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Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach

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The increased popularity and accessibility of social network analysis has improved our ability to test hypotheses about complex animal social structures. To gain a deeper understanding of the use and application of animal social network analysis, we systematically surveyed the literature and extracted information on publication trends from articles using social network analysis. We synthesize trends in social network research over time and highlight variation in the use of different aspects of social network analysis. The use of social network analysis in empirical articles has increased over time. In the context of social network methods, we found that many studies did not use an association index to account for missing individuals or observations of individuals; that the number and type of social network metrics calculated in a given study varied substantially (median = 2); and that focal observation was by far the most common method used to generate social networks, although the use of biologging devices increased over time. We also observed that most species studied using social networks are mammals (55%) or birds (23%), and that the majority are species of least concern (59%; International Union for the Conservation of Nature, IUCN, www.iucn.org). Based on our findings, we highlight four key recommendations for future studies: (1) the use of association indices is almost always necessary; (2) the a priori selection of specific network metrics and associated hypotheses increases transparency; (3) combination of focal observation with biologging devices could improve our understanding of remotely sensed behaviours; and (4) because most studies rarely study species of conservation concern, it may be practical to generate networks for similar species or populations, which could help inform management decisions. We highlight emerging trends in social network research that may be valuable for distinct groups of social network researchers: students new to social network analysis, experienced behavioural ecologists interested in using social network analysis and advanced social network users interested in trends of social network research. Our findings also shed light on past research and provide guidance for future studies using social network analysis.

Animal social network analysis has been used since the 1950s (for review see Krause, Lusseau, & James, 2009) and gained popularity among behavioural ecologists in two last decades. The emergence of network analysis to quantify social relationships has honed our questions and provided new avenues to test hypotheses about the causes and consequences of complex animal social structures (Croft, Madden, Franks, & James, 2011). As a result, animal social network analysis has become an important subdiscipline within behavioural ecology. Social dynamics, calculated using social network analysis, have been linked to a range of behavioural and ecological variables, including fitness (Stanton & Mann, 2012; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015), movement (Spiegel, Leu, Sih, & Bull, 2016), dominance (Bierbach et al., 2014), predation (Heathcote, Darden, Franks, Ramnarine, & Croft, 2017), animal personality (Wilson, Krause, Dingemanse, & Krause, 2013), information transfer (Firth, Sheldon, & Farine, 2016), pathogen dynamics (Webber et al., 2016) and quantitative genetics (Fisher & McAdam, 2017). Indeed, the application of social network analysis is widespread. Despite the current perceived popularity and historical significance of social network analysis, there remains no objective systematic overview of publication trends in animal social network analysis, although there are numerous comprehensive reviews (e.g. Krause, James, Franks, &

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Croft, 2015). Here, we synthesize trends in social network analysis and highlight variation in publication trends over time with an aim to guide future research using social network analysis.

Use of animal social network analysis involves three primary steps (Farine & Whitehead, 2015). First, information on social association, defined as spatial or behavioural circumstances in which interactions usually take place, or interaction, defined as action of one animal directed towards another, are used to construct social networks (Whitehead, 2008). Animals can be observed interacting or associating (Altmann, 1974), or association can be inferred with biologging technology (for examples see Croft, Darden, & Wey, 2016). Second, social interaction or association data are converted into pairwise matrices and association indices are often calculated. This form of data conversion often involves correction of the data; for instance, heterogeneity in the number of observations per individual is corrected using the half-weight index (Cairns & Schwager, 1987). Third, statistical or mathematical modelling of social networks to test hypotheses about underlying social network structure. For instance, individual or group-level social network metrics may be generated and combined with attribute data (sensu Farine & Whitehead, 2015). A wide range of social network metrics and association indices exist (for definitions see Tables 1, 2; Silk et al., 2017; Wey, Blumstein, Shen, & Jordán, 2008), many of which are used as individual-based proxies for animal social interaction, or association and can be used in statistical models. Despite the utility of network metrics for studies of individuals, most reviews on social network analysis do not explicitly provide guidance on the number or type of network metrics that should be quantified for a given type of analysis.

Although animal social network analysis is an important method for testing hypotheses about animal social structure (Croft et al., 2011), it is also relevant in an applied context (Makagon, McCowan, & Mench, 2012). Specifically, social network analysis has been used to quantify social structure for species of conservation concern as well as for captive and domestic species. In a killer whale, *Orcinus orca*, network, targeted removal of key individuals can fragment social networks and potentially reduce cohesiveness of highly dynamic social units (Williams & Lusseau, 2006). Moreover, social network analysis can also be used to predict pathogen dynamics (Drewe, 2010; Rushmore et al., 2013), which can have implications for reservoir hosts of infectious disease (Hamede, Bashford, Jones, & McCallum, 2012) or pathogen transmission from wild to domestic animals (Craft, 2015). Social network analysis of captive or domestic species also provides an opportunity to improve animal welfare and husbandry practices (Rose & Croft, 2015). Understanding social structure of captive and domestic species is important because many captive species are highly gregarious and housed in social groups while in captivity. For example, using social network analysis to quantify dominant–subordinate relationships between group members may be particularly important for captive species to reduce aggression and fighting (Makagon et al., 2012).

Despite the recent interest in animal social network analysis as a method, and subsequent emergence as a subdiscipline within behavioural ecology (Wey et al., 2008), there has been no systematic review of trends in social network publication. Here, we employ a bibliometric approach to synthesize research on animal social network analysis. Bibliometric approaches include objective measures of the content of a given research field. Recent examples within ecology and evolution include bibliometrics of conservation physiology (Lennox & Cooke, 2014), food web research (Tao et al., 2015), disease ecology (Manlove et al., 2016) and forestry (Bullock & Lawler, 2015). The intention of bibliometrics is to extract specific aspects of a research field to assess, track and analyse the status and trends within a research field. As a method of evaluating research, bibliometrics are traditionally intended to be nonprescriptive. By design, our bibliometric analysis is objective and is an empirical illustration of trends in social network research, and we encourage readers to investigate these trends. We do, however, also provide a series of recommendations based on our perspectives on key findings. Broadly, our four primary objectives were to:

(1) Assess trends in publication on animal social network analyses over time and identify the types of journals where social network articles are published.

