

Chapter 7

Seasonal Hormone Fluctuations and Song Structure of Birds



Manfred Gahr

Abstract Traditionally, it is assumed that singing of birds is a male-typical testosterone-dependent behavior. In this review I point out that singing outside the breeding season is common in males of many songbird species while their testosterone levels are low. Further, females of many tropical and temperate songbird species sing in various context in- or outside of the breeding season but testosterone levels of singing females are low in most cases. These findings question the testosterone-hypothesis of song production of songbirds. However, a key problem is the interpretation of “high” versus “low” testosterone levels, which would require a basic understanding of the quantitative interaction of testosterone and its estrogenic derivate with their specific receptors, as well as the dynamic abundance of these receptors in song controlling systems.

Bird songs are thought to mainly function in the realm of female mate attraction and defense of breeding territories against other males (Searcy and Andersson 1986; Kroodsma and Byers 1991; Catchpole and Slater 1995). Individual variation in song characteristics does affect reproductive success through mate choice and male–male competition (Andersson 1994). In relation, there is evidence of sexual selection for song traits such as song rate, repertoire size, structure of song motor units (syllables), and speed of syllable repetitions (for review: Podos et al. 2004). Current theory predicts that when senders and receivers have different evolutionary interests, as in sexual selection, signals must be subject to some costly constraint to constitute stable, honest indicators of quality (Grafen 1990). Individual variation in vocalizations will therefore depend on the condition of the adult male and its developmental history (Rowe and Houle 1996), but the costs of vocalizations are not well understood (Gil and Gahr 2002).

M. Gahr (✉)

Department of Behavioural Neurobiology, Max Planck Institute for Ornithology, Seewiesen, Germany

e-mail: gahr@orn.mpg.de

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T. Aubin, N. Mathevon (eds.), *Coding Strategies in Vertebrate Acoustic Communication*, Animal Signals and Communication 7,

https://doi.org/10.1007/978-3-030-39200-0_7

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Many temperate and tropical species, that breed seasonally, show seasonal singing activities, although there are surprisingly few quantitative data of circannual singing of bird species. In male songbirds, we can distinguish three categories (Fig. 7.1a): (MI.) males' singing activity is restricted to the breeding period; (MII.) males sing in the breeding season, and show a second period of singing activity in their post-molt nonbreeding period; (MIII.) males sing year-round. In the second and third cases the uttered song types and or the song pattern might change during the course of the year despite continuous singing activity. Although singing of females of temperate zone species is rare or not well documented, females of some temperate and of many tropical songbird species sing regularly. We can distinguish the following categories (Fig. 7.1b): (FI.) females' singing activity is restricted to the breeding period; (FII.) Females sing in the breeding season, are quiet during the autumnal molt and show again singing activity in their post-molt nonbreeding period; (FIII.) Females sing year-round; (FIV.) Females sing only in the nonbreeding season; (FV.) Females never sing. Clearly, these classifications must be an oversimplification in light of ca 4500 songbird species, but are useful for the discussion of (neuro)endocrine control of singing of males and females.

Due to the functions of male song for mate attraction and territorial defense, it is generally assumed that singing depends on the gonadal hormone testosterone. This predicts that males sing primarily in the breeding season and that females are not singing. However, as stated before, males of some temperate species and of many tropical species are known to sing outside of the breeding season and females of many tropical species sing regularly. In this review, I discuss the evidence for (1) seasonal singing activity, (2) seasonality of song structure, (3) testosterone dependency of song activity and song structure, (4) neural mechanisms of seasonal singing activity, and (5) neural mechanisms of hormone-dependent seasonal song structure. Based on the present survey of seasonal singing of songbirds, in the conclusion (6) I discuss the concept of singing as a testosterone-sensitive male sexual behavior. Although seasonal changes in singing/vocal activity are common in species of most avian orders (e.g., woodpeckers: Tremain et al. 2008; Malacarne et al. 1991) and seasonal changes in song pattern, too, are likely widespread (e.g., Galliformes: Fusani et al. 1993; suboscine-Passeriformes: Robertson et al. 2009), my review is focused on seasonal singing of songbirds (oscine Passeriformes). Songbirds are particularly interesting for this review, since they represent about half of today's bird species and since all songbirds have a homologous brain circuit that controls the song pattern, which facilitates species comparisons of underlying mechanisms.

7.1 Seasonal Singing Activity and Song Type Usage

7.1.1 Seasonal Singing Activity (Fig. 7.1)

In males of most temperate zone species singing activity varies during the breeding cycle being highest during mating and/or territory establishment and declines toward

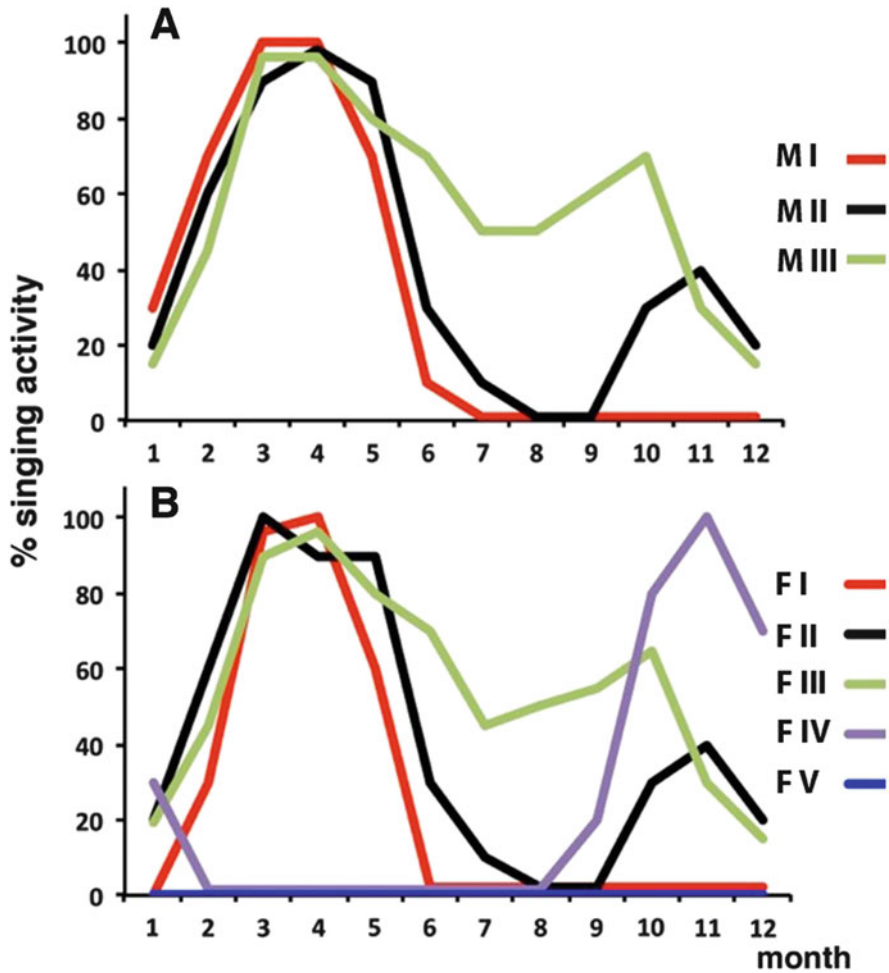


Fig. 7.1 Schematic representations of seasonal singing activity of male (a) and female (b) songbirds. In a, schematic drawings of three types of males' seasonal singing activities are depicted. The timing is based on a hypothetical average breeding season of the Northern Hemisphere: (MI.) Males' singing activity is restricted to the breeding period, (MII.) Males sing in the breeding season, and show a second period of singing activity in their post-molt nonbreeding period, (MIII.) Males sing year-round. In the second and third case the uttered song types and or the song pattern might change during the course of the year despite continuous singing activity. In b, schematic drawings of five types of females' seasonal singing activities are depicted: (FI.) Females' singing activity is restricted to the breeding period, (FII.) Females sing in the breeding season, are quite during the autumnal molt and show again singing activity in their post-molt nonbreeding period, (FIII.) Females sing year-round, (FIV.) Females sing only in the nonbreeding season, (FV.) Females never sing. % Singing activity is normalized to the month with highest singing activity of a species type. Month [1–12] represents January to December. (Modified after: Cox 1944; Immelmann 1969; Ritchison 1983; Langmore 1998; Schwabl 1992; Brunton and Li 2006; Price et al. 2008; Bezzel 2011; York et al. 2016; Gahr, unpublished observations)

the end of the breeding season. Typically, after the breeding season individuals of temperate species molt and show no singing activity in this period. In fall, the majority of species prepare for migration, while about 40% of species of the Northern hemisphere are resident or short-distance migrants. Observations by Alexander (1935) and a survey of Cramp and Perrins (1994) indicate that ca 60% of Palearctic-South-European or Palearctic-African migrants sing in their respective wintering grounds during northern winter, but good quantitative data are lacking. Thus, since the singing behavior during migration and in wintering areas is not well studied, the classification of species as “seasonal singing” is blurred for migratory species that depart briefly after the end of the breeding season. Likewise, little data about singing outside of the breeding season are available for tropical species that migrate within the tropics. In addition, for tropical species, the main problem is determining the breeding period per se that might differ strongly between species and between populations and individuals within a species (Stouffer et al. 2013). Further, since the amplitudes of fall and winter songs are frequently lower than that of breeding period songs, some species of category MI (FI) or MII (FII) might be category II or III, respectively. However, a confounding factor that might lead to false-positive category III species is the song development of juveniles; juvenile male songbirds practice singing in their first autumn/winter which might be confounded with singing adults in un-ringed populations. Last, the singing behavior in the nonbreeding period might differ within a species, in particular between sedentary and migrant populations.

