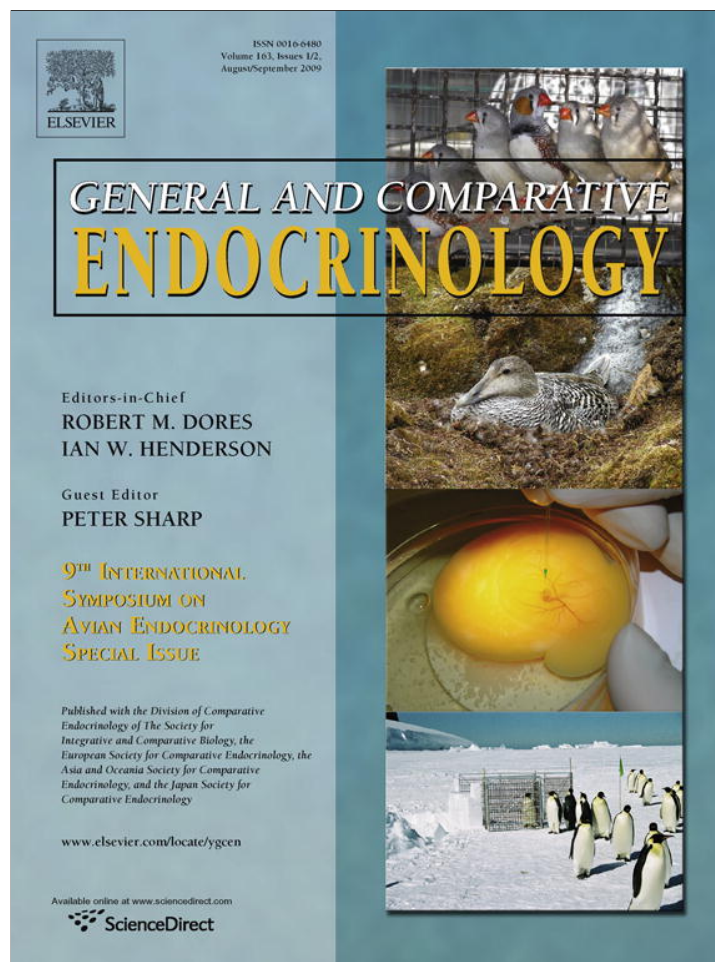


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## Seasonal neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding birds

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### ABSTRACT

The avian song control system is one of the primary models used to study neuroplasticity and neurogenesis in the adult vertebrate brain. A great deal of progress has been made in understanding the mechanisms controlling seasonal neuroplasticity of the song control system. However, relatively little work has been done to identify how prevalent this phenomenon is and if a diversity of environmental cues can regulate it. Photoperiod is the primary environmental cue used by mid- to high-latitude seasonally breeding birds to time growth of the song control system but many birds display flexible or opportunistic breeding patterns that are less reliant on photoperiodic cues. In addition, ~75% of birds are tropical and in only one such species has neuroplasticity of the song control system been studied. Our goal is to outline some of what is known and expand on the ways that studying tropical, flexibly, and opportunistically breeding birds can advance our understanding of plasticity in the song bird brain.

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### 1. Seasonal changes in brain structure and function associated with reproduction

The majority of animals exhibit seasonal changes in behaviors. Many seasonal behaviors, such as territoriality, migration, food caching, and reproduction can be linked with seasonal changes in the brain (Dawson, 2008; Lucas et al., 2004; Tramontin and Brenowitz, 2000). In the majority of birds that have been studied, the annual photoperiod cycle is the primary environmental factor used to time reproductive development. When a stimulatory photoperiod is reached in the spring (usually 12 h of light or more; often termed long days) release of gonadotropin-releasing hormone-I (GnRH-I) from the hypothalamus increases (Dawson and Sharp, 2007). As a result of GnRH-I release, luteinizing hormone (LH) and follicle stimulating hormone (FSH) increase in the blood, followed by gonadal growth, increased sex steroid production, gamete production and maturation, and reproductive behaviors (Dawson et al., 2001; Hamner, 1968). Long day stimulation maintains elevated sex steroids levels and reproductive function throughout the breeding period and if photoperiod is experimentally reduced below the minimal stimulatory length, sex steroid levels will decline and reproductive behaviors will cease (Hamner, 1968; Wingfield et al., 1993). However, in free-living temperate zone photoperiodic birds, reproduction is normally terminated by mid-summer, while photoperiods are still long. After prolonged exposure to long photoperiods (approximately 8 weeks, varying among species and