(2) Describe animal social network methods from peer-reviewed articles, including the type of data collection methods

Table 1
Glossary of definitions for the most commonly used animal social network metrics

Metric	Definition	Number of occurrences for each metric
Degree	The number of direct connections an individual has with other individuals. Degree can be separated into in- and out-degree, where in-degree is the number of connections directed towards the focal individual and out-degree is the number of connections direct to nonfocal individuals. Degree is often referred to as unweighted degree	97 (38 calculated in-degree; 36 calculated out-degree)
Graph strength	The combined weight (based on association indices or the frequency or duration of associations or interactions) of all of an individual's connections. Graph strength is often referred to as weighted degree	97 (14 calculated in-strength; 12 calculated out-strength)
Clustering coefficient	The density of the subnetwork of a focal individual's neighbours, usually operationalized as the number of connections between neighbours divided by the possible maximum number of connections between them	87
Betweenness centrality	The number of times an individual occurs on the shortest path length (see definition below) between two other individuals in a network	68 (2 calculated in-betweenness)
Eigenvector centrality	The influence, i.e. connections of an individual to other well-connected individuals, of an individual in a network based on the number and strength of the focal individuals connections	65
Path length	The shortest number of edges that connect two individuals in a network. Path length is either the average, or sum, of all shortest number of edges between a focal individual and all other individuals in a network	24
Closeness	The normalized mean path length from an individual to all other individuals	19 (4 calculated in-closeness; 4 calculated out-closeness)
Group metrics		
Graph density	The proportion of realized edges in a network	58
Modularity	Measure of the strength of division of a network into different modules, such as communities, clusters and social groups	50
Transitivity	The tendency for an individual's connections to associate with one another	13

Table 2
Glossary of definitions for the most commonly used association indices as well as comments on each index

Association indices	Formula	Comments[a]	Number of occurrences for each association index
Half-weight index (**HWI**$_{AB}$)	$HWI_{AB} = \frac{x}{\frac{1}{2}(Y_A + Y_B) + Y_{AB} + x}$	Less biased if individuals are more likely to be identified when not associated, or if not all individuals are identified	66
Simple ratio index (**SRI**$_{AB}$)	$SRI_{AB} = \frac{x}{x + Y_{AB} + Y_A + Y_B}$	Unbiased if all individuals are correctly identified and observed during each observation period	65
Gregarious-adjusted half-weight index (**HWIG**$_{AB}$)	$HWIG_{AB} = HWI_{AB}\frac{\Sigma HWI}{\Sigma HWI_A \times \Sigma HWI_B}$	Less biased than the HWI if individuals vary in their gregariousness	5
Twice-weight index (**TWI**$_{AB}$)	$TWI_{A,B} = \frac{(Y_{AB})}{[(Y_A) + (Y_B) + (Y_{AB})]}$	Less biased if individuals are more likely to be identified when associating	4

x: the number of instances where individuals A and B were observed together; Y_A: the number of instances where individual A was observed without individual B; Y_B: the number of instances where individual B was observed without individual A; Y_{AB}: the number of instances where individuals A and B were observed at the same time but not together; HWI_A: the half-weight index calculated for individual A; HWI_B: the half-weight index calculated for individual B.
[a] Comments are from Whitehead (2008).

and software used as well as the type of association indices and number of network metrics calculated.

(3) Identify which species are being studied using animal social network analysis including conservation status and the potential for taxonomic bias.

(4) Based on some of our key findings, we highlight recommendations for future research using animal social network analysis (Table 3). Our recommendations aim to complement empirical findings associated with our first three objectives.

METHODS

Data Collection

To evaluate the state of animal social network analysis within the peer-reviewed literature we conducted a literature survey using Thomson's Scientific Web of Science core databases. We used Web of Science because it allowed us to access large quantities of journal articles using thematic searches. We conducted our literature survey up to and including 2016 using a range of search terms that were likely to yield articles on social network analysis. We conducted four systematic searches of keywords on Web of Science that generated lists of articles that were likely relevant for our analysis. We searched the phrases ‘social network analysis’, ‘social network’, ‘network analysis’ and ‘contact network’ and filtered our searches using the following Web of Science categories: biology, ecology, zoology, behavioural sciences, evolutionary biology, epidemiology and psychology. Searches were conducted during 8–21 January 2017. In total, we identified 1603 unique articles through this method. We then used the ‘snowball approach’ (Horsley, Dingwall, & Sampson, 2011) to collect additional articles from the reference lists of all review and methodological articles (see below) identified through our Web of Science searches.

To meet the criteria for inclusion in our analysis, we used a conservative and systematic filtering process. We only included articles that explicitly stated their use of social network analysis and generated social networks based on pairwise social associations of nonhuman animals or, if empirical data were not included, discussed social network analysis in the form of a methodological, quantitative review or synthetic review (see below). Although animal social networks are occasionally constructed based on nodes

Table 3
Outline of implications, opportunities and future directions for research based on key findings from our study

Aspect of network analysis	Finding and implications	Opportunities and future directions
Association indices	The use of association indices in social network analysis is not ubiquitous. Potential bias if missing individuals, misidentified individuals, or more frequently observed individuals are not accounted for	Use of association indices in social network analysis is almost always required. We also recommend that summary statistics are presented on the number of observations per individual and for the association indices
Number of network metrics per article (Fig. 3c)	Studies using social network analysis generate a wide range of social network metrics (range 0–9) with apparent preference for certain network metrics	We recommend a priori justification of social network metrics and associated hypotheses. We also recommend that future studies include a statement indicating whether, or not, other network metrics were considered or used for analysis, but results were not included in the final results
Data collection method (Fig. 4b)	Focal observation is the most common form of data collection and is currently accepted as the most reliable form of data collection. Use of various biologging devices is less common, but has been increasing over time	Biologging technology represents an opportunity to test hypotheses about the ecology and evolution of social structure using existing data sets and increases the ability to measure social connections at certain times (e.g. at night or in winter) and for certain species (e.g. small or cryptic species) where focal observations are infeasible. Where possible we recommend the combination of focal observation with biologging devices to obtain information on fine-scale animal social interaction in the context of proximity measures obtained by biologging
Species of conservation concern	Studies generating social networks rarely study species of conservation concern, although there is increasing acknowledgment that social network analysis may be an important tool for species of conservation concern	We recommend future studies examine the social dynamics of species similar to those of conservation concern to ensure social network analysis will have conservation value for focal species. Deployment of biologgers may also be facilitated if species of concern require capture for other purposes, such as genetic sampling, relocation or tagging

that represent groups of individuals, such as harems or colonies, we only included articles where nodes were represented by a single individual. We also excluded articles that generated networks where nodes represented, for example, spatial locations, or edges represented parasite sharing, while we also excluded ecological, genetic and neural networks. In the case of ecological networks, we excluded these studies from our analysis because nodes represent species and edges represent some form of broad interaction between species, such as parasitism or predator–prey interactions. Although these fields use similar techniques to social network analysis, their inclusion was beyond the scope of our analysis. We also excluded articles that modelled social network processes because these articles were not explicitly based on empirically derived pairwise social associations, but, rather, the majority of articles that model social network dynamics are based on simulated data. In addition, we only included peer-reviewed research articles. We excluded peer-reviewed commentaries on, or responses to, previously published articles, editorials, letters to the editor, prefaces to theme issues, conference proceedings, theses, book chapters and books. Access to some of these sources of information can be sporadic, and typical bibliometric analyses exclude these sources because it is difficult to systematically search grey literature. From our original output of 1603 articles, only 293 articles matched our criteria. The snowball approach yielded an additional 135 articles for a total of 428 relevant peer-reviewed articles that used or where about social network analysis that met our criteria. For all articles we also extracted the Web of Science citation count on 8 January 2017. While it is possible we missed some published articles about social network analysis, we are confident that we identified a very large proportion of the literature up to 2016 in an unbiased manner, which accurately represents the trends in social network analysis implementation. All data collected are available as Supplementary Material.