With these caveats, in the following I list examples of the before mentioned three categories of seasonal singing activity of male songbirds: (MI.) males’ singing activity is restricted to the breeding period: temperate zone examples of the first category are the chaffinch (*Fingilla coelebs*; Bezzel 1988), the willow tit (*Parus montanus*; Bezzel 2011), the wood warbler (*Phylloscopus sibilatrix*; Fouarge 1968; Bezzel 2011), and the black-capped chickadee (*Poecile atricapillus*; Philmore et al. 2006). A tropical such species is the silver-beaked tanager (*Ramphocelus carbo*; Quispe et al. 2015, 2017).

(MII.) Males sing in the breeding season and show a second period of singing activity in their post-molt nonbreeding period: Examples are the black redstart (*Phoenicurus ochruros*; Apfelbeck et al. 2013), the canary (*Serinus canaria*; Leitner et al. 2001a, b; Voigt and Leitner 2008), the serin (*Serinus serinus*; Bezzel 2011), the European robin (*Erithacus rubecula*; Lack 1943; Bezzel 2011), the garden warbler (*Sylvia borin*; Bezzel 2011), the common chiffchaff (*Phylloscopus collybita*; Bezzel 2011), the song thrush (*Turdus philomelos*; Hegelbach and Spaar 2000; Alexander 1935), the great tit (*Parus major*; Bezzel 2011; Van Duyse et al. 2003), the stonechats (*Saxicola torquata*; V. Canoine personal communication), the nightingale (*Luscinia megarhynchos*; Kunc et al. 2006; Alexander 1935), the marsh warbler (*Acrocephalus palustris*; Kelsey 1988), and the great reed warbler (*Acrocephalus arundinaceus*; Sorensen et al. 2016). In these species, the postbreeding period of singing varies: some species start in fall and are able to sing throughout winter [e.g., the European robin (Lack 1943; Bezzel 2011) and black redstart (Apfelbeck et al. 2012; Bezzel 2011)] while others start singing only after their fall migration at the

wintering grounds [e.g., the great reed warbler (Sorensen et al. 2016)]. Further, interindividual differences in singing activity seem much more pronounced in fall and winter singing periods as compared to the reproductive season, to the extent that not all males of a species are singing or at least sing infrequent outside the breeding season (e.g., Alexander 1935; Bezzel 2011; Sorensen et al. 2016).

(MIII.) Males sing year-round: Temperate such species are the winter wren (*Troglodytes troglodytes*; Bezzel 2011), the coal tit (*Parus ater*; Bezzel 2011), the Eurasian nuthatch (*Sitta europaea*; Bezzel 2011), and the white-crowned sparrow (*Zonotrichia leucophrys*; DeWolfe and Baptista 1995). Tropical examples are the white-browed sparrow weaver (York et al. 2016; Voigt and Gahr 2011), the forest weaver (*Ploceus bicolor*; Wickler and Seibt 1980; Schmidl and Gahr unpublished data) and the red-cheeked cordon-bleu (*Uraeginthus bengalus*; Gahr and Güttinger 1986). The zebra finch (*Taeniopygia guttata*), originating of inner Australia, sings year-round, depending on water availability (Zann 1996; Johnson and Rashotte 2002). As stated above, for most tropical species quantitative data covering the whole year are missing.

Even in species that sing only in the breeding season (Category I) large call repertoires might be uttered year-round, e.g., the black-capped chickadee sings in the breeding season (Phillmore et al. 2006) but produces learned contact calls (the chick-a-dee call and the gargle call) year-round (Ficken et al. 1978; Ficken and Weise 1984; Hughes et al. 1998). This indicates a general complication of the categorization of seasonal singing, that is, to distinguish songs from calls in the first place. As the chickadee example indicates even vocal learning does not always help to distinguish songs from calls. In most studies included in this review, authors have used complexity such as being composed of several sequentially uttered sounds, of more than one sound type, and the length of the sounds to distinguish between songs and calls. This structural definition of a song must of course be a species-specific definition and there is not always a clear dichotomy between call and song, e.g., female canaries utter a call, the female-specific trill that is composed of several syllables in a mating context (Amy et al. 2015). This call is more complex than all other calls uttered by female canaries (Mulligan and Olson 1969), more structured than plastic songs uttered by some female canaries (Pesch and Güttinger 1985; Gahr, personal observation) but less complex than male canary songs. However, this canary call is as complex as, e.g., the “chit” songs of female red-winged blackbirds that are produced in a mating context (*Agelaius phoeniceus*) and more complex than the “teer” songs of these females (Beletsky 1983; Yasukawa et al. 1987).

In difference to all male songbirds, females of some species do not sing at all (e.g., the zebra finch: Morris 1954) and if they sing do not always do so in the breeding season (e.g., the European robin: Lack 1943; Hoelzel 1986; Schwabl 1992). Further, in reports of female singing of Northern temperate zone species, only a fraction of all females of a particular species are observed to sing (e.g., Arcese et al. 1988; Sandell and Smith 1997; Schwabl 1992; Bensch and Hasselquist 1992; Pesch and Güttinger 1985; Langmore and Davies 1997). Thus, the seasonal context of female singing seems to be more variable within a species and between species (for reviews: Ritchison 1983; Langmore 1998; Slater and Mann 2004). Like in

males, female songs might be part of duets or solo songs, a distinction that is relevant in the frame of seasonality only in case of multiple distinct song types of a species. Further, most examples of seasonal or year-round female singing lack circannual quantitative data. According to the females' singing behavior, species can be classified as follows (Fig. 7.1):

(FI.) Females' singing activity is restricted to the breeding period: Temperate zone examples are the alpine accentors (*Prunella collaris*: Langmore et al. 1996), the black-headed grosbeaks (*Pheucticus melanocephalus*: Ritchison 1983), the American dipper (*Cinclus americanus*: Bakus 1959), the Northern cardinal (*Cardinalis cardinalis*: Ritchison 1986; Laskey 1944). Although females of these and other species sing only in the breeding season, the context is varied, including nest-building, nest-relief, incubation, brooding, feeding chicks, pair-bond maintenance, family-group maintenance, and only rarely courtship and mate attraction (for review Ritchison 1983; Langmore 1998; Slater and Mann 2004). The example for the latter is the alpine accentor (Langmore et al. 1996).

(FII.) Females sing in the breeding season and have a second singing activity in their post-molt nonbreeding period: An example might be the streak-backed oriole (Price et al. 2008), but data covering the entire year would be required.

(FIII.) Females sing year-round: Examples are the New Zealand bellbird (*Anthornis melanura*; Brunton and Li 2006), the superb fairy wrens (*Malurus cyaneus*; Cooney and Cockburn 1995), the white-browed sparrow weaver (York et al. 2016; Voigt and Gahr 2011), and the forest weaver (Wickler and Seibt 1980; Schmidl and Gahr unpublished data), and likely females of many duetting tropical oscines, such as of the wren family (Slater and Mann 2004). As stated above, for most tropical species quantitative data in relation to phenology are missing.

(FIV.) Females sing only outside of the breeding season: Such examples are the canary (Pesch and Güttinger 1985; Ko and Gahr unpublished data), the European robin (European robin; Lack 1943; Schwabl 1992), and the starling (Pavlova et al. 2007). In the latter, presence of males and nest-boxes suppresses singing.

(FV.) Female never sing, e.g., the zebra finch and the Bengalese finch (*Lonchura striata domestica*) (Morris 1954; Immelmann 1969).

7.1.2 Seasonal Song Type Usage

In some species males produce several song types of which one or several are restricted to the breeding season. The species-typical songs uttered in the breeding season are frequently called full song (also called primary song or crystallized song). Here we use the term full song for songs loudly uttered in the breeding season or year-round. A well-studied such species is the colony-living white-browed sparrow weaver in which the dominant males sing two types of full song: the so-called morning song throughout the breeding season and the duet song throughout the year (Voigt et al. 2006; York et al. 2016) (Fig. 7.2a). The duet song is shared between the

dominant male, all subordinate males and the females of a colony (Fig. 7.2b). Duet song, which extends into chorus song if more than two individuals join, is uttered year-round. Solo song and duet song of the dominant male white-browed sparrow weaver differ in the temporal organization and in syllables' structures (Voigt et al. 2006).

There is no species known in which females sing multiple song types with at least one type restricted to the reproductive context. A potential such case might be the courtship songs of cordon bleus, in which males and females combine singing with other vocal and with visual displays (Gahr and Güttinger 1986; Ota et al. 2015).