dependant on the specific day length/light intensity) these seasonally breeding birds stop responding to light as a stimulus for reproduction. Plasma LH and FSH decline, and gonads regress (Dawson and Sharp, 2007). This change in response to photoperiod is termed absolute photorefractoriness and most photorefractory birds will not respond to long days as a reproductive stimulus until they are exposed to a period of short days (usually <12 h per day of light) for several weeks (Dawson et al., 2001).

In some birds, the timing of breeding can vary by months between years or between populations (Hahn et al., 2008). In many of these cases, reproduction is not closely correlated with changes in photoperiod and consequently photoperiod is thought to be less important or uninvolved in regulating reproductive function. For example, the majority of animals inhabit tropical latitudes where photoperiodic changes are minimal, but they still exhibit seasonal behaviors (Hau et al., 2008). In addition, some temperate zone species have highly flexible seasonal cycles that do not correlate with changes in photoperiod (Hahn and MacDougall-Shackleton, 2008). For our purposes, we will refer to species in which birds have been observed breeding during most or all times of the year as *opportunistically breeding* species. These species do not continuously breed year-round but they can apparently breed whenever favorable conditions occur. Further, we will refer to species that are able to breed whenever favorable conditions arise within a “window” of time during the year (often 6 months or more) as *flexibly breeding* species. In these species, there is at least one period of the year when these animals have never been observed breeding, even if environmental conditions appear to be conducive to reproduction. Finally, we will classify species that breed in the tropics simply as

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tropical breeding species (Table 1). Many tropical species have long breeding seasons with a great deal of spatial and temporal variability in the timing of reproduction (Hau et al., 2008). However, the data on breeding cycles in tropical species are often incomplete or limited to just a few years thus making it difficult to categorize them as either opportunistic or flexible breeders. It is important to emphasize that flexible, opportunistic and tropical breeding strategies are not mutually exclusive terms and are potentially very similar mechanistically. Many species may fall into multiple categories, often depending on the population.

## 2. Song control system

The seasonal growth and regression of the avian song control system has been at the forefront of vertebrate neuroplasticity research for the past three decades and is perhaps the best studied example of adult neurogenesis (Tramontin and Brenowitz, 2000). This system persists as a leading model in the field because the brain nuclei associated with learning and production of song are well defined. Further, the natural seasonal changes observed in the avian brain are the most pronounced and best defined changes of all vertebrates studied thus far (Brenowitz, 2004). For our purposes, we are defining neuroplasticity as organizational changes in the brain which can include changes in cell volumes, brain nuclei volumes, dendritic arborizations, neurogenesis, and apoptosis. Most studies on neuroplasticity of the song control system quantify volumetric changes of the song control nuclei. In some species, changing rates of neurogenesis and apoptosis in the brain contribute to increases and decreases in song nuclei volume. However, rates of neurogenesis and apoptosis have not been studied in all birds that experience changes in song nuclei volume (Tramontin and Brenowitz, 2000). Because of this, we will generally refer to changes in the brain as “neuroplasticity” and only discuss neurogenesis when specify data is available.

