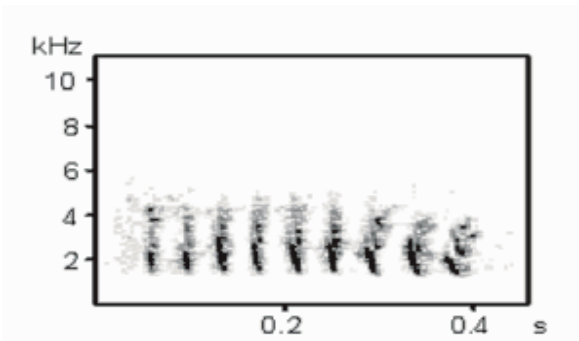
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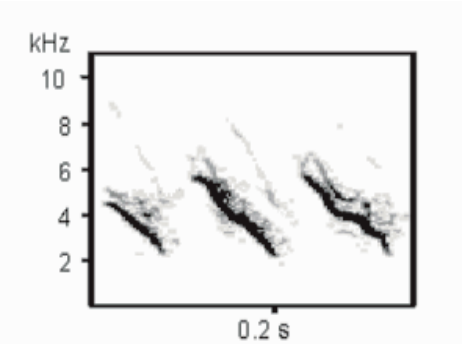
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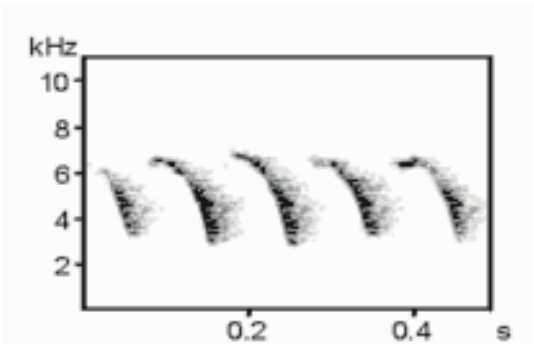
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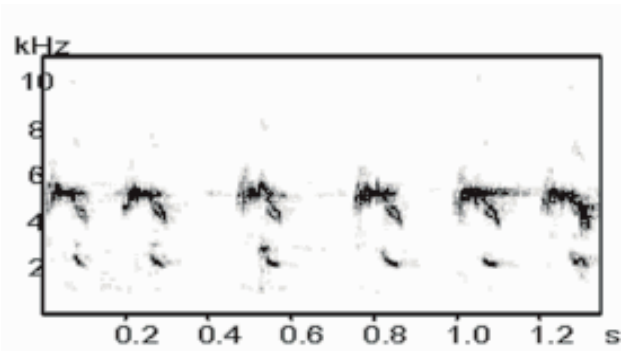
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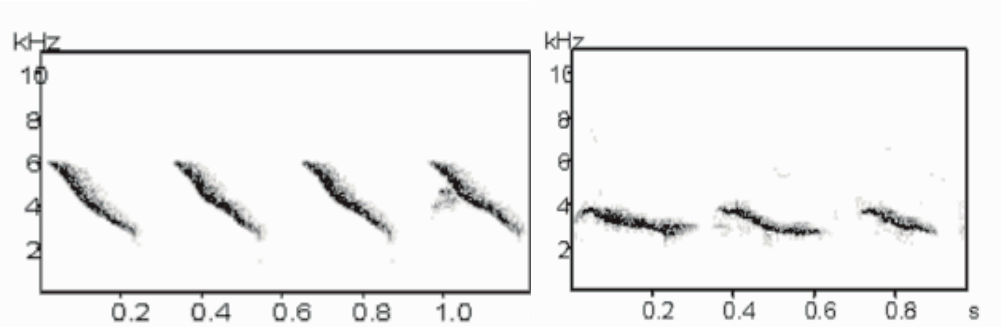
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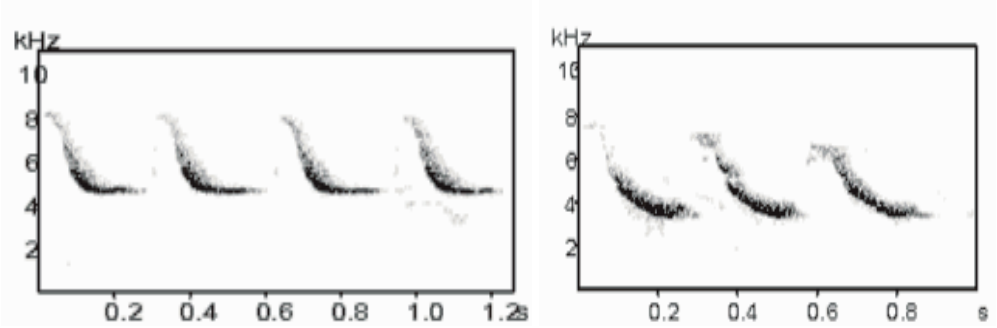
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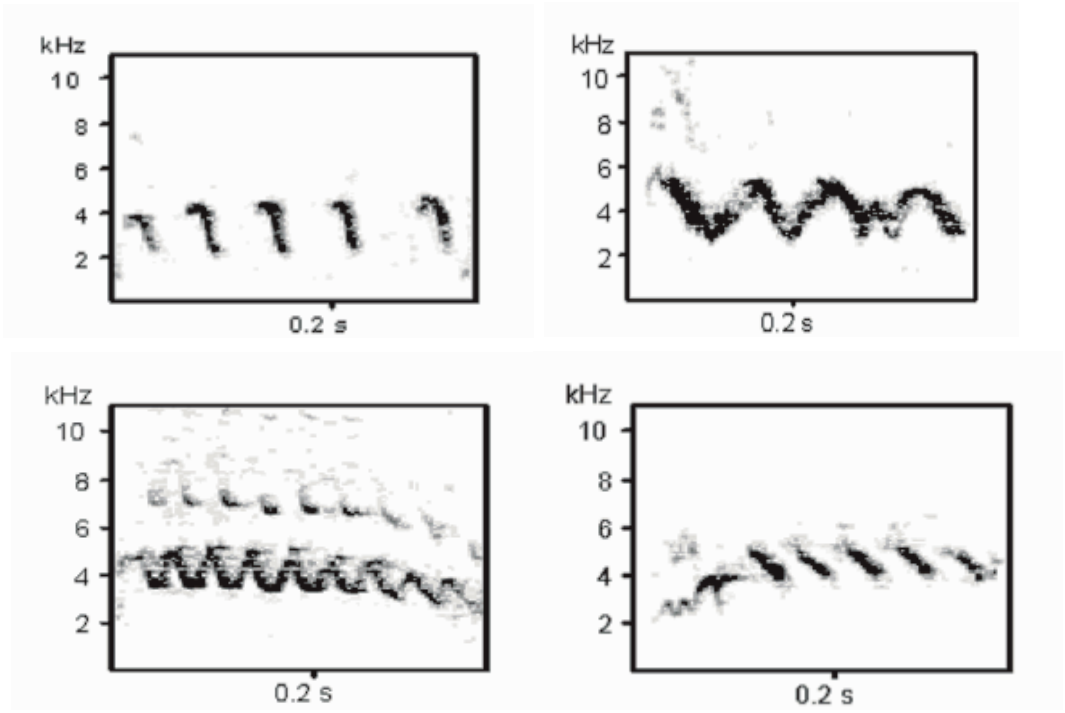
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SONDERAUFGABEN AM INSTITUT IN SEEWIESEN