However, the courtship song per se is similar to the song produced outside of the breeding season that might serve a pair-maintaining function. Song types that might be restricted to certain seasons are the so-called soft songs (also called quiet song, twitter song, whisper song) of males of certain species, which are low amplitude songs. According to calculations of Anderson et al. (2008), the full songs might be perceived by humans as about 4–8 louder than the soft songs of the same species, e.g., European robins (Lack 1943; Dabelsteen et al. 1997) and European blackbirds (*Turdus merula*; Dabelsteen 1984; Dabelsteen and Pedersen 1990) utter soft songs in

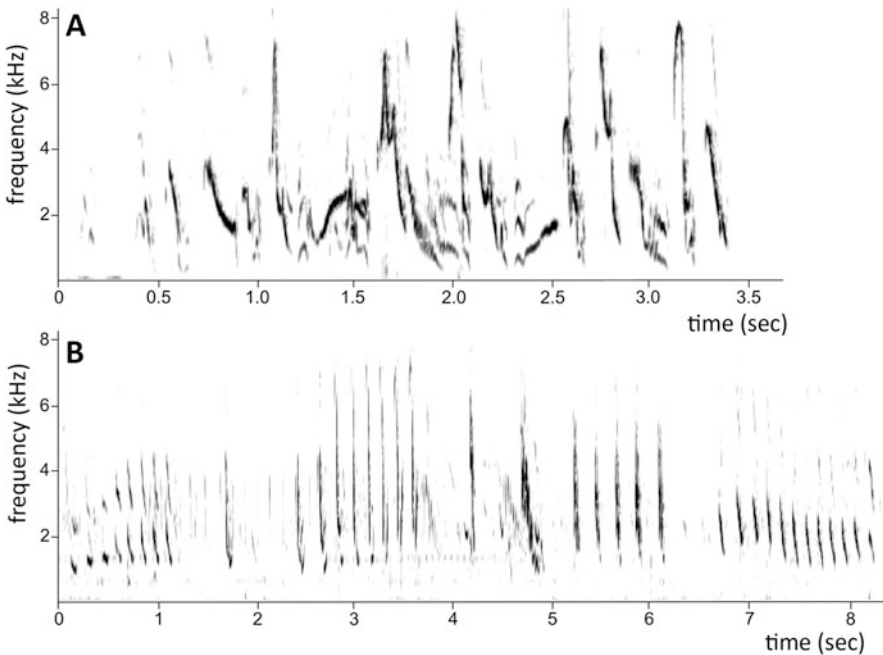


Fig. 7.2 White-browed sparrow weavers possess an extraordinary vocal communication system with two completely different types of song. Sonagrams from field recordings showing a duet song (a, similar in structure to chorus song) and a sequence from morning (solo) song (b) of white-browed sparrow weavers. While all group members engage in duet and chorus singing, morning song is only produced by the dominant male of the group. Note that time scales are different

winter. Likewise, the dunnock (*Prunella modularis*: Snow 1988), the alpine accentor (*Prunella collaris*: Langmore et al. 1996), the dark-eyed junco (*Junco hyemalis*: Titus 1998), the whitethroat (*Sylvia communis*: Balsby 2000), the swamp sparrow (*Melospiza georgiana*: Ballentine et al. 2008), and the song sparrow (*Melospiza melodia*: Anderson et al. 2008) produce soft songs that are only audible over a few meters. In case of the song sparrow, males broadcasted loudly their full song and two forms of soft songs, one similar in structure to the full song but with low amplitude and one that is unstructured, variable and sang with low amplitude (Anderson et al. 2007, 2008). The same males produce these songs types within short-time windows during the breeding season (Anderson et al. 2007, 2008). Likewise, male red-wings (Lampe 1991), European blackbirds (Dabelsteen 1984), and dark-eyed juncos (Titus 1998) produce soft songs that are described as being different in temporal organization, including more high-pitched elements and/or being more variable than the full songs during the breeding season. However, since soft songs are difficult to hear and to record over distance, it is in most species unclear if these songs represent a year-round song type that is uttered in the breeding season next to the loudly advertised full song, or a song type that is restricted to the nonbreeding season. Further, in most cases the low audibility of soft songs resulted in the lack of suitable recordings that would allow qualifying the soft songs as different or similar in structure to the full songs (Dabelsteen et al. 1998; Morton 2000; Anderson et al. 2008). It is unlikely that soft songs simply reflect production errors of the singer since the less structured soft songs of the swamp sparrows are nevertheless distinct reoccurring motor sequences (Anderson et al. 2007, 2008).

7.2 Seasonal Change of Song Structure

Autumnal/winter singing, i.e., “audible” singing outside of the breeding season as opposed to soft singing, has been reported for males of a number of nonmigratory temperate zone species such as the European robin, the winter wren, the black redstart, and the great tit (Armstrong 1955; Schwabl 1992; Apfelbeck et al. 2012; Van Duyse et al. 2003; Bezzel 2011). Likewise, males of various but not all long-distance migratory species have been reported to sing regularly on their wintering grounds (Cramp and Perrins 1994). In some of these species singing outside of the breeding period songs appear similar to the full song (e.g., the winter wren: Kreutzer 1973; the European robin: Lack 1943; Schwabl 1992; Ramenda and Gahr unpublished data). However, the males’ songs uttered in the nonbreeding period are in many species described as being less structured than the full songs and were termed subsongs. The term subsong originally described quite singing (i.e., soft songs) (Nicholson and Koch 1936) but was later used to label songs that were less structured than the typical full songs broadcasted during the breeding season (Lister 1953a). Nowadays, the term subsong is frequently used to describe the unstructured songs of juveniles uttered during song development. To avoid confusion, in this review we use the term “plastic song” for songs of adults uttered outside of the

Table 7.1 Seasonal change of song structures of species studied quantitatively in the wild

Song structure	Species	References
Syllable repertoire	Wild canary	Leitner et al. (2001a, b)
	Mockingbird	Howard (1974), Logan (1983)
	Tui	Hill et al. (2015)
	Starling	Van Hout et al. (2012)
Syllable repetition rate	Great reed warbler	Sorensen et al. (2016), Wegrzyn and Leniowski (2009)
Syllable stereotypy	Wild canary	Leitner et al. (2001a, b)
Phrase length	Song sparrow	Smith et al. (1997)
	Black redstart	Apfelbeck et al. (2013)
	Mockingbird	Howard (1974), Logan (1983)
	Starling	Van Hout et al. (2009)
Song length	Wild canary	Leitner et al. (2001a, b)
	Great reed warbler	Sorensen et al. (2016)
Song stereotypy	Wild canary	Leitner et al. (2001a, b)
	Song sparrow	Smith et al. (1997)

“Phrase” refers to larger subunits of the song that are composed of sequences of several syllables or repetitions of the same syllable or both

breeding season, i.e., autumnal/wintering songs that are structurally different from full songs.

Very few data are available in which the song pattern of the breeding period and the nonbreeding period within a species were compared statistically, and even fewer data are available, in which the song of the same individual singer uttered in different seasons were compared (Table 7.1). The best-studied example of seasonal song structure is the canary (Nottebohm et al. 1986; Leitner et al. 2001a, b; Voigt and Leitner 2008). Wild canaries form nonmigratory island populations at the Canary Islands, the Azores and Madeira. Both wild and domesticated canaries sing a less structured version of their full songs in autumn (Fig. 7.3). Besides a lower song amplitude and singing in groups, the males change their syllable repertoire partially, the syllable repetition rate, the stereotypy of syllables, the stereotypy of syllable sequences, and the song length (Nottebohm et al. 1986; Leitner et al. 2001a, b; Voigt and Leitner 2008). Other temperate zone examples likely singing plastic songs in autumn and winter are the song thrush, the European blackbird, the mistle thrush, the marsh warbler, the willow warbler, and the chaffinch (Thorpe 1958, 1961; Thorpe and Pilcher 1958; Kelsey 1988; Sorensen 2014). In fact, Thorpe states: “we may safely guess that as further material comes to hand, subsong will be found to be a very widespread phenomenon amongst song birds” (Thorpe 1961, p. 70). Similar, Lister (1953b) reported plastic song for many species of the Indian subcontinent. However, about 60 years later, the data situation is still mainly descriptive if not anecdotic:

Including the canary, quantitative comparisons of songs and plastic songs are available for only seven species (Fig. 7.4): In the song sparrow, song parts (trills) were composed of more syllables and syllables of the entire song were more

