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# Observing the unwatchable: Integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data

Jennifer E. Smith[1] 🆔 | Noa Pinter-Wollman[2] 🆔

[1]Biology Department, Mills College, Oakland, CA, USA

[2]Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA, USA

**Correspondence**
Jennifer E. Smith
Email: jesmith@mills.edu

## Abstract

1. In the 4.5 decades since Altmann (1974) published her seminal paper on the methods for the observational study of behaviour, automated detection and analysis of social interaction networks have fundamentally transformed the ways that ecologists study social behaviour.

2. Methodological developments for collecting data remotely on social behaviour involve indirect inference of associations, direct recordings of interactions and machine vision.

3. These recent technological advances are improving the scale and resolution with which we can dissect interactions among animals. They are also revealing new intricacies of animal social interactions at spatial and temporal resolutions as well as in ecological contexts that have been hidden from humans, making the unwatchable seeable.

4. We first outline how these technological applications are permitting researchers to collect exquisitely detailed information with little observer bias. We further recognize new emerging challenges from these new reality-mining approaches.

5. While technological advances in automating data collection and its analysis are moving at an unprecedented rate, we urge ecologists to thoughtfully combine these new tools with classic behavioural and ecological monitoring methods to place our understanding of animal social networks within fundamental biological contexts.

**KEYWORDS**

animal social networks, automated-sensing technology, behavioural methods, disease transmission, global positioning systems, reality-mining approaches, RFID readers, social behaviour

## 1 | INTRODUCTION

Since the time of Aristotle, humans have been observing the natural world from a distance. Such direct field observations are the historical basis for the now well-established field of behavioural ecology. Nearly 50 years ago, Altmann (1974) established a 'Rosetta stone' for the observational study of behaviour. In her paper, she outlined the most common methods used by behavioural ecologists and laid out the strengths and pitfalls of each. Altmann's paper has been the cornerstone of behavioural ecology research for the past 4.5 decades, as is evident by its nearly 16,000 citations (Google Scholar, 2020).

In recent years, rapid advances in automated sensing technologies have transformed how information about animal behaviour is collected. Examples of innovations include the use of monitoring systems and animal-attached devices (bio-loggers) to track animals' movements and social behaviour. Clearly, the availability of improved research methods, tools for obtaining data and the ability to relate observations to ecological and physiological processes have already transformed the field (Altmann & Altmann, 2003). On the 45-year anniversary of Altmann's (1974) seminal paper on the observational methods for the study of behaviour, the time is ripe for animal ecologists to reflect on the utility and integration of classic observational

methods, the use of new technologies and the incorporation of rapidly advancing analytical and computational tools.

Automated tracking offers opportunities to remotely quantify and study behaviour at scales that have not been possible previously (Dell et al., 2014). Bio-logging is broadly defined as the tracking of individual animals by attaching or implanting equipment to collect information about their identity, location, behaviour or physiology. These loggers include global positioning systems, accelerometers, video cameras and telemetry tags. The number and types of such bio-loggers have exploded in recent years (Dell et al., 2014; Williams et al., 2019; Wilmers et al., 2015). Specifically, these new tools allow monitoring of an animal's precise reaction to both its social and ecological environment (Amlaner & Macdonald, 1980; Evans et al., 2013; Krause et al., 2013; Ropert-Coudert & Wilson, 2005; Williams et al., 2019). These tools can improve the information available about the ecological drivers of individual differences in social decision-making, social interactions and emergent social structures. These tools have mainly been used to study population dynamics, movement ecology and conservation biology (Aikens et al., 2017; Block et al., 2011; Jacoby & Freeman, 2016; Merkle et al., 2016; Moll et al., 2007; Nathan et al., 2008; Patterson et al., 2008; Ropert-Coudert & Wilson, 2005). Recently, interest has increased in using technology to understand how animals construct and respond to their dynamic social environments (Figures 1 and 2).

