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Communication Networks and Spatial Ecology in Nightingales

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I. Introduction

In most animals, communication plays a central role in a variety of contexts, often having direct consequences for reproduction and survival. Among the diversity of signals used in communication, sexually selected elaborate displays have received specific attention in research on causes and consequences of complex behavioral traits (Danchin et al., 2008). Sexually selected signals usually provide information on the quality, condition, and motivation of the signaler and have important fitness consequences when being used in resource defense and acquisition and in mate attraction. Moreover, sexually selected signals often are long-range advertisement signals connecting distant individuals with each other, making such signals an important feature to be considered in social networks. Among the different advertisement signals, bird song as research model has provided important insights into the evolution of behavioral mechanisms and functions (Beecher and Brenowitz, 2005; Catchpole and Slater, 2008; Gil and Gahr, 2002; Searcy and Nowicki, 2005). In most songbirds that breed in the temperate zones, only males sing to defend a territory against other males and to attract or stimulate females (Catchpole and Slater, 2008); but female song in several species has been reported as well (Price, 2009; Riebel et al., 2005).

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A. Singing and Receiver Sex

One persistent question in sexual selection and in animal communication has been which kind of information is signaled when using structurally complex displays like bird song. Like most sexual displays, bird song is a multicomponent signal. Depending on the complexity of the signal, studies showed that the different song components can be under particular selection, such as repertoire size (Catchpole, 1980; Hasselquist et al., 1996; McGregor and Krebs, 1982; Rivera-Gutierrez et al., 2010), production quality of particular song components (Ballentine, 2009; Ballentine et al., 2004; Botero et al., 2009; Forstmeier et al., 2002), or use of songs that include specific song components (Vallet and Kreutzer, 1995; Vallet et al., 1998). In species with vocal repertoires, evidence from several studies suggests that repertoire size is intersexually selected, with males having a larger repertoire being more attractive to females and more successful in reproduction. Classic studies by Catchpole (1980) on sedge warblers, *Acrocephalus schoenobaenus*, by McGregor and colleagues on great tits, *Parus major* (McGregor and Krebs, 1982; McGregor et al., 1981), and by Hasselquist and colleagues (1996) on great reed warblers, *Acrocephalus arundinaceus*, are good examples of female preferences for males with a larger song repertoire, even though repertoire size presumably is also under other selection pressures (Byers and Kroodsma, 2009).

Because females and males may be interested in different characteristics of a singer, and different motivational and qualitative differences may be coded in different singing traits, the sexes may select for different structural traits. Females may be more interested in traits that signal parasite resistance or immune competence (Buchanan et al., 1999; Dreiss et al., 2008; Saino et al., 1997), in traits that reflect the genetic or developmental background (Holveck and Riebel, 2010; Nowicki et al., 1998a; Riebel et al., 2009; Searcy et al., 2010), or in traits that are linked to future parental care (Buchanan and Catchpole, 2000; Halupka and Borowiec, 2006). Males, in contrast, may be more interested in traits signaling resource holding potential and motivation to defend a resource (Naguib and Mennill, 2010; Searcy and Beecher, 2009). Traits like song rate may provide information on the personality of the singer (Naguib et al., 2010) or on the immediate condition of a singer, or of the territory, such as food availability (Berg et al., 2005; Clarkson, 2007; Strain and Mumme, 1988). Performance-related characteristics such as trills that depend on neuromuscular coordination (Westneat et al., 1993) are suggested to be affected specifically by developmental conditions (Hoese et al., 2000; Podos, 1996; Podos et al., 2009). Therefore, performance-related characteristics may be more relevant for females (Ballentine et al., 2004; Byers et al., 2010; Caro et al., 2010), as they can indicate male developmental background (Buchanan et al., 2003; Nowicki et al., 1998a; Searcy et al., 2010; but see Gil et al., 2006) or health (Dreiss et al., 2008), and thus predict qualitative aspects of the mate and possibly of its future offspring. Recent studies showed that such performance-related song traits are also used by males to assess the signaler (Cramer and Price, 2007; de Kort et al., 2009; DuBois et al., 2011; Schmidt et al., 2008; Sprau et al., 2010b). Thus, bird song as a multicomponent signal can reflect the different aspects of quality in different traits, which may also differ among species. Moreover, within the same signal, the relevant traits of a signal may depend on the sex of the receiver.

B. The Territorial Function of Bird Song

Many male songbirds respond aggressively to conspecific male intruders into their territories, but in some species, males may be more tolerant to intrusions as long as their reproduction or territory tenure is not at risk. Thus, silent intrusions without singing by the intruder may be tolerated to some extent. However, intruders that start singing within an already occupied territory typically elicit aggressive responses involving singing and approach by the territory holder. Playback experiments commonly simulate such intrusions by a singing rival to measure vocal and spatial responses of the territory holder (Catchpole and Slater, 2008; Gil and Gahr, 2002). Indeed, most of our knowledge on the territorial function of bird song is based on playback experiments, simulating an intruder into the territory or a rival singing nearby (Catchpole and Slater, 2008). A few studies tested directly the keep-out function of song using speaker-replacement experiments in which the resident male was temporally removed from a territory and replaced by a loudspeaker playing conspecific song or control sounds (Krebs et al., 1978; Nowicki et al., 1998b). A few other studies further investigated functions of singing over longer distances across territory boundaries (Simpson, 1985; Sprau et al., 2010a). All these studies support the idea that song serves as a keep-out signal to other males, and playback experiments have been powerful in determining which song traits and singing strategies yield strong responses by territorial males and their neighbors. The intensity of response toward simulated intruders usually is interpreted as reflecting the aggressiveness of the intruder as it is perceived by the resident male. Determining which signaling traits constitute an intensive and aggressive response is not always unambiguous, and there has been some debate on which criteria have to be met for a trait to be identified as an aggressive signal (Laidre and Vehrencamp, 2008; Naguib and Mennill, 2010; Searcy and Beecher, 2009; Searcy et al., 2006). Most commonly, changes in singing style such as more irregular singing, an increase in use of certain song traits, and physical approaches are interpreted as reflecting arousal. Traits that predict an escalation toward an actual physical attack have been argued to be of particular value in assigning an aggressive signal value (Searcy and Beecher, 2009). As signaling interactions commonly are used to avoid physical attacks, most commonly researchers rely on changes in vocal and spatial behavior to assess the function of a signal (Naguib and Mennill, 2010). Experiments using dummy birds which also add visual cues to the acoustic signal may prove to be a useful addition for some species (Balsby and Dabelsteen, 2002; Searcy et al., 2006), even though the use of dummies also has some limitations (Laidre and Vehrencamp, 2008) and is restricted to study short-range signaling. Thus, researchers usually rely on contextual changes in singing or on physical approach as measures of arousal and as an operational measure of aggressive response.

