1 **Animal social networks: towards an integrative framework embedding social**

2 **interactions, space and time**

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13 **Fifty years of social network analysis**

14 Social groups take a myriad of forms, reflecting the countless different ways in which

15 animals can interact and associate (Wilson 2000). This diversity calls for a broad and

16 dynamic toolkit that is both robust in allowing rigorous quantification of different

17 societies but also flexible in its ability to account for and control the nuances associated

18 with each ecological system. Since Sade (1972) first used social network analysis to

19 study heterogeneity in the affiliative social interactions of primates and their

20 relationship with dominance rank, this approach considerably developed for the

21 exploration and hypothesis testing of different aspects of animal social interactions

22 (Hasenjager, Leadbeater & Hoppitt; Hinde 1976; Brent, Lehmann & Ramos-Fernández

23 2011).

24 Over the last 50 years, social network analysis has grown into a diverse toolkit

25 that transcends animal behaviour and ecology allowing biologists to understand the

26 many facets of sociality, from mechanistic processes to ecological and evolutionary

27 functions (Cantor *et al.;* Hasenjager, Leadbeater & Hoppitt; Sosa, Sueur & Puga-

28 Gonzalez). For example, Bejder, Fletcher and Bräger (1998) proposed advanced

29 permutation techniques to examine  spatial associations between individuals, and

30 Croft, James and Krause (2008) together with Whitehead (2008) aggregated most of

31 our knowledge on the study of animal sociality in their seminal books. The growth in

32 the popularity of social network analysis in animal behaviour and ecology has been

33 favoured by methodological advances (Whitehead 2008), and automated monitoring

34 techniques (Smith & Pinter-Wollman) have also played a significant role by scaling up

35 research questions to new and previously intractable species and systems. Using
36 these tools for data collection and analysis has further engaged a lively community of
37 researchers that, together, have contributed a near constant refinement and evolution
38 of social network analysis methods and its application to animals.

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

48

49 **Controlling for biases in animal social network analysis**
50 Few wild biological data and analytical methods are immune to biases inflicted by
51 specifics of sampling protocols or study organism. Consequently, an important
52 challenge for ASNA studies is the need to consider the robustness of current
53 methodological approaches. In this joint Special Feature, Sosa, Sueur and Puga-
54 Gonzalez (consider network measures and their variants, and highlight the necessity
55 for future research to state the variant used as this may skew the interpretation of the
56 results. Once a network measure is selected, taking care to avoid multiple hypothesis
57 testing (Webber, Schneider & Vander Wal 2020), it is essential to ensure the reliability
58 of statistical tests. Puga-Gonzalez, Sueur and Sosa outline how limitations of current
59 permutation approaches extend to different data sampling scenarios, and Franks *et al.*
60 offer solutions to avoid spurious results that call for greater emphasis on effect sizes
61 as a means of making reliable statistical inference. Together, these three
62 methodological studies underline the continued need for caution when developing
63 analytical solutions and interpreting ASNA results. ASNA is continuously being refined
64 and improved (Franks *et al.;* Weiss *et al.*), but it will take continued efforts to keep
65 improving existing solutions and to address the multitude of remaining issues, such as
66 the appropriateness of different network measures, the rates of type I and type II errors
67 in standard null hypothesis-testing procedures, and finding robust solutions to
68 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), social drivers of animal movement (Milner, Blackwell & Niu) and to apply techniques developed for data collected using mark-release-recapture data (Silk *et al.*) and bio-logging methods (Gilbertson, White & Craft; Gomes, Boogert & Cardoso). The miniaturization of bio-logging devices now enable the study of a wider variety of organisms, from insects to cetaceans (Börger *et al.* 2020). Bio-logging 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). These advances, however, have led to a substantial methodological shift in network construction and analysis (Godfrey *et al.* 2014; Spiegel *et al.* 2016). One specific challenge that Gomes *et al.* tackle 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.

**Intrinsic and extrinsic factors shaping animal networks**

Research in ASNA has focused on how intrinsic and extrinsic factors shape individual social traits and their consequences on fitness (Silk *et al.* 2009; Silk *et al.* 2010; Brent, Ruiz-Lambides & Platt 2017), and species social diversity (Balasubramaniam *et al.* 2017). Studies have highlighted a broad range of intrinsic factors that shape heterogeneity in individual social traits such as age (Almeling *et al.* 2016), sex (Borgeaud *et al.* 2017), kinship (Hirsch, Stanton & Maldonado 2012), personality (Krause, James & Croft 2010), pathogens (Romano *et al.* 2016) etc. (see Cantor *et al.* & Sosa, Sueur and Puga-Gonzalez for an overview). Here, Brandl *et al.* provide a good example of how these intrinsic 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 *et al.* 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.*). 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.;* Milner, Blackwell & Niu; Pasquaretta *et al.*).

