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Social networks research in ex situ populations: Patterns, trends, and future directions for conservation-focused behavioral research

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Abstract

Social networks research using non-human animals has grown over the past decade, utilizing a wide range of species to answer an array of pure and applied questions. Network approaches have relevance to conservation, evaluating social influences on fecundity, health, fitness and longevity. While the application of network approaches to in situ populations with conservation concern appears in published literature, the degree to which ex situ and zoo-housed populations are the focus of “social networks for conservation research” is limited. Captive environments provide scientists with an ability to understand the social behavior of species that may be hard to observe consistently in the wild. This paper evaluates the scope of network research involving ex situ populations, analyzing output from 2010 to 2019 to determine trends in questions and subjects using ex situ populations. We show that only 8.2% of ex situ social network analysis (SNA) implications are of conservation-focus, apparent in papers relating to birds, carnivores, bats, primates, reptiles, and ungulates. Husbandry and welfare questions predominate in ex situ network research, but over half of these papers have nonpractical application (basic science). The chance of a citation for a basic science paper was 95.4% more than for a conservation-based paper. For taxonomic groups, primate-focused papers had the most citations. The focus of ex situ conservation-based networks research may be driven by the needs of conservation programs (e.g., population recovery outcomes) or by a need to evaluate the efficacy of ex situ conservation goals. We evaluate our findings considering the IUCN's One Plan Approach to conservation to show how in situ and ex situ network research is applicable to global conservation efforts. We have identified that there is a lack of application and evaluation of SNA to wildlife conservation. We highlight future areas of research in zoos and hope to stimulate discussion and collaboration between relevant parties.

KEYWORDS

animal behavior, ex situ conservation, horizon scan, One Plan Approach, zoo

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1 | INTRODUCTION

The current global extinction crisis calls for effective conservation action that is supported by sound biological, behavioral, and ecological evidence. Behavioral research of captive populations has potential for informing the conservation of their wild counterparts, but currently this is not being fully utilized. Zoos and aquariums are the most conventional way of enacting ex situ conservation aims (protection of species from extinction outside of a natural habitat) (Gusset & Dick, 2010, 2011). The main purpose of zoos and aquariums (hereafter referred to as zoos) has evolved from predominately public entertainment (Tribe & Booth, 2003) to educational, conservation and welfare aims being prominent. Guidance from subject-specific experts and regulatory bodies means the modern zoo has evolved into an ethical conservation center (Minteer et al., 2018) with the goals of meeting an animal's physical and physiological needs, the education of visitors, and tangible contributions toward species conservation programs (EAZA, 2013). Integrating zoo and field conservation efforts has become one of the most important population sustainability and conservation goals of an animal collection housed by the modern zoo (Rose, 2021; Traylor-Holzer et al., 2019).

Collaborative approaches to conservation by zoos and aquariums means information about (e.g., genetic and demographic) and the individual animals themselves are shared between institutions to build and maintain sustainable populations. Many zoos are involved in reintroduction programs by releasing captive-bred animals to re-establish wild populations (Gilbert & Soorae, 2017). Accredited zoos support overseas field projects by providing funding or resources, and World Association of Zoos and Aquariums members can collectively spend \$350 million US dollars annually on in situ conservation (Gusset & Dick, 2010). Zoos contributions to conservation research is evidenced in the scientific literature and this output is increasing each year, based on regional-specific (e.g., American Zoo Association) publications and when evaluating global journal repositories (Loh et al., 2018; Rose et al., 2019). Zoo data have been successful at filling knowledge gaps on biological and ecological traits of numerous wild species (Conde et al., 2019) that would otherwise have remained a mystery.

