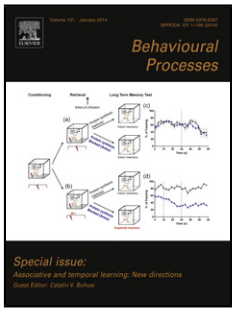
# Accepted Manuscript



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PII: S0376-6357(17)30179-1
DOI: https://doi.org/10.1016/j.beproc.2017.12.007
Reference: BEPROC 3556

To appear in: *Behavioural Processes*

Received date: 15-4-2017
Revised date: 19-7-2017
Accepted date: 14-12-2017

Please cite this article as: Rivera-Cáceres, Karla D., Templetron, Christopher N., A duetting perspective on avian song learning.Behavioural Processes https://doi.org/10.1016/j.beproc.2017.12.007

# A duetting perspective on avian song learning

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## Highlights

Avian song ontogeny is an important model system for language learning

Most past work has focused on song learning in species where only males sing

We review literature and propose future studies on song learning in duetting species

Duetting species could provide an important model for understanding vocal learning

## Abstract

Avian song learning has a rich history of study and has become the preeminent system for understanding the ontogeny of vocal communication in animals. Song learning in birds has many parallels with human language learning, ranging from the neural mechanisms involved to the importance of social factors in shaping signal acquisition. While much has been learned about the process of song learning, virtually all of the research done to date has focused on temperate species, where often only one sex (the male) sings. Duetting species, in which both males and females learn to sing and learn to combine their songs into temporally coordinated joint displays, could provide many insights into the processes by which vocal learning takes place. Here we highlight three key features of song learning—neuroendocrine control mechanisms, timing and life history stages of song acquisition, and the role of social factors in song selection and use—that have been elucidated from species where only males sing, and compare these with duetting species. We summarize what is known about song learning in duetting species and then provide several suggestions for fruitful directions for future research. We suggest that focusing research efforts on duetting species could significantly advance our understanding of vocal learning in birds and further cement the importance of avian species as models for understanding human conversations and the processes of vocal learning more broadly.

**Key words:**

Auditory-forebrain pathway, avian duets, conversation, duetting, duet learning, language, song learning, vocal interactions

Songbirds have become the one of the premier systems used to address questions concerning the development of behavior (Marler & Slabbekoorn, 2004), in part because of the many parallels that their vocal development shares with human language learning (Brainard & Doupe 2002; see Berwick et al 2011 for a discussion of potential differences between song and language). Like humans, songbirds learn their vocal signals during a critical period (most typically during the juvenile life phase), have specific neural circuits used in the learning and production of vocal signals, employ similar genetic mechanisms during vocal acquisition, and exhibit learning outcomes that are strongly determined by social factors. Several decades of song development research have produced a comprehensively detailed picture of how songbirds acquire their individual song structures (Catchpole & Slater, 2008). Yet, nearly all of this work has focused on species in which only a single sex—males—learn to sing.

In many species of birds, both males and females sing, and mated pairs in these species often join their songs to produce duets (Hall 2009). These species are largely concentrated in the tropics (Slater & Mann, 2004), and were for many years mostly disregarded by (primarily northern latitude) researchers, given the challenges of working on these species. Yet, better understanding the song learning process in these species has the potential to provide information on key aspects of vocal learning. Female song is ancestral (Odom et al., 2014), and thus understanding how female birds acquire their song repertoires could help us understand the evolutionary origins of song learning in birds. In addition, the interactive nature of duets allows one to approach the study of coding rule acquisition, that is, of the acquisition of the rules individuals need to use and interpret a signal. Finally, studying a different model system of song learning could provide a more general model for understanding human language learning. Here, we provide a brief overview of several key features of song learning in male birds, describe how these patterns might apply or be different in duetting species, and offer some suggestions for future directions that would be useful for better understanding song learning in the duetting context.

## Part I: Key Features of Song Learning (in species where only males sing)

The details of the song learning process vary across different species that have been studied to date (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005; Catchpole & Slater, 2008; Theunissen et al., 2008), but several key features stand out in many of these systems that could be particularly interesting to compare with duetting species.

### *Neural control of song learning*

First, vocal production and learning in birds are controlled by dedicated neural circuits in the songbird brain (Brenowitz & Beecher, 2005) much like in humans (Brainard & Doupe 2002). The song learning circuit includes a series of hormone-dependent nuclei in the anterior forebrain pathway (AFP) of the brain; these nuclei include the HVC, the robust nucleus of the arcopallium (RA), area X, the medial portion of the dorsolateral nucleus of the thalamus (DLM) and the lateral portion of the magnocellular nucleus of the anterior nidopallium (LMAN) (Brenowitz & Beecher, 2005). This architecture is similar to the architecture of many cerebral structures in mammals (Theunissen et al., 2008). HVC and RA are considered analogues of motor cortical areas specialized for vocal production, while area X is homologous to the basal ganglia and the auditory forebrain is analogous to auditory association cortex (Farries & Perkel, 2008).

Steroid hormones appear to be important in regulating both the production and learning of song in birds, with many of the song control nuclei possessing testosterone receptors. Testosterone (T), often considered the male sex hormone, can influence learning of sexually dimorphic song, with T levels being correlated with song activity and with the song learning timeline in many non-duetting birds (Catchpole & Slater 2008). Specifically, the presence of testosterone may act to help close the sensitive period, promote song stereotypy, and prevent future song learning (Brainard & Doupe 2002; Ball et al 2002, but see Templeton et al. 2012 for an exception to the last finding).

### *Timing and life history of song learning*

Songbirds possess critical periods for both the sensory and motor components of song learning (Beecher & Brenowitz, 2005). Juveniles develop their songs in two steps: first they listen to singing adults and memorize songs or parts of song (sensory phase); second, and typically later in the process, juveniles go through a period of rehearsal (sensorimotor phase), when they improve the accuracy of their songs through practice (Nelson & Marler, 1994). During the sensory phase of song learning, model songs are most likely stored in higher-order auditory forebrain areas (e.g. the caudal medial nidopallium) of young birds (Bolhuis et al., 2000). The memorized songs are then compared to auditory feedback from a bird's own song production, which is processed by the brainstem and relayed to the forebrain and song production systems. The difference between stored and produced song is then used as a corrective signal which in turn modifies neural circuits involved in vocal production (Theunissen et al., 2008). Based on anatomical lesions and pharmacological studies, it appears that the LMAN region is involved in preventing the crystallization of songs during the learning period (Scharff & Nottebohm, 1991), while the RA and HVC are involved in allowing the accurate production of memorized songs (Aronov et al., 2008; Simpson & Vicario, 1990). While the exact timing of, and degree of overlap between, these phases varies across different species of birds, both phases most typically occur early in development, during the juvenile life stage.