Studies have shown that male responses to playback depend on several factors including structural traits and the timing of playback songs relative to those of the subject (Todt and Naguib, 2000), the level of song degradation (Brumm and Naguib, 2009; Naguib and Wiley, 2001), changes in song amplitude (Naguib, 1997), or song familiarity (Falls et al., 1982). Moreover, responses may vary with time of day (Shy and Morton, 1986) or may depend on the habitat heterogeneity (Naguib and Todt, 1998). In addition, the nature of the territorial response also depends on the condition, rank, or quality of the territory owners themselves (Kunc et al., 2006; Mennill and Ratcliffe, 2004; Mennill et al., 2002; Schmidt et al., 2006; Sprau et al., 2010b), including elementary behavioral characteristics such as exploratory behavior that is commonly used as a proxy for personality (Amy et al., 2010), and previous experience with intruders (Amrhein and Erne, 2006; Godard, 1993; Hall et al., 2006; Schmidt et al., 2007). Moreover, recent studies simulating a more dynamically moving intruder revealed that spatial behavior of intruders effect responsiveness of residents (Amrhein and Lerch, 2010; Poesel and Dabelsteen, 2005).

C. Bird Song as Mediator in Social Networks

Bird song is a long-range signal, and a singing individual as well as its singing interactions with conspecifics usually can be heard by other individuals at various distances (Brumm and Naguib, 2009; Wiley and Richards, 1982). Thus, song can be seen as mediator connecting individuals over distances that are beyond actual close-range encounters. Such connectivity through long-range signals is important in understanding the network structure of a territorial neighborhood, where physical encounters are much more infrequent than in group living species. The signals connecting individuals are sources of information to be used in decision making in current and future territorial or mating contexts. Despite the territoriality, an individual's spatial behavior is not confined to its territory, as birds make silent excursions beyond the own territorial boundaries (Chandler et al., 1997; Hanski and Haila, 1988; Naguib et al., 2001, 2004; Pitcher and Stutchbury, 2000). Such excursions and singing by residents may partly have coevolved; territorial birds may sing to repel intruders, and intruders may use the song of residents to gather information that they may then use in future decision making, for example, for extrapair copulations, future encounters, or in decisions on settlement or mating in the following breeding season. Thus, to fully understand the function of song in a territorial neighborhood, the singing and territorial behavior of the resident individuals need to be considered along with the spatial and movement behavior of the territorial residents or nonterritorial floaters. Yet, as it is practically difficult to follow small songbirds over prolonged periods of time, there is still little information available on their spatial behavior and how it is linked to song. A few radio-tracking studies, including our own studies, have shown that the spatial behavior of nonterritorial prospecting individuals is linked to song, as we will discuss in Sections III.B and III.C. An additional consequence of singing in a social network is that vocal interactions between two individuals can be heard by others. These nonparticipating listening individuals (the audience; eavesdroppers) then can use asymmetries in vocal interaction to assess relative differences among the singers. Such eavesdropping has been shown to be an important source of information in communication networks (McGregor and Dabelsteen, 1996; Peake, 2005; Todt and Naguib, 2000), as discussed in Section III.C.

D. THE NIGHTINGALE

Male nightingales, *Luscinia megarhynchos*, have a high singing activity both at night and during the day (Amrhein et al., 2002; Thomas, 2002b), raising questions on functional differences in singing at different times of day. Nightingales are long-distant migrants and males start nocturnal song upon arrival from their wintering grounds on their breeding territories and usually cease nocturnal song once being paired (Amrhein et al., 2002). Females usually arrive about a week to 10 days after the males (Amrhein et al., 2007) so that data on singing behavior collected before pairing can be used to predict the future pairing success. In our study population, a large proportion of up to 50% of males remain unpaired throughout the season (Amrhein and Zwygart, 2004; Amrhein et al., 2004b, 2007), allowing us to compare song traits before pairing of males that become paired and males that remain unpaired (bachelors). Moreover, during nocturnal song, males engage in hourly long vocal interactions raising specific questions on the function of nocturnal song and on nocturnal male–male vocal interactions. Nocturnal song also has the practical advantage that functional aspects of vocal signals can be studied in the absence of visual cues or changes in spatial configurations. Moreover, in nightingales, territory boundaries are mostly defined by habitat characteristics such as bordering open fields, rivers, or grassland (Amrhein et al., 2002; Grüll, 1981; Wilson et al., 2005), so that loudspeakers can be placed at defined distances within or outside territorial boundaries. Nightingales also use a few preferred song posts during nocturnal song, and they spend about 90% of the time within their song territory (Naguib et al., 2001) so that the identity of the male can be determined by its singing location with high reliability. As in other songbirds, playback simulating territorial intrusions during the day elicit strong territorial responses including physical approach and singing (Sections II.C.4 and III.C). However, responses at night commonly are almost exclusively vocal and over longer distances with only rare occasions of approach (Section II.B).

By reviewing literature on the function of male song in nightingales, we integrate different aspects of communication and of the territorial system, and place our findings into a broader context of animal communication. Nightingales are an excellent model species to study song acquisition, song development, and the organization of large song repertoires (Hultsch and Todt, 2004; Kipper and Kiefer, 2010; Todt and Hultsch, 1996), as well as to study functional aspects of singing in the wild, which is the focus of this chapter. By bringing together different aspects of the singing behavior that has been studied both descriptively and experimentally along with more ecologically focused studies on settlement and spatial behavior, we provide a comprehensive overview of the complexity of the territorial system of a songbird. In Section II, we focus on descriptive studies on male singing activity in relation to pairing status and season (Section II.A) and on nocturnal vocal interactions (Section II.B). In Section III, we discuss playback experiments conducted during the day, which mainly were conducted within a communication network framework (Section III.C), and discuss translocation experiments with radio-tagged individuals in which we studied spatial behavior of prospecting males and females with respect to resident males' singing activity. In Section IV we integrate the main findings.

II. Singing and Territorial Behavior in Nightingales

The dual function of bird song, i.e.. territory defense and mate attraction, raises a number of specific issues on how the two functions of bird song are integrated into one signal (Ratcliffe and Otter, 1996). In addition to differences in the song traits to which males and females may attend to, as discussed above, another question is, whether females searching a mate and males listening to a rival's song both attend to song at the same time, as discussed in the following section.

A. Variation in Singing Activity with Time of Day, Season, and Pairing Status

One conspicuous aspect of bird song is that it varies on different time scales. Male singing activity varies over the year, with a peak of singing during the breeding season. Singing also varies within the breeding season, often with a peak in singing during earlier stages of the season. Moreover, singing varies with time of day and the actual timing of single songs varies with respect to the timing of songs of other males. Thus, one question is whether or not these various levels of temporal variation in singing have functional correlates that may explain the evolution of such time patterning.