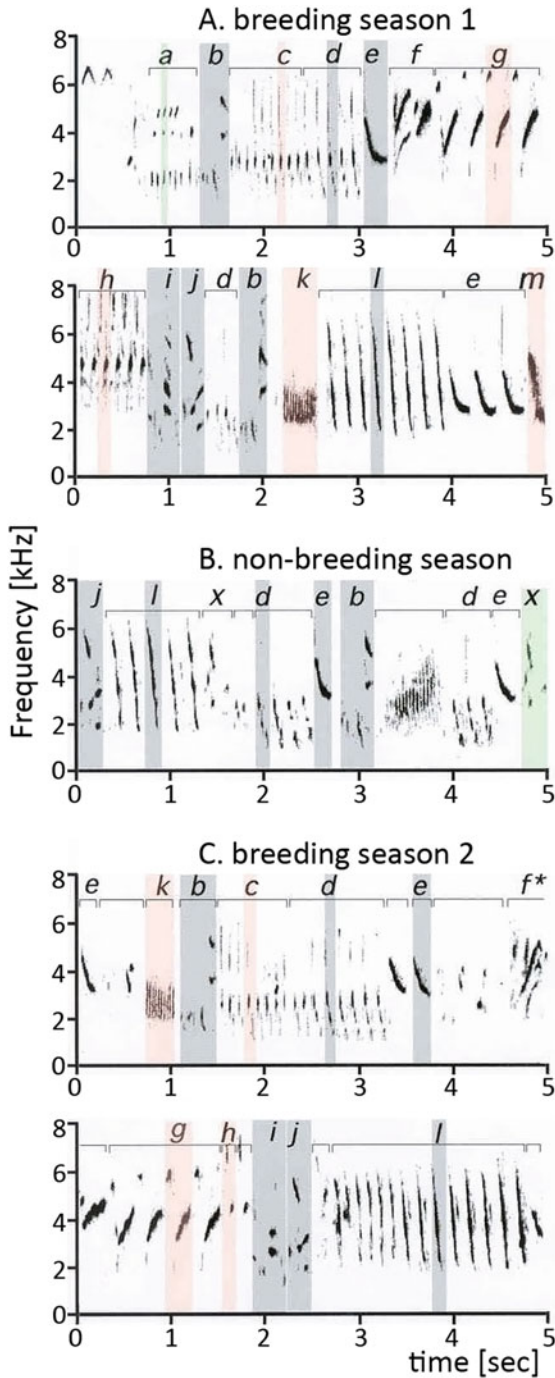


Fig. 7.3 Seasonal changes of the song pattern of wild canary males. Full songs of the breeding season (**a**) differ from plastic songs of the autumn (**b**) but are similar to the full songs uttered in the next breeding season (**c**). The repertoire composition, the number of unrepeated syllables and the

stereotyped in the full songs as compared to plastic songs (Smith et al. 1997). In black redstarts, full songs had more elements in two subparts (A and C) than songs of the nonbreeding period while other structural song parameters did not differ significantly between (Apfelbeck et al. 2013). In mockingbirds (*Mimus polyglottos*) the full song phrases are composed of significantly more repetitions of a given syllable type and the same individuals use partially different syllable repertoires in the spring breeding versus the autumnal nonbreeding season (Howard 1974; Logan 1983). In the New Zealand honeyeater, the tui (*Prosthemadera novaeseelandiae*), in the breeding season males' songs contained significantly greater proportions of trill components compared with songs in the nonbreeding season (Hill et al. 2015). In European starlings, full songs are characterized by longer song bouts and a larger repertoire (Van Hout et al. 2009). Further, although many species seem to sing during migration and on the wintering grounds (see above), only the great reed warbler (Sorensen et al. 2016; Węgrzyn and Leniowski 2009) was studied in detail in both periods. In difference to the song of the breeding season, songs of males wintering in Zambia were longer and less repetitive (Sorensen et al. 2016). In the willow warbler (*Phylloscopus trochilus*), songs recorded at the wintering grounds in Zambia seem to be somewhat longer with more variable syllable structure as compared to songs of breeding birds in Europe (Sorensen 2014), but this has not been analyzed statistically.

In summary, seasonality of the song structure has been studied quantitatively only in very few species (Table 7.1). Nevertheless, anecdotic reports on the seasonal occurrence of plastic songs suggest that it is a broad phenomenon occurring in various songbird families (e.g., Acrocephalidae; Fingillidae; Meliphagidae; Mimidae; Passerellidae; Phylloscopidae; Sturnidae; Turdidae). Seasonal structural changes such as song length, syllable repetition rates, syllable consistency, and repertoire composition are species specific (Table 7.1). However, individuals of some species



Fig. 7.3 (continued) song length change seasonally in wild canaries (Leitner et al. 2001a, b; Voigt and Leitner 2008); in domesticated canaries the syllable repetition rate changes in addition (Nottebohm et al. 1986; Voigt and Leitner 2008). Shown are spectrograms of song segments recorded from the same male in the field in April 1996 (breeding season 1, **a**), in November 1996 (nonbreeding season, **b**), and again in April 1997 (breeding season 2, **c**). Each syllable is a stereotyped set of one to several continuous sounds each with a typical frequency modulation. To illustrate this, some syllables are labeled with gray, green, or red. In a sequence, a syllable is repeated one to several times. Syllables that the bird produced year-round are labeled gray, those that are produced only in the breeding seasons are labeled red, those that were found only in one period are indicated green. A sequence of syllables from the 1996 breeding season (**a**) was marked with letters. Syllables that were produced in the following nonbreeding (**b**) and breeding season (**c**) are marked with the letters used in (**a**). About 75% of syllables such as b, d, e, i, j, l had correlation coefficients between 0.85 and 0.95 and are, therefore, produced year-round. About 25% of the syllables were produced seasonally. Half of those syllables (red) reappeared in the following year, i.e., are produced annually. Correlation coefficients for such syllables (for example c, g, h, k) were between 0.86 and 0.93. Certain syllables such as “a” and “x” (green) were not found in the subsequent seasons. “f” (**a**) and “f*” (**c**) are related syllables but with a correlation coefficients below 0.75 (after Leitner et al. 2001a, b)

species	song rate	song length	segment length	repertoire size	stereotypy	syllable rate	frequency range	references
zebra finch	x	x	-	-	-	-	x	2,4,6,18,28
Bengalese finch	x	-	-	-	n.a.	-	n.a.	19
black redstart	-	-	-	-	n.a.	x	x	1
blue tit	-	n.a.	-	-	-	n.a.	n.a.	11,12
blue-headed vireo	x	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	27
canary	x	x	x	-	x	x	n.a.	3,5,8
dark-eyed junco	x	-	-	-	-	-	-	9
house finch	x	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	23
pie'd flycatcher	x	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	20
red-winged blackbird	x	n.a.	n.a.	-	-	n.a.	n.a.	7,29
song sparrow	x/-	n.a.	x	-	x	-	n.a.	15,21,22,30
starling	x/-	-	n.a.	x	n.a.	-	n.a.	16,25,26
white crowned sparrow	x	n.a.	n.a.	n.a.	x	n.a.	n.a.	10, 14
white-throated sparrow	x	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	13
chaffinch	x	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	17,24

Fig. 7.4 Testosterone dependency of singing activity (song rate) and song structure (song length, segment length, syllable repertoire size, stereotypy, syllable rate, frequency range) of songbirds. Classifications are based on published studies that employed castration, hormone treatment and/or inhibiting of endogenous hormone production and androgen and estrogen receptor activity. Red: testosterone sensitive. Green: Estrogen sensitive. Yellow: Testosterone and estrogen sensitive. N. A. = not analyzed in the respective publication. References: 1 = Apfelbeck et al. 2012; 2 = Arnold 1975; 3 = Boseret et al. 2006; 4 = Cynx et al. 2005; 5 = Fusani et al. 2003; 6 = Harding et al. 1983; 7 = Harding et al. 1988; 8 = Heid et al. 1985; 9 = Ketterson et al. 1992; 10 = Konishi 1965; 11 = Kunc et al. 2006; 12 = Kurvers et al. 2008; 13 = Maney et al. 2009; 14 = Meitzen et al. 2007a; 15 = Nowicki and Ball 1989; 16 = Pinxten et al. 2002; 17 = Poulsen 1951; 18 = Pröve 1974; 19 = Ritschard et al. 2011; 20 = Silverin 1980; 21 = Smith et al. 1997; 22 = Soma et al. 1999; 23 = Strand et al. 2008; 24 = Thorpe 1958; 25 = Van Hout et al. 2009; 26 = Van Hout et al. 2012; 27 = Van Roo 2004; 28 = Walters et al. 1991; 29 = Weatherhead et al. 1993; 30 = Wingfield 1994 (From Gahr 2014)

such as the winter wren and the skylark (*Alauda arvensis*) change song parameters depending on the social context (Camacho-Schlenker et al. 2011; Geberzahn and Aubin 2014), which might be confounded with seasonal changes. Further, some observations of seasonal song structures might be due to juveniles that undergo song development in their first autumn and winter.

Another indication of seasonal changes in song structure is the occurrence of adult song learning. Adult learning of new song syllables likely affects overall song structure, particular in species that sing stereotyped songs in the breeding season such as canaries or song sparrow, in which changes of the syllable repertoire might affect syllable sequencing, song stereotypy, and or song length (Nottebohm and Nottebohm 1978; Leitner et al. 2001a, b; Nordby et al. 2001). Well-documented examples of changes of adult repertoires are the song sparrow (Nordby et al. 2001), the starling (Adret-Hausberger et al. 1990; Eens et al. 1992), the brown-headed cowbird (*Molothrus ater*; O’Loghlen and Rothstein 2002), and the mockingbird (Derrickson 1987). In light of seasonal structural changes, it is not relevant if adult song learning is de novo learning or altered syllable usage of material learned as juveniles.

Structural seasonal changes of the song of adult female songbirds have not been reported.