In most species, young males learn songs after they disperse from their natal territory. Zebra finches (*Taeniopygia guttata*) and Galapagos finches seem to be highly unusual species in that they learn songs directly from their fathers (Zann, 1990; Mann & Slater 1995; Grant & Grant, 1996); most other species learn their songs from other, typically unrelated, tutor(s) instead of their father, often resulting in song types shared with adults in the population or neighborhood where they recruit and establish a breeding territory but not shared with their natal neighborhood (Beecher & Brenowitz, 2005). In addition to these "close ended learners", some species continue to learn new songs after they first become sexually mature (Catchpole & Slater 2008).

### *The role of social factors in song learning*

Social factors appear to have a major role in guiding the song learning process in many young songbirds. Called the 'wildcard' of song learning (Beecher & Brenowitz, 2005), social interactions experienced by young birds can strongly impact the songs that they learn, sometimes overriding other factors. Comparing classic experiments with tape tutored birds (Marler, 1970) with those using live tutors indicates that the presence of live birds can influence song learning, with social interactions extending the sensitive phase (Nordby et al., 2001), or even prompting young birds to preferentially copy live tutors of a different species (Baptista & Petrinovich 1984). Different types of social interactions may be important at different phases of the song learning process; for example, patterns of song learning in young male song sparrows (*Melospiza melodia*) are influenced by the temporal pattern of when they hear tutors sing and also by the tutor's degree of interactiveness (Beecher, 2017). In addition to direct interactions, indirect, or eavesdropped, social interactions also appear to have important effects on song learning (Beecher et al 2007; Templeton et al 2010).

One overarching goal of song learning is for the young male to learn the songs that will facilitate communication with potential mates (females) and competitors (other males). Songbirds must therefore develop not only the ability to produce their individual songs, but also the ability to use those songs in the most effective way in interactively replying to other individuals. Important examples of vocal interactions in male songbirds are countersinging (Todt & Naguib, 2000), frequency matching (Otter et al., 2002), and song type matching (Beecher et al., 2000). Keeping with the example of western song sparrows, effective communication potentially requires that young birds learn songs that will be shared with their future neighbors in order to facilitate vocal interactions with these individuals (Beecher, 2017). Because most birds learn their songs from other males encountered after they disperse from their natal territory (Beecher & Brenowitz, 2005), the song learning program—including the sensory and sensorimotor phases and the importance of social factors—is such that most song learning takes place away from the natal territory.

There is some indirect evidence suggesting that male-only singing songbirds might learn more than song structure during early development; perhaps they also learn the rules for how to use their songs to communicate. Two hand rearing studies in Common Nightingales (*Luscinia megarhynchos*) found that when song types that males were tutored with were delivered grouped in set orders, individuals learned a) the individual song types b) the order in which each song type within a group was presented and c) the sequential association of different song groups (Hultsch, 1989; Hultsch, 1992). It has been argued that these results suggest that juveniles learn contextual information of when and how the songs should be used during vocal interactions (Geberzahn & Hultsch, 2004). Male song sparrows seem to be particularly attracted to vocal interactions (e.g. countersinging between two males) during the song learning phase (Templeton et al. 2010), leading researchers to speculate that in addition to allowing young birds to learn specific song types, eavesdropping on the interactions of adults could be a mechanism whereby young birds socially learn the cultural rules governing song use (i.e. for conventional signals such as song type matching) (e.g. Beecher et al. 2007; Templeton et al. 2010).

## Part II: Song learning in species that duet

### *Overview of song duetting*

Song duets are produced by hundreds of species of birds and have been the subject of much research effort, especially during the past 20 years. Here we provide a very brief definition and overview of song duetting, but we refer the reader to the excellent reviews by Farabaugh (1982), Hall (2004, 2009), Dahlin and Benedict (2014) and Logue and Krupp (2016), which carefully document various aspects of duetting, especially the evolutionary function(s) that duets serve in communication and social behavior.

At the simplest level, duetting involves two individuals producing acoustic displays that are at least somewhat temporally coordinated (Farabaugh, 1982). However, species vary dramatically in the form that their duets take (Dahlin & Benedict 2014). For example, the amount of coordination between the songs of the two individuals producing a duet varies across species, ranging from simultaneous singing (e.g., Radford 2003; Illes & Yunes 2009; Dowling & Webster, 2013) to intricately coordinated multi-part duets (e.g. Mann et al 2003; Logue et al 2008; Quirós-Guerrero et al in press) or choruses (e.g., Mann et al., 2006). Some of the most impressive duets, and those that are potentially most interesting from a song learning perspective, are the antiphonal duets produced by some songbirds, where two partners sing specific song phrases that are precisely timed to alternate rapidly with little or no overlap. Most typically these partners are male and female pair-mates, and in many cases they produce duets composed of sex-specific song phrases. Furthermore, in many species the song phrase that each individual selects from its (sometimes large) repertoire to sing in a given duet is non-randomly linked to a specific song phrase type from the repertoire of its partner, according to a pair-specific duet code (Logue, 2006). This type of singing style is exemplified by a number of species of new world wrens (Mann et al., 2009) for example the canebrake wren (*Cantorchilus zeledoni*; Figure 1).

In contrast to the abundance of functional studies of duetting, the ontogeny of song duets has largely been ignored. In part, it has been assumed that, at least in the oscine duetting species such as the neotropical *Thryothorus* wrens (Mann et al., 2009), repertoire acquisition should not differ from the non-duetting species (Hall, 2009). There is evidence that supports this view: slate-coloured boubous (*Laniarius funebris*) (Wickler & Sonnenschein, 1989) and bay wrens (*Cantorchilus nigricapillus*) (Levin et al., 1996) develop abnormal songs when raised in isolation, suggesting that song learning is important in duetting species. Some indirect evidence that supports the individual repertoire learning hypothesis is that the repertoires of birds from numerous duetting species vary on a micro-geographic scale, for example in canebrake wrens (Marshall-Ball & Slater, 2008) and rufous-and-white wrens (*Thryothorus rufalbus*) (Mennill & Vehrencamp, 2005).