1.1 | Ex situ conservation behavior research

Behavioral research is a key area of zoo science with the potential for expanded application to conservation aims (Caro, 1999). Understanding how animals interact with each other and their environment underpins successful conservation actions (Gosling & Sutherland, 2000). The emerging discipline "conservation behavior" focuses on behavioral research as a tool to solve conservation issues, similar to the terms and objectives of "conservation genetics" and "conservation ecology" (Blumstein & Fernández-Juricic, 2004; Swaisgood, 2007). Zoos are excellent places to study animal behavior due to their controlled and predictable environment, the range of species

housed and the replicates that are possible across facilities. Despite these positive aspects, it is not common to find empirical research conducted in zoos asking behavioral questions.

This lack of publication may be caused by the two fields of zoo research and field-based research traditionally seen as divergent, with academics from each discipline rarely attending the same conferences or reading the same literature (Blumstein & Fernández-Juricic, 2010). A lack of collaboration between these fields may be detrimental to the advancement of conservation research (Greggor et al., 2016). Conservationists do not always consider behavioral studies (Caro & Sherman, 2011; Caro & Sherman, 2013), and established researchers can consider animal behavior a theoretical subject that is not used for solving practical problems (Caro & Sherman, 2013). To help this, it has been suggested that behavioral research needs to make explicit links to conservation as opposed to plausible possibilities, to make behavioral studies more relevant to conservationists (Caro, 1999).

1.2 | Application of networks research

While there are several methods of assessing social relationships, hierarchy and associations in non-human animals, we focus our review social network analysis (SNA), to demonstrate an area of zoo research where conservation applications are missing. SNA is the study of animal social structure by quantifying the patterns of relationships. When implemented correctly SNA can be used to breakdown noisy data into key network features, and further used to evaluate relationships within a social group. SNA can be used to track the transmission of social information (Jones et al., 2017) and disease spread (VanderWaal, Atwill, et al., 2014) between and within populations, thus highlighting its potential as a tool for the planning and evaluation of conservation action. Many zoo-housed species of conservation concern, for example, western lowland gorilla (*Gorilla gorilla gorilla*), live in groups with a specific social structure important to individual health, welfare and fitness (Stoinski et al., 2003, 2013). Likewise, numerous "popular with visitors," charismatic zoo species, such as elephants, *Loxodonta* sp. and *Elaphus maximus* (Albert et al., 2018) are also social and have an role in promoting conservation efforts.

The potential of SNA's application to wild populations and conservation efforts is demonstrated in successful conservation of threatened socially complex species. High-profile reintroduction programs for species such as the golden lion tamarin, *Leontopithecus rosalia* (Kierulff et al., 2012; Kleiman et al., 1986), California condor, *Gymnogyps californianus* (Sheppard et al., 2013; Teixeira et al., 2007), and whooping crane, *Grus americana* (Kreger et al., 2005; Urbanek et al., 2010) have been successful in part thanks to the application of knowledge about their social behavior.

SNA studies are practical for modern zoos, as it is relatively easy to collect data in a controlled environment with known individuals, compared to in the wild. Current typical approaches for collecting social network data has been to sample "nearest neighbors" with

in-person observations (Rose & Croft, 2015). This is suitable for zookeepers as they are familiar with the subject individuals, is not time consuming, and does not require expertise. Analyzing the data, however, usually requires experience in mathematical modeling and computer coding, as this is typically where SNA can be performed best. There is also potential for automating the data collection and analysis in the future using biologging techniques (Ripperger et al., 2020). Zoo populations may appear limiting for network researchers, as not all facets of a natural environment are provided. However, SNA can be valid and reliable to apply across contexts (between captive populations and wild populations) if environmental differences are considered. It is possible to identify key social traits using ex situ populations (Abell et al., 2013), which have relevance to those investigating conservation aims and outcomes for such species and populations. For example, as translocation and population augmentation approaches are expanded to more species, it is important to understand how population management impacts upon social structure of animals in zoos. Recent work on giraffe (*Giraffa camelopardalis*) translocations in situ (Brown et al., 2019) shows the importance of movement of known social groups to ensure future viability of translocated population. Research on zoo-housed giraffes, showing strength and persistence of social bonds (Bashaw, 2011; Bashaw et al., 2007) can provide information to wild conservation scientists who require evidence for which individuals to select for the creation of a new population. Therefore, to represent how zoo research can be expanded into conservation planning and action, we use SNA as its potential for conservation is clear. As population management and in-zoo care become more species-specific and evidence based, there are less limitations surrounding use of zoo populations for conservation-themed social behavior research. For example, new approaches to southern ground hornbill (*Bucorvus leadbeateri*) management specifically mention the need to manage family groups together (EAZA Hornbill TAG, 2019) as per evidence from wild social structure, highlighting the two-way street of evidence of the wild improving the zoo and hence the zoo population being more useful to behavioral researchers.