Social network theory and machine learning have been instrumental in making connections between bio-logging technology and the study of social behaviour. Analysing the abundant data obtained from automated bio-logging of animals' behaviour requires dedicated analytic tools. Machine learning algorithms are starting to be employed to infer behaviour from movement data, including large movements across landscapes (Bastille-Rousseau et al., 2018), fine-motor movements measured with accelerometers (Hammond et al., 2016; Nathan et al., 2012; Williams et al., 2017) and a combination of both (Bom et al., 2014). Social behaviour can be inferred from remote-sensing tools, for example by inferring interactions through spatial and temporal proximity (Psorakis et al., 2012; Rutz et al., 2012; Ryder et al., 2012; Weihong et al., 2005). In some cases, the type of social interaction can be accurately inferred because of its duration and location. For example, when animals interact at a food patch, they can be inferred as co-feeding (Aplin et al., 2012; Chen et al., 2015; Tambling & Belton, 2009). Furthermore, direct food sharing can be quantified and detected automatically in some systems (Gernat et al., 2018; Greenwald et al., 2015). If the duration of an interaction between male and female tagged individuals is long, mating interactions can be inferred (Handcock et al., 2009; Hong et al., 2015; Psorakis et al., 2012).
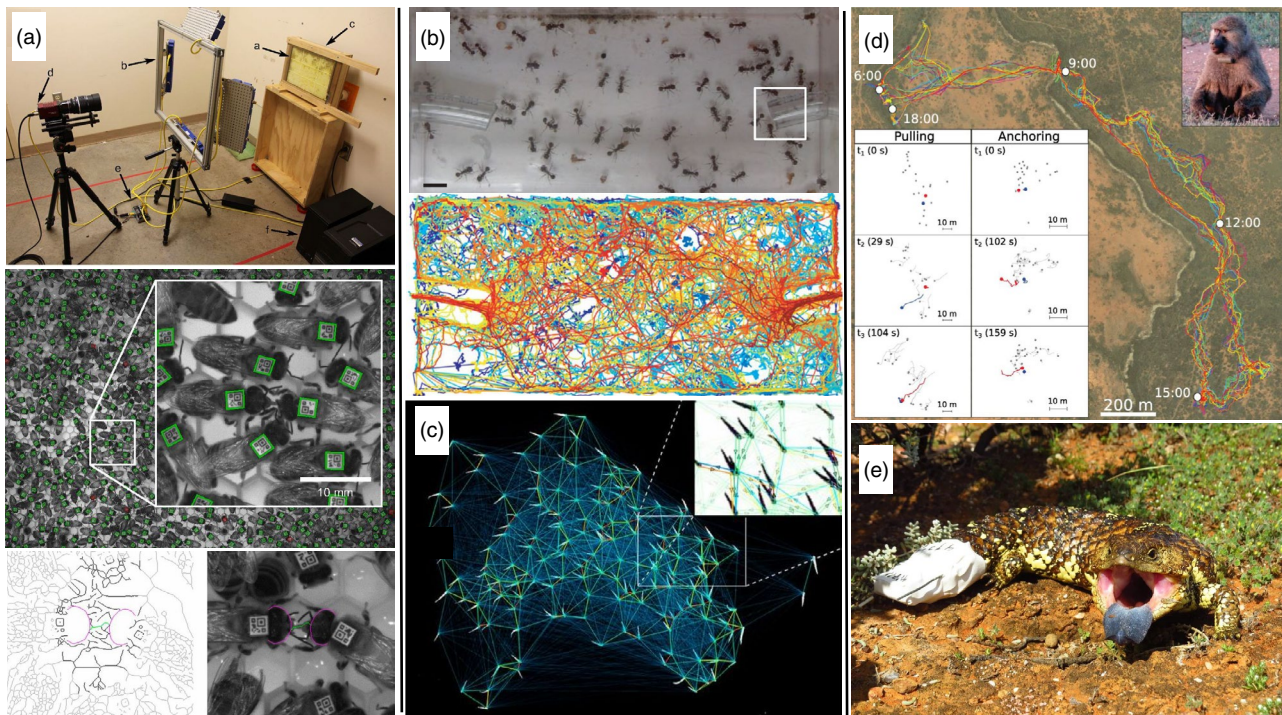


**FIGURE 1** High-throughput technologies are being used to monitor social phenomena, permitting for the observation of (a) 1.2 million social interactions among honeybees *Apis mellifera* within a single study (Gernat et al., 2018) [Copyright © 2018. Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND)], (b) previously hidden walking trajectories of red harvester ants *Pogonomyrmex barbatus* inside nests (Pinter-Wollman et al., 2011) (Reproduced with permission from the Royal Society of London), (c) sensory fields of fishes in moving schools *Notemigonus crysoleucas* (Rosenthal et al., 2015) (Published by PNAS. Reproduced with permission from Iain Couzin), and movements of mobile animals fitted with high-resolution GPS collars, including (d) baboons *Papio anubis* (Strandburg-Peshkin et al., 2015) (Published in Science. Reprinted with permission from AAA) and (e) sleepy lizards *Tiliqua rugosa* (Photo with permission by Orr Spiegel)
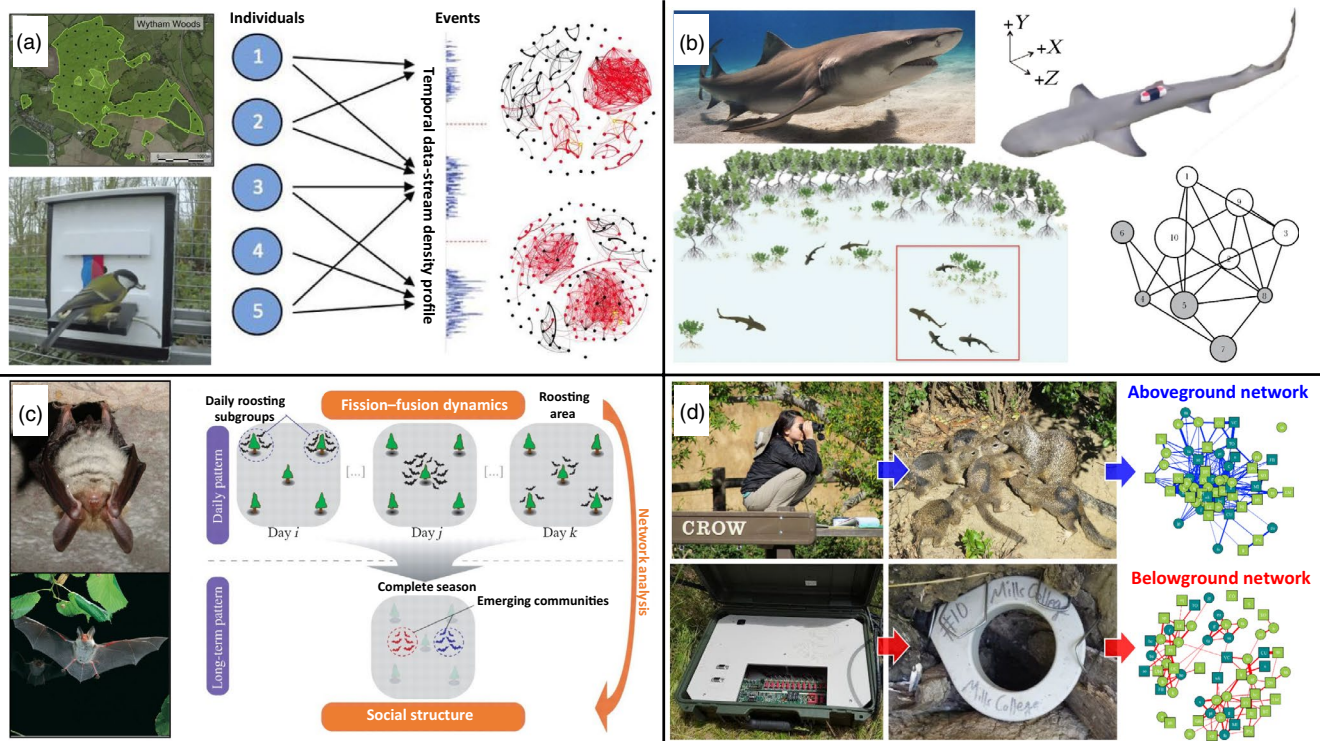
**FIGURE 2** Integration of naturalistic observations of behaviour, automated sensing and social network analysis is uncovering previously hidden phenomena. (a) RFID feeders track the diffusion of novel foraging techniques across social networks to document the persistence of culture via conformity in great tits *Parus major* (Aplin et al., 2015) (Published in Nature. Redrawn from original images with permission from Lucy Aplin). (b) Accelerometer tags reveal fine-scale patterns of leadership in lemon sharks *Negaprion brevirostris* as the sharks move behind coastal vegetation, which obscures direct observation (Wilson et al., 2015) (Reproduced with permission from Oxford University Press). (c) RFID readers at roosting sites reveal long-term social relationships of Bechstein's bats *Myotis bechsteinii* within their highly flexible social groups (Kerth et al., 2011) (Reproduced with permission from the Royal Society of London). (d) RFID readers combined with direct observations reveal that social network positions of individuals are consistent between two ecological contexts: aboveground and belowground in California ground squirrels *Otospermophilus beecheyi* (Smith et al., 2018) (Reproduced with permission from the Royal Society of London)