Data Extraction and Analyses

To address our first objective, which was to assess trends in publication on animal social network analysis over time, we assessed temporal changes in the number of articles published using, or about, social network analysis per year. We first assigned articles to one of four categories: empirical, synthetic review, methodological, or quantitative review. Empirical articles contained data collected in the field or laboratory that were used to generate social networks; synthetic review articles were data-free and outlined a broad synthetic or theoretical contribution to social network analysis; methodological articles may, or may not, have contained empirical data, but provided an overview or demonstration of a particular methodological aspect of social network analysis; quantitative reviews were categorized as articles that contained summaries or comparisons of empirically collected social network data from multiple species. For citation rate, measured as number of citations/years since publication, we determined whether different article types are disproportionately cited compared to others. We also assigned all articles to one of six general themes based on the journal of publication: behavioural (e.g. *Animal Behaviour*), general biology (e.g. *Proceedings of the Royal Society B*), general ecology (e.g. *Journal of Animal Ecology*), taxa-specific (e.g. *Journal of Fish Biology*), applied (e.g. *Applied Animal Behaviour Science*) or disease/parasitology journals (e.g. *Journal of Wildlife Diseases*). We recorded the year of publication for each article to demonstrate possible temporal changes in publication trends (see below).

To address our second objective, which was to describe animal social network methods, including the type of data collection methods and software used as well as the type of association indices and number of network metrics calculated, we extracted aspects associated with methods for all empirical articles. Our methodological overview comprised four key aspects of social network analysis. First, we determined the software used to generate social network analysis. Second, we assessed how networks were constructed, how many networks were constructed in each article and the number of uniquely identifiable individuals within each network. We considered networks as unique if they were constructed based on different behaviours (e.g. proximity versus grooming), different experimental treatments or trials, different groups, populations or species, or if they occurred across distinct temporal periods. We determined whether an association index was used, and, if not, whether network edges were weighted using another measure, such as frequency or duration of social interactions. Third, to consider the technological aspect of social network analysis, we recorded how data were collected to generate networks and the general type of behaviour used to quantify social relationships. Finally, we summarized the statistical aspect of social network analyses by recording the number and type of social network metrics quantified in each article as well as the number of individuals in each network. We separated social network metrics into individual and group-level metrics.

To address our third objective, which was to identify which species are studied using animal social network analysis, we extracted relevant information on the study species and the broad taxonomic group of the study species from empirical articles. For each species, we obtained IUCN (International Union for the Conservation of Nature, www.iucn.org) listing as well as the taxonomic class of each species in our data set.

RESULTS

Objective 1

We identified 428 animal social network articles from the peer-reviewed literature and classified 338 (79%) as empirical, 52 (12%) as synthetic reviews, 27 (6%) as methodological and 11 (3%) as quantitative reviews (Fig. 1a). The first article in our database was from 1999, and we observed an exponential increase in the total number of social network articles over time (Fig. 1a). Among the most cited articles in our database, we considered the top 25 cited articles for subsequent descriptive statistics, which were cited at least 13 times per year (range 13–42). Of these 25 articles, 13 (52%) were empirical, 10 (40%) were synthetic reviews, 1 (4%) was a quantitative review and 1 (4%) was a methods article (Fig. 1b, Fig. S1). The most common journal type where animal social network articles were published was behavioural journals (163/428, 38.1%), while social network studies were also published in general biology (126/428, 29.4%), taxa-specific (67/428, 15.7%), general ecology (44/428, 10.3%), applied (22/428, 5.1%) and disease/parasitology (6/428, 1.4%) journals (Fig. 2).

Objective 2

For empirical articles, the number of networks calculated per article was right-skewed, with a median of 3 networks per article (SD = 15.1, range 1–128; Fig. 3a, Table 1). The number of individuals in a given network was also right-skewed, with a median of 15 individuals per network (SD = 101, range 4–1406; Fig. 3b). The median number of social network metrics calculated per article was 2 (SD = 2.0, range 0–9; Fig. 3c), while the median number of network metrics per article that calculated at least one metric was 3 (SD = 1.8, range 1–9).

In total, at least one social network metric was calculated in 254 of the 338 empirical articles we identified (Table 1). Of the 254