The volumes and cytoarchitectural characteristics of the song control system change seasonally, paralleling changes in the activity of the reproductive system and singing rates (Nottebohm et al., 1976). During the breeding season, HVC, the robust nucleus of the arcopallium (RA), and Area X can more than double in volume in comparison to the nonbreeding season (Tramontin and Brenowitz, 2000). Numerous experiments support a role for testosterone in both singing behavior and the seasonal changes in the song control system (Ball et al., 2004; Tramontin and Brenowitz, 2000). Estrogens, such as estradiol, can also stimulate growth of HVC, RA and

Area X (Tramontin et al., 2003). Androgen receptors are present in HVC, RA, IMAN, Area X, and nXIIIs, while estrogen receptors are found in HVC of some species (Gahr, 2001). Taken together, these data suggest a complex relationship among neuroplasticity of the song control system, photoperiod, sex steroid release, and sex steroid receptor regulation in temperate zone species.

Although the majority of data support testosterone and its metabolites as the primary regulators of seasonal song system growth and singing behavior, there is evidence that non-sex steroid-dependent pathways are also important. The song control nuclei grow, although not to full size, in response to photostimulation in castrated species (Smith et al., 1997; Whitfield-Rucker and Cassone, 2000). Growth of the song control nuclei in photostimulated, castrated dark-eyed juncos, *Junco hyemalis*, is not enhanced by testosterone treatment and is greater than testosterone treated birds on a short, winter like photoperiod (Dloniak and Deviche, 2001). Similarly, intact photorefractory American tree sparrows, *Spizella arborea*, have larger HVC than short day photosensitive individuals, despite both groups having undetectable testosterone levels (Bernard et al., 1997). These data suggest that changes in the song control system during photostimulation are at least partially acting through non-gonadal pathways and may be sex steroid independent (Ball et al., 2004). However, a non-gonadal source of sex steroids, such as the adrenals or *de novo* steroid synthesis in the brain (neurosteroids), makes it difficult to determine how important steroid independent pathways are (Brenowitz, 2004; Schlinger and London, 2006).

In addition to testosterone, the hormone melatonin can influence growth of the song control system. Similar to mammals, melatonin regulates the circadian cycle of many bird species (Cassone et al., 2008; Gwinner et al., 1997) and melatonin may be important in mediating the reproductive response to photoperiod in *Galliformes* (Guyomarc'h et al., 2001; Ohta et al., 1989; Rozenboim et al., 2002). However, melatonin does not appear to influence seasonal photoperiodic regulation of the passerine gonadal cycle (Chakraborty, 1995; Rani et al., 2007; Wilson, 1991). Despite these findings, 125-Iodometatonin (IMel) binds throughout the song control nuclei of birds (Bentley et al., 1999; Whitfield-Rucker and Cassone, 1996). Exogenous melatonin treatment can also attenuate HVC growth in European starlings (Bentley et al., 1999) and house sparrows (Cassone et al., 2008). Additionally, melatonin binding in Area X is lower in European starlings that are photostimulated when compared to photosensitive starlings on short days and photorefractory starlings on long days (Bentley and Ball, 2000). These

**Table 1**  
General summary of song control nuclei (SCN) plasticity in four non-seasonally breeding models. Each species is placed in one or more general breeding strategy categories: opportunistic breeding, flexible breeding, or tropical. '?' next to species name indicates categorization is less clear.

Breeding pattern/species	Definition	Existing data on neuroplasticity	Potential future contributions
Opportunistic <i>Taeniopygia guttata</i> <i>Loxia leucoptera</i> ?	Can breed whenever favorable conditions arise	Neurogenesis occurs throughout the year but growth of SCN has not been observed in adult <i>Taeniopygia guttata</i> , a possible adaptation for year-round rapid initiation of breeding behavior	Could help identify the role of neurogenesis in SCN plasticity. Further, comparing the degree/absence of SCN growth during the year could indicate “preparedness” for reproduction
Flexible <i>Aimophila carpalis</i> <i>Zonotrichia capensis</i> ? <i>Loxia leucoptera</i> ?	Can breed whenever favorable conditions arise within a broad “window” of time	Neuroplasticity of the SCN occurs but it may not be strictly regulated by photoperiod and the volumetric changes are comparatively small for species in which we lack data from a full year ( <i>Aimophila carpalis</i> , <i>Zonotrichia capensis</i> )	Growth of SCN many occur in stages or progress slowly over the first few weeks/month of the breeding “window”. Could help identify critical stages in SCN growth that regulate singing behavior
Tropical <i>Zonotrichia capensis</i>	Species found in the tropics with long breeding seasons but too little data exists to define their breeding strategy	Neuroplasticity in SCN does occur in the tropical <i>Zonotrichia capensis</i> but it is unknown if it occurs in birds with entirely tropical phylogenetic histories	Could provide insight into non-androgen pathways regulating singing, non-photoperiodic regulation of neuroplasticity, and the evolution of neuroplasticity in the SCN

