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ANIMAL SOCIAL NETWORKS

Editorial

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Animal social networks: Towards an integrative framework embedding social interactions, space and time

Sebastian Sosa[1] | David M. P. Jacoby[2] | Mathieu Lihoreau[3] | Cédric Sueur[1,4]

[1]IPHC UMR 7178, CNRS, Université de Strasbourg, Strasbourg, France

[2]Institute of Zoology, Zoological Society of London, London, UK

[3]Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI), CNRS, University Paul Sabatier – Toulouse III, Toulouse, France

[4]Institut Universitaire de France, Paris, France

Correspondence
Sebastian Sosa
Email: S.Sosa@LIVE.FR

1 | FIFTY YEARS OF SOCIAL NETWORK ANALYSIS

Social groups take a myriad of forms, reflecting the countless different ways in which animals can interact and associate (Wilson, 2000). This diversity calls for a broad and dynamic toolkit that is both robust in allowing rigorous quantification of different societies but also flexible in its ability to account for and control the nuances associated with each ecological system. Since Sade (1972) first used social network analysis to study heterogeneity in the affiliative social interactions of primates and their relationship with dominance rank, this approach has been considerably developed for the exploration and hypothesis testing of different aspects of animal social interactions (Brent, Lehmann, & Ramos-Fernández, 2011; Hasenjager et al., 2020; Hinde, 1976).

Over the last 50 years, social network analysis has grown into a diverse toolkit that transcends animal behaviour and ecology allowing biologists to understand the many facets of sociality, from mechanistic processes to ecological and evolutionary functions (Cantor et al., 2020; Hasenjager et al., 2020; Sosa et al., 2020). For example, Bejder, Fletcher, and Bräger (1998) proposed advanced permutation techniques to examine spatial associations between individuals, and Croft, James, and Krause (2008) together with Whitehead (2008) aggregated most of our knowledge on the study of animal sociality in their seminal books. The growth in the popularity of social network analysis in animal behaviour and ecology has been favoured by methodological advances (Whitehead, 2008), and automated monitoring techniques (Smith & Pinter-Wollman, 2020) have also played a significant role by scaling up research questions to new and previously intractable species and systems. Using these tools for data collection and analysis has further engaged a lively community of researchers that, together, have contributed a near constant refinement and evolution of social network analysis methods and its application to animals.

The Joint Special Feature in *Methods in Ecology and Evolution* and the *Journal of Animal Ecology* is a celebration of research by animal social network scientists, introducing novel methods and questions pertaining to Animal Social Network Analysis (ASNA). It brings together research that highlights developments in computational methods, novel considerations about bias in ASNA, advances in the study of the factors shaping individuals and group social structure and how animal networks vary under different social environments. In doing so, we believe this Special Feature offers exciting directions for future research to better cope with the complexity of animal social structures.

2 | CONTROLLING FOR BIASES IN ANIMAL SOCIAL NETWORK ANALYSIS

Few wild biological data and analytical methods are immune to biases inflicted by specifics of sampling protocols or study organisms. Consequently, an important challenge for ASNA studies is the need to consider the robustness of current methodological approaches. In this joint Special Feature, Sosa et al. (2020) consider network measures and their variants, and highlight the necessity for future research to state the variant used as this may skew the interpretation of the results. Once a network measure is selected, taking care to avoid multiple hypothesis testing (Webber, Schneider, & Vander Wal, 2020), it is essential to ensure the reliability of statistical tests. Puga-Gonzalez et al., 2020 outline how limitations of current permutation approaches extend to different data sampling scenarios, and Franks et al., 2020 offer solutions to avoid spurious results that call for greater emphasis on effect sizes as a means of making reliable statistical inference. Together, these three methodological studies underline the continued need for caution when developing

Sebastian Sosa, David M. P. Jacoby, Mathieu Lihoreau and Cédric Sueur contributed equally.

analytical solutions and interpreting ASNA results. ASNA is continuously being refined and improved (Franks et al., 2020; Weiss et al., 2020), but it will take continued efforts to keep improving existing solutions and to address the multitude of remaining issues, such as the appropriateness of different network measures, the rates of type I and type II errors in standard null hypothesis-testing procedures, and finding robust solutions to measuring effect sizes.