In other cases, spatiotemporal co-occurrences offer insights about the timing and directionality of dyadic interactions to reveal leadership in mobile primates (Strandburg-Peshkin et al., 2015) or sharks (Jacoby et al., 2016).

Social network analysis has been instrumental in analysing social data for the past decade (Pinter-Wollman et al., 2014; Sih et al., 2009; Webber & Vander Wal, 2019; Wey et al., 2008), including data obtained through remote sensing technology. Network analysis takes into consideration the entire social system rather than focusing on pairwise interactions as independent social relationships within a group, revealing group-level phenomena (Flack et al., 2006; Smith et al., 2010). This analysis can only be achieved with modern computational tools and hardware, which were unavailable 4.5 decades ago. Graduate students did not have personal computers, figures in papers were often hand-drawn, and one had to look up critical values in tables to make statistical inferences. The revolutionary technological advances since Altmann's, 1974 paper have allowed us to pursue with increasing tenacity the same basic interests in animal social behaviour that motivated Altmann's fundamental work.

Here we explore ways in which the 'bio-logging revolution' (Williams et al., 2019) combined with advances in social network theory offer underexploited opportunities for behavioural field studies. In doing so, we identify biological questions for future research as well as potential challenges associated with integrating these technological advances into our research programs. Our goal is to provide a guide for behavioural ecologists of the best practices for quantifying and analysing social behaviour, particularly with respect to the burgeoning tracking tools and social network analysis methods.

## 2 | AN AUTOMATED TOOLKIT FOR STUDYING SOCIAL BEHAVIOUR

Reality mining involves collecting and analysing social behaviour data by machines. Common tools include bio-logging and biotelemetry technologies for mapping animal associations (Hughey et al., 2018; Krause et al., 2013). We briefly outline these new methods for collecting data, particularly in the context of social behaviour. We then evaluate the extent to which these methods are fundamentally different from those used in classical observational studies of behaviour in terms of their spatiotemporal scales and specificity in detecting behavioural interactions. Methods for collecting data remotely on social behaviour involve three major forms of detection: (a) indirect

inference of associations, (b) direct recordings of interactions and (c) machine vision, defined as automated inspection and analysis of images (Figure 1).

Animal encounters may be detected indirectly from co-locations of animals based on the recording of spatiotemporal animal movements from animal-borne tags (Krause et al., 2013). Importantly, these methods infer social associations from the spatial and temporal proximity of individuals. Because animal-borne tags provide data remotely (via VHF radio, ultrasonic acoustic telemetry, transmission of GPS data via the cellular network, etc.), they allow for the monitoring of animals with minimal disturbance (Tomkiewicz et al., 2010). To date, these tags can lack the resolution or accuracy to detect fine-scale interactions on free-living animals. Pairing video recordings and bio-logging data can help researchers to overcome these issues, as done to study hunting behaviour of tiger sharks (Andrzejaczek et al., 2019). Moreover, tags are constrained by a trade-off between their size and battery life that may lead to either high intensity monitoring over short periods or long-term monitoring with low sampling rates (Krause et al., 2013). The type of biological questions one is out to explore as well as the natural history and physiology of the study organism can help determine the duration and intensity of the remote sampling. For example, large-bodied animals that can carry large tags may be equipped with GPS loggers that record the position of animals in high spatial and temporal resolution for a substantial portion of their lives. GPS data can be downloaded remotely via the cellular network, or manually from the tags after they are retrieved from the animals; notably, the latter method of data retrieval is more invasive than the former. Additional recording devices can be added, including accelerometers, audio recorders and heartbeat monitors to augment the spatial data with behavioural, acoustic and physiological data (Williams et al., 2019). While these tags work particularly well for monitoring animals over large spatial scales and in open habitats, they can be expensive, limited by battery/memory size and potentially problematic in densely vegetated habitats and mountainous terrain (Hughey et al., 2018; Krause et al., 2013). They can also pose substantial challenges with respect to their needs for validation, calibration and management of devices (Brown et al., 2013). An alternative solution that does not require large tags is a radio frequency identification detection (RFID) system that detects passive-integrated transponder (PIT) animal-borne tags. These lightweight tags are inexpensive and small because they do not need to be powered with a battery or store information on board. Instead, the tag is activated when the animal passes near a tag-reader, which can be placed by a feeder (Evans & Morand-Ferron, 2019) or an entrance to a nest (Robinson et al., 2014) or burrow (Smith et al., 2018). RFID technology is suitable for tracking a large proportion of the population with little disturbance during data collection. However, it is limited in the spatial resolution because of the distances between the stationary tag-readers, which can result in missed detections of animal associations.