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LIST OF PUBLICATIONS

Salwiczek, L. H. and Wickler, W. (in press) The shaping of animals' minds. *Interaction Studies.*

Salwiczek, L. H. and Wickler, W. (in press) Bird song: An evolutionary parallel to human language. *Semiotika*.

Wickler, W. and Salwiczek, L. H. (2003) Foreign-language phenomena in birds: A means to understand the evolution of high level acoustic communication. pp. 395-412 In: *Europäische Sprachenpolitik / International Language Policy*, (eds. R. Ahrens, W. Hüllen & A. Raasch), Verlag Winter.

Salwiczek, L. H. (2002) Buchbesprechung in *Naturwissenschaftliche Rundschau*, 55. Jahrgang, Heft 4, Seite 220 von Geoffrey E. Miller: Die sexuelle Evolution Partnerwahl und die Entstehung des Geistes. Spektrum Akademischer Verlag. Heidelberg, Berlin 2001

Salwiczek, L. (2001) Grundzüge der Memtheorie. pp. 119-201 In: *Wie wir die Welt erkennen* (W. Wickler & L. Salwiczek eds.), Verlag Karl Alber, Freiburg.

Wickler, W. und Salwiczek, L.H. (eds.) (2001) Wie wir die Welt erkennen, Grenzfragen Band 27, Verlag Karl Alber, Freiburg, pp. 412.

Ich versichere, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe.