Nonlinear phenomena and song evolution in *Streptopelia* doves

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Abstract
The production of complex bird song is commonly achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. According to nonlinear dynamics theory, however, complexity can also emerge spontaneously from very simple and deterministic systems, without any external control. Thus far, studies linking bird song complexity with nonlinear dynamics are very rare. Here we explore the possibility that a number of complex acoustic phenomena in vocalizations of *Streptopelia* doves are caused by nonlinear dynamics intrinsic to their vocal organ. We show that the complex acoustic phenomena in species-specific coos resemble the nonlinear phenomena described earlier for mammalian vocalizations. These phenomena include the different attractor states that have been found in mammalian phonation (limit cycle, folded limit cycle, torus, and chaos), and sudden transitions within and between those states (bifurcations). We argue that large, qualitative differences between species-specific song in *Streptopelia* doves may correspond to different attractor states of the same type of dynamic system. If so, dramatic acoustic differences between species sounds do not necessarily reflect large differences in sound production mechanisms or evolutionary differentiation, but may be due instead to relatively small differences in syringeal structure and control mechanisms.

Key words: Vocal production, Nonlinear dynamics, Chaos, Syrinx, Evolution, *Streptopelia*

1 Introduction

One major challenge in the study of bird song is to explain the mechanistic origins of its complexity and diversity. Birds in general share the same basic mechanism for vocal production. The avian vocal organ, the syrinx, produces sound through the vibration of pairs of opposing labia or membranes that are driven by respiratory air flow (Larsen and Goller, 1999). Modulation of the sound generated comes about by changing the physical properties of this acoustic source, or of the vocal tract filter that shapes the source signal (Hoese et al., 2000). Such changes are often achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. It is not surprising, then, that the identification of neuromuscular correlates of acoustic modulation in birds has received considerable attention over the years (see Suthers et al., 1999).

Recent findings, however, show that simple nonlinear systems can also exhibit complex dynamics without any external, complex control. This is true even if the underlying mechanisms are simple and completely deterministic. Systems in nature are often nonlinear, meaning that the equations describing them include squared and higher-order terms; and the study of such systems using concepts developed in nonlinear dynamics theory has led to a better understanding of their behavior in such diverse fields as ecology, physics, and economics. Because the primary sound generators in birds are nonlinear oscillators, it seems logical to hypothesize that nonlinear system dynamics also contribute to the complexity of bird vocalizations. Surprisingly, the concept of nonlinear dynamics has been mostly ignored in the study of bird song (cf. Fee et al., 1998; Fletcher, 2000).

In this paper, we explore the possibility that part of the complexity in species-distinct coo vocalizations in the genus *Streptopelia* (turtle-doves) can be explained by nonlinear dynamics intrinsic in the sound-producing organ. The genus *Streptopelia*, family Columbidae, consists of 17 species with a known phylogenetic history (Johnson et al., 2001), each of which has its own specific species perch-coo (Slabbekoorn et al., 1999). Between species, coo sounds can differ qualitatively in tonal structure, a characteristic that is used by turtle-doves to discriminate between species coos (Beckers et al., 2003), and may be used for species recognition. If qualitative differences in tonal structure represent different states of the same nonlinear dynamic system, as opposed to qualitatively different production mechanisms, this has serious implications for our understanding of the kind of mechanistic changes that may be involved in the evolution of song in these birds.

We show that acoustic characteristics of the coos of *Streptopelia* match dynamics known to occur in nonlinear systems, and resemble those found in mammalian vocalizations, the production of which is better understood in terms of the dynamics of coupled, nonlinear oscillators.
and this not only gives rise to two independent frequencies (Neubauer et al., 2001). In nonlinear systems, desynchronized and vibrate at their own individual, different frequencies, becoming a different characteristic behavior, namely sudden transitions from one dynamic state to another. These are called bifurcations. Typical examples in mammalian vocalizations are the sudden transitions from harmonic to subharmonic regimes (period-doubling bifurcation), from harmonic to biphonation (secondary Hopf bifurcation), or from harmonic to chaotic regimes. Sudden transitions within one type of attractor are also bifurcations. Examples of this are mode-locking transitions, in which harmonic vibrations simultaneously jump from one frequency to another. Mode-locking occurs when a nonlinear interaction constrains two oscillating components of a system to maintain a small integer ratio of frequencies; it is known to occur in the song of zebra finches (Fee et al., 1998). Mode-locking transitions may arise when the characteristic frequency of one component is changed relative to the other, and the oscillation frequency suddenly jumps to achieve a new stable integer ratio.