Using a systematic literature review, we aim to characterize and quantify current implications being made of ex situ SNA research. Specifically, we identify trends among the number of citations, study taxa and research implications used in peer-reviewed, scientific publications focusing on ex situ SNA, over a 10-year period. We use SNA as an example research topic of animal behavior due to its wide literature background to demonstrate its use to species conservation initiatives. A 10-year period was chosen to capture an adequate sample while focusing on recent research. To improve the efficiency of behavior research between zoo researchers and conservationists we then provide examples of how zoo-based SNA research can be used to inform conservation actions. In line with the nascent “One Plan Approach” to conservation, where there is a sliding scale of management between zoo communities and field biologists (Conservation Planning Specialist Group, 2020; Rose, 2021; Traylor-Holzer et al., 2019), research should be efficiently used and communicated between parties to work toward a unified conservation

plan. Therefore, identifying currently unrecognized conservation areas where zoo behavioral research can contribute is of importance to the successful outcomes of this One Plan approach.

2 | METHODS

We compiled a database of recent publications that use SNA in captivity, to identify the research outcomes from these types of studies. Literature was collated using a Google Scholar query in the software “Publish or Perish” (Harzing, 2007). The query contained the following search criteria: (1) year published: 2010–2019. (2) All of the words: “social” and “animal” and “network.” (3) Any of the words: “captive” or “zoo.” (4) Title words: “social.” Title word “social” was included to reduce irrelevant search results, however we acknowledge that this may limit our literature sample. Search results were then filtered into relevant biological captive research papers, excluding review and methodology focused papers. We consider captive studies as those with subjects from a closed populations in a restricted/controlled environment. Studies from zoos, sanctuaries, rehabilitation/rescue centers were included, but most lab-based studies (e.g., medical companies) were excluded as these were generally studies without implications for the species studied.

Each paper was read in full or until it became clear what the research implications were. Methods and limitations were specifically considered to ensure that studies met the goals they had outlined. We classified research implications into husbandry evidence, animal welfare, population management and conservation evidence (Table 1). For papers that covered multiple implication topics, these were recorded and ranked into main and subsidiary implications (see Table S1). However, an implication topic could only be recorded once per paper. Papers that did not discuss any practical applications were recorded as basic science. In our database, for each paper, we recorded the taxonomic information of the study animals, the publication reference, the number of citations and the implication topics.

Using R version 4.0.2 (R Core Team, 2019), a negative binomial model was used to test if the number of citations (response variable) varied with main implication topic (Husbandry Evidence, Animal Welfare, Population Management, Conservation Evidence, Basic Science), and taxonomic group (bird, Carnivora, cetacean, Chiroptera, marsupial, multiple, primate, Proboscidae, reptile, rodent, ungulate) (predictor variables). Taxonomic grouping was determined by sorting animals into familiar taxa between Subphylum and Order. A negative binomial distribution was fitted to address overdispersion, with variance of the response variable (citations) greater than the mean. A default log-link function was used in the model as a natural fit for the count (response) variable. Basic science was chosen as the baseline for implication topics, and primates for taxonomic groups since they have the most citations overall and a relatively large sample size. The interaction of implication topic and taxonomic group was not included due to many combinations of these covariates having zero counts. Model coefficients were exponentiated (i.e., the reverse log