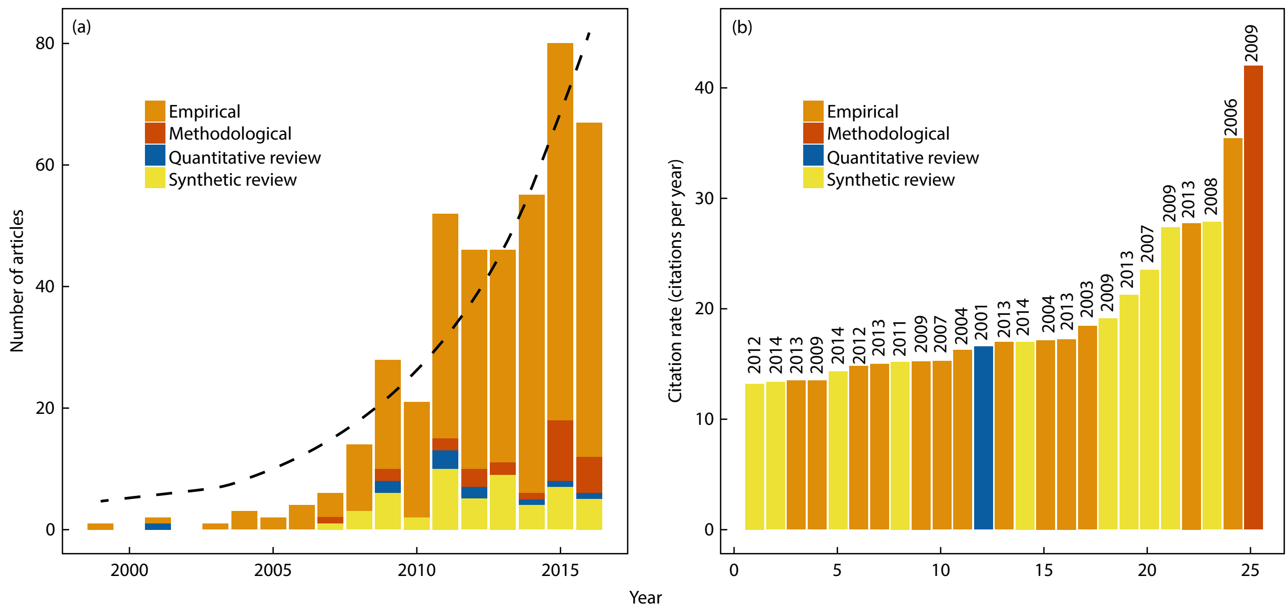

Figure 1. (a) Number of animal social network articles over time separated by article type. Note, the dashed line represents an exponential growth curve for the number of social network articles published each year. (b) Top 25 most cited articles based on citation rate (citations per year) that use, or are about, social network analysis (these articles were cited at least 13 times per year since they were published). Articles are separated by type: empirical, methodological, synthetic review and quantitative review. Note, the year of publication is included above each bar. Citations were extracted from Web of Science on 8 January 2017. See Fig. S1 for the references for each article presented here.

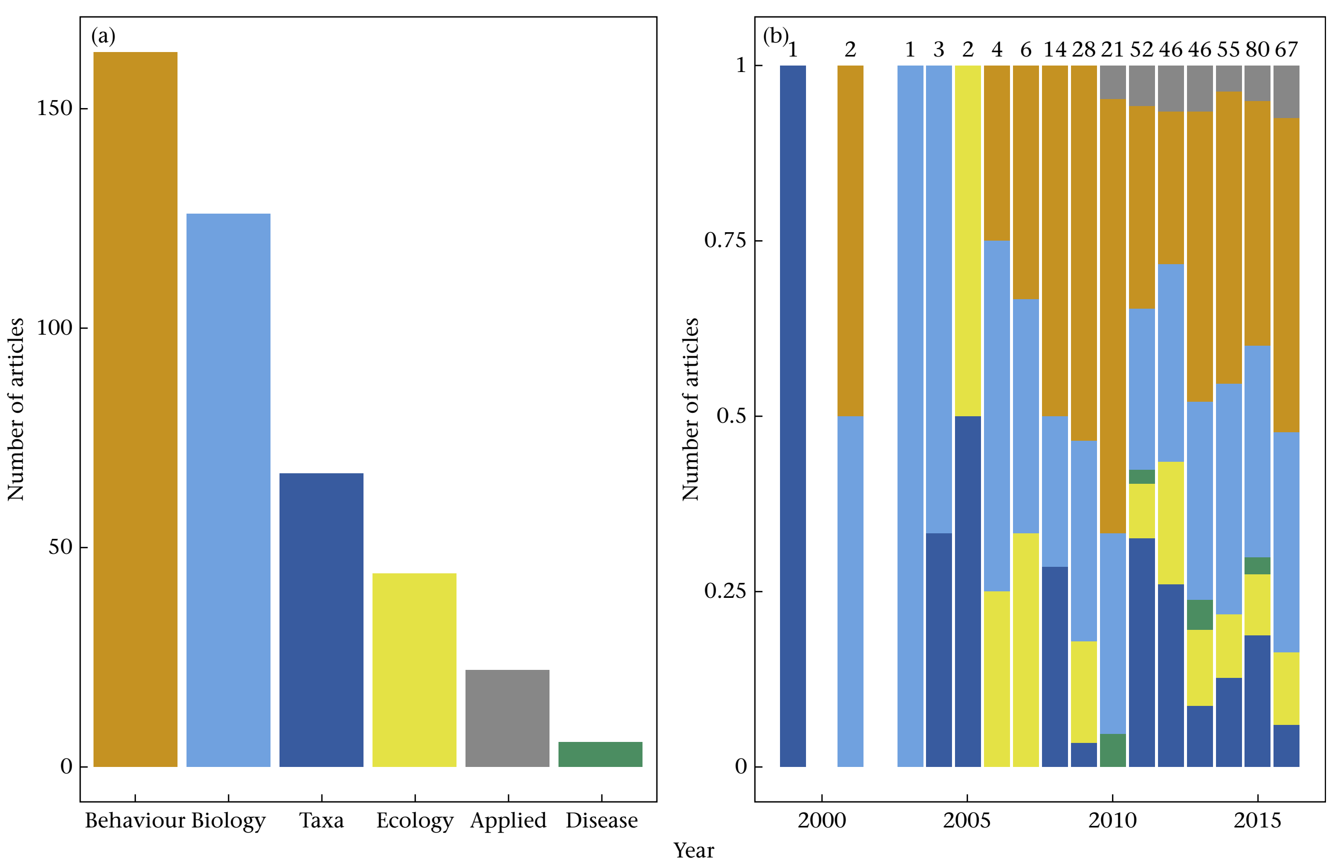

Figure 2. (a) Number of animal social network articles published in journals allocated to one of six categories: behaviour (orange), biology (light blue), taxa-specific (dark blue), ecology (yellow), applied (grey) or disease/parasitism (green). Social network articles are most commonly published in behavioural or general biology journals, while they are rarely published in journals categorized as applied or disease/parasitism. (b) Proportion of social network articles published in journals allocated to one of six categories over time. Total numbers of empirical articles are presented at the top of each bar in panel (b).