7.3 Testosterone-Dependent Seasonal Singing

7.3.1 Testosterone-Dependent Singing Activity

The gonadal dependency of singing of male birds was known for centuries based on the castration of roosters. Berthold with his seminal testis transplantation experiments was the first to recognize that a gonadal hormone, now known as testosterone, is controlling vocal activity and vocal structure (Berthold 1849). Likewise, in songbirds, seasonal singing activity was found to correlate with the hormonal activity of the testicles (Bullough 1942; Davis 1958; Armstrong 1973; Wingfield and Farner 1975). Testosterone is the main androgen released by the testicles and can be converted by the enzyme 5 α -reductase into the androgen 5 α -dihydrotestosterone (both androgens bind to the androgen receptor) and into the estrogen 17 β -estradiol (a potent ligand of both estrogen receptor α [ER α] and estrogen receptor β [ER β]) via the enzyme aromatase, which occurs in various tissues including the brain (Schlinger and Arnold 1991; Saldanha et al. 2000; Fusani et al. 2000, 2001; Schlinger and Remage-Healey 2012).

In temperate zones, the annual increase in day length triggers seasonal gonadal growth, which results in increased levels of circulating testosterone, an important initiator of reproductive behaviors. Supporting data of testosterone-dependent vocal activity (Fig. 7.4) come from hormone treatments of species of several avian orders including songbirds (e.g., Heid et al. 1985; Dloniak and Deviche 2001; Van Hout et al. 2009), subsocial passerines (Kroodsma 1985), parrots (Brockway 1968; Nespor et al. 1996), galliformes species (Marler et al. 1962; Andrew 1963; Chiba and Hosokawa 2006; Beani et al. 2000; Fusani et al. 1994), night herons (Noble and Wurm 1940), doves (Bennett 1940), and gulls (Terkel et al. 1976; Groothuis and Meeuwissen 1992). In particular, in all testosterone treatment experiments, male birds increased their singing activities (for review Gahr 2014). There is so far no report that testosterone treatment would fail to affect singing activity of birds. Further, males of MI species have maximal testosterone levels at the beginning of the breeding/singing period (e.g., Schwabl 1992; Fusani 2008; Goymann and Landys 2011; Apfelbeck et al. 2017).

In contrast to the testosterone hypothesis of singing, male birds of category MII and MIII sing outside of the breeding season when testicles are regressed (Armstrong 1973) and the levels of circulating testosterone are in many cases very low, around or below 100 pg per mL blood plasma (canary: Leitner et al. 2001a, b; Voigt and Leitner 2008/black redstart: Apfelbeck et al. 2013/song sparrow: Smith et al. 1997; Wingfield and Hahn 1994; but Soma et al. 1999/great tit: van Duyse et al. 2003/stonechats: Gwinner et al. 1994; Goymann et al. 2006). Because these values are close to the detection limits of most testosterone assays, (Wingfield and Farner 1975;

Leitner et al. 2001a, b; Gwinner et al. 1994; Goymann et al. 2006; Apfelbeck et al. 2013) the real blood testosterone concentration might even be lower. Since the detection of low amounts of testosterone is particularly sensitive to the sample volume and assay procedures, species differences of low testosterone levels might in part be procedural. In the breeding seasons, the amounts of circulating testosterone are in average 10–200 times higher: In the canary (Leitner et al. 2001a, b; Voigt and Leitner 2008), the great tit (Röhss and Silverin 1983; Van Duyse et al. 2003), the willow tit (Silverin et al. 1986), the black redstart (Apfelbeck et al. 2013), the European robin (Schwabl 1992), the mockingbird (Logan and Wingfield 1995), and the stonechats (Gwinner et al. 1994; Goymann et al. 2006) testosterone is high in the breeding singing season but low in the nonbreeding singing periods. It is unclear if these low levels of testosterone are relevant for the control of singing activity outside of the breeding season. In relation, inhibition of the androgen receptor did not affect singing outside of the breeding periods in male black redstarts and European robins (Schwabl and Kriner 1991; Apfelbeck et al. 2012, 2013).

Thus, testosterone data of seasonal (category MII) and year-round (category MIII) singing males support the notion that elevated levels are important for initiating singing in the breeding season but are not supportive for a testosterone-sensitive mechanism underlying autumnal and wintery singing. Further, although the overall relationship between testosterone and high singing activities is well established in the breeding season, there is mixed evidence of how individual variation in testosterone levels relate to individual variation in singing activity (e.g., Ketterson et al. 1992 but Saino and Moller 1995).

The effect of testosterone on song performance might involve androgenic and estrogenic action of testosterone and its metabolites. In the male zebra finch, aromatase inhibitor reduced the amount of directed (presumably courtship related) singing but not that of undirected singing (Walters et al. 1991). In great tits, estrogen might play a role for singing activity but this pathway was tested together with the androgenic control of singing (Van Duyse et al. 2005). However, singing rate was not estrogen sensitive in other species tested in this way, the canary (Fusani et al. 2003; Rybak and Gahr 2004), the black redstart (Apfelbeck et al. 2012), and the house finch (*Carpodacus mexicanus*; Strand et al. 2008).

As stated above, females of many species sing too. Testosterone is produced in the ovary as a precursor of estrogens (Johnson 1990). In relation, testosterone is highest in the chicken hen about 6–8 h before ovulation (Etches and Cheng 1981; Robinson et al. 1988). However, maximal concentrations of circulating testosterone (range: 50 pg–3.8 ng/mL) of female birds are four- to tenfold lower than in male conspecifics during the breeding season (Ketterson et al. 2005), and are around or below the detection limits in the nonbreeding periods (Ketterson et al. 2005). Concentrations of circulating estrogens in female songbirds are highest during the nest-building and the egg-laying period with concentration between 100 and 700 pg per mL blood plasma and are low throughout the rest of the year (Silverin et al. 1986; Wingfield and Farner 1978; Dawson 1983; Schwabl et al. 1980; Schwabl 1992; Gwinner et al. 1994).

In support of testosterone dependency of female singing, females that sing periodically or circumstantially are thought to secrete higher levels of testosterone in these periods. Such examples might be the female song sparrow (*Melospiza melodia*) (Arcese et al. 1988), the European robin (Schwabl 1992), the blue-capped cordon blues (Geberzahn and Gahr 2011), and female dunnocks, in which competition for male reproductive investment elevates testosterone (Langmore et al. 2002). Further, testosterone treatment induced singing in all adult female birds that differentiated the necessary song controlling brain structures during development (for reviews: Gahr 2007, 2014). However, these experimental concentrations of circulating testosterone are in average 10–500 times higher than those measured in untreated females and are higher than those found in males during the breeding season (e.g., Kriner and Schwabl 1991; Fusani et al. 2003; Hartog et al. 2009). On the other hand, female dark-eyed juncos have relatively high testosterone levels but do not sing regularly (Ketterson et al. 2005). Unfortunately, there are only little hormone data of females that spontaneously singing when circulating levels of testosterone are expected being low (e.g., female white-browed sparrow weaver: Wingfield et al. 1991 but York et al. 2016). Although estrogens have been shown to mediate some of the activational action of testosterone on vocalizations (Fusani et al. 2003; Fusani and Gahr 2006), these actions are due to estrogens derived from testosterone in the brain. Unfortunately, there are no estrogen data of females that were singing during nest-building/egg-laying period. Female European robins singing in winter had low to undetectable levels of estradiol (Schwabl 1992).

As stated above for the male birds, it is unclear if the low testosterone levels are relevant for the control of female singing behavior.

Thus, in summary, elevated levels of circulating testosterone correlate with males' singing activity in the breeding season but not with males' singing outside of the breeding season and not with the females' singing activities. A major problem of behavior–hormone correlations is the temporal resolution of data sampling, which is dense (e.g., daily) concerning the singing but sparse (weakly or biweekly or even less frequent) in case of the blood hormone measurements. In addition, testosterone production might undergo circadian changes. For these reasons short periods of high or elevated testosterone concentration are easily missed. Further, birds need to be caught for blood sampling. Thus, in most longitudinal field studies that cover one or more seasons, the singing activity data and testosterone data originate frequently from different individuals. Correlations of this type are particularly worrisome if the data sets originate from entirely different populations and years (e.g., Rost 1990, 1992) and should be avoided. Last, unfortunately the current testosterone assays cannot resolve low blood hormone concentrations. Thus, it needs to be seen if low levels of circulating testosterone are meaningful for song control.

7.3.2 *Testosterone-Dependent Seasonal Song Structure*

Vocalizations of some species (e.g., the canary, starling) change in structure after castration of adult males (Berthold 1849; Heid et al. 1985; Van Hout et al. 2009), can be reinstated with testosterone treatment after castration in adulthood (Heid et al. 1985), and can be induced in adult females by testosterone treatment (e.g., Shoemaker 1939; Leonard 1939; Konishi 1965; Kern and King 1972; Vallet et al. 1996). However, little attention has been paid to verify if testosterone-induced vocalizations of females are indeed “male-typical,” e.g., testosterone-treated female canaries sing male-like songs (Shoemaker 1939; Leonard 1939), which in average are composed of much fewer syllables compared to male canaries (Hartley and Suthers 1990; Fusani et al. 2003). However, some testosterone-treated female canaries produce songs with sexual release quality (Vallet et al. 1996). Likewise, in autumn, testosterone-induced songs of male chaffinches were reported being less structured than the full songs (Thorpe 1958).