While some features of duet song learning likely parallel those found in temperate species, there are several other factors that are unique to duetting species or at least to species in which both males and females produce songs. For instance, duetting requires engaging in vocal interactions that in several species involve specific relationships among the vocalizations from different individuals. Two key interaction rules arise from these relationships: precision in song answering (i.e. precise temporal coordination in the responses to a partner, Todt & Naguib, 2000) and non-random association of song phrases (i.e. duet codes, Logue, 2007). Furthermore, several duetting species produce sex-specific songs

(Hall 2009), which can differ significantly in their acoustic structure. Producing duets, especially those that involve high levels of temporal and spectral coordination, provides a number of challenges for song learning compared with learning solo songs. Here we review the information available to date on the proximate mechanisms and ontogeny of these emergent features of duets in songbirds.

### *Neural control of duetting*

Few studies have yet examined the brains of duetting birds in detail. Initial work by Brenowitz and colleagues (1985) demonstrated that the difference between male and female song control nuclei (RA) was much smaller in duetting species (bay wren and buff breasted wren, *Cantorchilus leucotis*) than in species in which only males sing, indicating that unlike in species where only males sing, the song nuclei responsible for song production and learning are of similar sizes in males and females of duetting species (Brenowitz & Arnold, 1985). Additionally, much like in species in which only males sing, the sizes of the song control regions in the brains of duetting bay wrens and rufous-and-white wrens are correlated with the song repertoire complexity, and this correlation extends both to males and females in these species (Brenowitz & Arnold, 1986). Males and females also have similar densities of steroid hormone receptors in their song control regions (HVC and lMAN) (Brenowitz et al. 1996). Given that lMAN is part of the anterior forebrain pathway devoted to song learning, this result suggests that steroid hormones are important for controlling song learning in both sexes in duetting species. Somewhat contradictory evidence comes from a study of a different duetting species, the African bush shrike (aka slate-colored boubous), which found that females have significantly smaller song nuclei (HVC and RA), lower numbers of neurons and smaller neurons than males, despite possessing song repertoires of comparable complexity (Gahr et al., 1998). Furthermore, Gahr and collaborators also found that across studied species in which females sing, there was no correlation between repertoire size and the degree of sex difference in brain specialization. However, they did find a significant increase in song nuclei size in female birds of those species in which females sing. Similar results to Gahr et al. (1998) have also been found in other species in which females sing: northern cardinal (*Cardinalis cardinalis*; Jawor and MacDougall-Shackleton, 2008), streak-backed oriole (*Icterus pustulatus*; Hall et al., 2010) and blue-capped cordon-bleus (*Uraeginthus cyanocephalus;* Lobato et al., 2015). Thus, it is now hypothesized that there is a threshold size for song nuclei to allow song production, but that the correlation between song nucleus size and song complexity or other features such as song output will vary across species once that threshold is met (Lobato et al., 2015). Overall, these studies suggest that similar brain centers control learning of song in both males and females. However, the fine details of how similarities and differences in brain structure affect the vocal repertoires of males and females across species where both sexes sing requires more study.

Understanding the mechanisms by which females and males acquire their individual vocal repertoires is important, but again, gaining this understanding is still not enough to clarify how duets are actually integrated in the brain. Some insights to how this interactive behavior could be encoded in song nuclei regions come from studies of only-male singing species. The areas of the brain involved in integrating auditory stimuli, like the HVC region of male (non-duetting) songbird species is tuned to respond preferentially to the bird’s own songs (e.g. McCasland & Konishi, 1981; Margoliash, 1986; Dave et al., 1998; Nick & Konishi, 2005) or to conspecific songs that closely resemble the bird’s own songs (Prather et al., 2008). However, the non-random association of songs between pair members (i.e. duet codes) presumably requires that duetting birds not only memorize their own vocalizations, but also memorize their partner’s vocalizations and the correct link between these songs (the duet code). Furthermore, temporal coordination in several duetting species is achieved by dynamic modifications to the singing tempo of individuals based on autogenous and heterogeneous cues (Fortune et al., 2011; Logue et al., 2008; Rivera-Cáceres, 2015; Templeton et al., 2013). Thus, to be able to integrate self and partner’s songs, the brains of duetting species ought to be tuned to respond to songs that might be very different from each other, especially in species with sex-specific song repertoires.

A single neurophysiology study has examined the activity of song nuclei in duetting birds. Fortune et al (2011) studied plain-tailed wrens (*Pheugopedius euophrys*) and showed that HVC of both males and females responds to both male and female song stimuli, but this region responds more to whole duets than to the isolated contributions of each sex. This study also revealed that the brains of both males and females are tuned to respond more to the vocalizations of females rather than to the vocalizations of males. Furthermore, this study demonstrated that, unlike non-duetting species, HVC preferentially responds to vocalizations that are performed with the correct temporal coordination. Thus it seems that the brains of duetting birds might differ from other species in that they are able to store more than the individual's own vocalizations. Seibt and Wickler (2000) suggest that song nuclei may function for storing not just a bird's own songs (the "overt repertoire") but also a "silent repertoire" of songs that the bird does not sing but which it must recognize and respond to. This silent repertoire could be especially important in duetting species in which one individual must recognize and rapidly respond to its partner's songs (Seibt & Wickler 2000). Fortune et al. (2011) lend further support to the idea that the brains of duetting birds store the entire vocal interaction, including the temporal patterns of this cooperative display and the role that each individual plays in it (i.e. the brains of males might respond more to female vocalizations because females lead the duets and males follow their lead). It is still unknown whether these nuclei function equally in both sexes during vocal production in addition to during auditory perception alone. If this is the case, it is possible that mirror neurons in this region provide the sensorimotor correspondence that individuals would need to produce duets with such a high temporal precision (Prather et al., 2008). The songs produced by the bird that starts the duet could activate the partner's auditory-vocal neurons in the HVC region. Those songs could then be compared a to representation of the stored vocal interaction and provide the cue needed for a rapid selection of the correct song type and precise temporal response.