data indicate melatonin inhibits the growth of the song control nuclei and decreased sensitivity to melatonin in Area X may be an important aspect of this regulation. However, it remains unclear if melatonin is an important regulator of song control nuclei growth under natural conditions.

As the complex interactions of hormones and photoperiod continue to be identified, it is becoming apparent that separating the effects of specific hormones from the multitude of photoperiodic effects is challenging in highly photoperiodic species. It is also unclear if environmental signals other than photoperiod can serve to mediate growth and regression of the song control system. Investigations of tropical, flexibly, and opportunistically breeding songbirds promise to be useful in expanding our understanding of seasonal changes in brain structure and function.

### 3. Neuroplasticity in tropical, flexibly, and opportunistically breeding species

Plasticity of the song control system has been studied in only a few species that are tropical and/or exhibit flexible/opportunistic breeding patterns. We present four examples of these non-traditional models for studying reproduction and neuroplasticity of the song control system. While not as extensively understood as temperate zone seasonal species, these species are advancing our understanding of the role of environmental cues other than photoperiod in regulating seasonal neuroplasticity of the song control system.

#### 3.1. Tropical rufous-collared sparrow

Rufous-collared sparrows (*Zonotrichia capensis*) are the first tropical vertebrate known to exhibit seasonal neuroplasticity (Moore et al., 2004b). This species ranges from Southern Mexico to Southern Argentina, and breeds seasonally on the equator (Moore et al., 2005). In equatorial populations of this species, reproduction appears correlated with decreasing rainfall at the end of the rainy season, a time period when food availability is probably increasing. Different populations at the same latitude often breed at different times of the year, consistent with the different wet/dry seasonal patterns that these populations experience (Moore et al., 2004b).

Similar to temperate zone species, the song control nuclei of rufous-collared sparrows increase in size at the beginning of the breeding season (Moore et al., 2004b). Free-living individuals from two populations at the same latitude were sampled during breeding and non-breeding periods. In both populations, HVC, RA, and Area X were larger in breeding versus non-breeding males. Similar to the timing of reproduction, the song control nuclei grew at different times of year when compared between sites. The asynchronous changes between the two populations, and the fact that these birds only experience a ~3 min annual shift in photoperiod (US Naval Observatory), strongly suggests that photoperiod is not a significant regulator of the reproductive system or song control nuclei size in the wild (Moore et al., 2004b).

Similar to temperate zone species, rufous-collared sparrows have enlarged song control nuclei when testosterone is elevated and males sing more (Moore et al., 2002). These data suggest a similar causal relationship between testosterone, song production, and song control system neuroplasticity as is observed in higher latitude species. In addition, 3 weeks of testosterone treatment stimulated growth of HVC and RA, but not Area X, in captive, adult, male rufous-collared sparrows (Small et al., 2007a). Similar to findings in free living individuals, HVC and RA increased <30% in volume. This is far less of an increase than commonly observed in temperate zone species (Tramontin and Brenowitz, 2000). How-

ever, free living pre-breeding birds may have had partially developed song control nuclei, thus minimizing the observed magnitude of change. Also different from temperate zone species, the testosterone treated captive males did not sing despite having enlarged HVC and RA (Small et al., 2007a). These birds were individually housed in cages in an outdoor aviary (Quito, Ecuador) and were visually isolated from other males. The captive housing conditions could have suppressed singing behavior, however, these data are consistent with free living testosterone treated males showing no changes in singing behavior associated with aggression (Moore et al., 2004a). These data suggest that elevated testosterone is less important in regulating behaviors such as singing and aggression in comparison to temperate zone birds. These data also indicate that increased expression of singing behavior is not essential for growth of HVC and RA in rufous-collared sparrows, although, it is unclear if singing behavior facilitates growth of Area X. In addition to understanding seasonality in tropical species, continued research on rufous-collared sparrows could provide insight into non-androgen dependent pathways regulating singing behavior and regulation of song system growth independent of singing behavior.