Direct social interactions may be detected remotely via proximity loggers that record tag-to-tag communication when they are in a certain range of each other (Böhm et al., 2009; Haddadi et al., 2011; Rutz et al., 2012). This method requires both interacting animals to wear tags. As stated above, tags are limited by the trade-off between their weight and on-board data storage and battery life. Furthermore, proximity tags require extensive calibration to ensure accuracy (Boyland et al., 2013; Ripperger et al., 2016), and tagging a large proportion of the population to obtain a substantial number of interactions can be costly. A major benefit of proximity loggers over other automated technologies is that interaction data can be inferred from individuals of known identities coming within a specified distance from one another (Krause et al., 2011). That said, recent advances in Unmanned Aerial Vehicles (UAVs, e.g. 'drones') could offer an exciting alternative to proximity loggers for social monitoring. UAVs may capture social interactions of all group members simultaneously with limited disturbance to the subjects (e.g. no tags or human presence). However, drones can be expensive to deploy and are not allowed in certain locations (e.g. national parks in the United States), thier tracking duration is limited by short battery life spans, their noise can interfere with animal communication, and post-processing of the data captured can be laborious and require elaborate and intensive computation. To date, research reliant upon drones mostly focuses on conservation questions, such as monitoring numbers of elephants (Vermeulen et al., 2013) or deer (Chrétien et al., 2016). Drones have captured the behaviours of social animals, including feral horses (Inoue et al., 2019; Ozogány & Vicsek, 2014) and whales (Torres et al., 2018). Going forward, we anticipate these tools to advance the study of the animal social networks.

Machine vision tools are creating opportunities for remote sensing of context-specific animal interactions at high spatial and temporal resolutions. First, automated video analysis is used to determine the position of animals and detect interactions (Weinstein & Ben Weinstein, 2018). Machine learning algorithms recognize the type, nature and context of the interaction (Robie et al., 2017). For reviews that detail the intricacies of machine learning and realty mining in animal behaviour, see Krause et al. (2013) and Valletta et al. (2017). Reviews that expand on interpreting accelerometer data provide information on specific algorithms, such as random forests (Fehlmann et al., 2017), simulations (Barkley et al., 2020) and decision tree methods (Nathan et al., 2012). Many of these machine vision tools have been developed for animals that are tagged (e.g. with two-dimensional barcodes in laboratory environments: Gernat et al., 2018; Greenwald et al., 2015; Heyman et al., 2017; Stroeymeyt et al., 2018; Figure 1a). Untagged animals may also be detected (Bozek et al., 2020; Gal et al., 2020; Hein et al., 2018; Pinter-Wollman et al., 2011; Rosenthal et al., 2015; Strandburg-Peshkin et al., 2013; Figure 1b,c). Furthermore, recent developments in drone technology and acoustic monitoring are bringing these machine-vision-based tools into the field; cameras deployed on drones can monitor the behaviour of animals in their natural environment (Torres et al., 2018). These approaches are extremely computationally intensive, and may require substantial time for tagging individuals. Moreover, long-term monitoring requires the hardware and software to store, access and analyse terabytes of image data. Still, the potential to obtain data

on both the location and timing of social interactions as well as the nature of the behaviour during, before and after the interactions, remotely, without disturbing the animals, is alluring.

In light of the bio-logging revolution and recent advances in social network theory, it is time to revisit the major observational methods outlined by Altmann (1974): (a) ad libitum sampling, (b) sociometric matrix completion, (c) focal animal surveys, (d) all-occurrence sampling, (e) sequential sampling, (f) instantaneous and scan sampling and (g) one-zero sampling. We consider the value added by automated approaches, as well as their shortcomings, by evaluating the limitations of traditional approaches, improvements due to automation and limitations of automation, for each sampling method (defined in Table 1); we exclude one-zero sampling from our table because of the inherent biases identified by Altmann (1974).