Implication topics	Definition
Husbandry evidence	Referring to the daily care and management regimes of captive wild animals
Animal welfare	Referring to upholding the physical health and psychological wellbeing of captive wild animals
Population management	Referring to the maintenance of sustainable ex situ populations (e.g., animal moves or creating new breeding groups)
Conservation evidence	Referring to management of threatened species to reduce a decline and prevent extinction
Basic science	Theoretical findings or advancing knowledge without practical application

TABLE 1 Definitions used to categorize practical implications of zoo social network analysis literature

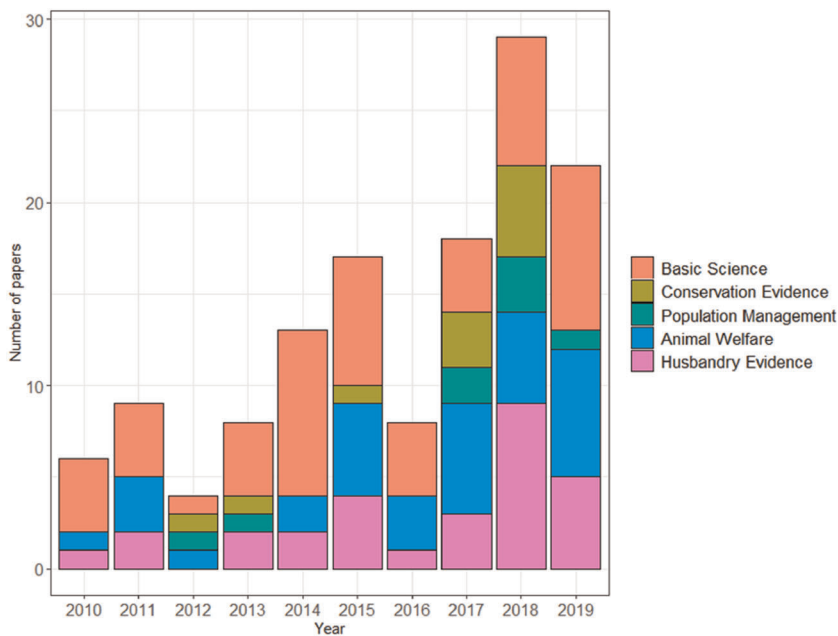


FIGURE 1 The total number of papers on each implication topic that used a social networks approach in captivity between 2010 and 2019 [Color figure can be viewed at wileyonlinelibrary.com]

was calculated) to estimate the odds ratios between predictor variables, which were then interpreted. A Tukey's pairwise comparison was then run using R packages "lsmeans" (Lenth, 2016) and "pbkrtest" (Halekoh & Højsgaard, 2014) to determine specific predictors of citation score.

3 | RESULTS

In total 103 papers were identified, and the most referenced practical implication topic was Animal Welfare (24.6%), followed by Husbandry Evidence (21.6%), Conservation Evidence (8.2%), and Population Management (6.0%) (Table S1). The remaining papers (40.0%) were recorded as Basic Science and did not discuss any practical applications to their findings. Alternatively, Basic Science papers commonly referred to methodological improvements and knowledge building.

The number of SNA zoo papers increased over time, where Basic Science dominated the literature consistently over the 10 years

(Figure 1). Husbandry Evidence and Animal Welfare persisted across the 10 years, whereas Conservation Evidence and Population Management were only present in half of the years. Practical application papers (i.e., not basic science) usually consisted of two topics, a main topic and a subsidiary topic. For example, frequently paired topics were Animal Welfare and Husbandry Evidence, which consisted of over half of all pairings noted. Conservation Evidence was one of the topics that paired the least with other topics, occurring with Population Management in 6/103 papers, Husbandry Evidence in 3/103 papers, and Animal Welfare in 2/103 papers.