In difference to overall testosterone sensitivity of singing activity, song structure such as song length, song fragment length (e.g., motif, tour, phrase), song unit repertoire (element, syllable, song type), song unit stereotypy, song unit repetition rates, or the frequency range are sensitive to testosterone treatment in a species-specific manner (Fig. 7.4; Gahr 2014). Thus, there are large species differences to the extent of which the song pattern is testosterone-sensitive, from little in the zebra finch to stark in the canary. In relation, acute levels of testosterone do not correlate with song structure such as repertoire size in the red-winged blackbird (*Agelaius phoeniceus*) (Weatherhead et al. 1993) or the canary. This might be due to fact that song structure depends on the organizational effect of testosterone, that is, there is a delay between testosterone’s effect on neuronal and neural endophenotypes and the occurrence of the overt phenotypes such as the song. In general, the relation between individual changes in testosterone levels and changes in song structure as well as interindividual differences in testosterone levels and such differences in song structure are vague.

The only example of brain-derived estrogens that control the song structure comes from the adult canary; estrogens are required to sing songs with high syllable-repetition rates (Fusani et al. 2003; Rybak and Gahr 2004; Fusani and Gahr 2006), a feature that is important for the sexual quality of canaries’ songs (Kreutzer and Vallet 1991).

7.4 Neural Mechanisms of Seasonal Singing Activity

Singing activity seems not controlled directly by the neural vocal control system that controls the structure of the song as detailed in the next paragraph. Even male canaries with bilaterally lesioned HVC (an important song control region of the songbird brain, see Fig. 7.5), try to sing although with no or little audible outcome

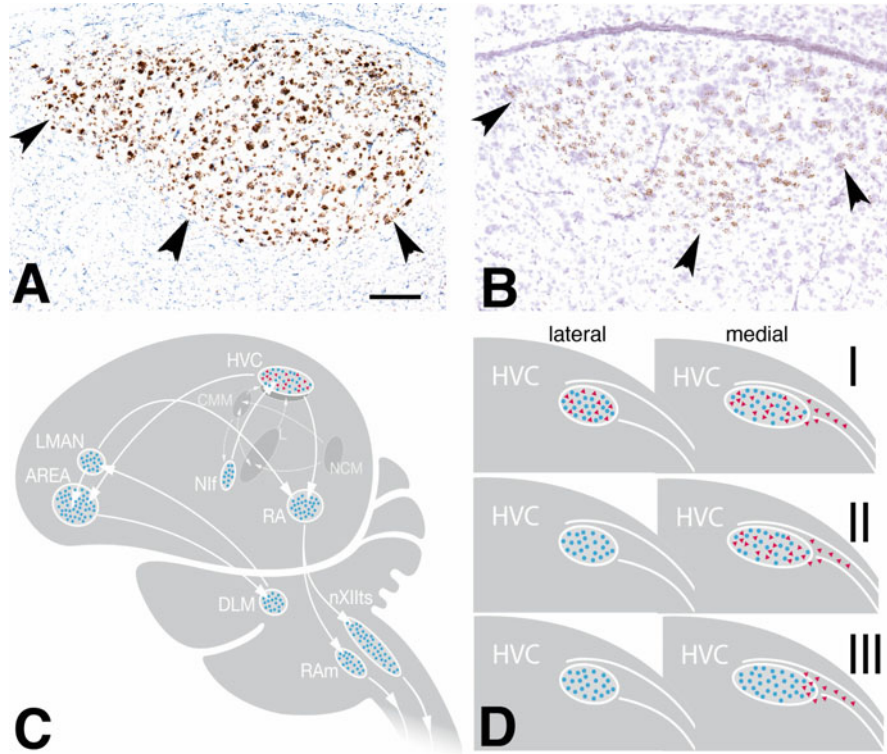


Fig. 7.5 Distribution of androgen receptors (AR) and estrogen receptors ($ER\alpha$) in the vocal control system. In **a**, we depict the expression of AR mRNA in the HVC of a male canary and in **b**, the $ER\alpha$ mRNA in the HVC of a great tit (*Parus major*) of the reproductive season. The mRNA expressing cells (brown) were labeled with a nonradioactive in situ hybridization method. In **c**, we show the distribution of AR (blue dots) and of $ER\alpha$ (red triangles) in the areas of a schematic vocal control system of songbirds. Some thalamic brain areas that appear important for coordination of the left and right vocal control network are omitted (see Wild 1997). Note that ER expression in vocal areas is limited to HVC and differs strongly between species (see **d** and Table 7.1). In **d**, we represent the distribution of AR and $ER\alpha$ in the lateral and medial part of the HVC: in type I, $ER\alpha$ is expressed throughout the entire HVC, in type II $ER\alpha$ is expressed in the medial HVC but not or very low in the lateral part, in type III $ER\alpha$ expression is low even in the medial part of HVC. In all songbirds, AR is expressed throughout HVC and $ER\alpha$ is found ventromedial to HVC. In Area X, AR is abundant only in some individuals. *Abbreviations*: Area X; DLM, nucleus dorsolateralis anterior, pars medialis; DM, dorsomedial nucleus of the midbrain nucleus intercollicularis; HVC, proper name; Field L; IMAN, lateral magnocellular nucleus of the anterior nidopallium; mMAN, medial magnocellular nucleus of the anterior nidopallium; NC, caudal nidopallium; NIF, nucleus interface of the nidopallium; nXIIIts, tracheosyringeal portion of the nucleus hypoglossus; RA, robust nucleus of the arcopallium; RAm, nucleus retroambigualis; rVRG, rostro-ventral respiratory group (after Frankl-Vilches and Gahr 2017)

(Nottebohm et al. 1976). In a non-songbird, the adult male ring dove (*Streptopelia risoria*), estrogens derived from testosterone in the preoptic area are important to stimulate sexual vocal displays (Hutchison and Steimer 1984). Likewise, in

songbirds the testosterone-inducible singing activity (see above; Gahr 2014) might be mediated by androgen or estrogen receptors that are abundant in preoptic neurons: Alward et al. (2013) showed that singing rate was increased by testosterone implants into the medial preoptic area of castrated male canaries while this treatment did not enhance the song structure such as song stereotypy. In relation, implants of estrogens plus dihydrotestosterone near HVC of white-crowned sparrows did not affect song rate (Meitzen et al. 2007a). How testosterone affects cellular mechanisms of preoptic neurons and how those would activate the vocal control areas needs to be seen.

However, such testosterone-dependent mechanisms acting in the preoptic region would not explain singing in seasons when testosterone levels are baseline. Riters and colleagues suggest that song intensity involves neuro-peptidergic mechanisms in limbic regions outside of the vocal control system such as preoptic and septal nuclei (Riters and Ball 1999; Riters 2012; Kelm-Nelson et al. 2013; Merullo et al. 2016). Others speculated that the hormone DHEA (dehydroepiandrosterone) would mediate singing in periods of low testosterone levels (e.g., Soma et al. 2002; Maddison et al. 2012), but there is conflicting evidence (e.g., Pintér et al. 2011). Further, limbic neurons are sensitive for modulatory action of monoaminergic systems, melatonin and opioids and might increase or decrease the probability to sing, although as stated before, the connections of these regions to the vocal control areas need to be identified (e.g., Wild 2017). Such neuro-modulating mechanisms might explain the impact of the sociosexual and physical environment (e.g., food and water availability in zebra finches: Rashotte et al. 2001; Johnson and Rashotte 2002) on singing activity independent of gonadal hormones (e.g., Gulledge and Deviche 1998; Bentley et al. 1999; Deviche and Gulledge 2000; Tramontin et al. 1999).

An alternative possibility of testosterone-sensitive singing activity in times of low testosterone is the increased sensitivity of vocal neurons for testosterone and its androgenic and estrogenic derivatives. Such an example is the vocal neurons of the silver-beaked tanager (*Ramphocelus carbo*), an endemic neotropical songbird from the Amazon region. In these males, seasonal activation of full song correlated with an increased expression of androgen receptors in the HVC, while testosterone levels remained basal for several weeks after onset of song activity (Quispe et al. 2016). Circulating levels of testosterone started to rise later in the breeding season and coincided with consummatory sexual behaviors. This indicates that equatorial silver-beaked tanagers expands the annual period of singing by transiently increasing the sensitivity of the vocal control system to testosterone, a mechanism that avoids potentially detrimental effects of prolonged periods of elevated testosterone (Quispe et al. 2016).

7.5 Neural Mechanisms of Testosterone-Dependent Seasonal Song Structure

As detailed before, in many tropical and some temperate zone birds, the same song pattern (full song) can be heard year-round (e.g., winter wren: Kreutzer 1973; the great tit): while others sing additional song types in the breeding period (e.g., morning song of white-browed sparrow weaver: Voigt et al. 2006; directed song of zebra finches: Pröve 1974; Sossinka and Böhner 1980; Kao and Brainard 2006) or sing plastic songs in the nonbreeding period (e.g., great reed warbler: Sorensen et al. 2016; canary: Nottebohm et al. 1986; Leitner et al. 2001a, b; Voigt and Leitner 2008). Species and sex differences in seasonal stability versus seasonal plasticity might depend on the testosterone sensitivity of neural vocal control regions, on the sensitivity of the genome to changing testosterone levels, and might depend on species-specific effects of testosterone-induced gene expression on neural circuit formation. Alternatively, seasonal vocal pattern might be influenced by testosterone sensitivity of auditory processing (Henry and Lucas 2009; Velez et al. 2015) in auditory areas that give input to the vocal control system. In relation, androgen receptors (ARs) are expressed in many neurons of the auditory forebrain (Metzdorf et al. 1999). This scenario is not further discussed in the present review.