*Timing and life history of song learning*

Song acquisition seems to occur only during early development in those duetting species studied to date. For instance, slate-colored boubous raised in captivity seem to maintain a fixed song repertoire after the first six to eight months of life (Wickler and Sonnenschein, 1989). Furthermore, the acoustic structure of striped-back wren (*Campylorhynchus nuchalis)* songs does not change once individuals reach adulthood (Price, 1998). Finally, the individual song repertoires of adult canebrake or riverside wrens (*Cantorchilus semibadius)* do not appear to change from one season to another, even after a bird changes mates (Rivera-Cáceres et al., 2016; Quiros Guerrero & C.N.T. unpublished data). Based on these preliminary indications, the overall timing of the song learning patterns in duetting species is similar to the learning pattern of most species of closed-ended learners in which only males sing. However, within early development, the onset and duration of sensitive periods for song learning and vocal interaction rule learning might differ greatly between duetting and non-duetting species (Figure 2).

While there is much variation in the timing of song learning across species in which only males sing (Beecher and Brenowitz, 2005), with only a few exceptions most species appear to memorize and produce songs after they disperse from their natal territory (Figure 2a). In contrast, observational and hand-rearing studies have found that juvenile birds of duetting species stay in their natal territories for several months and individuals memorize and produce new song types throughout this period (slate-colored boubous, Wickler and Sonnenschein, 1989; stripe-backed wren, Price, 1998; superb fairy-wrens, *Malurus cyaneus*, Evans and Kleindorfer, 2016; canebrake wren, K.D.R.C, unpublished data; riverside wren, Quiros-Guerrero & C.N.T. unpublished data; Figure 2b).

One possible difference between species in which only males sing and species in which both sexes sing is that within the same species, males and females might differ in the duration of their sensitive periods to song memorization. A single study has provided evidence to support this idea: male blue-capped cordon-bleus (*Uraeginthus cyanocephalus*) appear to learn for a longer time compared to females (Geberzahn and Gahr, 2013). Differences in the duration of sensitive periods or dispersal patterns between sexes could provide mechanisms that allow individuals to learn sex-specific repertoires; however no study to date has addressed this issue.

In addition to each sex learning to produce component song phrases, duetting birds must learn the rules that govern the use of these songs in the creation of interactive duets . Duetting species might differ from male-only species in terms of when they acquire the rules governing song use (i.e. contextual learning rather than production learning; Janik & Slater 2000). Juvenile canebrake wrens acquire both their song phrases and the rules (i.e. temporal precision and duet codes) needed to use those phrases to perform duets while still on their natal territories (Rivera-Cáceres et al. in review), and it is likely that other species that have delayed dispersal also learn rules governing duet composition during this stage. However, despite learning the rules related to duet codes and timing during early ontogeny, when these young birds disperse from their natal territory and attract their own mate, this mate will very likely not share some or all of the song phrases the bird originally learned. Thus, new rules governing the association of song phrase types into duets, in terms of the timing and the duet codes, may need to be acquired later in life. The duets of magpie-larks (*Grallina cyanoleuca*; Hall & Magrath 2007) and canebrake wrens (Rivera-Cáceres et al., 2016) are more precise in terms of timing in established pairs than in newly formed pairs, though studies in other species have not always shown this same pattern (Arrowood 1988; Levin 1996; Marshall-Ball & Slater 2008; Benedict 2010). In terms of duet codes, a removal study conducted in the field by Rivera-Cáceres et al. (2016) showed that adult canebrake wrens do in fact learn new song-type associations when they obtain new mates.

It is therefore quite likely that duetting birds learn  duet codes during at least two different stages in life: one duet code is learned in the juvenile stage from parents and additional duet codes are learned in adulthood each time a bird obtains a new mate (Logue 2007; Logue & Krupp 2016).  Overall, it seems that there is some evidence that duetting rules may have a different developmental history than individual song repertoires, at least in some species. Nevertheless, because different species have different duetting styles, not all species might need to learn duetting rules during adulthood. The ontogeny of duetting rules has been ignored in the literature until recently, so it is unknown just how general this learning pattern really is and future study is necessary.

### *The role of social factors in duet learning*

Because duetting is, by definition, a social activity, it seems logical that social factors might affect the acquisition of the elements that a bird needs to participate in a duet. However, little research has directly addressed this question to date. There is some evidence that, unlike most species in which only the male sings, duetting species, and other species in which both males and females sing, might learn their repertoires from their parents (e.g. slate-colored boubous, Wickler and Sonnenschein, 1989; stripe-backed wren, Price, 1998; forest weavers, Seibt et al 2002; superb fairy-wrens, Evans and Kleindorfer, 2016; canebrake wren, K.D.R.C, unpublished data; riverside wren, Quiros-Guerrero & C.N.T. unpublished data). It is also possible that this difference in dispersal is driven by latitudinal gradients, instead of singing styles, but further research is necessary to disentangle these effects. Additionally, duetting birds could require social interactions to acquire sex-specific repertoires, temporal coordination, and duet codes.

Many duetting species have sex specific repertoires (Hall, 2009). In the three species studied to date—bay wrens (Levin et al., 1996), slate-colored boubous (Wickler and Sonnenschein, 1989), and blue-capped cordon-bleus (Geberzahn and Gahr, 2013; Lobato et al., 2015)—females and males have the ability to produce both sexes' song and thus either a sex-specific template, social factors or a combination of both are the cause of the sex-specific repertoires observed in adults. In bay wrens, when female and male juveniles were tutored with duet song recordings played from a single speaker, individuals learned to produce full duets, instead of only producing the component songs of their own sex. However, when exposed to duets where the sex-specific components were played from different stereo speakers, individuals tended to produce both full duets and solo songs that corresponded to their genetic sex (Levin et al., 1996). Thus the authors suggest that while an innate template might exist, social interactions with tutors are essential for juveniles to learn the correct song repertoires. Furthermore, juvenile female slate-colored boubous did not learn songs from playbacks alone, but juveniles that were raised in an aviary by their parents or other adult pairs did learn their correct sex's song repertoire. These results also support the idea that social interaction with tutors is essential to learn the correct song repertoires in duetting birds. A later study attempted to determine if phenotypic cues could help juvenile slate-colored boubous to figure out which parent they should use as a model for song-repertoire acquisition (Wickler, 1996). This study revealed that there are only very subtle differences in the coloring patterns of the underside of the wings, which the authors argue is an unlikely trait to be used by juveniles because there is no flight display during duetting. The authors also found a slight difference in size and weight between males and females, but it still remains to be tested if these or other unstudied characteristics aid juveniles in learning the correct repertoires during early development. Finally, blue-capped cordon-bleu juveniles do not seem to possess a sex-specific template given that both males and females produce songs with similar duration and their repertoire size is comparable throughout most of their ontogeny (Lobato et al., 2015). Song repertoires only become sexually dimorphic (in size) during adulthood in this species, mainly due to females eliminating more song elements than males from their final repertoires. However, it is unknown whether this change is socially or genetically driven.