With these considerations in mind, new methods continue to be presented, allowing researchers to address novel challenges in ASNA such as accurate estimates of social trait heritability (Radersma, 2020), social drivers of animal movement (Milner et al., 2020) and to apply techniques developed for data collected using mark-release-recapture data (Silk et al., 2020) and biologging methods (Gilbertson et al., 2020; Gomes et al., 2020). The miniaturisation of biologging devices now enable the study of a wider variety of organisms, from insects to cetaceans (Börger et al., 2020). Biologging provides access to new data sources, using less invasive methods and continuous collection, considerably expanding our knowledge of how animals and groups behave in the wild (Smith & Pinter-Wollman, 2020). These advances, however, have led to a substantial methodological shift in network construction and analysis (Godfrey, Ansari, Gardner, Farine, & Bull, 2014; Spiegel, Leu, Sih, & Bull, 2016). One specific challenge that Gomes et al. tackles is how to determine cut-offs while delimiting social associations and, thereby, providing a standard procedure for building social networks from proximity-based association data collected through radio frequency identification detection.

3 | FACTORS SHAPING ANIMAL NETWORKS

Research in ASNA has focused on how phenotypic attributes and environmental factors shape individual social traits and their consequences on fitness (Brent, Ruiz-Lambides, & Platt, 2017; Silk et al., 2009, 2010), and species social diversity (Balasubramaniam et al., 2017). Studies have highlighted a broad range of individual attributes that shape heterogeneity in social traits such as age (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016), sex (Borgeaud, Sosa, Sueur, & Bshary, 2017), kinship (Hirsch, Stanton, & Maldonado, 2012), personality (Krause, James, & Croft, 2010), pathogens (Romano et al., 2016) etc. (see Cantor et al., 2020; Sosa et al., 2020 for an overview). Here, Brandl et al., 2020 provide a good example of how these factors might interlink by showing how synchrony in reproductive timing can shape present and future individual social bonds.

Although ecologists and evolutionary biologists have extensively explored the effects of variation in the physical environment on the development and fitness of individuals and their consequences on population dynamics, these aspects remain overlooked in the study of animal societies (Spiegel, Leu, Bull, & Sih, 2017; Webber & Vander Wal, 2018), but see (Moscovice, Sueur, & Aureli, 2020). Space use is often implicated as strongly influencing social dynamics, as this constrains the frequency or time with which individuals can interact or be associated (Webber & Vander Wal, 2018). As a result, space use represents an important dimension for many social processes, such as disease spread (Albery et al., 2020). A particular focus of this joint Special Feature is on the study of how habitat constraints or spatial ecology can shape group social structure through individual movements (Albery et al., 2020; Milner et al., 2020; Pasquaretta et al., 2020).

In addition, few studies have investigated the multivariate aspects of individual sociality (Brandell et al., 2020) and movements (Milner et al., 2020). Here, Brandell et al., 2020 determine the relative influence of environmental factors, biotic interactions, infectious disease and group composition on group spatial networks in two social species of carnivores. Such a multivariate approach is of considerable interest to understand the relative influence of habitat structure and/or social factors in shaping social structure and to better understand their dynamics, host pathogen dynamics, or species–species assemblages (Massol et al., 2020). The new methods presented in this joint Special Feature (Albery et al., 2020; Massol et al., 2020; Milner et al., 2020; Pasquaretta et al., 2020) will help better understand such complex related processes.

4 | ANIMAL NETWORKS UNDER DIFFERENT ENVIRONMENTS

Social structure represents the most plastic aspect of animal societies as individuals can, through social interactions, regulate conflicts (Aureli & de Waal, 2000), create affiliative bonds (De Waal & Roosmalen, 1979), cooperate (Seyfarth & Cheney, 2012), transmit information and learn (Hoppitt & Laland, 2013). This allows them to cope with ecological constraints specific to their living environment. There is growing evidence for a dynamic eco-evolutionary feedback between the (social) environment and social structure (Cantor et al., 2020; Romano, Macintosh, & Sueur, 2020; Smolla & Akçay, 2019; Sueur, Romano, Sosa, & Puga-Gonzalez, 2019; Udiani & Fefferman, 2020) as individuals that better adjust their behaviour in response to the challenges, both external to and inherent in social relationships, within the context of their own dynamic social networks, might increase their own fitness (Romano et al., 2020).