Taxonomic analyses showed that Animal Welfare and Husbandry Evidence were the most common implications across taxa for ex situ social network research and included all but three taxonomic groups (Figure 2). Birds, Carnivora, primates, and ungulates were the most popular and diversely studied taxonomic groups. Half of bird and primate SNA papers related to basic science, whereas no Carnivora papers were used to answer these types of questions. Conservation-themed SNA implications were present in papers that focused on Primates ($N = 4$), carnivores ($N = 2$), ungulates ($N = 2$), bats

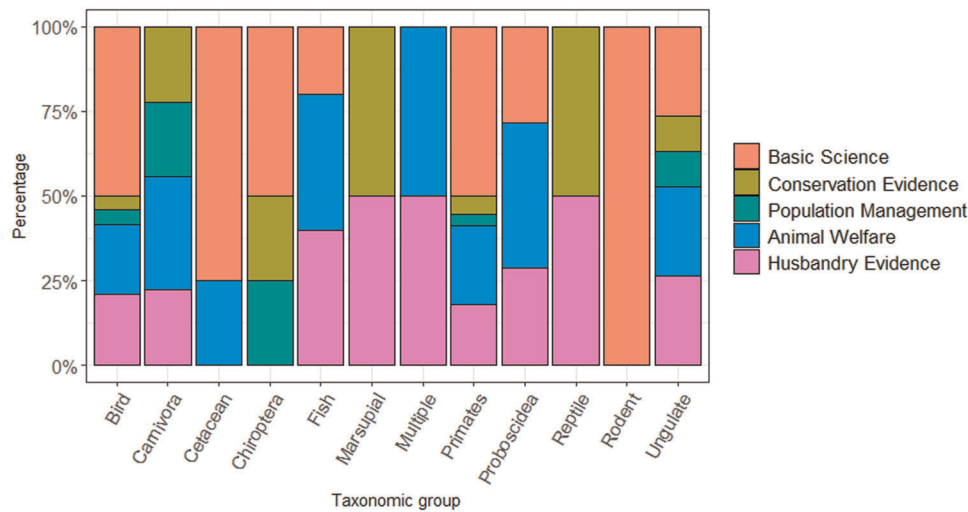


FIGURE 2 Proportions of each taxonomic group of animal subjects used for each of the five categories from this sample of social networks papers between 2010 and 2019. “Bird” included passerines and nonpasserines and papers on domestic poultry. “Multiple” refers to papers with multiple species across taxa as subjects. “Ungulate” includes papers on wild hoofed mammal species as well as domestic cattle and pigs. Sample sizes: bird = 11; Carnivora = 5; cetacean = 4; Chiroptera = 3; marsupial = 1; multiple = 5; primate = 28; Proboscidea = 3; reptile = 1; rodent = 1; ungulate = 6 [Color figure can be viewed at wileyonlinelibrary.com]

(Chiroptera) ($N = 1$), birds ($N = 1$), reptiles ($N = 1$), and marsupials ($N = 1$).

We found a significant effect of some implication topics on the number of citations, with fewer citations for Animal Welfare and Conservation Evidence topics, compared to Basic Science (Table 2). Odds ratios showed that the chances of a citation for a Basic Science based paper was 55.7% more than Animal Welfare and 95.4% more than Conservation Evidence. We also found that taxonomic groups cetaceans, carnivores, bats, proboscids, and ungulates had fewer citations, while fish had more citations than primates. The chances of a citation for a primate paper was 75.5% more than cetaceans, 81.4% more than proboscids, and 68.8% more than ungulates. The conditional model explained 19.7% of the variation in citations. A Tukey's pairwise comparison of each implication topic across all taxonomic orders showed significantly fewer Conservation Evidence papers (estimate = 3.080 ± 1.088 ; z ratio = 2.831; $p = .037$) were cited compared to those on Basic Science. All other pairwise comparisons were nonsignificant.