3 Nonlinear dynamics in the song of *Streptopelia* doves

We used recordings of perch-coo vocalizations that had been collected for earlier studies (Slabbekoorn et al., 1999; Beckers et al., 2003) to search for phenomena linked to nonlinear dynamics. All of the above-described nonlinear phenomena in mammalian vocalizations (Wilden et al., 1998; Fitch et al., 2002) appear in the perch-coo vocalizations of *Streptopelia* doves.

3.1 Limit cycles
Fourteen of the seventeen species have pure-tonal perch-coos, the simplest form of a limit cycle (Fig. 1a). Seven of these have trill-like coos, which consist of fast, repetitive pulses of pure-tone sound, and could therefore be regarded as amplitude-modulated and interpreted as a torus in nonlinear dynamics theory. The repetition rate of these pulses, however, is relatively low (< 30 Hz); they do not give rise to multiple frequencies in human and probably dove perception, and their production may not be intrinsic to the dynamics of the syrinx.

Subharmonics (folded limit cycles) do not occur normally in coo sounds emitted by Streptopelia doves, but vocalizations recorded in the interclavicular air sac of ring doves, S. risoria, occasionally do (Fig. 1b; Beckers et al., 2003), even though the harmonic and subharmonic components are filtered out before the sound radiates.

3.2 Torus

Two harmonically unrelated frequencies, “biphonation”, occur in the normal perch-coos of at least one species, S. orientalis. An example is the third sound element, labeled “B” in Fig. 2. In this example, a multi-harmonic signal with a fundamental frequency of 460 Hz (f) is modulated by a lower signal (g) of about 180 Hz, leading to the “side-bands” of 180 Hz at each harmonic of f.

3.3 Chaos

In three species (S. orientalis, S. tranquabarica and S. lugens), normal coo vocalizations consist completely or partly of elements with a chaotic structure. The S. orientalis sound elements labeled “C” in Fig. 3 are examples. Slabbekoorn et al. (1999) classified these vocalizations as “noisy”, but we believe that they are true chaotic sounds because there is often some harmonic structure within the irregular patterns, as described for mammalian chaotic sounds by Wilden et al. (1998). The regular sudden transitions from harmonic or biphonic sound to very irregular regimes (element ‘B/C’ in Fig. 2), and the varying degrees of irregularity in time-frequency patterns, are consistent with this interpretation. In an exceptional case, we found short chaotic regimes in the perch-coos of S. risoria, a species that normally produces harmonic coos. Although it is hard to prove the chaotic nature of sounds from acoustic analysis alone, some mathematical tools can be helpful in its identification (Fletcher, 2000; Tokuda, 2002).

3.4 Bifurcations

Frequency jumps are common sudden dynamic state transitions in all Streptopelia species with harmonic vocalizations. At these transitions, the gradual time-frequency contour is momentarily disrupted, as the fundamental frequency jumps almost instantaneously to a different frequency range without interrupting phonation (the first element in Fig. 1b). Such frequency shifts probably reflect mode-locking dynamics. In S. orientalis, transitions from harmonic to chaotic states are common (Fig. 2), and in S. risoria, coos showing subharmonics, transitions from harmonic to subharmonic regimes, and vice versa, occur suddenly without a stop in phonation.

4 Implications for evolution of song

One of the key features of nonlinear systems is that small and gradual changes in control parameters can cause large, sudden, and qualitative changes in dynamics. If true in bird song, the intrinsic dynamics of the sound production organ itself would provide a source of major and qualitative acoustic variation. Presence of transitions within species shows that these can be readily achieved. Such transitions may also be at the basis of vocal differences between species. Seemingly strong interspecific differences, e.g. between the tonal coos of S. risoria and the noisy ones of S. orientalis or S. tranquabarica, might thus have resulted from minor changes in underlying mechanisms of vocalization, without the need for large changes in syringeal structure or control mechanisms.
References