**TABLE 1** Revisiting Altmann (1974): Observational study of behaviour in the age of big data

| Sampling method[a] | Limitations of traditional approach | Improvements due to automation | Limitations of automation |
|---|---|---|---|
| **Ad libitum:** Opportunistic recordings of behavioural states or events without systematic constraints | The observer records only what they can see and what they think is relevant at a given time | - Continuous gathering of a diversity of behaviours, including those previously hidden (e.g. too subtle to detect or in hidden spaces)<br>- The spatial and temporal resolution of sampling has increased with automated sensing<br>- Interference to animals and bias about the relevance of the data collected have decreased | - Not all acoustic and visual information can be recorded<br>- Devices attached to animals are limited by their size, battery life, visual/auditory scope and budget |
| **Sociometric matrix completion:** Recording behavioural acts of dyads during direct observations in the field | Social network analysis has transformed the utility of sociometric matrices completion; these grids are the basis for most animal network analyses today | - Continuous data collection of large datasets over vast spatial and temporal scales increases opportunities for studying network dynamics<br>- Pairing of proximity loggers with on-board cameras and bio-loggers to track physiology could prove useful | - Most proximity loggers fail to quantify the nature of exchanges (e.g. asymmetric, friendly, agonistic) |
| **Focal animal surveys:** Collection of all states or events for one individual over time | A human must follow an animal and record all its behaviours; this is very time-intensive and produces data on only one individual at a time | - Permits for the recording of multiple focal individuals simultaneously over a variety of temporal and spatial scales<br>- Reveals sequential patterns, nearest neighbours and activity budgets at multiple levels of social organization<br>- Limits biases from human presence on behaviour | - While technologies may detect some behaviours that are too subtle for the human eye to observe, they can miss certain states or events (lack realism) |
| **All-occurrence sampling:** Collection of previously specified sets of events | Limited to a small subset of all possible behaviours at any given time | - Permit for recording and extraction of all behaviours in visual and/or audio range, including those that have not been previously identified<br>- Records data on multiple individuals at once<br>- Analytic improvements provide insights into the synchrony of collective behaviours | - Many automated methods are limited in their ability to distinguish among various ecologically relevant behaviours (e.g. grooming, coalition formation)<br>- Synergy between direct and automated methods can overcome these shortcomings |
| **Sequential sampling:** Recording all behaviours in the order of occurrence until the sequence ends | Method can introduce biases due to the way sequences are selected because observer must decide when to start and end collection of sequences | - High sampling throughput<br>- Standardizes detection of the timing of sequences through the continuous recording of multiple social interactions before they start and after they end | - Limitations in ability to distinguish among different ecologically relevant behaviours<br>- Synergy between naturalistic observations and automated methods can overcome these shortcomings |
| **Instantaneous and scan sampling:** Recording of activity or state at preselected time points | Collecting data at prescribed intervals misses behavioural acts that transpire between samples | - Continuous collection of data allows for subsequent data filtering into scans as needed (e.g. using machine learning algorithms) | - Difficulties in distinguishing among different behaviours<br>- Scan sampling could be used to increase battery life and space for data storage |

[a]One-zero sampling is excluded due to the inherent biases detailed by Altmann (1974).

## 3 | SOCIAL NETWORK ANALYSIS OF HIGH-THROUGHPUT DATA

Social network theory offers a powerful suite of statistical tools to model and predict the influence of salient ecological parameters (Farine & Whitehead, 2015; Jacoby & Freeman, 2016; Pinter-Wollman et al., 2014; Sih et al., 2009, 2017; Wey et al., 2008). Although network analysis offers the potential to disentangle multiple ecological drivers that underlie animal social behaviour, its implementation requires careful consideration, particularly with respect to hypothesis testing and statistical inference (Croft et al., 2011; Farine, 2013, 2017; James et al., 2009; Silk et al., 2017). Specifically, there is no single approach for analysing social network data. Because of the interdependencies among individuals, comparing observed data to null models (also, referred to as reference models; Gauvin et al. (2018)) is a common approach. Reference models can be generated using a number of randomization procedures. The randomization procedures must be very carefully chosen and will depend on the biological question asked. Thus, while there are useful tools for conducting randomizations of animal social networks, they should be used judiciously to avoid testing hypotheses that are irrelevant to the biological system or question of interest.

Automated behavioural tracking systems provide new opportunities for studying social behaviour in different ecological situations (Williams et al., 2019), and at different temporal scales (Dell et al., 2014). The pairing of social network theory with information on the physical environment in which the interactions occur is offering new insights into these processes. Another such opportunity for technological synergy is the integration of multiple data streams on the physical environment, such as from light detection and ranging, e.g., NEON and satellite images, with social network and animal movement data (He et al., 2019; McLean et al., 2016). For example, a study of decision-making in wild baboons (Strandburg-Peshkin et al., 2015; Figure 1d) integrated information on habitat features with information on social interactions (Strandburg-Peshkin et al., 2015, 2017). Furthermore, a study of sociality in sleepy lizards integrated the effect of animal social movements with information on social interactions (Spiegel et al., 2017; Figure 1e). High-frequency multivariate data can be used to test hypotheses about the ecological and evolutionary contexts of social behaviour. For example, Markov chain Monte Carlo (MCMC) approaches offer a powerful means for analysing large, complex datasets (Handcock et al., 2007). Such advances will inform our understanding of the ecological forces that shape social behaviour and generate predictive models of social behaviour.

## 4 | CONFRONTING OBSERVER BIAS: NEW CHALLENGES AND OPPORTUNITIES

Traditional observational methods of behavioural data collection may generate biased samples by influencing the subject's behaviour, or due to observer biases (Altmann, 1974). Automated sensing of behaviour has the potential to mitigate these biases by standardizing data collection techniques and permitting data collection with little disturbance by the human observers (Table 2). Specifically, automated tracking permits the monitoring of undisturbed animals for long uninterrupted periods, offering clues to how animals react to each other and other features of their environment in real time (Cooke et al., 2004; Dell et al., 2014; Kabra et al., 2013; Ropert-Coudert & Wilson, 2005; Williams et al., 2019; Wilmers et al., 2015). It is worth noting that the presence of a tag on an animal may change a subject's behaviour (Coughlin & van Heezik, 2014) or its interactions with other individuals (Burley, 1986). GPS loggers, proximity loggers and accelerometers require catching the animals and attaching the device to them. Unless automated drop off mechanisms are available, researchers must recapture subjects to retrieve the tracking equipment. Drones may offer a less invasive alternative (Hodgson & Koh, 2016), especially if flown high with a telescopic lens as to not disturb subjects (Fettermann et al., 2019) or after a short habituation period (Ditmer et al., 2018). Second, automated methods facilitate the measurement of multiple variables at once, thus reducing the likelihood of missing measurements of previously unknown drivers of sociality. These new candidate variables may be used to parameterize social network models to partition out their relative effects on social processes and test meaningful hypotheses.