4 | DISCUSSION

Our results indicate that Basic Science had the most citations and was the most frequent type of paper in zoo SNA literature. Conservation Evidence on the other hand was the least cited type of paper and was rarely an application covered. Animal Welfare and Husbandry Evidence had few citations compared to basic science but were frequent applications of zoo SNA literature. Population Management also had few citations compared to basic science and was the least frequent type of paper. Fish and Primate papers had the most citations out of taxonomic groups.

It is perhaps not surprising that husbandry evidence and animal welfare are key reasons for SNA studies to be conducted on ex situ populations, given the direct benefits. Also, given the increased scrutiny of zoo animal welfare states by professionals and zoo visitors alike (Maple & Perdue, 2013; Sherwen & Hemsworth, 2019). Unsurprisingly, primates are common subjects for zoo-based social networks research, with 46 papers (44%) in our sample focused on this taxonomic group. Given the complexities of their social systems and similar evolutionary relationships to humans, social network techniques can be easily transferred over to non-human primate research.

4.1 | Future directions of ex situ SNA research

Our results show the need for more ex situ SNA across taxa and its application to conservation. Studies of SNA in captive populations can be directly informative to the management of wild populations. For example, investigating social composition over resources and shared space can be important for understanding disease transmission. Such research has practical application for both captive management and conservation. Balasubramaniam et al. (2018) used SNA to investigate pathogen transmission in a captive population of rhesus macaques (*Macaca mulatta*), with results that support the idea that social communities act as bottlenecks by reducing the distribution of infectious agents in a population. Central or highly connected individuals can act as a “super-spreaders” of infection (Balasubramaniam et al., 2019) and therefore affect the health and welfare of close associates. As such, captive studies using SNA can directly inform disease control strategies in wild populations, which may be relevant for zoonosis in ecotourism (Muehlenbein et al.,

	Estimate	SE	z value	Pr(> z)
Implication topic				
Basic science (intercept)	3.038	0.270	11.23	<0.0001
Husbandry evidence	-0.457	0.482	-0.95	0.343
Animal welfare	-0.815	0.410	-1.99	0.047
Population management	-1.032	0.825	-1.25	0.210
Conservation evidence	-3.080	1.088	-2.83	<0.005
Taxonomic group				
Bird	-0.216	0.432	-0.50	0.616
Carnivora	0.296	0.842	0.35	0.725
Cetacean	-1.406	0.845	-1.66	0.096
Chiroptera	-0.714	1.039	-0.69	0.491
Fish	0.878	0.818	1.07	0.282
Marsupial	-36.883	17,043,722.849	-0.00	1.000
Multiple	1.360	1.594	0.85	0.393
Proboscidea	-1.684	0.800	-2.10	0.035
Reptile	-36.883	17,043,723.084	-0.00	1.000
Rodent	-0.042	1.574	-0.03	0.978
Ungulate	-1.166	0.524	-2.23	0.026

Note: Estimates are reported on the log scale.

TABLE 2 Model estimates, SEs, Z value, and *p* values for significant output from a negative binomial regression with a log-link function, comparing the implication topics, taxonomy of study subject and cumulative citation score of each article

2010; Rwego et al., 2008), and help reduce disease spread in populations of conservation concern. SNA can also be used for assessing reintroductions by comparing preintroduction analysis in a captive environment and postreintroduction analysis in the wild environment. Franks et al. (2018) adopted this method for translocating hihi (*Notiomystis cincta*) and found that there was a significant tendency for higher mortality for translocated juveniles that lost the most associates.

For some species with limited captive social networks papers, more extensive literature on wild studies is available. For example, the giraffe features in numerous field-based social network papers (Bercovitch & Berry, 2013a, 2013b; Berry & Bercovitch, 2015; Carter, Brand, et al., 2013; Carter, Seddon, et al., 2013; Saito & Idani, 2017; VanderWaal, Atwill, et al., 2014; VanderWaal, Wang, et al., 2014), but we found only three papers that measure social preferences of captive giraffe over time, one with a networks approach (Lewton & Rose, 2019) and two without (Bashaw, 2007; Bashaw et al., 2007). The social interactions of wild giraffe are noted to be weaker when animals are exposed to more human interaction (Muller et al., 2019) and such social networks findings have relevance to captivity. If giraffe social behavior can be altered by human presence, and zoological collections are encouraging visitor interaction events with their giraffe (Orban et al., 2016), SNA research should be implemented to define any impact on animal-to-animal bonds with increasing contact with humans.

