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Preface

The social network and communicative complexity: preface to theme issue

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The complex social worlds of many animal species may be linked to complex communicative systems in those species. We now have evidence in diverse taxa and in different communicative modalities suggesting that complexity in social groups can drive complexity in signalling systems. The aim of this theme issue is to develop the theory behind this link between social complexity and communicative complexity, and to provide an overview of the lines of research testing this link.

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It is news to no one that our world is highly connected. It might be news to those whose everyday experience involves updates of Facebook, Twitter feeds and text messaging, but our world was highly connected even before the age of the Internet. The average human being lives in a socially complex world of family members, close friends and neighbours and acquaintances—an exceedingly complex network of relationships with other human beings. Indeed, the complexity of our social networks is one of the defining features of being human [1–3].

We have known for centuries that many non-human animal species (hereafter, animal species) live in groups—from relatively small and fairly stable social groups of individuals who interact with one another repeatedly over long periods of time to immense aggregations of individuals who may interact on one particular day and never interact with one another again. We have only recently begun to realize how socially complex the lives of many animal species are. Theory and hypotheses from social network approaches are rapidly being put to the test in a wide range of species [4–8]. The complex social worlds of many animal species are thought by many researchers to represent selective environments for increased cognitive processing ability in those species [9–11].

The complex social worlds of many animal species may also be linked to complex communicative systems in those species. Beginning with the first explicit test of this idea by Blumstein & Armitage [12], we now have evidence in diverse taxa and in three different communicative modalities (auditory, visual and chemical) suggesting that complexity in social groups can drive complexity in signalling systems. The aim of this theme issue is to develop the theory behind this link between social complexity and communicative complexity, and to provide an overview of the lines of research testing this link. The impetus for this theme issue was a symposium on social complexity and communicative complexity during the 'Behavior 2011' joint meeting of the Animal Behavior Society and the International Ethological Conference, held at Indiana University in Bloomington, IN, USA. Many of the contributors to this theme issue were part of that symposium.

The first three articles of this issue describe some of the key theoretical issues related to the 'social complexity hypothesis' for communicative complexity. First, Freeberg *et al.* [13] develop this hypothesis and provide some of the historical background to the idea that complex social groups might demand complex signalling systems. This article raises a number of the key predictions that stem from the hypothesis. Next, Flack [14] describes the mechanics of complex social structure and how complex systems maintain themselves or undergo change over time. This work focuses on individual power and social structure in a non-human primate species, and how that social structure relates to signalling among individuals. The 'social complexity hypothesis' for communicative complexity is a relatively recent notion. Despite a number of studies providing support for the hypothesis, a key limitation of the hypothesis as it currently stands is that it has rarely been tested against alternative explanations for communicative complexity. This is the major argument of the article by Ord & Garcia-Porta [15], and they use powerful comparative

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One contribution of 13 to a Theme Issue 'The social network and communicative complexity in animals'.

approaches to test the hypothesis against alternatives. They find that in many cases alternative hypotheses—such as species ecology or a phylogenetic null model—better explain changes in signalling complexity than the 'social complexity hypothesis'. Their work points to the need to consider these alternatives in future testing of the 'social complexity hypothesis'.

The next four articles in the theme issue address the link between social complexity and communicative complexity from the standpoint of vocal signalling in primate species. Nettle [16] discusses some of the important components of human languages that contribute to complexity in this most complex signalling system, and that vary enormously across different languages. This article calls attention to the need to assess whether this variation in language parameters is associated with differences in social contexts of language development. In the next article, Dunbar [17] also addresses the topic of language, but from the standpoint of the kinds of communicative changes that may have evolved in the origins of language. This work focuses on the nature of social bonds within groups of primates, and how increases in group size generate a greater need for vocal and visual signalling complexity, including novel non-verbal signals such as laughter. Gustison *et al.* [18] compare two closely related primate species—chacma baboons and geladas—in terms of the size of their vocal repertoire. Geladas have a more complex social structure than chacma baboons, and also have a larger vocal repertoire. Most of the work testing for either correlational or causal relationships between complexity of social groups and complexity of signalling systems has focused on the production side of the system—the displays and calls produced by signallers. Ramsier *et al.* [19] extend a comparative test of the 'social complexity hypothesis' for communicative complexity to the perception side of the system. They find that individuals in socially complex primate species have greater overall hearing sensitivity and higher frequency hearing than individuals of less socially complex primate species.

Most of the work to date that has tested the 'social complexity hypothesis' has done so with non-human primate species and with vocal signalling systems. The remaining articles in this theme issue expand tests of the hypothesis to other taxonomic groups or to other signalling modalities. Pollard & Blumstein [20] find that social complexity in ground-dwelling sciurid rodents predicts vocal signalling complexity. Importantly, they demonstrate that different attributes of social complexity—such as group size compared with the diversity of functional roles within groups—may be associated with different components of vocal complexity. Krams *et al.* [21] address the 'social complexity hypothesis' from the standpoint of a group of songbird species. Members of the Paridae—chickadees, tits and titmice—generally have complex social structures and this article discusses whether this social complexity might explain the structural complexity of one of the primary calls used by parids in social organization. White *et al.* [22] also focus on songbirds, but instead of assessing variation in calls, they assess song and singing behaviour in cowbirds. This article describes work demonstrating that male cowbirds exposed to changing and complex social groups are more effective at attracting females and subsequently have greater reproductive success in comparison with male cowbirds exposed to static social groups. In a return to non-human primate species, Dobson [23] assesses the 'social complexity hypothesis' from the perspective of visual signalling systems—in this case, the diversity of facial expressions in many primate species. The article details strong relationships among variables related to social complexity—group size, time spent allogrooming and size of the neocortex—and variables related to visual signalling complexity such as facial nucleus volume size and number of facial expressions. Finally, delBarco-Trillo *et al.* [24] focus their efforts on understanding the relationship between social complexity and chemical signalling complexity. In a comparison of several *Eulemur* species, the authors find that chemical odour complexity is greater in female lemurs belonging to species exhibiting multimale–multifemale groups compared with female lemurs belonging to species exhibiting single female–male pair bonds.

As mentioned above, the 'social complexity hypothesis' for communicative complexity is still a relative newcomer to our attempts at understanding the evolution of complex signalling systems [25]. The articles in this theme issue collectively articulate the 'social complexity hypothesis' and provide evidence in support of the hypothesis. Importantly, several of the contributions raise critical limitations and concerns related to the hypothesis—limitations and concerns which our future work must address if we seek a greater understanding of communicative system complexity. We hope that this theme issue serves as a foundational document on which to build this future work.

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