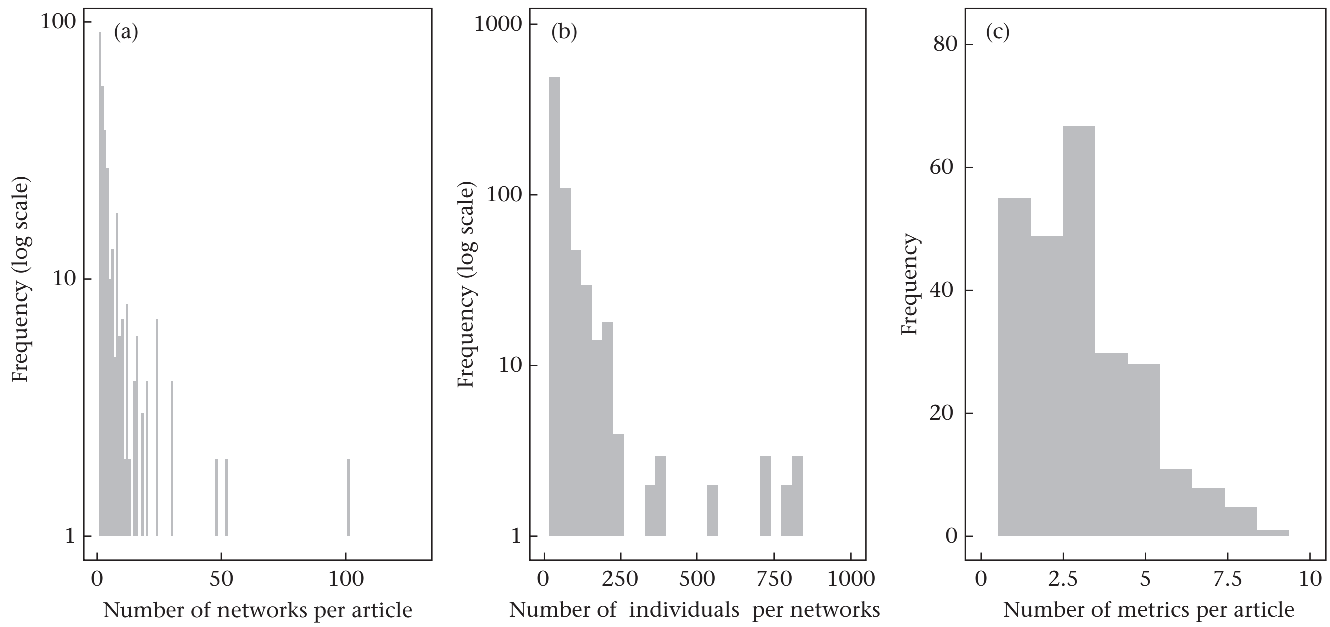

Figure 3. (a) Number of animal social networks generated per empirical article included in our study; median number of networks generated per article was 3 (range 1–128). (b) Number of individuals per network generated; median number of individuals per network was 15 (range 4–1406) from a total of 2674 networks generated across all 338 empirical articles. (c) Number of social network metrics generated per empirical article; the median number of metrics per article was 2 (range 0–9).

studies that calculated at least one metric, we identified 35 unique social network metrics, and, in general, different network metrics were not used equally. The most commonly quantified individual-level social network metrics were degree and graph strength (both quantified in 97/254 articles, 38.2%), while node-based clustering coefficient (87/254, 34.3%), betweenness centrality (68/254, 26.7%) and eigenvector centrality (65/254, 25.6%) were also commonly quantified (Table 1). The most commonly quantified group-level social network metrics were graph density (58/254, 22.8%) and modularity (50/254, 19.7%; Table 1). Meanwhile, of the 83 studies that did not calculate any social network metric, social network analysis was still used in some capacity, e.g. for visualization, network-based diffusion analysis or multiple regression quadratic assignment procedure, among other techniques.

A variety of animal social network software programs were used across articles. The most commonly used software program was R (76/338 of empirical studies, 22.5%), including 'asnipe', 'igraph', and 'sna' among others (Fig. 4), while SOCPROG (63/338 empirical studies, 18.6%) and UCINET (51/338 empirical studies, 15.1%) were the second and third most commonly used software programs, and 18.0% (61/338) of articles used multiple software programs and 5.9% (20/338) of articles used other software programs (Fig. 4a). We were unable to determine what software program was used in 19.8% (67/338) of empirical articles.

Data collection techniques were skewed towards focal observation (267/338, 79%; Fig. 4b). A range of biologging technologies, including passive integrated transponders (20/338. 5.9%), proximity devices (12/338, 3.5%), VHF telemetry (12/338, 3.5%), GPS

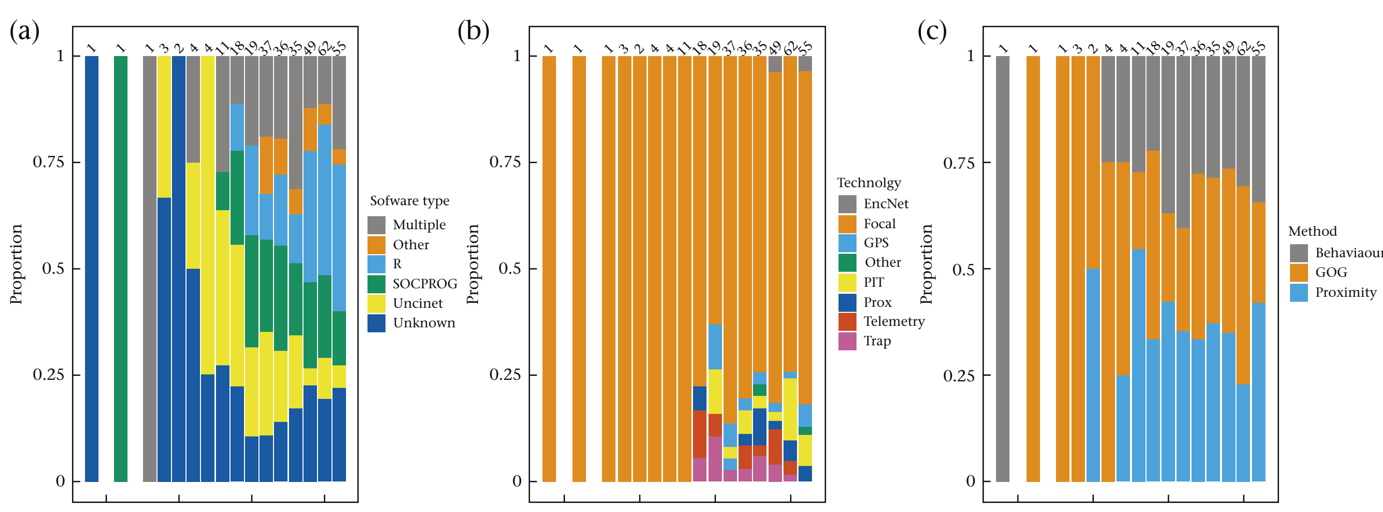

Figure 4. (a) Proportion of empirical animal social network articles that used different software programs to generate social networks over time. Note, most articles use at least one R package, although many articles use SOCPROG or UCINET, or some combination of R, SOCPROG and UCINET. (b) Proportion of empirical social network articles that used different data collection techniques over time (EncNet: Encounternet; GPS: global positioning system; PIT: passive integrated transponders; Prox: proximity devices; Trap: trapping data). (c) Proportion of empirical animal social network articles that used different types of data collection methods over time. Note, GOG refers to gambit-of-the-group data collection. Total numbers of empirical articles are presented at the top of each bar.

telemetry (11/338, 3.3%), trapping data (10/338, 2.9%), Encounternet (4/338, 1.2%) and other techniques (2/338, 0.6%), were also used to collect data (Fig. 4b).