#### 3.2. Opportunistically breeding zebra finch

Zebra finches, *Taeniopygia guttata*, are a classic example of an opportunistic breeder. Free-living zebra finches found in arid regions of Australia breed during any month of the year, often after periods of irregular rain (Keast and Marshall, 1954). This rain associated activation of the reproductive system may result from increased food availability. In support of this, captive zebra finches can breed year round, regardless of photoperiod, if mates and *ad libitum* food are provided (Perfito et al., 2008; Zann, 1996). Free-living males can have enlarged “semi-activated” testes year round (Farner and Serventy, 1960; Zann, 1996), although in some populations males fully regress their gonads during non-breeding periods (Hahn et al., 2008; Perfito et al., 2007). Male zebra finches exposed to photoperiods exceeding natural photoperiods grew their gonads (Bentley et al., 2000), but this response may be an indirect effect resulting from increased food intake during long day exposure (Perfito et al., 2008). Thus, while photoperiod may play a role in regulating reproductive function in this species, it does not appear to be the primary stimulus for reproduction development.

Male zebra finches can sing year around but they increase singing behaviors focused on nearby females (directed song) during courtship (Zann, 1996). Changes in song control nuclei volumes have not been documented in adult zebra finches, yet neurogenesis can occur throughout adulthood (Wilbrecht and Kirn, 2004). These data could indicate that male zebra finches have “semi-active” song control systems throughout the year, similar to their gonads in some populations. However, studies on free-living population may reveal a period of regression, similar to that of gonadal function (Perfito et al., 2007). It is also unknown whether photostimulation or diet manipulation could influence song control nuclei volumes.

#### 3.3. Opportunistically/flexibly breeding white-winged crossbill

White-winged crossbills, *Loxia leucoptera*, are nomadic birds that are found in the boreal coniferous forests of North America and reproduce during periods of unpredictable food availability (Benkman, 1990). Demonstrating the opportunistic nature of their breeding pattern, these birds have been reported reproducing during any month of the year including during the shortest and longest photoperiods of the year (Benkman, 1990; Deviche and Sharp, 2001). However, these birds apparently do not respond to good conditions for breeding during autumnal molt which suggests

they have more of a flexible breeding pattern rather than a strictly opportunistic breeding schedule (Deviche and Sharp, 2001; Hahn et al., 2008).

Captive male and female white-winged crossbills had larger HVC, RA and Area X when exposed to long, summer like photoperiods in comparison to birds exposed to shorter winter and spring like photoperiods (MacDougall-Shackleton et al., 2001). Females had smaller song control nuclei than males but still demonstrated a similar seasonal pattern in response to changes in photoperiod. Males exposed to long photoperiods also have developed testes and elevated plasma LH (Hahn et al., 2004; MacDougall-Shackleton et al., 2001) and they do not appear to become absolutely photorefractory (Hahn et al., 2004). These data indicate that photoperiod can influence reproductive system activity and growth of the song control system in white-winged crossbills.

MacDougall-Shackleton et al. (2001) argue that testosterone is the most likely hormonal signal mediating the effect of photoperiod on the song control system. Based on this, they postulate that crossbills breeding during the short days of winter should also have high testosterone and enlarged song control nuclei. This hypothesis remains untested but if song control nuclei are enlarged during short day breeding, this species could provide insight into the interaction of photoperiod and other environmental cues to regulate neuroplasticity. Alternatively, if song control nuclei are not enlarged during short day breeding, this species could provide insight into the importance of neuroplasticity in regulating singing behavior.