No hand-rearing studies have yet been carried out to determine whether individuals require social experience as they acquire temporal coordination or duet codes, or the specific types of social experiences that facilitate learning these aspects of song usage. Only one field study has addressed these questions in canebrake wrens and found that juveniles are significantly less coordinated than adults and do not adhere to a duet code as consistently as adults during early stages of development (Rivera-Cáceres et al. in prep) but both features improve with time (K.D.R.C. unpublished data). Furthermore, Rivera-Cáceres et al (in prep) showed that the duet code that each juvenile follows is the same as the one used by the adults that raised that juvenile. These results suggest that duet coordination and duet codes are learned during early development and that juveniles need an adult model to copy these duetting rules from. Studies rearing birds under controlled acoustic environments would be beneficial to further test these ideas.

## Part III: A framework for future research on duet ontogeny

Species in which both sexes sing provide many possibilities for increasing our knowledge of vocal development. Thus far, most work has focused on male song learning and an obvious direction for future research would be to increase the scope of research to examine many of the above topics from the perspective of female song. In addition to understanding the processes of vocal learning when both sexes learn their songs, species in which males and females produce joint duet songs could dramatically advance our understanding of vocal learning, specifically because of the interactive nature of duetting. Below we focus on the importance of understanding the ontogeny of vocal interactions and suggest several specific lines of inquiry that could help further establish duetting bird species as an ideal model investigating this phenomenon.

### *Studies to examine individual and collective song learning*

Hand rearing studies have provided a powerful methodology for testing questions related to song acquisition in male birds since pioneering work in the 1950's (Thorpe 1954) and we suggest that performing similar studies with duetting species would provide many possibilities for expanding our understanding of how animals learn to produce and use duets. While hand rearing studies under controlled acoustic conditions could shed light on many different aspects of duet song ontogeny, we especially encourage research that focuses on the following two topics.

### i. Acquisition of individual male and female song repertoires

Duetting species and species in which females also sing provide an ideal model for studying similarities and differences in vocal learning between sexes. We have discussed several studies examining this topic at the neuroendocrine level above, but we suggest that examining similarities and differences that exist during the acquisition of individual-song repertoires at the behavioral level could also be a fruitful topic for future research. For instance, within species sex differences would be particularly interesting to investigate in relation to the duration of the sensitive period and the nature of social factors that affect how individuals acquire their song repertoires. Furthermore, a number of duetting species have sex-specific song repertoires (i.e. male song phrases are categorically or quantitatively different from female song phrases) and it would be interesting to determine whether the sex differences in ontogeny are pronounced or even constrained to species with sex-specific repertoires. We additionally encourage scientists to test whether sex-differences in the factors mentioned above in fact function to facilitate individual birds in acquiring the repertoire that corresponds to their genetic sex. Finally it would be equally important to assess what acoustic cues could confirm the hypothesized sex-specific auditory template, if one indeed exists.

### ii. Acquisition of rules governing duetting interactions

While the acquisition of individual-repertoires is an important and interesting aspect of duet learning, especially in species with sex-specific repertoires, duetting species also provide an exciting model system for studying the ontogeny of vocal interactions. Studying the ontogeny of duetting as a collective behavior (Logue and Krupp, 2016), by considering how pairs of birds learn interdependent song features, including duet codes and the temporal coordination of duets, will help create a fuller appreciation of the social factors required to develop such a complex behavior as duetting.

The first unanswered question in this regard is whether individuals require experience listening to duets to be able to engage in a duet later in life or if performing this coordinated behavior is an innate ability. An experiment in which isolated hand-reared birds are exposed either to solo renditions of the species' songs or to the same songs but linked in duets would address this question. The second unanswered question is whether the species-specific temporal patterns (e.g. alternating vs. overlapping or loose vs. precise temporal coordination) are acquired from the adult tutors. Lastly, Rivera-Cáceres et al (in prep) showed that juvenile canebrake wrens learn their duet codes from the adult tutors. However, it is unknown whether the tendency to follow a duet code is a learned or innate trait. Thus, laboratory experiments are required to test whether birds tutored with duets that do not follow a duet code are able to create duet codes as adults.

In addition to the hand rearing experiments proposed, we would also like to encourage the performance of more field experiments that address the ontogeny of temporal coordination and duet codes in species with different duetting styles. One intriguing possibility is that species with high temporal precision and/or pair-specific duet codes require learning of those rules during both early development and adulthood but that learning in species with loose temporal precision and/or population-wide duet codes is restricted to early development. To understand the evolutionary trajectory of these complex rules it is vital to take a comparative approach and this will only be possible if more species, including songbird and non-oscine duetting species, are studied.

### *Duetting birds as a model for turn-taking vocal interactions*

As we discuss above, humans and songbirds share many similarities in the brain architecture in charge of controlling vocal learning and vocal production of single vocalizations, and for this reason birds have become a major model for better understanding language learning (Doupe & Kuhl, 1999; P. Marler, 1970). Perhaps these similarities extend to how vocal interaction rules are encoded in the brain as well. One key feature of human language is the degree of its interactivity. Turn-taking, in which individuals avoid overlapping each other's utterances but at the same time keep silent gaps short (~200ms) is a universal vocal interaction rule in humans (Levinson, 2016). Levinson (2016) diagrams the three steps of cognitive processes by which turn taking takes place in humans and examines these processes in other primates. We suggest that, as is true for many other features of vocal learning, songbirds could provide a particularly useful parallel model for studying the cognitive processes underlying turn taking behavior (Figure 3). The temporal scale with which duetting birds answer their partners is very similar to the timing in turn taking (within hundreds of milliseconds, Figure 1a in Levinson, 2016 and Figure 3a in this article), while the time scale of turn taking in marmosets can differ by three orders of magnitude (Takahashi et al., 2013). The brain processes that control rapid vs. slow responses could differ substantially. Below we discuss each of the three requirements for turn taking (Levinson 2016) in relation to duetting birds.