Part of the temporal variation of singing behavior may have evolved as a result of different selection pressures by male and female receivers. Females usually make decisions on mating at specific periods in the season, when choosing a social mate or when making decisions on extrapair copulations. Males are most vigorous in territory defense also during this period, but the territorial function of song usually persists beyond the period of female reproductive decision making. In several species, males sing differently during the period of mate attraction compared to when singing to other males in a territorial context. For example, before attracting a mate, males in some species sing more complex songs and show higher singing activity than after mate attraction (Catchpole and Slater, 2008), suggesting that in such cases the primary function of male song is to initially establish a territory and to attract a female.

In Section II.A.1, we will consider variation of nocturnal and diurnal song in nightingales with respect to the time of season and the pairing status of males. The focus of this section is on descriptive data from nightingales allowing to make inferences on the possible function of singing at different times of day with respect to receiver sex. The timing of single songs within nocturnal vocal interactions will be discussed in Section II.B.1 where it is linked to other aspects of singing and territorial behavior. Responses to diurnal playback are considered within Sections II.C.4 and III.C.

1. *Variation in Nocturnal Singing Activity*

The most apparent characteristic of the temporal variation of singing in nightingales is the extensive nocturnal song in addition to diurnal song (Amrhein et al., 2002; Hultsch and Todt, 1982; Thomas, 2002b). Nightingales have a diurnal singing routine like most other songbirds, so that nocturnal song is an extension of the diurnal singing routine rather than merely a temporal shift away from times when most other songbirds sing. As nocturnally singing males lose more weight over night than males which do not sing, nocturnal song may carry substantial physiological costs (Thomas, 2002a). Even though nocturnal song is more widespread across birds than often thought (Amrhein et al., 2002), the predictability and regularity of nocturnal song in nightingales along with its sibling species, the thrush nightingale (*Luscinia luscinia*; Griessmann and Naguib 2002), is outstanding, as males then sing at high song rates over several hours without changing song posts. The existence of diurnal as well as of nocturnal song raises the question of whether the function of song differs between times of the day. The observation that the number of nocturnally singing males decreases with the ongoing breeding season has led to the idea that males sing at night to attract nocturnally migrating females (Glutz von Blotzheim, 1988; Hultsch, 1993). In surveys on the occurrence of nocturnal song and on the pairing status of territorial males, we indeed found that males usually cease singing at night after a female has settled in their territory (Amrhein et al., 2002, 2004a, 2007). These findings suggest that nocturnal song plays an important role in female attraction. Findings that females prospect an area by sampling several singing males at night (Roth et al., 2009), as discussed in Section III.B, support this conclusion.

Interestingly, paired males often resume nocturnal song for some nights at a later stage, mainly during female egg-laying (Amrhein et al., 2002; Kunc et al., 2007). These findings suggest that while nocturnal song appears to be import in attracting a female for social pair formation, the function is not restricted to that (see also Section II.B). The nocturnal song of a paired male during its mate's egg-laying period is likely to have a different function given that social pair formation with several females is an extreme exception in nightingales (Glutz von Blotzheim, 1988). Nocturnal song during the egg-laying period may have several other functions (Amrhein et al., 2002), such as to stimulate his mate to invest more into egg production (Gil et al., 2004), to mimic a bachelor and thus to reduce the probability of intrusions by males seeking extrapair copulations, or to attract females seeking extrapair copulations. Despite this correlative evidence suggesting that nocturnal song is under main selection by females, experimental studies show that nocturnal song also is of intrasexual relevance, as discussed in Section II.B.1.

2. *Variation in Dawn Singing Activity*

In contrast to nocturnal song, singing activity at dawn does not vary significantly with pairing status or with the stages of the breeding cycle (Amrhein et al., 2004a). Also, dawn song rate does not correlate with subsequent pairing status and with the breeding stages, contrasting some studies in other species (Kunc et al., 2005a). Currently, we cannot exclude that the specific characteristics of singing at dawn differ over the season or among males differing in pairing success. Yet, the mere presence of dawn song over the season suggests that its function is important to defend the territory against rival males and for regulating social relationships among territorial neighbors. A high singing activity at dawn is widespread among songbirds (Staicer et al., 1996) and has been linked to female fertility (Cuthill and Macdonald, 1990; Mace, 1987; Welling et al., 1997), nest defense, parental care and survival (Welling et al., 1997), territory defense (Poesel et al., 2004), male rank (Otter et al., 1997), previous territorial intrusions (Amrhein and Lerch, 2010; Erne and Amrhein, 2008), population density (Sexton et al., 2007), or to ecological factors like environmental pollution (Gorissen et al., 2005). The link between dawn song and female fertility, as reported in some studies (also see Suter et al., 2009), suggests a specific intersexual function of dawn song. Yet, even in species with a peak of dawn singing around female fertility, dawn singing often extends beyond the fertile period of the mate (Amrhein et al., 2008; Saggese et al., 2011), and it can involve a complex signaling network among many individuals (Fitzsimmons et al., 2008a,b; Foote et al., 2008, 2010). Dawn song thus may well be of general importance for males and females to assess singers, even if it may have evolved initially due to stronger selection pressure from one sex.

Thus, the temporally different singing behavior of paired and unpaired males at night and the lack of differences at dawn along with apparent sex-specific differences in the time of day at which nightingales explore the area (Amrhein et al., 2004b; Roth et al., 2009; see Section III.B) suggest that intra- and intersexual selection has led to the temporal segregation of singing and prospecting.

B. Vocal Interactions

When males sing, they often also vocally interact with each other. Such vocal interactions are characterized by temporal and/or structural relations of the songs of the singers to each other (Todt and Naguib, 2000). Males occasionally reply with the same song type to each other (song type matching) or specifically select songs with certain structural characteristics when counter singing with each other. Moreover, song birds (Brumm, 2006; Ficken et al., 1974, 1985) as well as chorusing insects and frogs (Grafe, 1996; Greenfield, 1994; Schwartz, 1987) generally avoid acoustic masking so that call or song alternating is widespread. However, males frequently also start a song before the other male has finished, thus overlapping the song of