7.5.1 *Seasonal Testosterone Sensitivity of Vocal Control Regions: Androgen and Estrogen Receptors in Vocal Neurons*

In songbirds, neural song control is achieved by a chain of interconnected brain areas in the fore-, mid-, and hindbrain (Nottebohm et al. 1976; Wild 1997; Hahnloser et al. 2002; Amador et al. 2013) (Fig. 7.5c). In particular, forebrain vocal control areas such as the HVC are evolutionary novelties of songbirds (Gahr 2000; Petkov and Jarvis 2012). In addition to the control of the song pattern, these areas are active during call-based vocal communication (Ter Maat et al. 2014; Benichov et al. 2016). The forebrain vocal circuit of songbirds connects to general avian vocal areas in the mid- and hindbrain via a projection of archistriatal neurons (the RA, robust nucleus of the arcopallium), in particular to the syringeal motonucleus (nucleus hypoglossus pars tracheosyringalis) and to respiratory pre-motor nuclei (Wild 1997).

One mode of steroid action in the brain is the alteration of gene expression by binding to intracellular steroid receptors that transactivate transcription of target genes in a ligand-dependent manner (Carson-Jurica et al. 1990). The androgen receptor (AR) has a high affinity for the testosterone and 5 α -dihydrotestosterone, but not for 5 β -dihydrotestosterone (Grino et al. 1990). The two types of estrogen receptors (ER α , ER β) bind 17 β -estradiol with high affinity. The AR gene codes for the AR protein, the ESR1 gene for ER α protein, and the ESR2 gene for ER β protein. The AR and ER α but not ER β occur in the vocal control system (see below).

In songbirds, AR mRNA or AR protein were reported for HVC, RA, and IMAN of all species studied (Balthazart et al. 1992; Bernard et al. 1999; Gahr et al. 1998, 2008; Metzdorf et al. 1999; Fusani et al. 2000; Voigt and Gahr 2011; Fraley et al. 2010; Quispe et al. 2016). Since these include species of various songbird families, among which are the basal Maluridae, the Corvidae, the Malaconotidae, and the derived Fringillidae and Thraupidae, the AR expression in HVC, RA and IMAN seems a general characteristic of songbirds (Frankl-Vilches and Gahr 2017). Further, AR mRNA and protein are reported for mMAN (medial magnocellular nucleus of the anterior nidopallium) and NIF (nucleus interfascialis) in canaries and zebra finches (Balthazart et al. 1992; Metzdorf et al. 1999; Fusani et al. 2000), but these areas have not yet been surveyed in other species. Extrapolating from the HVC, RA and IMAN data, we assume that AR expression in mMAN and NIF is also a common feature of songbirds. In Area X of zebra finches and canaries, ARs occur in only some individuals for unknown reasons (Gahr 2004; Kim et al. 2004). In another Estrildid finch, the wild white-rumped munia (*Lonchura striata*) and its domesticated relative the Bengalese finch (*Lonchura striata domestica*), ARs are expressed in a strain-specific pattern in Area X (Wada et al. 2013). In the brainstem, ARs occur in all respiratory-vocal areas and in syringeal motoneurons (Gahr and Wild 1997; Gahr 2000).

Among forebrain vocal areas, ESR1 mRNA and ER α protein is only expressed in HVC and around the dorsal aspect of RA of canaries and zebra finches (Gahr et al. 1993; Metzdorf et al. 1999). Further comparative data are available for ER α expression and protein abundance in the HVC of various species. These data suggest three types of distribution pattern (Frankl-Vilches and Gahr 2017) (Fig. 7.5d): (I) High expression of ER α throughout the entire HVC (e.g., canary, East-African shrike); (II) High expression of ER α only in the medial part of HVC (e.g., the forest weaver, the black redstart); and (III) No expression in the lateral part and low levels of ER α in the medial part of HVC (e.g., zebra finch, Bengalese finch). In all songbird species, large populations of ER α expressing neurons are found ventromedial to HVC aligning the lateral ventricle, an area including the so-called para-HVC (Johnson and Bottjer 1995), but extending much further medial than the latter (Gahr et al. 1993, and unpublished data).

In summary, all forebrain vocal control areas express or have the potential to express AR. Females of species of Maluridae, the Corvidae, the Malaconotidae, and the derived Fringillidae and Thraupidae that develop a vocal system, AR and ER α are expressed in the same areas as in their male conspecifics (Gahr unpublished data). Thus, since the expression pattern between species is very similar, AR and ER α distribution does not explain species differences in the degree of testosterone sensitivity of song features. In difference, ER α distribution of HVC varies considerably between species and suggests species indifference in estrogen dependency of vocal structures. Further, sexual differences of testosterone-dependent singing are not explained by sex differences in hormone receptor abundance in vocal areas.

Nevertheless, species differences in seasonal dynamics of both AR and ER α expression in vocal control areas might be involved in seasonality of song pattern and neural endophenotypes in a species-specific way (Fusani et al. 2000; Fraley et al. 2010). In the

canary, AR expression in HVC is similar in the breeding and the nonbreeding season and low during the molt while ER α expression is high in the nonbreeding season and at the beginning of the breeding season but lower during the later breeding season and the molt (Gahr and Metzdorf 1997; Fusani et al. 2000). In the white-crowned sparrow, AR expression in HVC is higher during the breeding season as compared to the nonbreeding season while AR expression in other vocal areas is similar in the two seasons (Fraleay et al. 2010). In general, AR expression in vocal control areas is rather invariant throughout the year except during the molt (Gahr and Metzdorf 1997; Gahr unpublished data).

7.5.2 Seasonal Changes of Transcription of Vocal Control Neurons

The same set of genes was found in genomes of various songbird species (Frankl-Vilches et al. 2015; Lovell et al. 2014; Warren et al. 2010). These findings suggest that the evolution of species-specific testosterone-sensitive song structures and related endophenotypes of songbirds does not result from the gain and loss of genes, but from the species-specific hormone-sensitive gene regulation (Frankl-Vilches et al. 2015). In contrast to the global similarity of songbird genomes, on the nucleotide level there are considerable species differences as shown above for the AR promoter of chicken and zebra finch. Such species differences can impact binding motifs of the ER α , the so-called estrogen response element (ERE) and of the AR, the so-called androgen response element (ARE) as shown for genes expressed in the HVC of the canary and the zebra finch (Frankl-Vilches et al. 2015). About 35% of the ERE-bearing and about 11% of ARE-bearing genes expressed in HVC of canaries were lacking these sites in the corresponding zebra finch orthologous promoters (Frankl-Vilches et al. 2015). Thus, species-specific evolutionary loss or gain (e.g., through point mutations) of EREs and AREs might underlie a species-specific gene pool that can be regulated by the activation of AR and ER α via testosterone and its androgenic and estrogenic metabolites in HVC.

This species-specific sensitivity of genes for AR and ER α together with species-specific testosterone profiles might lead to species differences in seasonal transcriptomes. In the white-crowned sparrow, seasonal comparisons of HVC and RA showed that gene expression is area-specific and time-specific across different reproductive conditions (Thompson et al. 2012). In the European robin, examination of HVC transcriptomes and histological analyses of song control nuclei showed testosterone-induced differentiation processes related to neuron growth and spacing, angiogenesis and neuron projection morphogenesis. Similar effects were found in female canaries treated with testosterone (Dittrich et al. 2014). In contrast, the expression of genes related to synaptic transmission was not enhanced in the HVC of testosterone treated female robins but was strongly upregulated in female canaries. A comparison of the testosterone-stimulated transcriptomes indicated that brain-

derived neurotrophic factor (BDNF) likely functions as a common mediator of the testosterone effects in HVC (Dittrich et al. 2014; Frankl-Vilches et al. 2015). BDNF is an important regulator of neuronal and neural plasticity (Kowiański et al. 2017). However, other modes of testosterone action, notably related to synaptic transmission, appeared to be regulated in a more species-specific manner in the HVC of robins and canaries. Divergent effects of testosterone on the HVC of different species might be related to differences between species in regulatory mechanisms of the singing behavior.

7.5.3 Comparisons of Seasonal Testosterone-Induced Differentiation of Song Control Regions and Song Structure

Comparisons of the neuroanatomy of male songbirds suggest that seasonal changes in song structure parallel seasonal changes in HVC size of several species (Nottebohm 1981; Tramontin and Brenowitz 2000). However, this pattern is not universal and a number of species do not show such a correlation (Gahr 1990, 1997; Brenowitz et al. 1991; Leitner et al. 2001a, b; Reeves et al. 2003; Phillmore et al. 2006). Next to HVC size, testosterone and its estrogenic metabolites affect various parameters of song control neurons of adult songbirds in a song-area-specific manner. These effects including synapse density and dendritic arbores in RA (DeVoogd and Nottebohm 1981), GAP-junctions in HVC (Gahr and Garcia-Segura 1996), spiking activity of RA neurons (Meitzen et al. 2007b, 2009), synapse protein expression in HVC (Voigt et al. 2004), and neurotransmitter content (Ball and Balthazart 2010). Although these neuronal features are closer to neural function than song-area size, their relations to testosterone-dependent vocal pattern remains to be seen.