Research in ASNA is increasingly integrating the concept of social plasticity, the degree to which an individual varies its social behaviour dependent upon environmental factors. This is important not only for exploring the mechanisms driving individual heterogeneity in sociality but also for understanding how plasticity manifests at both the individual and the group level (Ilany & Akçay, 2016; Montiglio, McGlothlin, & Farine, 2018). The study of social dynamics, such as how individuals sociality changes in response to demographic changes (Borgeaud et al., 2017), is made possible thanks in part to the application of time-aggregated network analysis (Hobson, Avery, & Wright, 2013) for which specialised analysis packages exist now (Bonnell & Vilette, 2020; Sosa et al., 2020). Several studies in this joint Special Feature explore these aspects by addressing, for example, how mechanistic factors allow animals to cope with demographic changes (Farine, 2020), how networks are shaped by group phenotypic composition (Dakin et al., 2020) and environmental conditions (Burns et al., 2020), and how inter-group encounters shape overall network structure (Preston et al., 2020). Together, these studies highlight that individual sociality is not the only plastic trait but that there are also numerous extrinsic and intrinsic constraints that drive group social structure dynamism.

Similarly, while past research has established that sociality affects fitness (Brent et al., 2017; Silk et al., 2009, 2010), Formica et al., 2020 show that this effect may be condition-dependent while Turner et al., 2020 (show that different types of social interactions have different effects on individual fitness according to ontogenetic stages. Such dynamics in individual sociality, group structure as well as condition-dependent effects of sociality on fitness may help better explain evolutionary processes such as population structure and gene flow dynamics (Zonana et al., 2020). These two studies highlight the important necessity to integrate the heterogeneity of social and ecological environments in which individuals live when studying evolutionary processes responsible for the emergence, maintenance and selection of group phenotypic composition (Vander Wal, 2021).