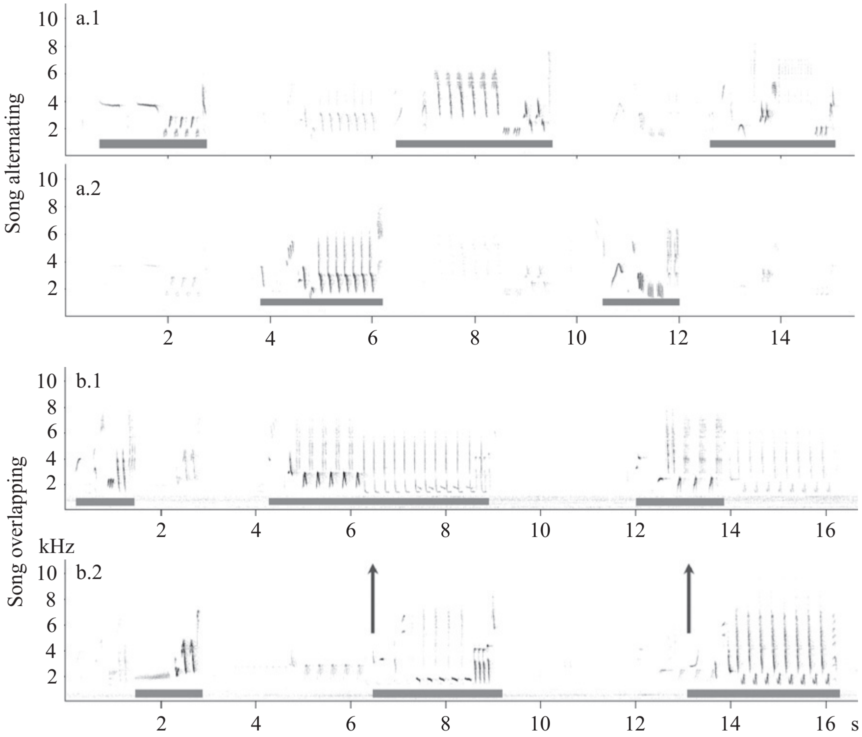

FIG. 1. Sound spectrograms from two vocal interactions in male nightingales, exemplifying song alternating (a.1 and a.2) and song overlapping (b.1 and b.2). Overlapping events are marked with arrows and the duration of a song is highlighted by gray bars below each song. Songs from interacting individuals are faintly visible also in the spectrogram of songs from its counterpart.

the counterpart (Fig. 1). Possibly resulting from such general mechanisms to avoid signal overlap, persistent song overlapping by playback simulating close rivals in songbirds often elicits changes in singing and aggressive responses such as approach to the loudspeaker (Naguib and Mennill, 2010). Song overlapping has been shown in many species to act as a signal and indeed can be used more universally than song type matching, which requires a song repertoire as well as songs that are shared among singers. Vocal interactions in nightingales are most apparent during long nocturnal singing bouts, but males also vocally interact with each other during the day. In the following sections, we will first address experiments in which we tested vocal response of male nightingales to song overlapping during nocturnal song (Section II.B.1) and then (Section II.B.2) the relation between nocturnal singing interactions between unpaired males and their future pairing success. As most of the playbacks that we conducted during the day were conducted in a communication network framework or tested the territorial response to specific song traits, we consider these diurnal responses in Sections II.C.4 and III.C.

1. Song Overlapping at Night

During nocturnal song, nightingales often interact vocally with each other mainly by alternating songs and by occasional song type matching or overlapping (Todt and Naguib, 2000). Even though the primary function of nocturnal song appears to be attracting females, as discussed in Section II.A.1, descriptive and experimental data suggest that nocturnal song is relevant also in male–male interactions. Playback studies on nightingale nocturnal song have shown that males respond in specific ways depending on the timing of an opponent's song, such as when their songs are overlapped by playback or when playback songs alternate with them (Hultsch and Todt, 1982; Naguib, 1999; Naguib and Kipper, 2006; Schmidt et al., 2006; Sprau et al., 2010b; Fig. 1). The most frequent response to song overlapping during nocturnal song in nightingales is a more irregular singing pattern (Naguib and Kipper, 2006; Naguib et al., 1999; Schmidt et al., 2006), suggesting that males try to avoid being overlapped and perceive song overlapping as a disturbing and presumably aggressive signal (Naguib and Mennill, 2010; Todt and Naguib, 2000). Most commonly, interacting nightingales alternate their songs during nocturnal singing interactions, with 20–30% of songs overlapping the songs of a rival during long distance interactions between neighboring males (Naguib and Kipper, 2006). Nightingales also have been shown to increasingly interrupt their nocturnal singing the more their songs are being overlapped during nocturnal playback (Naguib and Kipper, 2006). Interestingly, after playback, males continued to sing with the more interruptions the more songs were overlapped by playback, indicating that responses to song overlapping are not just reactions to avoid jamming but lead to more persistent arousal. This also suggests that song overlapping can be used as a graded signal by adjusting the number of songs of a rival that are overlapped (Naguib and Kipper, 2006). Yet, to date studies have treated song overlapping as a strategy with binary options for choice, that is, song alternating or song overlapping. Thus, there is still little understanding on how the signal value of song timing varies on a more gradual level, and whether or not the function of song overlapping is also affected by the latency with which a male starts a song after the rival started its song and thus by the proportion of a song that is being overlapped.

While playback experiments at night provide insights into which song traits males use and respond to vocally, the territorial consequences of such singing strategies are not as apparent as during the day, when patterns of singing can have immediate consequences leading to physical retreat or approach. The value of the information obtained during nocturnal listening or interacting thus can be expected to be important also in decision making during the day. As proposed by the social dynamic hypothesis discussed in the context of dawn singing (Staicer et al., 1996), males may exchange information during nocturnal interactions that is relevant for their general social relations. This could include learning individual characteristics of the song of particular male rivals (Kiefer et al., 2010) or assessing motivational characteristics that may affect also territorial behavior during the day. If so, one would predict that during the day males would respond more aggressively to a male which they already had experienced as singing aggressively at night. To test this idea, Schmidt et al. (2007) presented males with either an alternating or overlapping playback at night, played from outside their territory. When simulating an intrusion the next morning using a standard noninteractive playback, males showed a stronger territorial response when they had been exposed to an overlapping rather than to an alternating playback the night before (Schmidt et al., 2007). These findings show that male vocal interactions at night have consequences for territorial behavior during the day and that song overlapping at night leads to more aroused singing during the night as well as to more aggressive territorial responses during the day. Such long-term effects are also supported by playback studies on banded wrens, *Thryothorus pleurostictus*, and on winter wrens, *Troglodytes troglodytes*, which revealed changes in singing and territorial behavior 1–5 days after an intruder was simulated (Amrhein and Erne, 2006; Amrhein and Lerch, 2010; Erne and Amrhein, 2008; Illes et al., 2006).

2. *Correlates of Future Pairing Status*

The vocal interactions between males provide information on differences in motivation or quality of the male, or they may be linked to differences in territory quality. Such information is also relevant for females, which thus may impose a selection pressure on male–male nocturnal interactions. Females may attend specifically to these interactions and be influenced in their mating decisions depending on relative differences in the performance of males in their vocal interactions (Wiley and Poston, 1996). A network of nocturnally singing males thus even may be considered as a sort of hidden lek in which territorial males display relative to each other (Cockburn et al., 2009; Wagner, 1998) during the time of female prospecting (Roth et al., 2009). Studies on diurnal song in other species support this idea, as laboratory studies on canaries, *Serinus canaria*, showed that female song preference is affected by the way songs are used in a vocal interactions between males (Amy et al., 2008; Leboucher and Pallot, 2004). Also field studies on great tits (Otter et al., 1999) and black-capped chickadees, *Poecile atricapilla*, (Mennill et al., 2002) showed that females attend to male–male vocal interactions and subsequently use the obtained information in their mating decisions.