Next, I discuss the consequences of local manipulation of testosterone and estrogen concentration and of testosterone- and/or estrogen-controlled proteins in particular song control regions. First, testosterone infusion into song areas suggest that local action of steroids in one song control area affects downstream areas (Brenowitz and Lent 2002; Meitzen et al. 2007a). In particular the works of Meitzen et al. (2007a) show that estrogenic and androgenic metabolites of testosterone act in HVC to increase firing rate of RA neurons, which correlates with song stereotypy but not with song performance in adult white-crowned sparrows. Such testosterone-induced firing rates of RA neurons reflect seasonality of RA neurons since spontaneous firing rates of such neurons are much higher in spring compared to autumn in white-crowned and song sparrows (Meitzen et al. 2007b, 2009). Likewise, testosterone infusion into RA of adult canaries increased the firing of RA neurons (Breutel and Gahr unpublished data). How HVC neurons affect the firing rate of RA neurons is not known.

In canaries, songs are composed of syllables that are repeated identically several times (so called tours) before switching to the next syllable. Fusani et al. (2003) induced singing in adult female canaries through testosterone treatment, but inhibited in one group of such females the aromatization of testosterone into estrogens with an aromatase inhibitor. Testosterone-induced development of male-like song in female canaries is accompanied by an increase in the expression and enzymatic activity of aromatase in the telencephalon near HVC (Fusani et al. 2001), the only vocal areas with higher levels of estrogen receptors (Fig. 7.2). After 3–4 weeks of testosterone treatment, females developed a male-like song, with exception that such females sang few different syllables. In correlation with the male-like songs (long sequences of repeated syllables), the HVC size of singing females increased and was different from untreated non-singing control females (Fusani et al. 2003). The estrogen-deprived singing females differed, however, in that they produced syllable sequences with lower repetition rates compared to the non-deprived singing females (Fusani et al. 2003). On the behavioral level, similar results were obtained for male canaries (Rybak and Gahr 2004).

The local action of testosterone on HVC and the song structure has been studied in some detail in canaries. Testosterone induces the production of vascular endothelial growth factor (VEGF) and its receptor (VEGFR2 tyrosine-kinase) in the canary HVC, which in turn leads to an upregulation of BDNF production in HVC endothelial cells (Louissaint et al. 2002). Systemic inhibition of the VEGFR2 tyrosine-kinase was sufficient to block testosterone-induced singing of female canaries, even though testosterone exerts its inductive action on HVC morphology such as increased volume and increased total number of HVC neurons (Hartog et al. 2009). Expression of exogenous BDNF in HVC, induced locally by *in situ* transfection, reversed this VEGFR2 inhibitor-associated blockage of song development. The VEGFR2-inhibited, BDNF-expressing females developed elaborate male-like full song features such as syllable repertoires and high repetition rates of song syllables (Hartog et al. 2009).

The work of Fusani et al. (2003) and Hartog et al. (2009) suggests that androgen-dependent overall HVC morphology (reflected in HVC volume) is necessary for the production of certain (basic canary pattern such as repetition of identical syllables) song structure of canaries while other (estrogen-dependent) song structures (high repetition rates of syllables) require neuronal properties that are independent of vocal area size. The association/dissociation of brain area size and a particular neuronal phenotype might be a species-specific phenomenon since HVC volumes appear estrogen sensitive in song sparrows (Soma et al. 2004) and white-crowned sparrows (Tramontin et al. 2003 but Baker et al. 1984) but androgen sensitive in the canary (Fusani et al. 2003; Fusani and Gahr 2006) and hormone insensitive in the Mexican house finch (Strand et al. 2008).

7.5.4 Males Versus Females

As stated above, the differences between testosterone sensitivity of singing activity and of song pattern, seasonal or not, of male and female songbirds are not explained by the expression of AR and ER α in vocal control areas. A similar conclusion comes from the comparison of the neuroanatomy of the song system of males and females of several species. In species with singing females sexual dimorphisms are found in a species-specific, area-specific way to a varying degree at all organizational levels of the song control areas, the gross-anatomical, ultrastructural, electrophysiological, biochemical, and molecular (gene-expression) level (Nottebohm and Arnold 1976; Nottebohm 1980; Gahr and Metzdorf 1997; Del Negro and Edeline 2002; Ritters and Ball 2002; Nealen 2005; Voigt and Gahr 2011; Duncan et al. 2011). Most notable, even in species such as the forest weaver, the East-African shrike and the Northern cardinal, in which male and female sing identical or nearly identical songs, respectively, there are sex differences in the size and organization of forebrain song control areas (Gahr et al. 1998, 2008; Jawor and MacDougall-Shackleton 2008; Voigt and Gahr 2011). Likewise, there is no correlation between song performance and song system anatomy since song areas are smaller in female streak-backed orioles that have a larger song output than the males of this species (Hall et al. 2010). Further, even in females that produce male typical songs due to testosterone treatment, the neuroanatomy is sexually dimorphic and does not allow relating neural features and hormone-dependent song pattern of males or females (Nottebohm 1980; Fusani et al. 2003; Hartog et al. 2009; Voigt and Leitner 2013).

7.5.5 Testosterone-Independent Seasonal Control of Song Structure

Vocal neurons express receptors for glucocorticoids (Suzuki et al. 2011; Senft et al. 2016), retinoic acid (Denisenko-Nehrbass et al. 2000), and melatonin (Gahr and Kosar 1996; Jansen et al. 2005; Fusani and Gahr 2015). Further, vocal neurons are sensitive for modulatory action of monoaminergic systems (Li and Sakaguchi 1997; Ball and Balthazart 2010) and opioids (Gulledge and Deviche 1998; Dloniak and Deviche 2001). These neurochemical phenotypes suggest that song phenotypes are under the control of multiple environmental signals that directly act on song neurons, bypassing the gonadal hormones or acting in concert with the gonadal hormones. The most direct evidence suggesting non-gonadal plasticity of singing comes from works on adult male zebra finches: melatonin affects their song pattern and the electrophysiology of RA neurons transiently (Jansen et al. 2005; Deregnacourt et al. 2012). Unfortunately, the impact of melatonin on song and vocal neurons of seasonal singers such as the canary has not been tested.

A common mechanism of song control, dependent and independent of gonadal hormone, might be BDNF-sensitive mechanisms of HVC. As explained above for

the canary, BDNF activity in the HVC is important for the production of sexually salient song pattern (Hartog et al. 2009). Whatever upregulates BDNF in HVC might facilitate differentiation of song structure. This notion is supported by the findings that BDNF expression, at least in rodents can be modulated by many factors that reflect environmental conditions, next to sex hormones (Dittrich et al. 1999; Louissaint et al. 2002; Scharfman and MacLusky 2005; Berton et al. 2006). In this scenario, BDNF upregulation in the vocal control system, even in birds with low levels of gonadal hormone production should show some form of singing.

7.6 Conclusion. Seasonal Singing: Who, How, and What for?

Traditionally, it is assumed that singing of songbirds and song-like vocalizations of other bird species such as the crowing of the chicken are male-typical behaviors (Thorpe 1961, pp. 41–48). This idea was particularly sponsored by the observation of many naturalists that male birds of the Northern hemisphere sing intensely during the breeding season but not in fall or early winter (Fry 1916; Cox 1944; Saunders 1947, 1948). However, the reconsideration of old observations (Fry 1916; Alexander 1935) and new studies of species of the Northern and Southern hemisphere (e.g., Kelsey 1988; DeWolfe and Baptista 1995; van Duyse et al. 2003; Kunc et al. 2006; Bezzel 2011; Apfelbeck et al. 2013; Sorensen 2014; Sorensen et al. 2016) clearly demonstrate that singing outside the breeding season is a common behavior of male songbirds while their testosterone levels remain low (e.g., Schwabl 1992; Apfelbeck et al. 2013; York et al. 2016). Further, detailed studies of tropical and temperate species in the last three decades and reconsideration of old studies of Australo-Asian species led to the conclusion that singing of female songbirds is an ancient and widespread behavior (e.g., Gahr and Güttinger 1986; Hoelzel 1986; Ritchison 1986; Odom et al. 2014), while testosterone levels of singing females are low in most cases (for review: Ketterson et al. 2005). These findings question the testosterone hypothesis of song production. However, a key problem is the interpretation of “high” and “low” testosterone levels, which would require a basic understanding of the quantitative interaction of testosterone molecules, androgen receptor (AR) and estrogen receptor (ER) densities, and transcriptional regulation, e.g., would the transient upregulation of AR in HVC or the vocal system in general be a mechanism to maintain song structures in seasons when testosterone production is low? Or do other endocrine systems induce singing in males outside of the breeding season and in females at various annual periods? Or are males and females able to regulate AR and ER dependent mechanisms via non-endocrine pathways? These are just a few possibilities to explain the mismatch of the seasonal profiles of testosterone and of singing behavior. More detailed field studies of hormone production and singing of males and females as well as detailed molecular analysis of hormone-receptor-hormone interactions are needed to elucidate the neuroendocrine control of seasonal

singing. Insights into the endocrine control of male singing outside the breeding season and of female singing are essential for understanding the proximate and ultimate mechanisms of seasonal singing.

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