In addition, few studies have investigated the multivariable aspects of individual sociality (Brandell *et al.*) and movements (Milner, Blackwell & Niu). Here, Brandell et al. 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 multivariable 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.*). The new methods presented in this joint Special Feature (Albery *et al.;* Massol *et al.;* Milner, Blackwell & Niu; Pasquaretta *et al.*) will help better understand such complex related processes.

**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.;* Smolla & Akçay 2019; Sueur *et al.* 2019; Romano, Macintosh & Sueur 2020; 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, Macintosh & Sueur 2020).

Research in ASNA is increasingly integrating the concept of social plasticity, the degree to which an individual varies its social behaviour dependent upon external 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

137 2018). The study of social dynamics, such as how individuals sociality changes in
138 response to demographic changes (Borgeaud *et al.* 2017), is made possible thanks in
139 part to the application of time-aggregated network analysis (Hobson, Avery & Wright
140 2013) for which specialised analysis packages exist now (Bonnell & Vilette; Sosa *et al.*
141 2020). Several studies in this joint Special Feature explore these aspects by
142 addressing, for example, how mechanistic factors allow animals to cope with
143 demographic changes (Farine), how networks are shaped by group phenotypic
144 composition (Dakin *et al.*) and environmental conditions (Burns *et al.*), and how inter-
145 group encounters shape overall network structure (Preston *et al.*). Together, these
146 studies highlight that individual sociality is not the only plastic trait but that there are
147 also numerous extrinsic and intrinsic constraints that drive group social structure
148 dynamism.

149 Similarly, while past research has established that sociality affects fitness (Silk
150 *et al.* 2009; Silk *et al.* 2010; Brent, Ruiz-Lambides & Platt 2017), Formica *et al.* show
151 that this effect may be condition-dependent whilst Turner *et al.* show that different types
152 of social interactions have different effects on individual fitness according to
153 ontogenetic stages. Such dynamics in individual sociality, group structure as well as
154 condition-dependent effects of sociality on fitness may help better explain evolutionary
155 processes such as population structure and gene flow dynamics (Zonana *et al.*).

156

157 **Anthropogenic impacts on animal societies.**
158 At the heart of understanding the intrinsic link between habitat, movement and social
159 behaviour is the pressing acknowledgement that animals are increasingly inhabiting a
160 world impacted by anthropogenic-driven disturbances. As so, it is important that we
161 understand the response of social animals to such change (Bond et al.). The major
162 question of how social structure is shaped by the broader environment represents a
163 substantial challenge to address. Do networks change in response to environmental
164 changes in a consistent way? For example, Bond *et al.* test how the social structure of
165 communities of giraffes are impacted by human disturbance, revealing a signature of
166 network structure that matches those detected in small captive groups of birds exposed
167 to social disturbances (Maldonado-Chaparro *et al.* 2018).

168 As humans and wildlife increasingly share space, new methods that integrate
169 biologging technologies (Gilbertson, White & Craft; Gomes, Boogert & Cardoso) and/or
170 that use citizen scientists to collect and record data on grouping animals (Aplin *et al.*),

171    will no doubt prove invaluable for anticipating how and to what extent animal groups
172    and populations will be affected by future environmental changes during the
173    Anthropocene. In doing so researchers will also need to consider carefully how these
174    approaches can be optimised to reduce our impact on animal welfare. Thus, future
175    adaptations in ASNA methods must also be mindful to align with a changing ethical
176    landscape (Soulsbury *et al.* 2020).

177

178    **Networks beyond social interactions: cascading effects across levels of**
179    **organisation**

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

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

pollination ecology through the application of predictive models (Pasquaretta *et al.* 2019).

**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, Fletcher & Bräger 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 inform 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 *et al.* 2019) of animal societies and heterospecific assemblages (Farine, Garroway & Sheldon 2012).