In nightingales, several nocturnal playback experiments showed that males that are unpaired at the time of playback but later become paired respond differently to playback than males that remain unpaired throughout the breeding season. Males that remain bachelors overlap fewer playback songs (Kunc et al., 2006), interrupt their singing more when their songs are overlapped (Schmidt et al., 2006), and more frequently add high-frequency whistles to their songs than males that will become paired (Sprau et al., 2010b). Moreover, during the period when females of paired males lay eggs, their mates respond with a lower song rate and lower extent of song overlapping to nocturnal playback compared to bachelors' responses during the same time of the season, indicating that males become less aroused when challenged by nocturnal song after pairing (Kunc et al., 2007). In contrast, males that remain unpaired throughout the breeding season do not strongly vary in their response to an opponent across the season. Thus, males apparently vary the level of aggression in vocal interactions according to their pairing status and to the stage of the breeding season (Kunc et al., 2007). Yet, it remains to be shown whether the relation between singing and successful pairing results from females preferring males that interact more aggressively or whether males interacting more aggressively also differ in other traits affecting female choice.

C. Structural Song Traits and Their Specific Functions

In the following subsections, we will highlight some structural characteristics of nightingale song and consider the currently available data from nightingales on the possible function of different structural traits.

1. *Song Repertoires*

Nightingales are renowned for their singing versatility and their large vocal song repertoire consisting of 150–200 different song types (Kipper et al., 2006). Further, each song is composed of a complex series of repeated and unrepeated elements (Todt, 1970). The repertoire and its organization are acquired through vocal learning during early life (Hultsch, 1992; Hultsch and Todt, 1989, 1992, 1996a). Yet, males can also be inventive when developing their repertoire (Hughes et al., 2002) and modulate their repertoire later in life, with the main changes occurring from the first to the second breeding season (Kiefer et al., 2006, 2009), leading to more repertoire similarities among males in their second breeding season (Kiefer et al., 2010). In line with such repertoire modulation, male nightingales actually may sing songs learned early in life only when hearing that particular song. Otherwise they retain certain songs as ‘‘silent song types’’ that are not produced during noninteractive singing (Geberzahn and Hultsch, 2003; Geberzahn et al., 2002).

While the song repertoire has been intensively studied to address questions on rules of song acquisition and of storing and retrieving large amounts of serial information, less is known on the factors that have led to the evolution of the large repertoires in the first place. To date, a few studies have shown that the song repertoire of male nightingales provides information that could be relevant in female choice. Kipper et al. (2006) showed that males arriving earlier in the season have larger song repertoires and a larger body mass, suggesting that repertoire size encodes information on male quality. Moreover, 1-year old males have smaller repertoires than older males (Kiefer et al., 2006) and age can be one of the important factors reflecting quality. Given that the vocal repertoire is delivered in singing bouts lasting over several hours at night, which is the time of female mate prospecting, it seems reasonable to assume that females indeed attend to structural singing traits in nocturnal song, even though they probably will not actually count the number of song types to determine repertoire size. Neighboring males also share a substantial proportion of their song repertoire of up to 60% (Kipper et al., 2004) and commonly alternate songs with each other during nocturnal singing with occasional song type matching and overlapping songs of the rival (Todt and Naguib, 2000). The fact that male nightingales acquire both the songs shared by many males as well as songs that are not shared with others may enable them to match the songs of rivals as well as to avoid being matched by rivals (Sprau and Mundry, 2010). Such social effects may thus also have played a role in the evolution of large repertoires (Byers and Kroodsma, 2009).

2. *Whistle Songs*

Among the diversity of nightingale songs, one song category sticks out syntactically and auditorily, which are the so-called whistle songs (Hultsch and Todt, 1996b; Kunc et al., 2005b). Unlike most other nightingale songs that start with a series of nonrepeated structurally different notes, whistle songs begin with a series of repeated notes with a narrow frequency bandwidth leading to a whistle-like structure. Each male has a repertoire of different whistle songs differing in frequency, duration, and modulation of the whistles (Kunc et al., 2005b; Naguib et al., 2002). Whistle songs are used at all times of the day but are most common during nocturnal song where up to 20% of the songs can be whistle songs (Kunc et al., 2005b; Naguib et al., 2002). Early in the breeding season, whistle songs sung at dawn make up less than 14% of songs (Kunc et al., 2005a). In contrast to soft initial whistles (see Section II.C.3), the conspicuous whistles at the onset of whistle songs appear to be designed for long-range transmission and as alerting component (Richards, 1981), and whistle songs have a considerably longer transmission distance than more broadband frequency song components (Naguib et al., 2008). The increased use of whistle songs at night, their decreased use during male–male close-range interactions (Kunc et al., 2006), and their long transmission range combined with nocturnal migratory and mate searching behavior of females suggests that they have a specific function in alerting and attracting females. Nevertheless, males also are responsive to whistle songs at night as they occasionally match the same song category and thereby often even use whistles that also match the frequency of the whistles of rival males (Naguib, 2005). Such frequency matching occurs more often and with more precision with increasing distance (Naguib et al., 2002) and thus can be seen as a less aggressive long distance signal to attract attention. Such whistle frequency matching over long distances possibly serves to draw attention of females to the song of the matching male and away from competitors. This long distance matching adds a new aspect to the general view on the function of signal matching as it contrasts the more common findings that vocal matching is associated with aggressive close-range contexts (Searcy and Beecher, 2009; Todt and Naguib, 2000).

3. Songs Preceded by High-Frequency Whistles

In addition to the distinct song category of whistle songs, nightingales occasionally also use softer high-frequency whistles as the first elements preceding any song. Such an initial whistle is of higher frequency compared to the whistle in whistle songs, it is of lower amplitude, and usually it is not repeated (Fig. 2). The more frequent use of initial whistles in territorial disputes and short-range vocal interactions suggests that they function primarily as short-range signals in aggressive contexts (Sprau et al., 2010a,b). These findings suggest that initial whistles are functionally similar to soft song that has been described in other songbird species as agonistic signal in intrasexual interactions (Anderson et al., 2007; Dabelsteen et al., 1998; Hof and Hazlett, 2010; Searcy and Nowicki, 2006). Soft song with its low amplitude is considered to signal high arousal to an opponent, while reducing the probability that eavesdroppers receive the signal content (McGregor and Dabelsteen, 1996). Initial whistles could expand on this function, as the low amplitude may signal high arousal only to close rivals while hiding this arousal from more distant individuals that are exposed to the regular songs (Sprau et al., 2010a).