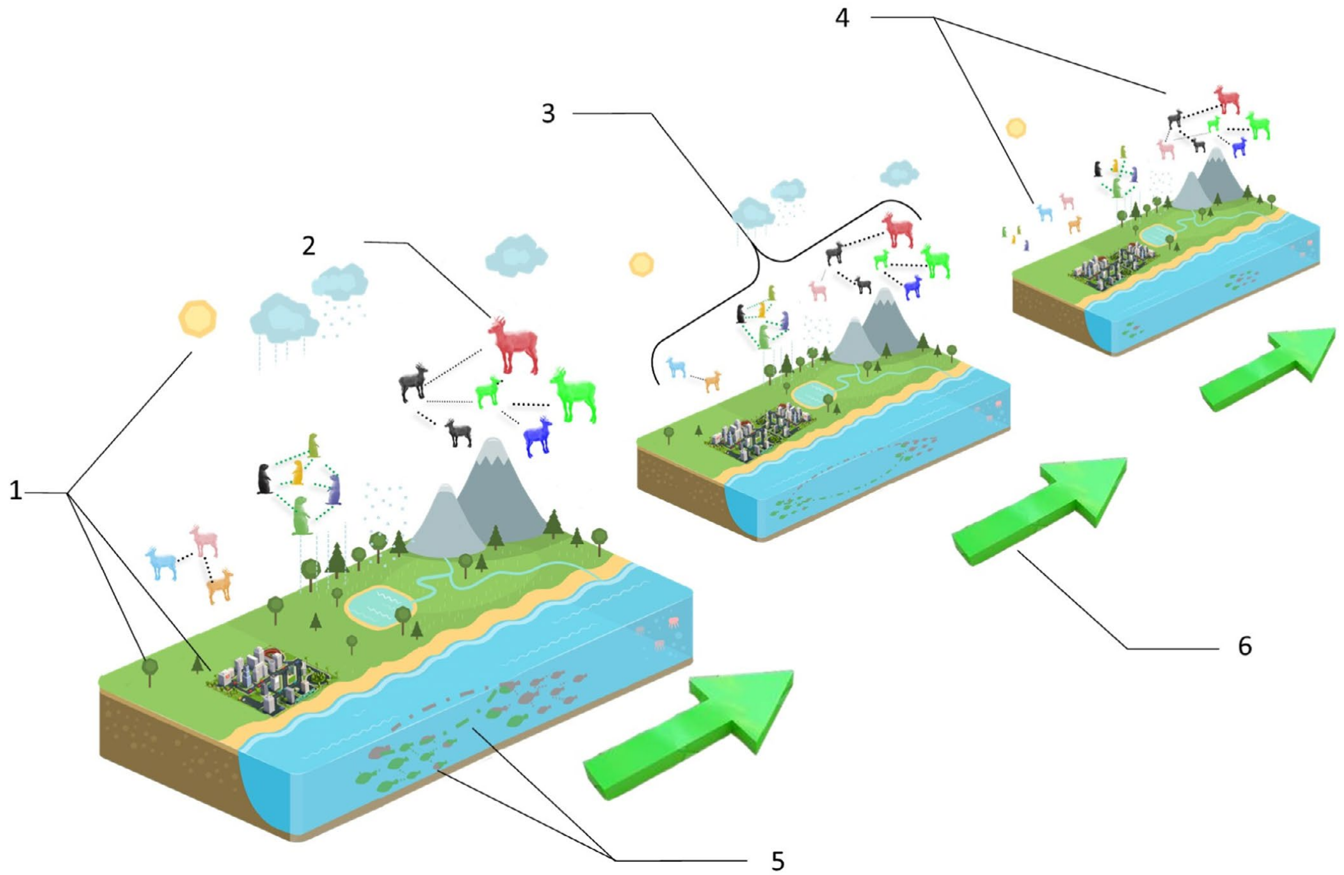

FIGURE 1 ASNA synthetic framework for integrating social, spatial and temporal network features in the study of animal social networks. Below we highlight some questions that could be addressed by this approach. (1) Which, how and why biotic (e.g. resource dispersion, pathogens) and abiotic factors (e.g. habitat heterogeneity, entropic disturbances) affect social behaviour, group-level dynamics and population-level social structure? For example, climatic factors that shape habitats through plant phenology and resource dispersion may affect animal social structure and habitat use (Albery et al., 2020; Brandell et al., 2020; Burns et al., 2020; Gilbertson et al., 2020; Milner et al., 2020; Pasquaretta et al., 2020). (2) Which, how and why behavioural or physiological factors (e.g. social organisation, individuals' development, physiological markers) shape individual- group- and/or population-level social structure? Variation in biotic and abiotic factors can affect physiological markers, propensity to cooperate, propensity to disperse in individuals, which may, in turn, affect sociality and group structure (Brandl et al., 2020; Dakin et al., 2020; Turner et al., 2020). (3) How and why these factors can drive interactions between groups (e.g. group size, group encounters), species (e.g. host–pathogen, plant–pollinator) and ecosystem assemblages? The impact of biotic and abiotic factors on sociality may affect group-group encounters and competition for resources, and shape species–species assemblages and ecosystem structures (Massol et al., 2020; Preston et al., 2020). (4) Which, how and why physiological, behavioural and environmental factors drive individual- and group-level social plasticity, inter-group social structure, and ecosystem dynamics (e.g. spatial network variation across seasons)? Considering the hypothesis in points 1, 2, 3, we may expect inter- and intra-group differences according to seasonality or social organisation of species (e.g. Brandell et al., 2020). (5) Which, how and why are the consequences of such social plasticity on developmental, life history traits, ecological genetics, evolutionary biology, populations and community ecology? Considering influences determining sociality and plasticity, as well as condition-dependent effects of sociality on fitness (Formica et al., 2020; Turner et al., 2020), facilitates a better understanding of evolution processes such as group/population structures, sexual selection and gene flow (Zonana et al., 2020). (6) Points 1 to 5 focus on the drivers shaping sociality in the same time point and space of the observed sociality. However, a temporal analysis of how past individuals' sociality, physiological, behavioural and environmental factors may shape current individuals' sociality (Farine, 2020), space use Albery et al., 2020, groups and populations social structures, and species–species assemblages is needed to better understand global system dynamics

5 | ANTHROPOGENIC IMPACTS ON ANIMAL SOCIETIES

At the heart of understanding the intrinsic link between habitat, movement and social behaviour is the pressing acknowledgement that animals are increasingly inhabiting a world impacted by anthropogenic-driven disturbances. As so, it is important that we understand the response of social animals to such change (Bond et al., 2020). The major question of how social structure is shaped by the broader environment represents a substantial challenge to address. Do networks change in response to environmental changes in a consistent way? For example, Bond et al., 2020 test how the social structure of communities of giraffes are impacted by human disturbance, revealing a signature of network structure that matches those detected in small captive groups of birds exposed to social disturbances (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby, & Farine, 2018).