Using ex situ populations as research models can help drive sustainable conservation initiatives (Traylor-Holzer et al., 2019).

Several species mentioned in the paper by Traylor-Holzer et al. (2019), pack-hunting canids and hyaenids, have highly complex social environments (such as the African wild dog, *Lycaon pictus*, and the bush dog, *Speothos venaticus*) and therefore make suitable candidates for SNA research. These authors also state that ex situ populations can help mitigate primary threats to in situ populations via investigations into improving gene flow, reproductive success and the survival of life stages, and these questions can be answered with a network approach. SNA is a preferable method due to its quantitative approach and ability to easily analyze changes over time, therefore it should be at the forefront of scientists' minds when answering conservation questions, such as why a species is not breeding at sustainable or viable levels.

4.2 | One plan and SNA: Promoting ex situ behavioral study and conservation in the zoo and beyond

This case study focused on SNA related research, but the lack of conservation implications is likely a general trend across all types of zoo research. Most zoo research is based on welfare or husbandry questions as those are immediate concerns of zoos (Binding et al., 2020). However zoo animals can have a real role in promoting the three scientific aims of the modern zoo (education, conservation, and research) (Rose, 2018). One way to achieve the One Plan Approach,

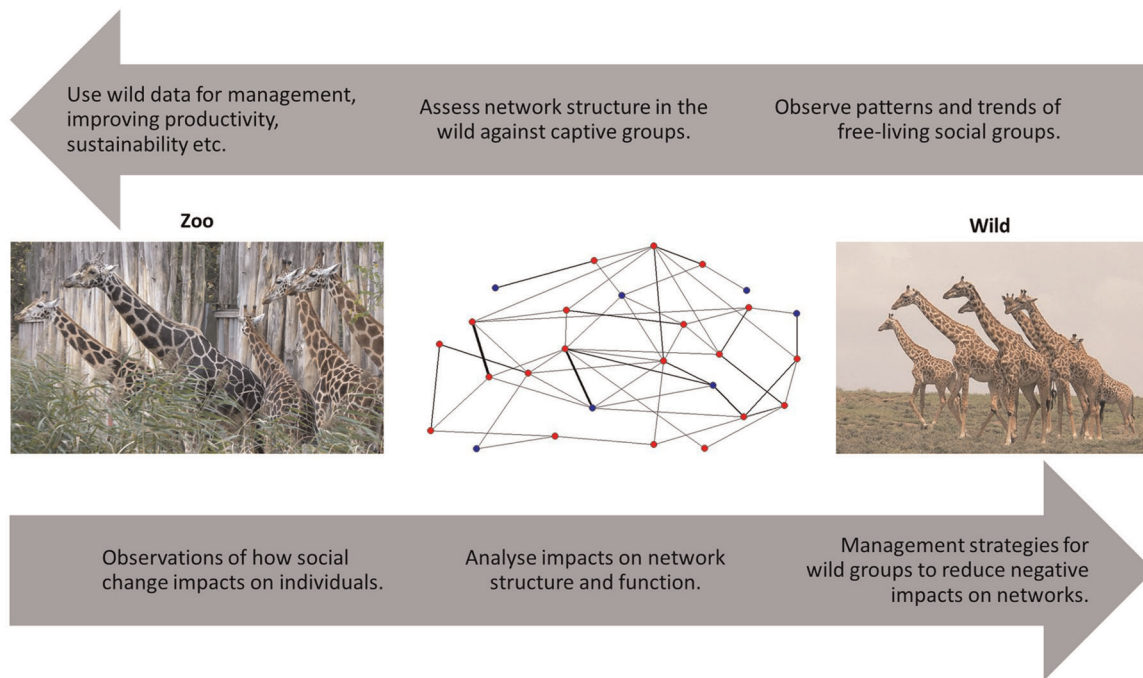


FIGURE 3 Use of zoo animal studies can inform conservation action in the field by assessing social network changes with alterations to physical or social environment. Species-appropriate social groupings can be created based on comparative wild data, to ensure ex situ population sustainability, appropriate breeding rates and lifespan of zoo-housed animals. Photo credits: P. Rose & Wikimedia Commons [Color figure can be viewed at wileyonlinelibrary.com]

is by integrating the zoo environment more into conservation projects. Some zoo animals have the potential to be the perfect test subjects for behavior research, with the ability to manipulate their environment and easy ways to record their behavior. Zookeepers and other zoo professionals can also help collect behavior data by adopting a research assistant role in projects. Collaborations with university-based research projects, will help address the research aim of their zoo and promote research career opportunities for their staff. Such collaborations can benefit project budgets by saving on time, expenses, and resources.

The One Plan Approach seeks a metapopulation management plan for animals in the field and in zoos (Conservation Planning Specialist Group, 2020). Figure 3 provides an example of the flow of information from ex situ animals to in situ animals and how SNA research in each population has implications for conservation. Work on the social relationships of wild flamingos acknowledge important social bonds (Diawara et al., 2014), and further research in captivity has revealed the presence of strong bonds can remain across years (Rose & Croft, 2018)—thus showing how knowledge of behavior in captivity