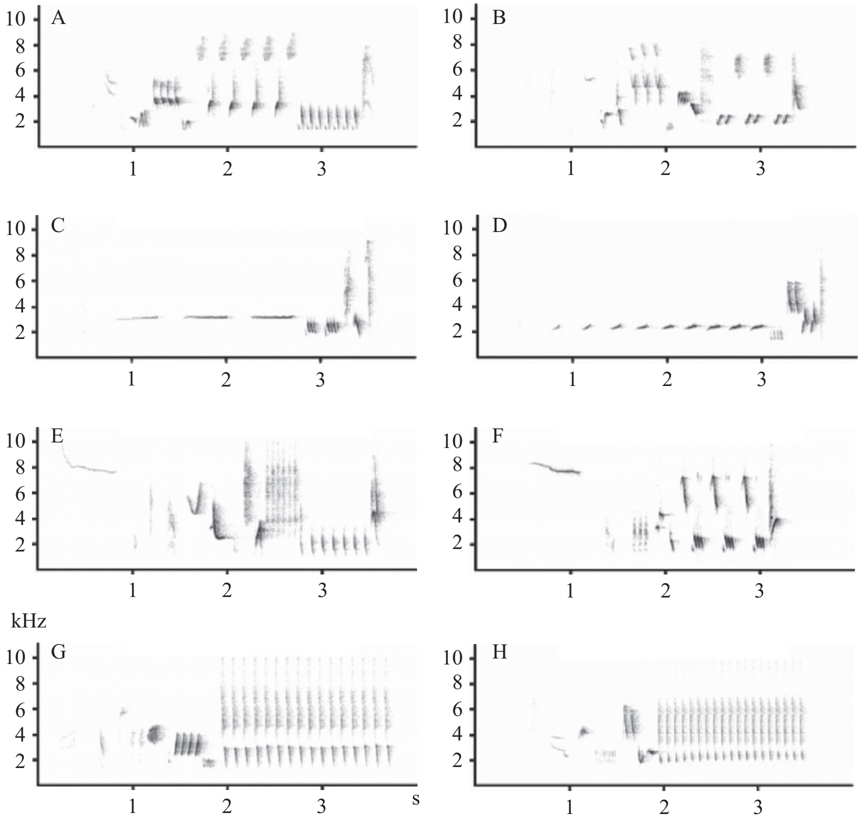

FIG. 2. Sound spectrograms nightingale songs with different structural components. (A) and (B) represent ordinary nightingale songs; (C) and (D) represent whistle songs, characterized by the series of whistles in the first part of the song; (E) and (F) represent songs preceded by initial whistles which are higher in frequency and lower in volume than the whistle in whistle songs. They also are usually not repeated within a song but often precede subsequent ordinary songs; (G) and (H) represent songs containing rapid broadband trills.

4. *Songs with Rapid Broadband Trills*

Another song category that appears to have a specific signal value consists of songs that contain rapid broadband trills. Trills occur in many songbird species and often are used in aggressive contexts (Cramer and Price, 2007; DuBois et al., 2009; Illes et al., 2006), but they have also been shown to be used by females to assess males (Ballentine et al., 2004; Caro et al., 2010; Vallet and Kreutzer, 1995). Because the production of trills is physically constrained (Hoese et al., 2000; Podos, 1996), they can contain specific information on the quality of the singing male that can be used by females (Ballentine, 2009; Ballentine et al., 2004; Caro et al., 2010; Draganoiu et al., 2002) as well as by males (Illes et al., 2006; Schmidt et al., 2008). Rapid trills degrade quickly over distance (Naguib, 2003; Naguib et al., 2008) so that the signal content is probably most easily received in close-range interactions even though in nightingales rapid broadband trills are still perceived as an aggressive signal at far distances (Sprau et al., 2010a). We also found that males increase the percentage of songs containing rapid broadband trills in response to nocturnal playback (Kunc et al., 2006; Schmidt et al., 2006; Sprau et al., 2010b) and sing more songs with rapid broadband trills to near than to far nocturnal playback (Sprau et al., 2010a). Further, in a playback experiment during the day using two loudspeakers, we showed that territorial males approach and respond more to the loudspeaker playing songs with rapid broadband trills than to the loudspeaker playing songs without trills (Schmidt et al., 2008). Males approached faster and stayed longer and sang more near the loudspeaker broadcasting songs with these trills, compared to the loudspeaker playing songs without such trills. These findings suggest that rapid broadband trills have an aggressive signal value, confirming the interpretation from studies on rapid broadband trills during nocturnal songs (Kunc et al., 2006; Sprau et al., 2010a,b).

Rapid broadband trills thus seem to have a similar signal value as song overlapping (also see Section II.B.1). Unlike song overlapping, though, trills can be sung independently of whether or not a rival is singing and thus are suitable signals also in noninteractive singing bouts. In a study testing whether trills can enhance the agonistic function of song overlapping, we found a moderate enhancing effect of trills on song overlapping (Sprau et al., 2010b).

III. SPATIAL ECOLOGY AND COMMUNICATION NETWORKS

A. SONG AND TERRITORIAL SETTLEMENT

Territorial songbirds are model organisms to address a number of issues in behavioral ecology that are related to division of space and defense of resources. At the onset of each breeding season, space has to be divided up among individuals, as many resident species are not strictly territorial outside the breeding season (Stamps, 1994; Stamps and Krishnan, 1997, 2001), and because migratory birds have to establish territories upon arrival on the breeding ground. The factors affecting the decisions where to settle are often difficult to disentangle. Presumably, a complex set of factors is involved in the decision process including individual-specific traits such as the experience with a particular site, individual age, time of arrival, as well as environmental factors such as territory location, quality, and spatial arrangement of the males that are already present (Hoover, 2003; Naguib, 2005; Reed et al., 1999).

In a survey of settlement patterns in nightingales, we found that males that arrive earlier are more likely to become paired than later arriving males. Early arriving males on average also were older than late arriving males, but this difference was not significant (Amrhein et al., 2007). Nevertheless, these data fit well with findings by Kipper et al. (2006) that males arriving earlier have larger song repertoires, and that song repertoire also increases with age, at least from the first to the second breeding season (Kiefer et al., 2006; Kipper and Kiefer, 2010). Even though it is not possible with our current data to disentangle the role of male characteristics and territorial characteristics with respect to female choice, the data suggest that it is beneficial for males to arrive a few days before the majority of females arrive. Such an earlier male arrival generally might have evolved as a consequence of male–male competition for the best territories (Kokko et al., 2006). It may also make them more attractive, as longer residency could have positive effects on current physical condition after a long migration. Longer residency and familiarity with the site and the neighborhood may also affect other behavioral traits that females may attend to, such as attention and response to stimuli, or exploratory and foraging behavior.