The most common type of network edge weighting was based on the duration or frequency of interactions (133/338, 39.4%), while fewer articles used association indices (Table 2). The half-weight index (HWI) was the most commonly used association index (66/338, 19.7%), followed by the simple ratio index, SRI (62/338, 18.5), the half-weight index corrected for gregariousness, HWIG (5/338, 1.4%) and the twice-weight index, TWI (3/338, 0.1%), while in 45/338 (14.3%) articles, the association index or matrix weighting procedure was unknown, and 20/338 (5.9%) of articles used a binary association matrix.

Data collection methods were similar among the three types of data we considered. The use of gambit-of-the-group was more common in studies from earlier in our database, while the proportion of use for each method stabilized around 2008 (Fig. 4c). Gambit-of-the-group was the most commonly used type of association data (121/338, 35.8%), while proximity to conspecifics (114/338, 33.7%) and behavioural interaction (103/338, 30.5%) were also relatively common.

Objective 3

In total, 201 unique species from 12 taxonomic classes were studied in empirical social network articles and there was variation in the species studied based on their IUCN Red List status. The most commonly observed listing was least concern (119/202, 59%), while species that were not listed (23/202, 11.3%), vulnerable (15/202, 7.5%), endangered (14/202, 7.0%), not threatened (12/202, 6.0%), critically endangered (7/202, 3.5%), data deficient (5/202, 2.5%) and domestic (4/201, 2.0%) were less commonly studied (Fig. 5).

The majority of species studied were in classes Mammalia (111/202, 55%) and Aves (47/202, 23%), while fewer were from classes Actinopterygii (14/202, 7%), Insecta (12/202, 6%), Chondrichthyes (5/202, 2.5%), Reptilia (4/202, 2%) and Hymenoptera (2/202, 1%). Meanwhile, there was a single (1/201, 0.005%) species studied in classes Malacostraca, Sauropsida, Amphibia and Arachnida. The most common species studied in all empirical social network articles were great tits, *Parus major* (17/338 empirical articles, 5%), guppies, *Poecilia reticulata* (14/338, 4.2%), chimpanzees, *Pan troglodytes* (13/338, 3.9%), rhesus macaques, *Macaca mulatta* (12/338, 3.6%), bottlenose dolphins, *Tursiops truncatus* (11/338, 3.3%), and sleepy lizards, *Tiliqua rugosa* (10/338, 3.0%).

DISCUSSION

Animal social network analysis has increased in use over the past two decades, and within this growing body of literature we found substantial variety in the number, and type, of network metrics calculated across studies, the use of association indices and the species studied. We found that most empirical social networks contain relatively few individuals and the use of specific association indices varied considerably. We also found taxonomic bias in the species being studied, where the majority of species studied were birds or mammals, and of these, most were listed as being of least concern by the IUCN. Based on key findings and observations from our bibliometric analysis, we also provide a series of recommendations for future studies using social network analysis. After two decades of modern social network analysis, our study provides insight into some trends in social network research within the field of animal behavioural ecology.

Objective 1: Trends in Publication Analysis

It is clear the use of animal social network analysis has increased in popularity over the past two decades, a trend which is broadly consistent with the general increase in academic publication. The number of empirical studies increased slowly during 1999–2007 before an exponential increase in the number of articles per year after 2008. Similar to many natural populations, there could be a carrying capacity for the number of articles using social network

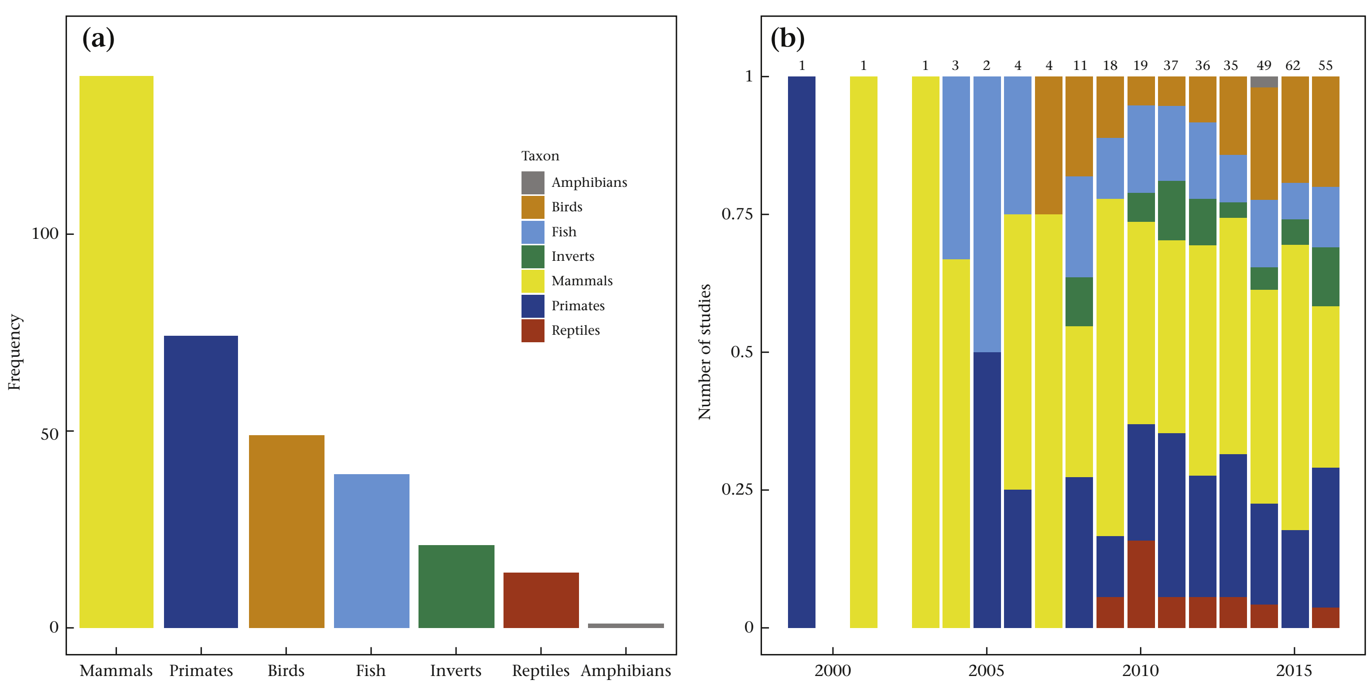

Figure 5. (a) Number of species from empirical animal social network articles from one of seven broad taxonomic groups, where the colours representing each taxonomic group in this panel carry over to panel (b). Primates were separated from nonprimate mammals because of the large number of social network studies on primates. (b) Proportion of species from empirical social network articles separated by broad taxonomic group over time. Note, the trends in species are similar over time with few observable discrepancies in the proportion of a given taxonomic group studied at any given time.

analysis in a given year, but we may still be far from the actual carrying capacity. Interestingly, the number of review and methods articles did not follow the same proportional increase as empirical articles, although in the final two years of our analysis (2015 and 2016) there was an increase in the number of methodological articles published. The recent increase in methods articles may be a function of a field that was largely missing a coherent and up-to-date set of guidelines. Prior to 2015, when a number of important methods articles were published (e.g. Farine & Whitehead, 2015; Whitehead & James, 2015), few comprehensive 'how to' articles explicitly provided guidance on social network analysis (although comprehensive books did exist: Croft, Ruxton, & Krause, 2008; Whitehead, 2008). Importantly, an increase in methodological articles, as well as reviews about specific methods highlights an attempt to achieve a higher standard for social network methods up to the end of our data collection in 2016 (see references above) as well as in the short time since (e.g. Hoppitt & Farine, 2018; Silk & Fisher, 2017).