The first requirement in turn-taking in humans is that individuals waiting their turn need to predict the rest of the incoming utterance as soon as possible after the other individual starts talking (Stivers et al. 2009). In black-bellied wrens, Logue (2006) has shown that females are able to predict the song type that the male will sing based on the first or last part of the male's song. This study suggests that duetting birds are also able to predict the content of the song of their partner based on partial information, though similar studies with other species would help confirm the generality of this finding. Furthermore, studies assessing the latencies for auditory responses of duetting and non-duetting birds towards different types of stimuli (e.g. innate calls, vs. songs that do not require a coded response vs songs that require a duet code) would help to better understand the predictive nature of song answering in duetting birds in comparison to human turn taking (Figure 1b in Levinson, 2016 and Figure 3b in this article).

The second requirement in human turn-taking is that individuals have to plan a response based on available information before the previous speaker's turn ends (Levelt, 1993). In duetting birds, the memory of the own bird's and its partner's duet code could represent a way in which individuals plan a correct response. In a behavioral experiment, Rivera-Cáceres et al. (2016) showed that female canebrake wrens know the duet code with which males answer to the female's phrases. In a neuroscience experiment, Fortune et al. (2011) suggests that duetting birds store whole duets in their memories. No studies to date have shown whether the bird's own duet code and its partner's duet code are stored in both individuals' brains and demonstrating this would be an important step forward. One possible approach to addressing this issue could be performing readings of song control nuclei (HVC, RA, etc.) when individuals of both sexes are exposed to either correct or incorrect duet codes.

The last requirement during human turn taking is that individuals use the syntax and semantics of the speaker in turn to estimate the likely duration and thus predict its ending. As the songs that many birds use during duets are of fixed length, it seems that this requirement could be fulfilled by the first step. However, it has also been shown that the different sexes within the same species might use different cues to determine their response timing. For instance, the best predictor of male black-bellied wren response timing is the beginning of the female's song, while the best predictor of female response timing is the end of the male's song (Logue et al., 2008). Male happy wrens adjust the timing of their responses to their partner's song tempo, even when it is manipulated under experimental conditions devoid of other cues (Templeton et al. 2013). In canebrake wrens, both female and male response times depend on the duration of their partners' song types, but in females that dependence is weak while in males it is very strict (Rivera-Cáceres, 2015). Future work examining how syntax and semantics impact neural recognition and behavioral responses to partner song phrases could help further establish parallels between humans and duetting birds in terms of the predictive abilities in turn taking vocal communication (Figure 2c).

### *Duetting birds as models for the acquisition and use of conventional signal rules*

As stated above all species of songbirds must develop the ability to produce their individual songs. However, even species in which only the males sing must also develop the ability to use those songs during vocal interactions. For instance, during countersinging interactions, males can associate their songs with specific temporal patterns (Geberzahn & Hultsch, 2004). Males can also select song types non-randomly with respect to the songs sung by other individuals, for example in song-matching (Beecher 2017). Because temporal coordination is not nearly as precise as in duetting species and because the non-random associations between song types in non-duetting species are less strict than in duetting species the ontogeny of these rules has been often overlooked despite the vast body of research on the ontogeny of individual song structure. Recent studies in duetting species have shown that duetting rules have a complex ontogeny and can be acquired both during early development and during adulthood (Rivera-Cáceres and Quirós-Guerrero, 2014; Rivera-Cáceres et al., 2016). Studies on duetting birds could in fact lead the way in understanding how communication rules are learned more broadly (e.g. in species where only males sing). Furthermore, the approaches taken in duetting species studies could also be applied to studying the ontogeny of temporal coordination during countersinging and song-matching events.

There is some speculation that male birds may learn the rules associated with territorial countersinging interactions in addition to song structures (Hultsch, 1989; Hultsch, 1992) during early development which might take place by eavesdropping on adult male interactions (Beecher et al. 2007; Templeton et al. 2010), potentially in a similar way in which duetting birds acquire their duet codes (Figure 2). However, it is also possible that, like duetting birds, males in non-duetting species are also able to learn their vocal interaction rules during adulthood when they interact with other territorial males. For instance, a recent study in zebra finches showed that temporal associations between innate calls of birds can be learned during adulthood (Benichov et al., 2016). Presumably, temporal patterns are also learned for other types of singing interactions, but this is not known in zebra finches or other species.

Observational field studies (e.g. Rivera-Cáceres et al in prep) and playback experiments (e.g. Templeton et al., 2013, Rivera-Cáceres et al., 2016) with juvenile and adult birds could help elucidate whether non-duetting males show the same patterns of temporal coordination and song-matching at different life stages. Furthermore because it is easier to perform hand rearing experiments in temperate males, testing whether individuals raised by tapes are able to follow complex rules, such as aggressive escalation through song type matching, later in life similarly to birds raised by live tutors or interactive virtual tutors would be relatively straight forward.

### *Duet learning in non-oscine birds*

While we have focused primarily on songbirds because they have become such important model systems for studying vocal learning, it is also important to note that two other clades of birds, parrots (Psittaciformes) and hummingbirds (Trochilidae), also learn their individual song repertoires (Baptista & Schuchmann, 1990; Gahr, 2000; Zhang et al. 2014). In both groups, a few species have been shown to perform coordinated song performances, such as the duets of Yellow-Naped Amazons (*Amazona* *auropalliata*, Wright & Dahlin, 2007) and grey parrots (*Psittacus erithacus,* Todt, 1975), and the alternating songs of lekking long-billed hermits (*Phaetornis longirostris*, Araya-Salas et al., 2017). Many duetting species also belong to clades in which song repertoires are not learned, such as the suboscine passerines (e.g. rufous hornero, *Furnarius rufus*, Laje & Mindlin, 2003; the warbling antbird, *Hypocnemis cantator*, Seddon & Tobias, 2005), the Anatidae (e.g. Bar-headed Geese, *Anser indicus*, Lamprecht et al., 1985), the Strigidae (e.g. the barred owl, *Strix varia*, Odom & Mennill, 2010) among others. The development of behaviors that allow individuals to sing in coordination with one another (i.e. interaction rules governing duetting) has been little studied in songbirds (Levin, 1996, Rivera-Cáceres et al., 2016, Rivera-Cáceres et al., *in review*) but to our knowledge it has not been addressed at all in non-oscine species. We argue that these types of studies should be performed a) in the other groups of vocal learners mentioned above (i.e. hummingbirds and parrots), especially because it has been shown that species in both groups are able to modify their songs during adulthood (e.g. budgerigars, *Melopsittacus undulates*, Farabaugh et al., 1994) and b) in species that do not learn their vocalizations, given that the development of the individual vocal repertoire and the rules that allow those repertoires to be combined in duets might differ. Furthermore, controlled laboratory experiments are required to determine whether an innate predisposition to learn these rules exist in both vocal learner and non vocal learner species.