Male songbirds often are highly philopatric, with males returning to the same territory they had occupied the previous year (Greenwood, 1980), and this is also common in our nightingale population. Using long-term territory-occupancy data, Roth and Amrhein (2010) proposed a new model to estimate local survival, which is the probability that a male survives from one breeding season to the next and settles in the same territory as in the previous breeding season. They then compared local survival with apparent survival obtained from a traditional analysis of the capture–recapture data from the same population, determining the probability an individual survives from one breeding season to the next and settles in the same study area (as opposed to the same territory in local survival). As local survival in nightingales is virtually the same as apparent survival, it appears that most of the surviving males settle not only in the same study area, but also in the same territory as in the previous breeding season. For the moderate proportion of males that switch territories, males may often select new territories at some larger distance from the previous territory and thus also outside our study site (Roth and Amrhein, 2010).

The spatial configuration of territories is the result of the decision of each individual where to settle and may explain part of the variation in breeding success among males (Formica et al., 2004). It is also likely that the spatial configuration of the territories have direct implications on vocal communication and likewise that vocal communication may affect the spatial configuration (Naguib, 2005; Waser and Wiley, 1980). For instance, it is known for several bird species that distance to the closest neighbor or the number of neighbors may affect singing (Cockburn et al., 2009; Liu, 2004). A survey of the settlement pattern in male nightingales confirmed that the distance to the closest neighbor decreases and the number of neighbors increases during the course of the breeding season (Naguib et al., 2008). One thus may argue that a seasonal change in the spatial configuration of territories could explain at least part of the seasonal variation in singing of nightingales (Amrhein et al., 2004a; Kunc et al., 2005a) as well as the seasonal changes in vocal interactions (Kunc et al., 2006, 2007). Although still understudied, the interplay of the spatial configuration of territories and of song received increasing attention over the past years. Current research indicates that vocal communication in many species is best viewed as a communication network with stationary as well as moving senders and receivers.

B. SPATIAL BEHAVIOR WITHIN AND BEYOND TERRITORY BOUNDARIES

While a territory is the most obvious central component of a territorial individual's spatial ecology, behavior does not stop at a territorial boundary. For example, singing interactions usually involve communication across territory boundaries among two or more territorial males. Moreover, many territorial systems also incorporate nonterritorial individuals, so-called floaters (Bruinzeel and van de Pol, 2003; Campioni et al., 2010; Kempenaers et al., 2001). Male floaters usually do not sing (Amrhein et al., 2004b), but they may impose selection pressures on territorial males that are difficult to assess, given the often hidden behavior of floating individuals (Smith, 1978). Due to the general difficulty of observing individual songbirds over a prolonged time while they are exploring space, most information on spatial behavior beyond territorial boundaries results from radio-tracking studies (Chandler et al., 1994, 1997; Hanski, 1992; Maciejok et al., 1995; Naef-Daenzer, 1994; Pitcher and Stutchbury, 2000; Rätti and Siikamki, 1993; Stutchbury, 1998). These studies have well documented that males as well as females can leave their territory and explore the neighborhood, showing that understanding territorial systems requires a more holistic view incorporating a larger area.

In a series of studies, we investigated the spatial behavior of both male and female nightingales, combining radio-tracking and translocation studies with descriptive and experimental work on singing behavior of territorial males. Our aim was to determine whether and to what extent spatial relations exist among individuals within a larger neighborhood and how these are linked to or mediated by the singing behavior of residents. By radio-tracking males throughout the breeding season, we found that most of the time, males indeed remain on their territory, defined as the area they use for singing (Naguib et al., 2001). Interestingly, males that sang at higher rates also made more forays while receiving fewer forays from neighbors. Yet, we found the opposite pattern when following males whose neighbor was challenged by a simulated territorial intrusion using playback (Naguib et al., 2004). In this case, males were more likely to intrude into a neighbor's territory when that neighbor sang more in response to a simulated intruder. These findings show that song has both repelling and attracting functions to other males, depending on the context in which it is used.

On a larger scale, male song also appears to have an attracting function to rival males exploring a neighborhood. We occasionally observed that during extraterritorial forays, radio-tagged males move straight close to the song posts of their singing neighbors. We made similar observations in a radio-tracking study where males were translocated from a remote site to our site. Translocated males almost exclusively prospected the neighborhood at dawn, which also is the time of day with the highest probability to encounter a resident male singing (Amrhein et al., 2004b). During these dawn excursions, translocated males visited several resident males (Fig. 3), often sitting close to the singing resident, suggesting that they were attracted by the song of the residents (Amrhein et al., 2004b). Interestingly, translocated males spent more time in territories of paired males than in those of unpaired males, suggesting that the short period of prospecting at dawn is sufficient to assess the pairing status of a resident. We do not know whether this information is provided by a possibly different singing style at dawn of paired and unpaired males or by the female itself. Information on pairing status otherwise is more readily available at night, when paired males usually do not sing (Amrhein et al., 2002, 2004a). Yet, due to an apparent lack of nocturnal movements by males, they are unlikely to use nocturnal song to assess pairing status of males within a larger neighborhood.

In contrast to territory-prospecting males, prospecting unpaired females moved over large distances specifically at night and moved less at dawn or other times of the day (Roth et al., 2009). These findings support the idea that females use nocturnal song to assess pairing status and quality of males. Yet, it remains unclear whether nocturnal singing is a cause for, or an effect of, nocturnally prospecting by females, and how nocturnal song evolved in the first place (Roth et al., 2009). Both, the translocated females at night and the translocated males at dawn, covered distances during one prospecting foray of up to 6 km. Such extended movements of potential receivers reveal that singing males indirectly compete with other singing males that are further away than the hearing distance. As a consequence, coevolution

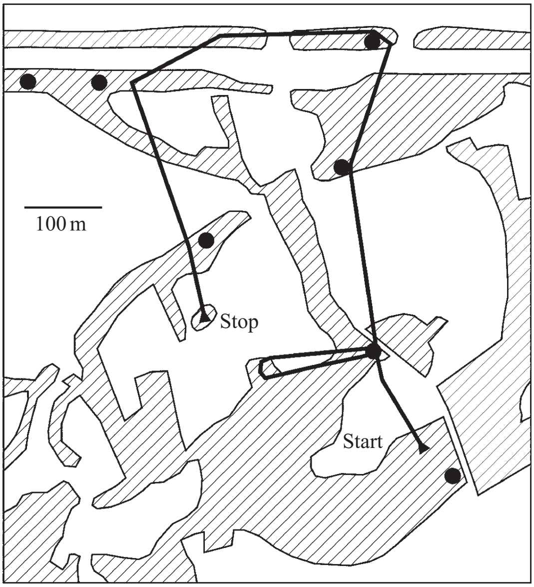

FIG. 3. Dawn prospecting path (black line) of a translocated and radio-tagged male nightingale (based on data in Amrhein et al., 2004b). Hatched areas indicate reed, bushes, or woods separated by fields and meadows. Black dots indicate singing territorial males.

between vocal and spatial behavior warrants an integrated view of vocal signaling on the one hand and of use of space on the other hand. Studies on spatial behavior of information-seeking individuals have a great potential to improve our understanding of vocal communication, as the movements of receivers within and among territories may influence and connect individual males singing in their territories, resulting in social networks (Croft et al., 2007, 2009). Such an integrated view is emphasized by studying vocal communication within a network of signalers and receivers, as discussed in the following section.