Our citation analysis suggests that empirical articles are similarly cited to synthetic review articles, which were among the most cited articles in our database. This trend is similar to other subdisciplines within behavioural ecology (animal personality: Davis, Payne, & Sih, 2015; Dirienzo & Montiglio, 2015). While the two most highly cited articles in our database were the SOCPROG guide (Whitehead, 2009) and a seminal empirical social network article (Flack, Girvan, de Waal, & Krakauer, 2006), review articles were more highly cited than we may have expected based on their overall prevalence in the database (Fig. 1). While most behavioural ecologists rely on empirical hypothesis testing, it is clear that a relatively small proportion of all empirical articles become highly cited, compared to a larger proportion of all synthetic review papers. Interestingly, the most highly cited review papers of social network analysis are approximately a decade old and describe the functional role and potential applications of network analysis in behavioural ecology (Fig. S1). As we reflect on the field, these articles may represent classic 'early' descriptions of how we thought about social network analysis in the modern era. Moving forward, reviews with more specific focus may become a more common form of review, and we expect that citation patterns will shift to reflect a more nuanced understanding of how we test hypotheses using social network analysis.

Objective 2: Methods

The advancement, availability and accessibility of computer programming has undoubtedly contributed to the rise in popularity of animal social network analysis over time. Until the advent of open access software and relatively easy-to-use social network R packages (e.g. Csárdi & Nepusz, 2006; Farine, 2013, 2014), our findings suggest the social network subdiscipline went through some degree of methodological disarray. The increase in the proportion of methods articles published in 2015 and 2016 may have stimulated the formation, and implementation, of guidelines for social network analysis. For example, the selection and implementation of association indices is an important example of an aspect of social network methodology with considerable variation in implementation practices. Our analysis suggests that many studies do not use association indices, but rather, network edges are weighted based on the frequency or duration of social interactions. We recommend future articles quantifying social networks use an association index to account for missing observations (Hoppitt & Farine, 2018). The simple ratio index (SRI) and half-weight index (HWI) were the most commonly used indices and, depending on data collection methods, either the SRI or HWI are appropriate in almost all situations. The SRI is applied when every individual is observed and correctly identified in all sampling periods. Meanwhile, the HWI accounts for missing observations of individuals at any given sampling period and the potential for certain individuals to be observed more regularly (Cairns & Schwager, 1987). Although our results suggest that SRI and HWI are the most commonly used association indices in social network research, the recent publication of several important reviews suggests potential alternative options for specialized situations (e.g. Godde, Humbert, Côté, Réale, & Whitehead, 2013; Hoppitt & Farine, 2018; Weko, 2018; Whitehead & James, 2015). For better interpretation of association indices, we recommend that future studies report the summary statistics for association indices. For example, mean, standard error and range of the total number of observations per individual accompanied by similar statistics for the actual association indices. Finally, knowledge of the approximate proportion of the total population included in network analysis is also important for reducing bias associated with missing or unidentified individuals (Hoppitt & Farine, 2018).

The use of different animal social network software has also changed over time. SOCPROG and UCINET were widely used in the first decade of social network analysis. More recently, R packages, including 'asnipe', 'igraph' and 'sna' have been more commonly used, while more specialized packages are becoming increasingly available ('spatsoc': Robitaille, Webber, & Vander, 2018; 'ant': Sosa et al., 2018). The implementation of social network analysis in R makes it more compatible with other analytical techniques, such as quantitative genetics (Thomson, Winney, Salles, & Pujol, 2018; Wilson et al., 2010), geographical patterns of space use (Spiegel et al., 2016), exponential random graph models (Silk & Fisher, 2017), or multilayered social networks (Silk, Finn, Porter, & Pinter-Wollman, 2018).

We also found the vast majority of empirical animal social network studies collected data by focal observation. A logical explanation for these findings is that focal observation is less expensive, involves less data processing, does not require animal handling and generally has lower standards of animal ethics. Focal observation is also reliable because observers are certain of the exact behaviours of one or more animals (Altmann, 1974). We expect it is these reasons that focal observation has remained the most common type of data collection for social network analysis over time. However, despite the reliability of focal observation, biologging with various devices is increasingly being used in many ecological studies (Wilmers et al., 2015), and social network analysis is no exception. Specifically, biologging allows for continuous and simultaneous monitoring of multiple individuals, giving a more comprehensive understanding of social network dynamics. The most popular biologging device used to generate social network data is radiofrequency identification devices (RFIDs), such as passive integrated transponder tags (PIT), although most articles using RFIDs are from the same system of great tits in the United Kingdom (e.g. see Aplin et al., 2013). We expect the availability of various types of biologging devices should increase the popularity of remotely collected social network data. GPS telemetry data, autonomous fixed arrays and proximity collars are relatively underused technologies in social network research, despite the fact that both have potential to test a variety of hypotheses about animal social structure (Jacoby & Freeman, 2016); for example, proximity collars may be used to test hypotheses about disease transmission in small or cryptic species (Hamede, Bashford, McCallum, & Jones, 2009; Silk, Weber et al., 2018). Automated barcode tracking systems are a relatively new technique for generating social networks (Alarcón-Nieto et al., 2018), although there were no studies in our bibliometric analysis that used these devices. Accelerometers are also a relatively new biologging technique, which, in combination with proximity loggers, could provide insight into the behavioural time budgets in a social context (Jacoby & Freeman, 2016). Moreover, the use of accelerometers in combination with proximity loggers could enable the continuous monitoring of individuals through space and time, a form of data collection that is difficult or impossible for most other types of biologging devices and impossible for focal observation. While we expect the use of biologging technologies will continue to increase in use over time, focal observation remains the most popular and reliable data collection method because it is inexpensive, requires less data processing, and specific behaviours can be recorded. We recommend that, where possible, future studies validate biologging devices by observing individuals with biologging devices to develop an understanding of what individuals are doing when they are in close proximity to one another (Carter, Lee, & Marshall, 2015; Castles et al., 2014; Farine, 2015).