## Conclusions

Avian song duets are some of the most remarkable displays of any animal in terms of their complexity and temporal precision. Although there has been a rich history of studying the adaptive function of duets, relatively little information exists on the ontogeny of this fascinating behavior. Yet, better understanding how song learning progresses in duetting species, where both sexes learn to sing and learn to combine their songs into joint acoustic displays, could provide a number of key insights into vocal learning more generally and further help solidify the importance of songbirds as a model for better understanding the evolution and ontogeny of our own language.

## Figure Legends

**Figure 1.** Spectrograph of one duet song from a pair of canebrake wrens. Each duet song type in a pair's repertoire begins with a male introductory phrase, which is followed by rapid alternation of male and female song phrases. The spectrograph has been colored to reflect the male (blue) and female (red) components of the duet.

**Figure 2.** Schematic of song learning timing and life history in a) a species in which only males sing (song sparrow), and b) one where both sexes learn songs and learn to combine them according to duet codes (canebrake wren). Bird cartoons courtesy of Arthur de Wolf and Amy Evenstad (www.birdorable.com). Two potential key distinctions exist between these systems, the location of song learning and the nature of the interactions in which songs are used at different stages. First, most male-only singing species tend to learn their songs from tutors after they disperse from the natal territory, but both memorization and production phases take place on the natal territory in neotropical wrens. Second, while young birds practice singing at many points during development, most of the singing interactions in male-only singing species take place with other territorial males as the young bird establishes his breeding territory, in contrast, duetting species begin using their songs interactively while still on their natal territory by participating in duets with their parents and siblings. After dispersal and territory establishment, duetting wrens must also learn a new duet code and temporal coordination pattern in order to interactively sing a repertoire of duets with its new mate. In addition to duet interactions between members of a pair, pairs also interactively use their duet songs to communicate with other pairs (neighbors), similarly to male-only singing species. It is likely that male-only singing birds must learn the

rules governing these types of conventional signals (e.g. song type matching, panel a) colored in red), but this has been little studied to date.

**Figure 3**. Avian duetting as a model for turn taking in vocal communication. a) Responses between phrases of a duet are rapid, with average latencies for response for different species ranging from -70 to 140 milliseconds (average across species=24 millisecond response time). Data are taken from previous publications: yellow-crowned gonolek, *Laniarius barbarus*, (Grimes, 1965); black-headed gonolek, *Laniarius erythrogaster*, (Thorpe, 1963); canebrake wren (Rivera-Cáceres, 2015); black-bellied wren (Logue et al., 2008); happy wren (Templeton et al., 2013). We also included the mean latency of human turn-taking (Stivers et al. 2009) to show that duetting bird latencies are more comparable to duetting turn-taking rather than latencies observed in marmoset turn taking (modal response time: 5.63s; Takahashi et al, 2013). b) Response latencies (i.e. the latency for instantaneous production of a song as a response to another song with which there is no memory association) for the production of single song phrases are unknown in duetting species. c) Like in humans, predictive comprehension (i.e. the ability to understand the whole utterance by just listening to part of it), or at least predictive auditory processing, may be used by birds to anticipate the termination of each song phrase in order to initiate production early enough to maintain both the duet code and rapid temporal responses. Figure based on a human model put forward by Levinson (2016).

## Acknowledgements

We thank William A. Searcy for providing helpful advice and comments on this manuscript and for his involvement in the canebrake wren project. We also thank Esmeralda Quirós-Guerrero who helped KDRC with data collection for the canebrake wren project and leads much of the unpublished riverside wren research described here. This work was supported with funds from Pacific University and the M.J. Murdock Charitable Trust (to C.N.T.) and a Doctoral Dissertation Improvement Grant (DDIG) provided by the National Science Foundation (NSF), a Student Research Grant provided by the Animal Behavior Society, a Research Grant provided by the Organization for Tropical Studies (OTS), and funds from the University of Miami (to K.D.R.C.).

## Author Contributions

The authors contributed equally to both developing the ideas presented here and to the writing of this manuscript.