#### 3.4. Flexibly breeding rufous-winged sparrow

Rufous-winged sparrows, *Aimophila carpalis*, are residents of the Sonoran Desert that breed after irregular summer monsoon rains. Field and captive data demonstrate that increased photoperiod stimulates testicular development in March and maintains it until early September (Small et al., 2007b). In captivity, exposure to stimulatory long days for periods up to 11 months does not cause spontaneous reproductive regression and birds regressing gonads in the wild are still photosensitive (Small et al., 2007b). These data indicate that in this species reproductive regression is not caused by absolute photorefractoriness. Further, captive males transferred from a non-stimulatory short day treatment (8 h of light per day; 8L) to a long day treatment (13 or 14L) will develop their reproductive systems, however, transferring birds from a longer photoperiod (16L) to 13L or 14L results in reproductive regression (Small et al., 2008a). These data indicate that captive long day exposure causes reduced sensitivity to day length as a reproductive stimulus, similar to relative photorefractoriness. Despite photoperiodic regulation of the testicular cycle, plasma LH and testosterone normally do not increase in the spring during testes development. Instead plasma LH and testosterone commonly stay low throughout the summer and increase in July within a few days of the first summer monsoon rains and concurrent with reproductive behaviors (Deviche et al., 2006; Small et al., 2007b; Strand et al., 2007). The specific environmental cues that stimulate increased plasma LH and testosterone are not known, but increased food availability may be important (Small et al., 2005).

Rufous-winged sparrows also exhibit plasticity of the song control system. HVC and RA grew 23% and 38%, respectively, between July 2 (pre-breeding; one week prior to the first monsoon rain) and July 29 (breeding) (Strand et al., 2007). This growth occurred during decreasing day length, however, plasma testosterone and singing rates were likely to have increased during this same time period (Deviche et al., 2006; Strand et al., 2007). Currently it is unknown whether testosterone influences growth of the song control system in rufous-winged sparrows. Total neuron numbers in HVC and RA did not change between sampling dates, suggesting that

song control nuclei volumes did not increase as a result of changes in the rate of neurogenesis and/or apoptosis.

Similar to equatorial rufous-collared sparrows, pre-breeding song control nuclei volumes may not be representative of the minimal annual volumes of these nuclei. Thus the degree of growth and regression, in comparison with more traditional temperate zone seasonal breeders, is unclear. Further investigations could help determine if growth of the song control system occurs in stages in rufous-wing sparrows, possibly starting in the spring concurrent with testes growth, or if it occurs very slowly throughout the summer prior to the normal breeding period.

#### 4. Future questions regarding neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding birds

The studies described above demonstrate how non-traditional models are expanding our understanding of neuroplasticity of the song control system. Here, we present some future research areas that we feel will be profitable. While some are specifically targeted towards the song control system, others are broader in scope. Generally speaking, until we develop a greater understanding of the environmental and hormonal cues that mediate seasonal neuroplasticity, we will not understand how it operates or how widespread the phenomenon is.

##### 4.1. How prevalent is seasonal neuroplasticity of the song control system?

Most studies on the seasonal neuroplasticity of the song control system have been done on relatively few species (Tramontin and Brenowitz, 2000). Thus far, only one study (Moore et al., 2004b) has demonstrated (or even studied) seasonal neuroplasticity of the song control system in a tropical bird despite the fact that the vast majority of birds are tropical (Stutchbury and Morton, 2001). While that study of rufous-collared sparrows demonstrated that neuroplasticity of the song control system can exist in a tropical species, it does not let us know if it is common in tropical birds (or animals) in general. Rufous-collared sparrows are the only tropical member of the genus *Zonotrichia*. By studying rufous-collared sparrows, data can be compared to findings in white-crowned sparrows, *Z. leucophrys*, a well established model in song system research. This comparison minimizes phylogenetic confounds, but the data on rufous-collared sparrows does not inform us if neuroplasticity is seen in birds with entirely tropical phylogenetic histories. If seasonal neuroplasticity of the song control system exists in a tropical bird from a purely tropical lineage, it would provide substantial evidence that neuroplasticity evolved independently of photoperiodicity and is likely to be common in tropical birds.