C. STRATEGIES IN COMMUNICATION NETWORKS: SIGNALING AND INFORMATION GATHERING

One aspect of territorial systems that has been emphasized in recent years is that animals using long-range signals can be heard simultaneously by several receivers. Animals are well known to be able to obtain information about relative differences between individuals by observing their interactions (Danchin et al., 2004; Whitfield, 2002). Signaling interactions with asymmetries in the way signalers use their signals provide information on relative differences among individuals. This information may be important for nonparticipating eavesdroppers such as potential mates or rivals that may benefit from using information obtained from signaling asymmetries. To emphasize this way of information gathering, McGregor and Dabelsteen (1996) introduced the term communication networks highlighting the potential for individuals to eavesdrop on signaling interactions between others and to extract information from the relation of their signals to each other. Signalers even may interact in certain ways to signal specifically to eavesdroppers rather than to their direct interacting counterpart (Zahavi, 1979). The idea of communication networks stimulated research activities focusing on more than two individuals being involved in a communication event in a range of organisms (McGregor, 2005). In nightingales, we used two-loudspeaker setups to test whether territorial males extract information from signaling interactions and respond differently depending on the relation between the two signals. Song overlapping and other temporal asymmetries in singing appeared as a particularly suitable example, as the two loudspeakers could be set to only differ in the temporal relations of the songs but not to differ in any absolute trait, such as song rate or song complexity. The experiments showed that males responded more aggressively to a loudspeaker playing song that overlapped the songs of another loudspeaker placed 20 m away (Naguib and Todt, 1997). These findings indicate that males can indeed extract information from signaling interactions between other males, and that song overlapping is interpreted as aggressive signal also by eavesdroppers and not only by the individuals directly involved in the interaction. Moreover, a subsequent experiment in which songs from two loudspeakers alternated with each other in asymmetric ways revealed that asymmetries in vocal interactions are relevant for eavesdroppers also in the absence of song overlapping (Naguib et al., 1999). The experiment demonstrates the existence of vocal leader–follower relations, with males responding stronger to vocal leaders when songs were alternating asymmetrically without any vocal overlap (Naguib et al., 1999). Also Mennill and colleagues found a stronger response by male black-capped chickadees to the overlapping speaker (Mennill and Ratcliffe, 2004), and they further showed that females are more likely to engage in extrapair copulations when they heard their mate losing a vocal interaction as imposed by interactive playback (Mennill et al., 2002). Studies on great tits also found that females respond differently depending on whether or not their mate is overlapped by playback (Otter et al., 1999), but this did not lead to changes in extrapair paternity (Otter et al., 2001). Peake and colleagues showed that great tit males use information obtained by eavesdropping differently depending on whether they are themselves challenged by a winner or a loser of the interaction they could listen to (Peake et al., 2001; Peake et al., 2002). The presumably most common context for eavesdropping on others' interactions involves an interaction of a territorial male with a singing stranger or a neighbor. Interactions of a territorial male with a stranger can be valuable to eavesdropping neighboring males, because they could use the response by their known neighbor as yard stick to assess the stranger. In order to test this idea, we conducted playback experiments with males but focused on the spatial behavior of their neighbors, which we recorded using radio telemetry (Naguib et al., 2004). This experiment revealed that nightingales indeed attend to their neighbors' interactions and respond depending on how their neighbor responds. Males intruded into the neighboring territory earlier when the challenged neighbor responded stronger. Yet, they did not intrude when the rival was simulated to have left the territory shortly after the intrusion (Naguib et al., 2004). Such eavesdropping on neighbor interactions and responses that depend on the neighbors behavior toward an unfamiliar rival may be adaptive as any new individual settling in the neighborhood may cause an at least temporal instability of an established system. Some studies indeed showed that birds benefit by being surrounded by familiar neighbors (Beletsky and Orians, 1989). Other laboratory studies showed that eavesdropping females respond differently to overlapped and overlapping songs (Amy and Leboucher, 2009; Garcia-Fernandez et al., 2010; Leboucher and Pallot, 2004). These studies show that signaling interactions provide important information for decision making, in addition to information derived from a single male singing. Recently, Amy et al. (2010) even showed that great tits respond to playback in their neighboring territory depending on personality traits of that neighbor. These findings indicate that individual information about the neighbor affects their own decision making in response to threats in the neighborhood. Such eavesdropping, extraterritorial forays, or in resident birds also previous encounters in winter flocking suggest that territorial systems should be seen as a larger social network with social relations extending in time and space beyond a mere presence and defense of territorial boundaries.

Taken together, the studies outline three lines of evidence that a songbird communication system such as in nightingales is best viewed as a large-scale communication network. First, singing is likely to depend on the spatial configuration of the territories. Second, because prospecting individuals are exposed to the singing of several males over a large spatial range, singing males may compete for access to females or territories with many other males, some of them even outside their own hearing distance. And third, songbirds obtain information by listening to the contests of other individuals, thus emphasizing the network character of communication systems involving multiple senders and receivers.

IV. SUMMARY AND CONCLUSION

Here we synthesize studies on vocal communication and spatial behavior in nightingales with research on other songbirds and emphasize the functions of advertisement signals in territorial systems and their role linking individuals in a social network. Nightingales with their hour-long singing bouts at night and their substantial singing activity at day have been a rewarding model to provide answers for a number of functional issues in vocal communication. Studying vocal behavior at night has yielded insights into the functions of vocal signals in the absence of changes in spatial location and the risk of immediate physical escalation. Playback experiments during the day have complemented nocturnal playbacks and revealed the importance of vocal interactions for eavesdropping territorial males and their neighbors. The combination of descriptive and experimental studies on song with a communication network approach and translocation experiments to test prospecting behavior of males and females have provided insights into a more ecological perspective of communication, enhancing the understanding of general principles of temporal and structural variation in advertisement signaling across species. The integration of singing and spatial behavior emphasizes the importance of network characteristics in the evolution of communication systems, with selection pressures imposed by territorial neighbors and nonterritorial individuals that intrude into occupied territories or eavesdrop from the distance on singing and singing interactions. More research on singing and spatial behavior will be important to broaden our view on such complex communication systems. Also playback studies may continue to develop a more dynamic approach, simulating intruding strangers as well as intruding neighbors that show natural spatial behavior by moving within the territory of a resident. Automated devises for song recordings and tracking movements and the use of populations with well-characterized individuals may become an essential component for future studies. Such studies will be able to generate novel insights into animal communication by integrating signaling and spatial behavior, as we have highlighted in this chapter.

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