As humans and wildlife increasingly share space, new methods that integrate biologging technologies (Gilbertson et al., 2020; Gomes et al., 2020) and/or that use citizen scientists to collect and record data on grouping animals (Aplin et al., 2020), will no doubt prove invaluable for anticipating how and to what extent animal groups and populations will be affected by future environmental changes during the Anthropocene. In doing so researchers will also need to consider carefully how these approaches can be optimised to reduce our impact on animal welfare. Thus, future adaptations in ASNA methods must also be mindful to align with a changing ethical landscape (Soulsbury et al., 2020).

6 | NETWORKS BEYOND SOCIAL INTERACTIONS: CASCADING EFFECTS ACROSS LEVELS OF ORGANISATION

We now have access to unprecedented amounts of data including, for example, biologged individual physiological measurements, remotely sensed environmental variables or heterospecific space use and behaviour. Importantly, these data span phenotypic (e.g. physiological, ontogenesis) and environmental (e.g. habitat, climate, parasites, other species and/or groups) factors, and their variation over time. Contributions in this Joint Special Feature provide insight into these developments that are sharpening the picture of the various evolutionary processes involved in shaping social heterogeneity and plasticity. Figure 1 provides a comprehensive view of the different levels of organisation embedded in the study of animal social networks, that is, individuals, social structure, habitat, environment and their dynamics.

We hope that this will serve as a basis for novel questions and for identifying the methodological challenges to come in order to determine the relative influence of each of these factors by integrating interaction networks across levels of organisation (Brandell et al., 2020; Jacoby & Freeman, 2016; Sueur et al., 2019). A particularly promising line of research is the development of multi-layered networks (Fisher & Pinter-Wollman, 2020; Mourier, Ledee, & Jacoby, 2019; Silk, Finn, Porter, & Pinter-Wollman, 2018), hierarchically embedded interaction networks (Montiglio, Gotanda, Kratochwil, Laskowski, & Farine, 2020), or bipartite networks (Massol et al., 2020) that can expand exploration of interactions beyond social groups, spanning from cells to whole ecosystems, and their dynamics. For instance, Massol et al., 2020 used bipartite networks to analyse the structure of host-microbiota interaction networks. The method by Massol et al., 2020 considers and assesses multiple drivers of network structures across species. Importantly, this approach can be adapted to study other aspects of connectivity in networks. For example, it could be used to study the multifactorial drivers embedding social and spatial networks of pollinators, spatial patterns of pollen flow, and reproductive networks of plants, potentially revolutionising research in pollination ecology through the application of predictive models (Pasquaretta et al., 2019).

7 | CONCLUDING REMARKS

Considerable progress has been made since the first application of social network analysis to animals (Sade, 1972) and the first specific ASNA approaches were developed (Bejder et al., 1998). This joint Special Feature is reflective of the milestones reached in the past few years in ASNA, presenting new methods that redefine analytical standards and covering topics as diverse as social transmission, epidemiology, quantitative genetics, social structure plasticity, fitness consequences, habitat use and applied conservation. Although social network analysis enables to examine many facets of social phenomena, there is still much to be done to build bridges across disciplines. As the research tools and questions developed for animal social network analysis strengthen, they will also have the potential to inform on pressing global events (Firth et al., 2020). Opening up a dialog across disciplines will be particularly important in the development and application of holistic frameworks that embed social interactions, space and time, to address topics such as the diversity (Sah, Méndez, & Bansal, 2019) and complexity (Kappeler, Clutton-Brock, Shultz, & Lukas, 2019) of animal societies and heterospecific assemblages (Farine, Garroway, & Sheldon, 2012).

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