##### 4.2. When should we expect to see neuroplasticity of the song control system?

Similar to white-winged crossbills and rufous-winged sparrows, many birds with flexible breeding schedules are likely to exhibit seasonal neuroplasticity of the song control system. In these species, the specific timing of breeding often varies within a broad "window" during the year. The primary question that arises for these species is when we would predict growth of the song control nuclei to occur: at the beginning of the "window", or concurrent with the beginning of reproductive behaviors, or at both times? When rufous-winged sparrows and rufous-collared sparrows (which share similarities with flexible breeders) were sampled in pre-breeding and breeding condition (a few weeks apart) song con-

control nuclei grew, indicating growth concurrent with reproductive behaviors. However, volumetric changes during this period were much smaller than are observed in many photoperiodic seasonal species (Moore et al., 2004b; Strand et al., 2007). Interestingly, when male white-winged crossbills were sampled three times over 12 months, thus increasing the chances of sampling the extremes of song nuclei volume, the magnitude of volumetric changes were comparable to photoperiodic seasonal species (MacDougall-Shackleton et al., 2001). These data suggest that sampling flexibly breeding birds solely in pre-breeding and breeding condition may not be sufficient to obtain the full range of volumetric change.

In flexibly breeding models, growth of the song control nuclei may begin many months in advance of changes in singing behavior. This growth may occur in stages or progress slowly over a broad period of the year. If slow or staggered growth of the song control nuclei does occur, it could provide a unique opportunity to study the stages of song control nuclei plasticity over time. If this slow/staggered growth does not occur, it suggests that the magnitude of growth of the song control system is far less in some flexibly breeding birds than in seasonal photoperiodic birds. Understanding how and why these less pronounced changes differ from the more dramatic changes seen in other models could also provide insight into critical stages in the regulation of singing behavior.

Opportunistically breeding birds may employ different patterns of song control system plasticity depending on the species. Opportunistically breeding males have to be prepared to use song to attract mates and defend territories during any time of year. In such cases it may not be adaptive to have a song system that regresses and thus limits their ability to perform these tasks. This model is consistent with the absence of documented song control nuclei growth in adult zebra finches. However, zebra finches still exhibit neurogenesis throughout the year which may be important for regulating changes in singing behavior. White-winged crossbills can exhibit a seasonal cycle in song control nuclei growth and regression, but it is unclear how consistent this seasonal cycle is in free-living crossbills. Together, these data suggest that opportunistically breeding species could employ a variety of different strategies for regulating singing behavior and song control nuclei plasticity. Continued investigations into song system plasticity in opportunistic models may help differentiate between breeding strategies used by birds categorized as “opportunistic” by further elucidating the animal's preparedness to engage in reproductive behaviors at any time of year.

#### 4.3. What are the environmental cues and hormonal mechanisms mediating neuroplasticity of the song control system in tropical, flexibly, and opportunistically breeding species?

In the absence or decreased importance of initial predictive cues, it is possible that tropical, flexibly, and opportunistically breeding birds use more *reactive cues* to time seasonal reproduction. Rainfall, food abundance, and social cues could be examples of more reactive cues because birds use them to evaluate and respond to their current environmental conditions. In temperate zone species, rainfall and diet cues have been considered supplementary cues or short-term cues (Hahn et al., 2008) to the overall initial predictive cue of photoperiod. That is, these cues are still predictive but on a shorter time frame. In the absence or decreased importance of photoperiodic cues, these other cues may play a more important role. This more important role could be to inform the animal about the current breeding conditions because longer term predictions are difficult to make. In other words, while cues such as diet may be less predictive of future environmental conditions, they do provide a way for the animal to respond to the prevailing environmental conditions.

