
A Spatial Dance to the Music of Time in the Leks of Long-Tailed Manakins

DAVID B. McDONALD

DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY, UNIVERSITY OF WYOMING
LARAMIE, WYOMING, USA

I. INTRODUCTION

“What better time than now? What better place than here?”

Rage Against the Machine

Since its inception, behavioral ecology has focused on the distribution of resources, in time and space, as a key driver of variation in social systems (Emlen and Oring, 1977). My title comes from the series of novels “A Dance to the Music of Time,” by Anthony Powell, which in turn was named for a painting by Nicholas Poussin. Coordinated dancing, whether by two or more humans (<http://sneakmove.com/2007/06/awesome-new-european-dance-craze/>) or partnered manakins, is inherently a patterned interplay of space and time. By my count, Darwin (1859) used the word “time” 222 times in the “Origin of Species.” He used the word “space” less frequently (39 times). His main concern, of course, was the gradual descent of forms over time, such that the natural world becomes the tangled bank that we now enjoy and destroy. Behaviorists have also long been interested in time and space, but their focus is generally on more detailed variation over shorter periods of time and smaller spatial scales.

Most theoretical models for themes involving behavior include time as an implicit or explicit factor. Subjects such as the development of behavior or seasonal variations in behavior obviously focus on time as a central organizing principle. Ontogenetic changes in behavior as well as the temporal scale and stability of episodic events, such as breeding seasons, have been an important focus for a host of behavioral studies. My own interests now include the challenges of incorporating temporal dynamics into social network models (Sih et al., 2009). That is, moving from a static view of a social

network to one that incorporates social fluidity and dynamics provides an opportunity to view the multidimensional fabric and stability of social organization as the components (individuals or groups) undergo fission and fusion (Croft et al., 2004), develop or change status (McDonald, 2007), or as the network as a whole expands or shrinks.

Space has necessarily always been of central importance to the field of patch dynamics and foraging ecology (Caraco et al., 1980; MacArthur and Pianka, 1966) and to such behavior-related problems as the influence of dispersal on genetic structure (Bohonak, 1999) or population dynamics (Pulliam, 1988). Parker (1978) explored the problem of searching for a mate with a spatial framework derived from optimal foraging. Partly due to the advent of more sophisticated technology for handling spatial data, a focus on how space affects social dynamics plays an expanding role in behavioral ecology. For example, spatially explicit models have become important for modeling the evolution of social behaviors. This emphasis on the importance of spatial context is especially evident in the study of the evolution of cooperation among unrelated individuals (Nowak et al., 1994). Working from simulations in which individuals occur on a lattice, Nowak et al. (1994) showed that cooperation among unrelated individuals is much more likely to persist when cooperators occur in spatially contiguous and relatively stable associations. Spatial contiguity and stability means that cooperators can receive as well as disburse benefits and has been shown repeatedly to enhance the stability of cooperation or the likelihood that it will evolve.

The processing of information is a cornerstone of behavioral ecology, whether at the level of organismal function or the behaviorist's attempt to extract meaning from a welter of observational or experimental data. Clearly, information matters to animals in their environments, as a problem of intake, processing, storage, and retrieval that culminates in decision-making. Almost any consideration of information reception, transmission, and processing leads one naturally to attend to the brain as the center for processing of information. Cognition in general, and spatial memory in particular, provide mechanisms that link time and space. Biological representations of space are almost always temporally dynamic, as the distribution of resources changes rhythmically or stochastically over a range of time scales. While spatial memory has been well explored in the contexts of foraging and food storage (e.g., Brodin and Bolhuis, 2008; Healy et al., 2005) and of host-nest location by brood-parasitic cowbirds (Sherry et al., 1993), its importance in other ecological contexts has received less attention. Recent attention to episodic memory (Clayton and Russell, 2009; Emery, 2006) and recent evidence that temporal capacity for spatial memory fluctuates over time (Dunlap et al., 2009) are examples of how cognitive processing acts as a control on behavioral organization. The costs and

benefits of information storage and retrieval affect each of us in obvious ways in the computer age, but they have also clearly shaped the evolution of vertebrates from the level of individuals to social groups to populations.

The aim of this chapter is to synthesize some of the ways that temporal and spatial factors influence or even determine the unusual social system of lek-mating long-tailed manakins, *Chiroxiphia linearis*. Lek mating systems are often invoked as one of the circumstances in which sexual selection should act in its purest or most extreme fashion (Höglund and Alatalo, 1995). Because lek-mating males do not provide parental care or resources valuable to breeding females (Bradbury, 1981; Wiley, 1974), variance in male mating success should depend exclusively on female choice and male-male competition, especially the former. Whether vying for access to females by displays or by interactions with other males, one would expect males to compete intensely. Why therefore, are males in the manakin genus *Chiroxiphia*, especially *C. linearis*, unique among animals in performing cooperative courtship displays with males to whom they are not related (McDonald and Potts, 1994)? Time, at scales ranging from daily to tens of years, and space, particularly the way that females use and remember space in foraging and mate choice, have become increasingly important to how I think about the differences between the social system of long-tailed manakins and that of all other animals. Although the cooperative displays of *Chiroxiphia* males are unique, understanding the forces that drive these behaviors provides a reference point for the workings of sexual selection, the evolution of cooperation and the organization of social behaviors in animals of all sorts. I will outline two alternative hypotheses for the evolution of male-male cooperation. One emphasizes the possible constraints imposed on males by unanimity of female choice, while the other emphasizes the stability of male-male associations. Toward the end, I will tie these themes to the idea of information as a resource (Frank, 2009; Miller, 1983). Behavioral ecologists seem likely to benefit in many ways by attending explicitly to information as a resource that emerges from, is conserved within, and may sometimes even drive the evolution of behavior.

II. NATURAL HISTORY

“Listen to the Pretty Sound of Music as She Flies”

The Beatles

The manakins (Pipridae) are a Neotropical family of approximately 51 species of suboscine birds (Remsen et al., 2010 for the 47 South American species; I add *C. linearis*, *Manacus vitellinus*, *M. candei* and *M. aurantiacus*