Automated tracking is not free of biases, and animal ecologists must carefully consider potential sources of new errors or biases introduced by automation (Table 2). Automated tracking can lead to statistical dependencies and require selecting appropriate statistical methods. First, automated methods could lead to statistical non-independence because of their capacity to record multiple streams of high-throughput data, particularly in systems for which movement patterns covary predictably with sociality (Albery et al., 2020). For instance, high-resolution proximity loggers reveal that two correlated behaviours—an individuals' social network position and ranging behaviour—explain epidemic outcomes in free-ranging domestic dogs (Wilson-Aggarwal et al., 2019). Second, each automated method must be carefully validated using naturalistic observations. For example, accelerometer data need to be validated with direct observations of the animals' behaviour to provide reliable training sets for the machine learning algorithms that later automate the inference of behaviours from accelerometer data streams (Hammond et al., 2016; Wikelski et al., 2007). Similarly, researchers must select biologically meaningful criteria for defining social network ties rather than deferring the definition of an interaction to the limits of the technology that is collecting the raw data (Psorakis et al., 2012). For example, a long range of a sensor or low sampling frequency might force a researcher to use larger spatial and temporal thresholds in their definition of interactions through spatiotemporal co-occurrence than would be relevant according to the sensory capacity of the species (Haddadi et al., 2011). Third, tracking technologies may be restricted to only a few individuals in a social group because tags are expensive or could harm the growth of juveniles. Thus, researchers may have a limited 'social resolution' of the group activity and be potentially limited in the scope of inference to the specific demography (e.g. adults) that is being tracked (Shizuka & Johnson, 2020; Spiegel & Pinter-Wollman, 2020). In other cases, sensors that require retrieval may be intentionally deployed on

**TABLE 2** Comparisons and synergies of classic versus automated tools for sampling behaviour

| | Most apparent Pro | Most apparent Con | Opportunities for synergies |
|---|---|---|---|
| **Classic, observational methods for the study of behaviour** | | | |
| Direct observations | High level of realism and cost-effective | Labour-intensive, observer bias in applying ethogram to subjects, low spatial and temporal resolution | Can augment automated data to provide an ecological and social context or to compare between contexts that are easily observed versus those hidden from observers using non-automated methods |
| **Automated tools for studying animal behaviour** | | | |
| *Location detection* | | | |
| GPS, VHS, satellite tags | Low observer bias | Expensive | Data acquired automatically can be augmented with direct behavioural observations to provide context; automated data may also augment direct observations of interactions with encounters in locations that cannot be accessed or seen by researchers |
| Passive tags | Relatively cheap | Low spatial resolution | |
| Proximity loggers | Remote sensing of contacts when animals cannot be observed directly | Low 'social resolution' because the cost and mass of units prohibit the tagging of all individuals in a population | |
| Image analysis | Little disturbance to subjects | Computation power required | |
| *Behavioural assignment* | | | |
| Accelerometers | Remote sensing of behaviours when behaviours cannot be directly observed, or observed at the desired scales, using traditional methods | Time required for validation; costs and mass of units prohibit the tagging of all individuals in a population | Increase sampling quantity and efficiency; allows inferring behaviours when animals cannot be observed directly to augment direct observations in other situations |
| Computer vision | Collection of high-throughput data of behavioural sequences with limited labour from humans | Time required for validation and computational processing time of large datasets | |

animals that are bold or easily captured. This biased tagging can lead to unintended dependencies on the personalities of the individuals that are being tracked. Such a bias in sampling might, for example, influence network studies aiming to understand how individual differences in behaviour shape social networks (Krause et al., 2010; Sih et al., 2009; Wilson et al., 2015). Fourth, researchers must be mindful of the duration over which tags remain active on animals because animals differ in how easy they are to locate or simply in the duration over which the tags remain on them. If such differences are not accounted for, animals that are tracked for longer durations might seem more central in a social network than others simply because of differences in the amount of data available for them (Spiegel & Pinter-Wollman, 2020). Finally, researchers must match the statistical tools they use to the tracking data they obtain. For instance, using statistical tools developed for continuous data might not be appropriate for discrete data and vice versa.

Computer simulations can aid in assessing different biases for data collected from direct observations and when using automated methods. Such simulations can uncover the extent to which social networks are affected as a result of different biases and different sampling methods and efforts (Aguiar et al., 2018; Davis et al., 2018; Silk et al., 2015). Simulations are often used by ecologists to estimate bias in abundance calculations, such as when using acoustic monitoring (Balantic & Donovan, 2019), but are still an underutilized tool in social network studies. For example, simulations uncovered that telemetry data can result in overly connected networks and create biases in global and node-level network measures (Gilbertson

et al., 2020). One useful approach is to compare the robustness and certainty of animal social network measures collected via direct (e.g. human observers) and automated (e.g. high-resolution GPS collars) methods (Davis et al., 2018). Such comparisons must be done carefully because networks constructed based on different methods are not always comparable (Castles et al., 2014). Moreover, when the goal is to infer social interactions from spatiotemporal proximity, researchers must keep in mind that interactions may result from the joint use of resources, rather than from social preference, when data are explicitly linked to ecological information (Spiegel et al., 2016). Researchers may use spatial information about resources and associations to tease this apart (Spiegel & Pinter-Wollman, 2020). Furthermore, simulations may be useful to disentangle whether spatial constraints or social preferences are the drivers of the social associations using agent-based models (Pinter-Wollman, 2015), gregariousness-corrected association indices (Godde et al., 2013) or permutations of movement data (Spiegel et al., 2016).