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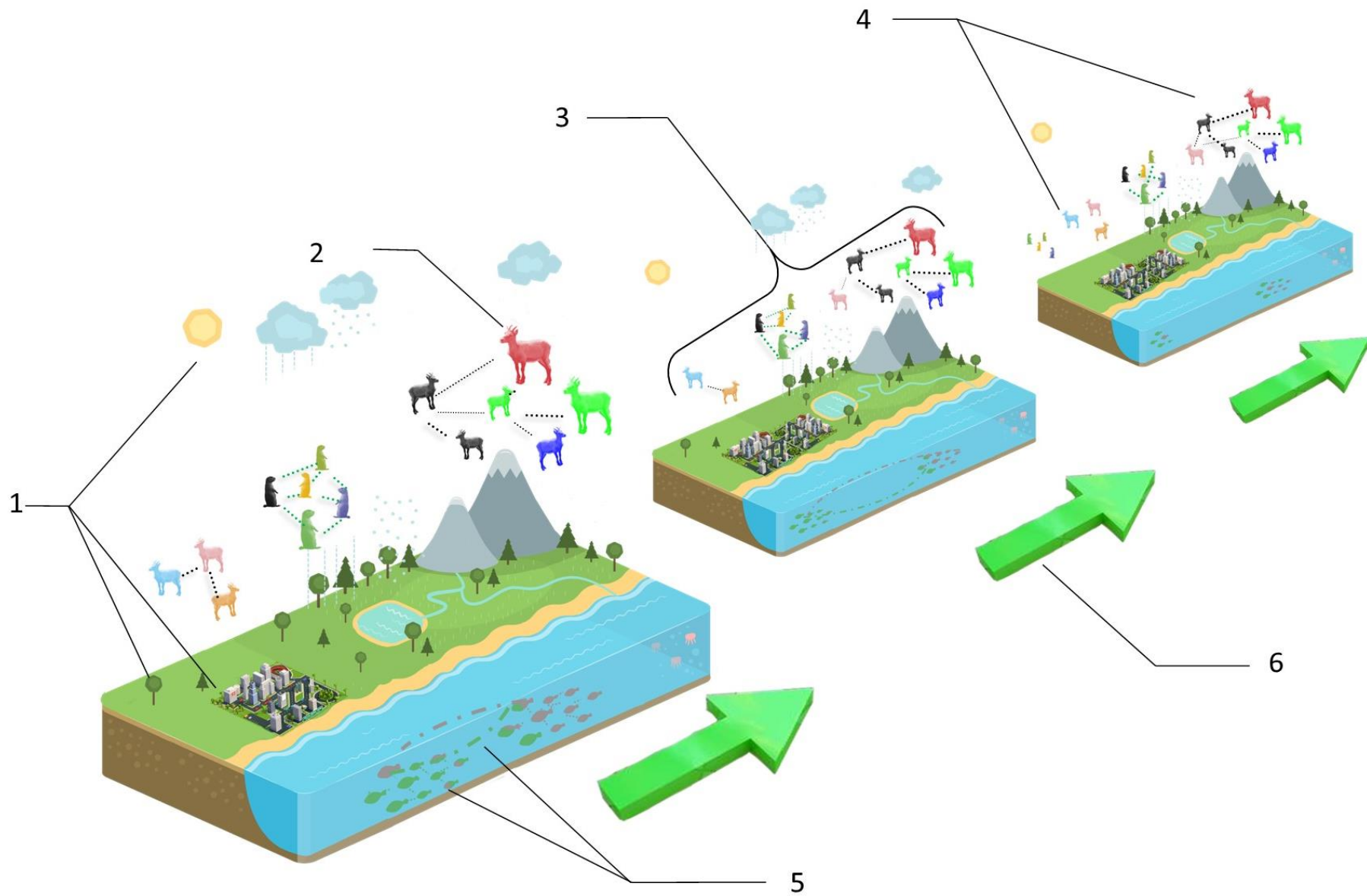
**Figure 1.** ASNA synthetic framework for integrating social, spatial and temporal network features in the study of animal social networks. Below we highlight some questions that could be addressed by this approach.

1. Which, how and why extrinsic 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.;* Brandell *et al.;* Burns *et al.;* Gilbertson, White & Craft; Milner, Blackwell & Niu; Pasquaretta *et al.*).

2. Which, how and why intrinsic factors (*e.g.* social organization, 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.;* Dakin *et al.;* Turner *et al.*).

3. How and why extrinsic and intrinsic 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.;* Preston *et al.*).

4. Which, how and why extrinsic and intrinsic 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.)*].

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.;* Turner *et al.*), facilitates a better understanding of evolution processes such as group/population structures, sexual selection and gene flow (Zonana *et al.*).

251   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

252   analysis of how past individuals' sociality, extrinsic and intrinsic factors may shape current individuals' sociality (Farine), space use

253   Albery *et al.* (), groups and populations social structures, and species-species assemblages is needed to better understand global

254   system dynamics.

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