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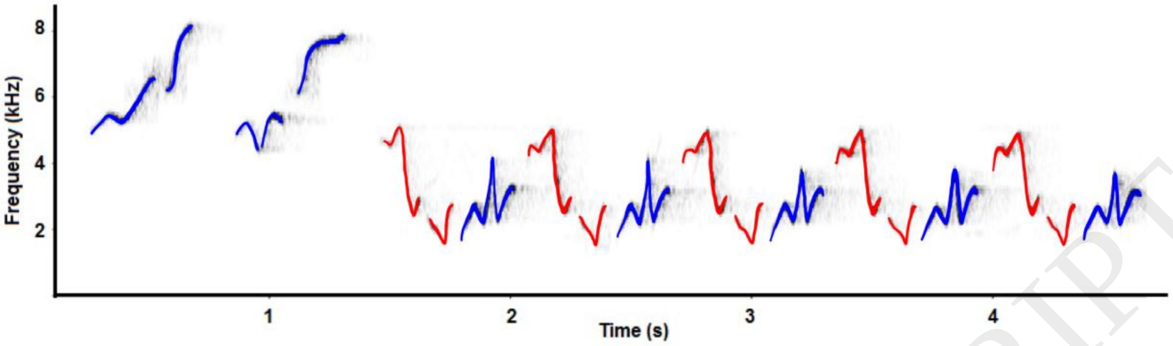
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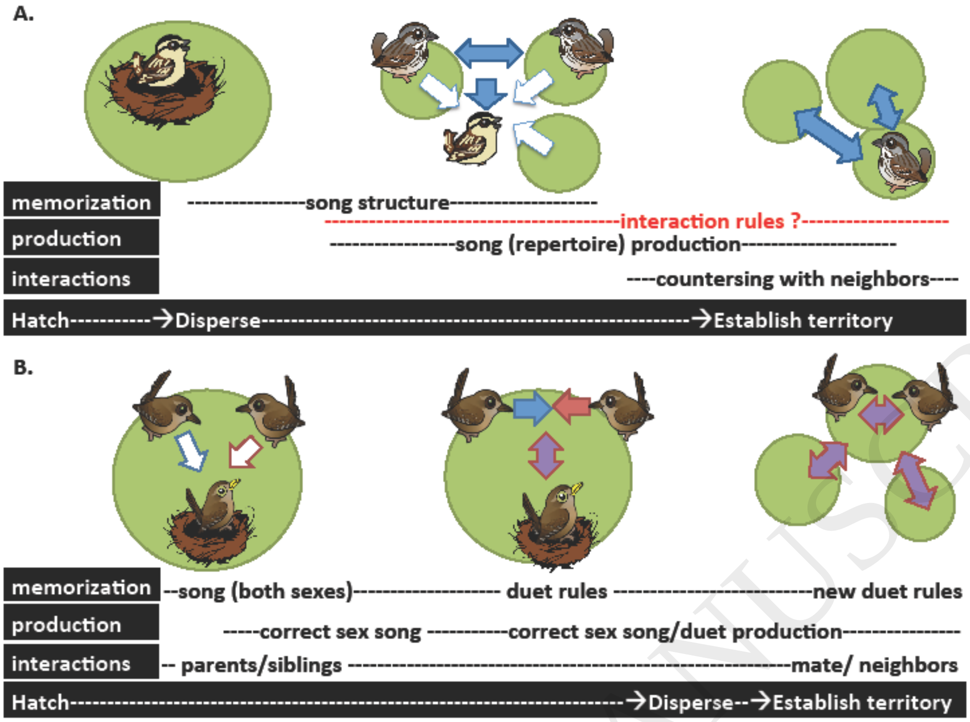
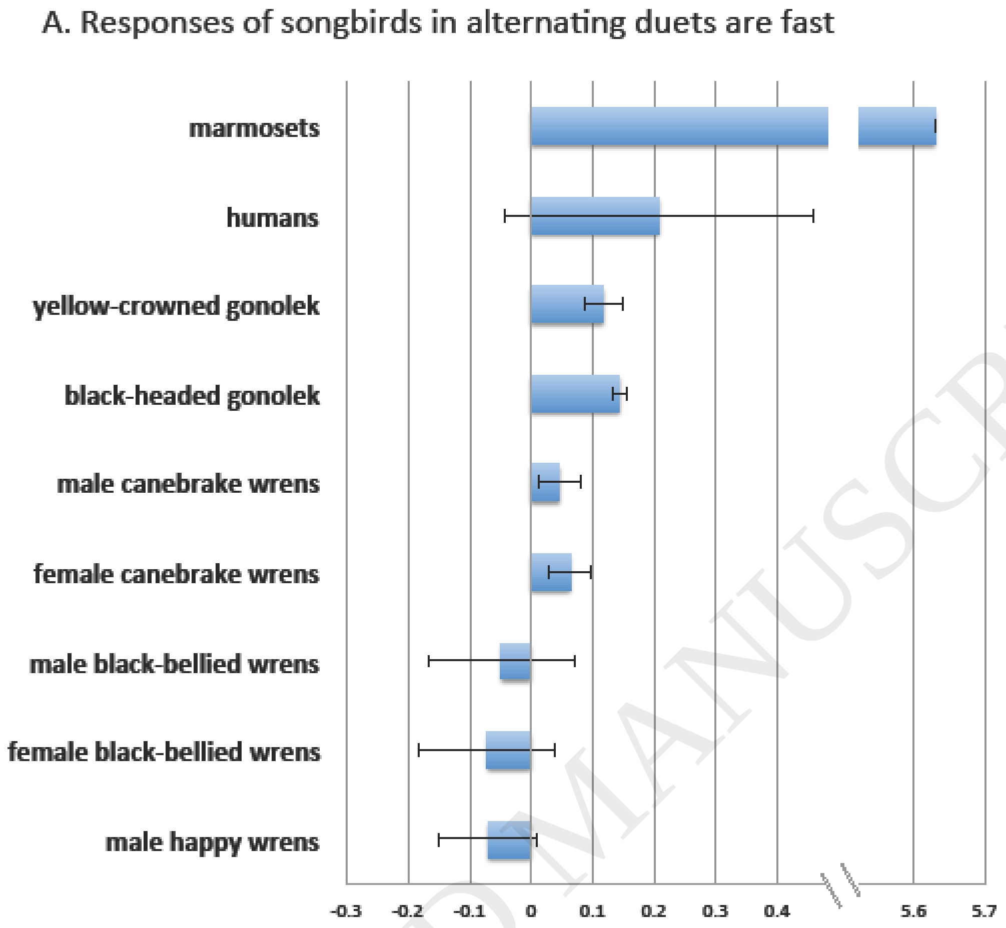
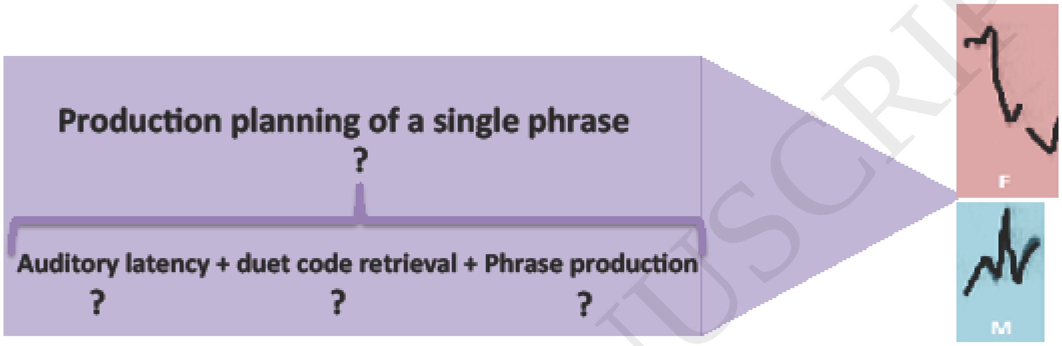

A.
memorization
production
interactions
---------------song structure-------------------
-----------------------------------------interaction rules ?-------------------
----------------song (repertoire) production--------------------
----countersing with neighbors----
Hatch----------→Disperse----------------------------------------------------------→Establish territory
B.
memorization
production
interactions
--song (both sexes)------------------ duet rules -------------------------new duet rules
-----correct sex song ----------correct sex song/duet production---------------
-- parents/siblings ---------------------------------------------------------mate/ neighbors
Hatch----------------------------------------------------------------------→Disperse--→Establish territory



A. Responses of songbirds in alternating duets are fast

B. Latencies in sound production are unknown



C. Production of response could overlap with comprehension of incoming phrase