## 5 | INTEGRATING THE BEST OF TWO WORLDS: DIRECT OBSERVATION AND AUTOMATED DATA COLLECTION AND CLASSIFICATION

Altmann (1974) recognized the value of sampling using more than one method in a study. She suggested that samples may be taken

successively, under favourable conditions, or even concurrently. Use of these standardized methods for direct observation by human observers has yielded numerous long-term datasets that have greatly contributed to our understanding of animal social systems, particularly for free-living mammals (Alberts, 2019; Hayes & Schradin, 2017; McDonald et al., 2018; Smith, Lehmann, et al., 2017). Automated-sensing tools extend these traditional approaches by permitting observation of social behaviours from the animal's perspective (Table 2). This is particularly useful for studying animals that socialize in spaces that are challenging to observe, such as in the ocean or terrestrial refugia (Figure 2). For example, tracking with RFID allows documenting phenomena that are otherwise hidden from human observers, including the diffusion of novel foraging techniques across social networks in the nests of great tits (Aplin et al., 2015; Figure 2a), long-term social relationships of Bechstein's bats across roosting sites (Kerth et al., 2011; Figure 2b), social monogamy in prairie vole nests (Sabol et al., 2018) and consistent social network traits of California ground squirrels aboveground and belowground (Smith et al., 2018; Figure 2d). Accelerometers are revealing fine-scale patterns of leadership in the social networks of lemon sharks when hidden behind coastal vegetation (Wilson et al., 2015; Figure 2c). Similarly, acoustic telemetry data permit tracking marine fishes (Finn et al., 2014) or marine predators (Williams et al., 2018) whose social networks would otherwise be challenging to observe. In these ways, automated tracking tools are particularly valuable in that they offer opportunities to overcome long-standing and widely recognized methodological issues (Altmann, 1974) associated with the study of secretive, cryptic and/or highly mobile free-living animals. For example, in wildlife conservation, ecologists combine the use of automated acoustic monitoring and occupancy modelling of species; this combination improves detection while reducing false-negative detections (Campos-Cerqueira & Aide, 2016). Integration of automated and manual classification could reduce biases in the study of social behaviour. Even in controlled laboratory settings, integration of direct observations, image analysis and social network tools is sometimes required to reveal otherwise hidden information (Fewell, 2003; Mersch et al., 2013; Pinter-Wollman et al., 2011; Stroeymeyt et al., 2018). For instance, combining insights from automated tracking, controlled pathogen exposure, transmission quantification and simulations revealed that infected animals socially isolate themselves from the group (Gernat et al., 2018; Stroeymeyt et al., 2018). Notably, these behaviours were only apparent when researchers implemented a combination of many tools.

Social network analysis of data collected from animal-borne sensors can improve our understanding of processes that are challenging to quantify or visualize due to their elaborate or dynamic nature (Blonder et al., 2012; Pinter-Wollman et al., 2014; Silk et al., 2018). Recent advances include uncovering the ecological drivers of associations (Cross et al., 2013), factors stabilizing cooperation (Patzelt et al., 2014) and covariates of disease transmission within (Craft, 2015; Hamede et al., 2009; Silk et al., 2017; Stroeymeyt et al., 2018; White et al., 2017) and between species (Böhm et al., 2009). Furthermore, multilayer network approaches now allow for the integration of ecological and social processes into a single framework (Silk et al., 2018)

and for combining behaviours in different situations and across time (Finn et al., 2019). When integrating direct observations and automated data collection, one should keep in mind potential associated pitfalls. For example, automated acquisition and direct observations may occur at different times (e.g. night and day) and/or locations (e.g. near a field site or in a remote location that is challenging to reach). The different types of data can further be recorded at different temporal and/or spatial resolutions. For example, automation might record events every second while observations might be recorded only every few minutes. If one chooses to combine measurements that are collected at different temporal resolutions, they might need to aggregate or subsample the automated measures. Alternatively, one could use both types of measurements to learn about different aspects of the system and keep their statistical analyses separate.

# 6 | NEW OPPORTUNITIES AND UNANSWERED QUESTIONS: A PATH FORWARD

Advances in bio-logging science have offered remarkable insights into understanding locomotion, feeding behaviour, energy expenditure, physiological thresholds and other biological processes (Evans et al., 2013). Animal-borne sensors and remote sensing data about the environment could uncover new insights on animal sociality (Table 3). Although rarely paired with the study of social behaviour, bio-loggers can provide information on behaviour (e.g. foraging, grooming, etc.), heart rates and body temperatures of recognizable individuals over time (Le Grand et al., 2019; Wassmer & Refinetti, 2019). The value of this added information is especially evident when combined with tracking technology that offers high-resolution spatial data (Kays et al., 2015; Krause et al., 2013). Combining information from multiple sources of automated monitoring systems can be challenging, as detailed in Table 1 in Krause et al. (2013). To date, multi-modal data on free-living animals have been underutilized to test hypotheses about social behaviour. Within the context of social networks, data on contacts among animals may be integrated with knowledge about ecological context, physiological state of individuals and acoustic information. For example, multilayer network approaches could offer insights about how the relationship between microhabitat features and social connections influences group dynamics (Finn et al., 2019).