can complement wild research for further ecological study. As wild animals become more heavily managed, and space restrictions caused by nature reserve boundaries, for example, limit carrying capacity, data from zoo studies on numbers to keep within a specific area and overall breeding rates are relevant to the management of these free-living (if constrained) individuals. Mills et al. (2014) explain in detail that a networks approach can bring together stakeholders to make effective conservation planning and implementation

of conservation action. These authors also note some of the challenges that using a network approach can face, such as understanding the changes in stakeholder networks and what roles are played by individuals.

5 | CONCLUSIONS

Overall, we found that Conservation Evidence is seldom used as a stand-alone implication for social network research using ex situ populations, whereas Husbandry Evidence, Animal Welfare, and Basic Science dominated this sample of SNA literature. Conservation Evidence based papers also received the lowest citations. We have explored the potential uses SNA research has for conservation, with a specific relevance to answering questions that can relate to implementation of a One Plan Approach. We have also provided examples of how research on ex situ populations can answer conservation questions in species that may be familiar, but seldom used as research populations in captivity. Therefore, our results suggest that conservation-relevant SNA studies in zoo settings are underutilized. SNA is expected to be relevant in future behavioral ecology and applied husbandry research and so we encourage an interdisciplinary approach, which involves more studies of in situ populations for conservation-relevant ex situ implications (e.g., breeding aims, population sustainability outcomes and best practice husbandry guidelines). Alongside these goals, behavioral ecology researchers should further consider the questions that can

be answered by using ex situ populations that would add evidence to wildlife management plans, our understanding of anthropogenic effects on wildlife and the importance of social groups for fitness and long-term population viability. We hope that this review encourages researchers to explore the application of SNA, together with other areas of the behavioral sciences, further. The current conservation crisis suggests that it is more important than ever for field researchers and zoo biologists to share methods and resources and collaborate in the successful implementation of conservation actions.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

Formal ethical review was not undertaken as data were taken from already published sources using a freely available data searching tool.

AUTHOR CONTRIBUTIONS

Methods were written by the Jack Lewton, and developed with advise and guidance from the Paul E. Rose plus information and feedback from colleagues with experience in structured literature reviewing and meta-analysis.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. The spreadsheet of raw data that includes all information on the articles collected for the literature is included as supplementary material.

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