Increased food availability is believed to be an important ultimate factor for the timing of reproduction in birds. However, food availability/quality may also be a particularly important proximate/reactive cue regulating reproduction in less photoperiodic animals (Hahn et al., 2005). Food supplementation can advance the timing of reproduction in a variety of species of birds and species found at lower latitudes tend to be more responsive to this effect of food (Schoech and Hahn, 2007, 2008). Increased food availability stimulates both testes growth and singing in zebra finches (Johnson and Rashotte, 2002) and spotted antbirds (Hau et al., 2000; O'Brien and Hau, 2005). It is unknown if the song control system is affected by dietary changes or what mechanisms might mediate this effect.

Photoperiod has been shown to influence the reproductive system in a variety of tropical, flexibly, and opportunistically breeding birds (Bentley et al., 2000; Hahn, 1995; Hau et al., 1998; Small et al., 2007b) although it appears to play a less significant role than in higher latitude species. Light intensity could also play an important role in some species that appear to be less photoperiodic or non-photoperiodic (Gwinner and Scheuerlein, 1998). Day time light intensity is often higher during the dry season in comparison to the rainy season (Hau et al., 2008; Kumar et al., 2007) and these changes in light intensity correlate with the breeding seasons of many birds that breed during or after periods of heavy rain (Moore and Wingfield, 2002; Small et al., 2007b; Zann, 1996). Lower light intensity is less stimulatory to gonadal development and plasma LH in European starlings, *Sturnus vulgaris* (Bentley et al., 1998), which in turn could influence sex steroid levels and song control nuclei growth. Furthermore, melatonin can influence the plasticity of the song control system (Bentley et al., 1999; Cassone et al., 2008) and day time light intensity does directly affect melatonin levels in stonechats, *Saxicola torquata axillaris* (Kumar et al., 2007). Together, these data suggest that light intensity, possibly mediated through melatonin or gonadal hormones, could play an important role in regulating song control system plasticity in birds that breed during/after irregular rainfall.

Social cues have also been shown to enhance growth of the song control system. Photostimulated white-crowned sparrows housed with females had larger HVC and RA than photostimulated males housed alone (Tramontin et al., 1999). Additionally, testosterone treated male canaries, *Serinus canaria*, housed with females had larger HVC than testosterone treated males housed with another male (Boseret et al., 2006). The need to be synchronized with a mate may be particularly important in animals that are less seasonal and breed asynchronously with other pairs in the population (Moore et al., 2005). Alternatively, males within a population may also be stimulated by other males' reproductive behaviors as a form of “public information” (Danchin et al., 2004) to help in assessing the proper timing of reproduction. The reproductive system of brown-headed cowbirds, *Molothrus ater*, is stimulated by visual and vocal cues from conspecific males (Dufty and Wingfield, 1990). However, male rufous-winged sparrows exposed to conspecific song recordings had larger testes but not larger song control nuclei volumes when compared to controls (Small et al., 2008b). Social cues derived from females appear to augment growth of the song control system in males but further studies are needed to understand the extent to which social cues can stimulate neuroplasticity independent of other cues.

From a proximate or mechanistic perspective, we would expect to see that testosterone plays a primary, but not necessarily exclusive role, mediating seasonal plasticity of the song control system. Tropical birds provide an interesting case because they often have levels of testosterone that are much lower than temperate zone species (Goymann et al., 2004), yet relatively high receptor densities may compensate for these low levels (Canoine et al., 2007). To our knowledge, it is unknown if species differences in the sensitiv-

ity of the song control nuclei to testosterone exist and thus careful construction of dose–response curves should be interesting.

In summary, studies of temperate zone seasonal breeders have served as the traditional models for understanding neuroplasticity of the song control system. While these studies have opened up a whole field of neurobiology, they have limitations. For example, efforts to decouple photoperiodic cues from other cues can be challenging. Studies of tropical, flexibly, and opportunistically breeding species offer advantages that should be utilized (Table 1). While we present these three groups as separate alternatives to temperate zone species, indeed they are not mutually exclusive and individual species may exhibit characteristics of each group. By studying these non-traditional models we can expand our knowledge of both the prevalence of as well as the environmental and hormonal mediators of neuroplasticity of the song control system.

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