Sensors of animal physiology can track socially relevant biomarkers to address the largely understudied proximate mechanisms of social network structure (Croft et al., 2016). For instance, heart-rate monitors can reflect states of arousal (Wascher et al., 2008) and responses to social (Viblanc et al., 2012) and non-social (Ditmer et al., 2018) stressors. These devices could be paired with proximity loggers to track real-time physiological responses to social interactions. Although limited examples link social behaviour to these on-board measures, monitors have revealed significant increases in the heart rates of greylag geese in social versus non-social contexts (Wascher et al., 2008). In naturalistic settings,

**TABLE 3** Classic versus automated tools for sampling non-behavioural traits of subjects and their environments

| | Most apparent Pro | Most apparent Con | Opportunities for synergies |
|---|---|---|---|
| **Classic methods:** *Biological samples and measures collected directly from animals* | | | |
| Blood and tissue | Provides ample physiological data on immediate hormonal status and for genetic analysis | Labour-intensive, invasive sampling (e.g. requires live capture of subjects) | Direct measures of hormonal levels, gene expression, physiological state, body condition and growth have the potential to provide proximate explanations for data collected using automated methods and/or direct observations |
| Faecal samples | Minimally-invasive sampling of glucocorticoid metabolites, microbiome; provides long-term insights into physiological status | Labour-intensive, provides metabolized version of hormones and microbes of interest, both of which may degrade between time of deposition and processing | |
| Mass and body measurements | Direct and simple measures | Limited information | |
| **Automated methods:** *Animal-borne sensors, image capture and high-throughput environmental sampling* | | | |
| *Sampling of non-behavioural traits of subjects* | | | |
| Animal-borne sensors (e.g. heart rate/temperature monitors, magnetometers, accelerometers, light sensors) | Real time and accurate data with little disturbance to subject | Deployment and recapture of units could be invasive; cost and mass prohibit tagging all individuals in a population | Provide proximate explanations for location data collected automatically and/or direct observations |
| Indirect measures of body size or growth (e.g. photogrammetry, image analysis) | Permits for measurements of animals from a distance and without capture using photographs and/or lasers | Validation required to connect measures of growth to measures of maturity and health; expensive and still labour-intensive | Can offer insights into life-history stage of animals observed |
| *Sampling of the external environment* | | | |
| Data on the physical environment (e.g. image analysis, weather sensors) | High spatial and temporal resolution with limited disturbance to subjects | Computation power required | Provide ecological context for both remotely sensed data and direct observations; May be collected remotely and independently from the subjects that are being monitored |

animal-mounted physiological sensors can provide opportunities for investigating natural environmental perturbations to study how ecological processes, such as drought, shape—or are shaped by—social processes (Henzi et al., 2009; Holekamp et al., 2012; de Silva et al., 2011; Smith et al., 2018). Internal temperature loggers could offer new ways to examine how social integration buffers mammals from environmental stressors, such as thermal stress (Young et al., 2014). Skin-associated patches are being developed to track physiological variables, including cortisol to monitor stress reactivity in humans (Lee et al., 2016). These tools could also elucidate the physiological mechanisms triggering prosocial and antisocial behaviours in natural settings (Montgomery et al., 2018; Smith, Petelle, et al., 2017). Applications of these technologies to free-living animals could offer insights into real-time reactivity—as well as accumulated physiological responses across the life span—to social and ecological stressors.

Recording devices such as microphones, accelerometers and light sensors can augment studies of social behaviour in ways that have not been explored yet. Microphones and other acoustic recording instruments can be used to investigate stressful environments. For example, while developmental 'stress' predicts network position in captivity (Boogert et al., 2014), evidence of a causal link between basal 'stress' and network attributes in free-living animals is mixed (Szipl et al., 2019; Wey & Blumstein, 2012). Animal-worn acoustic monitors and microphone arrays could offer insights into

the mechanisms that promote social interactions or disrupt cohesion. For example, vocalizations recorded may be associated with territorial defence, mate attraction, predator deterrence, foraging or group cohesion (Blumstein et al., 2011). Automated recordings can further provide insights on the spread of social information across networks. However, to date, only a few studies have integrated acoustic signalling with social network studies. Accelerometers could uncover energetic costs of social cohesion for mobile foragers. Light sensors, accelerometers and magnetometers (which detect an individual's position relative to the earth's magnetic field) could together map social networks hidden from observers because animals are below-ground or inside nests. For example, dead-reckoning, the calculation of an animal's positions using estimates of speed and course over time, is being used to track underground path use of a gregarious carnivore, the European badger, within its underground sett (Walker et al., 2015). Researchers could use graph theory to analyse overlapping paths of animals over time to reveal new information about their social lives in contexts previously hidden from observers.

## 7 | CONCLUSIONS

Recent technological developments are leading to an explosion in data streams that are available for the study of animal sociality.

Going forward, these advances offer numerous opportunities for collaboration among ecologists, behaviourists, physiologists, statisticians, mathematicians, physicists, engineers and computer scientists to apply new tools—grounded in classic natural history studies of animals—to address long-standing questions and motivate new ones about the complexity of animal social lives.

## AUTHORS' CONTRIBUTIONS

J.E.S. conceived of the idea for the article; J.E.S. and N.P.-W. wrote the manuscript jointly and approved the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

This manuscript does not contain data.

## ORCID

*Jennifer E. Smith* https://orcid.org/0000-0002-3342-4454
*Noa Pinter-Wollman* https://orcid.org/0000-0002-0448-8037

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