Social network metrics are arguably the most appealing aspect of network analysis because they can be interpreted relatively easily and used in statistical models. We observed apparent preference for certain social network metrics. Strength and degree were the most commonly calculated social network metrics, while clustering coefficient, betweenness and eigenvector centrality were also relatively common. Among the synthetic review and methods articles that we identified, there was little discussion or guidance on the number or type network metrics to calculate in a given study. While we do not advocate for the use of any particular network metrics, the use of a large number of social network metrics may be problematic. We therefore recommend explicit justification for the use of any given metric and suggest that social network users avoid the practice of HARKing (hypothesis after results are known: Kerr, 1998). Although HARKing and data mining, or dredging, can be problematic, transparency about the selection and use of biologically relevant network metrics reduces uncertainty or confusion about whether a study may be guilty of HARKing. We also recommend that future studies include a statement indicating whether, or not, other network metrics were considered during data exploration (Lewis, Vander Wal, & Fifield, 2018). This type of statement will increase transparency in the field of animal social network research. Similar to other required statements, e.g. regarding observer bias or animal ethics, will at worst force researchers already prone to HARKing to consider their use of network metrics and at best will increase transparency in the practice of justifying the use of certain network metrics.

Randomization is an important social network method that we did not incorporate into our bibliometric analysis. While the awareness of randomization procedures has improved substantially in recent years (Farine & Whitehead, 2015), it was prohibitively difficult to extract relevant information on randomization procedures from empirical studies. Many studies did not provide sufficient detail about the type of randomization procedure used, e.g. node-based or data-stream, or whether the randomization procedures included statistical analysis. Methods for conducting randomizations for various types of data have also improved (see Farine, 2017), but it is clear greater transparency about the type and extent of randomizations used is required. We suggest that future studies provide open-access code and data to help readers and social network users better understand the types of randomization being used (for discussion on the 'data-pipeline' see Lewis et al., 2018).

Objective 3: Species

The most common species in our data set were model species from well-established systems, most of which are relatively abundant and easy to work with. The use of model species improves our understanding of the ecology and evolution of social behaviour, and in support of this line of research, many of species in our database were listed by the IUCN as being of least concern. Conservation is becoming an increasingly important issue across ecological disciplines. Among behavioural ecologists, understanding conservation implications for species is often cited as an important conclusion of empirical work. Meanwhile, several recent reviews have also highlighted the relative complacency of behavioural ecologists in a conservation context (Caro & Sherman, 2011, 2013), and our findings generally support these views. Despite the paucity of studies quantifying social networks for species of conservation concern, it may not be reasonable to have expected a large number of studies on these species. Specifically, by their very nature, species of conservation concern are rare and can be difficult to observe, both of which can be problematic in the context of collecting data for social network analysis. We do, however, wish to highlight that studies quantifying social networks for species of conservation concern represent an important advance in our understanding that behaviour is relevant in a conservation context (e.g. mountain gorillas, *Gorilla beringei*: Rosenbaum, Maldonado-Chaparro, & Stoinski, 2015). The use of biologgers may also be facilitated if species already require capture for other purposes, such as genetic sampling, relocation or tagging. Moreover, the field of ‘conservation behaviour’ (Blumstein, 2010; Macdonald, 2016) has highlighted social network analysis as a potentially important tool to help inform management plans, particularly for highly gregarious species in the wild (Snijders, Blumstein, Stanley, & Franks, 2017).

Little is known about the relationship between social behaviour and population dynamics, and animal social network analysis represents a potential method that could improve our understanding of this relationship (Webber & Vander Wal, 2018). Allee effects, a phenomenon described as a positive relationship between fitness and group size or population density (Stephens & Sutherland, 1999), are an important conservation issue for some social species (Angulo et al., 2018). We recommend that future studies assess whether social network analysis could be used to help predict whether individuals with high centrality may have higher fitness (e.g. Stanton & Mann, 2012; Vander Wal et al., 2015) or whether groups of translocated individuals are able to maintain social structure or integrate with new group members (e.g. Jesmer et al., 2018; Poirier & Festa-Bianchet, 2018). Similarly, we also suggest that in cases where it is at least plausible that social network analysis could help understand the relationship between social structure and population dynamics, that networks are first generated for similar nonthreatened populations or species to ensure data collection methods are appropriate and effective. As is the case for methods being applied to managed populations, social network analysis is likely most beneficial when applied directly to a given population because context of a species, population or system is critical for social network analysis.

Conclusion

We synthesized trends in animal social network research using a bibliometric approach. Social network analysis has increased exponentially over time, and we assessed a wide range of data collection and analytical methods used in studies that generate social networks. Our assessment of social network methods suggests there is substantial variation in the number, and type, of network metrics calculated across studies, the use of association indices and the species studied. Although our bibliometric analysis was objective, we provide four broad recommendations for future studies using social network analysis (Table 3). First, in the context of association indices, we recommend the inclusion of summary statistics for the number of observations per individual as well as for association indices. Second, we recommend a priori selection and justification of network metrics to reduce the likelihood of HARKing in studies using social network analysis. We also suggest including a statement indicating whether other network metrics have been analysed during data exploration. Third, while focal observation is the most common, and presumably, the most reliable type of data collection method for studies using social network analysis, biologging is the most comprehensive. Thus, we recommend the combined use, and validation, of biologging devices with focal observation. Fourth, we recommend and support the continued effort to study species of conservation concern using social network analysis. Studies of similar species or populations may help justify potential costs associated with studying groups or populations of conservation concern.

The field of animal social network analysis has clearly advanced during the last two decades. In their seminal paper, Wey et al. (2008, p. 342) concluded by stating: ‘We expect in the next decade there will be a fundamental increase in our understanding of social relationships and behaviour resulting from the widespread adoption of social network analyses, and we look forward to these insights’. Indeed, in 2018 the widespread adoption of social network analysis has clearly enabled a fundamental increase in our understanding of social relationships and behaviour, for example, an increased emphasis on the effect of direct and indirect social relationships on fitness. Our analysis highlighted some of the trends in social network analysis. As basic social network methods become standard operating procedure and transparency about certain types of methods (e.g. randomizations) increases and research shifts towards open science, we expect an increase in meta-analyses or other large-scale syntheses to emerge (e.g. Sah, Mann, & Bansal, 2018). Finally, in the next decade we also expect that the ever-changing analytical, methodological and theoretical boundaries of social network analysis will allow empiricists to continue testing new and exciting hypotheses with increased rigour.

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Supplementary Material

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