Review

Reality mining of animal social systems

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The increasing miniaturisation of animal-tracking technology has made it possible to gather exceptionally detailed machine-sensed data on the social dynamics of almost entire populations of individuals, in both terrestrial and aquatic study systems. Here, we review important issues concerning the collection of such data, and their processing and analysis, to identify the most promising approaches in the emerging field of 'reality mining'. Automated technologies can provide data sensing at time intervals small enough to close the gap between social patterns and their underlying processes, providing insights into how social structures arise and change dynamically over different timescales. Especially in conjunction with experimental manipulations, reality mining promises significant advances in basic and applied research on animal social systems.

Origin and potential of reality mining

The existence of 'digital footprints', which humans leave behind when they go about their daily lives in the modern world, has fundamentally changed the way in which human behaviour can be studied [1]. 'Reality mining' (see Glossary), which is one aspect of digital-footprint analysis, can be defined as the collection and analysis of machine-sensed data regarding human social behaviour with the goal of modelling behavioural patterns (*sensu* Eagle and Pentland [2]). Reality mining enables researchers to investigate the social behaviour of almost entire human populations, in extraordinary detail and with exceptional spatiotemporal resolution [2–4]. The sample sizes achieved by state-of-the-art human reality-mining studies are staggering. For example, more than 95% of the human inhabitants of most western countries carry and use mobile phones, Facebook currently has approximately 900 million users worldwide, and more than 400 million messages are posted on Twitter every day [5]. Tapping into these rich data sources provides unique insights into human daily activity patterns, the topology and dynamics of social networks, and the flow of information within and across populations [6,7]. In this review, we argue that, thanks to the advent and increasing refinement of a range of miniature tracking technologies, biologists will soon be able to emulate this powerful reality-mining approach in their studies of animal social behaviour and ecology, recording field data sets of unprecedented size and quality. This will progressively shift the focus from the challenges of data generation to issues concerning data management and analysis.

Systematic, disturbance-free observation of free-ranging animals is often difficult, or impossible, in species that have secretive life styles or live in inaccessible habitats. To overcome these constraints, field biologists are increasingly using miniature animal-attached tags that can aid in the remote collection of data about the movements, behaviour, physiology, and/or environments of animals [8–12]. Although reality mining in humans and animals differs in some fundamental ways (see below), basic research objectives and methodological approaches have much in

Glossary

Association matrix: quadratic matrix whose cells reflect association patterns between individuals.
Biologging and biotelemetry: use of miniature animal-attached tags for logging and/or transmission of data about the movements, behaviour, physiology, and/or environments of animals.
Global positioning system (GPS): satellite-based system that provides location and time information.
Hidden Markov model (HMM): a probabilistic model comprising an underlying stochastic process that is hidden and can only be observed through other stochastic processes that produce the observable output.
Logger: an electronic device (animal attached or field deployed) that collects, and subsequently stores, data.
Passive integrated transponder (PIT) tag: a small microchip that transmits its identification code when moved past a reader at a short distance.
Proximity logging: biologging system that enables the dynamic mapping of animal-to-animal distances, using animal-borne transceiver loggers.
Radio-frequency identification (RFID): a non-contact data transmission technology comprising a transponder (e.g., attached to an animal) and a receiver; passive transponders use the energy of the electric field of the receiver and have a smaller detection range compared with active, battery-powered transponders.
Reality mining: the collection and analysis of machine-sensed data pertaining to the social behaviour of animals or humans, with the goal of modelling behavioural patterns.
Received signal strength indicator (RSSI): RSSI values are recorded by proximity loggers and, following appropriate system calibration, can be converted into estimates of animal-to-animal distance.
Transceiver: an electronic device that can both transmit and receive information (usually, radio pulses).
Wireless sensor network (WSN): data collection system comprising fixed and/or roaming (e.g., animal-borne) transceivers ('nodes') that collect and exchange data through wireless radio transmission.

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common, and we see considerable potential for cross-fertilisation between these two young fields.

Instead of using traditional data-collection techniques, such as standardised resighting of a comparatively small sample of individually identifiable animals once per month, week, or day, a reality-mining approach employing cutting-edge, animal-borne technologies can be applied to entire local populations, enabling automated charting of individuals' daily activities and social associations with a temporal resolution of hours, minutes, or even seconds [3,13,14]. Such near-continuous and simultaneous sampling of social encounters for all individuals in a group or population provides the basis for comprehensive descriptive and predictive models of a range of dynamic processes in free-ranging animals, such as disease transmission, predator–prey interactions, information flow within and between populations, formation of social hierarchies, cooperation between individuals, and responses to sporadic ecological events (e.g., sudden changes in food availability). Importantly, for the first time, it will be possible to gather robust empirical evidence on how population-level social structure emerges from highly dynamic, individual-level associations, which is one of the major unresolved challenges in the field of animal social network research [15,16].

Here, we examine how a reality-mining approach can be applied to animal systems, discussing human case studies where appropriate. Reality mining integrates machine-based data collection, analysis, and modelling, and the scope and structure of our review reflects this combination of different sets of methodologies. In particular, we: (i) review the most promising tracking technologies for recording social behaviour and activity patterns in wild animals; (ii) discuss challenges posed by large tag-generated data sets, in terms of data screening and processing; (iii) highlight opportunities for modelling data sets with a range of analytical techniques; and (iv) illustrate the potential of reality mining in biological field research, by summarising recent breakthroughs with avian applications. To conclude, we identify several areas where a reality-mining approach could significantly advance our understanding of animal behaviour and ecology.

Data collection

Most reality-mining studies on humans opportunistically harvest data that are generated through subjects' natural use of omnipresent electronic devices or services, such as mobile phones, websites, or credit cards [5]. Such studies require careful processing of large, complex data sets, but biologists face the additional challenge of generating suitable data in the first place, by deploying tags on study subjects and subsequently recovering tag-generated information. In 'biologging' applications, data are stored in the internal memory of animal-borne loggers, and later retrieved through download from recovered devices or uplink transmission to receivers (Table 1). By contrast, in 'biotelemetry' applications, a signal from a transmitter is sent immediately to a receiver where it can be either stored or interpreted in real time by fieldworkers; telemetry systems are usually classified as 'active' (internal power source) or 'passive' (transmission induced by external readers). Terrestrial and aquatic animal-borne technology is based on the same basic rationale, although the mode of signal transmission and the specifics of device construction differ [12].

One of the key challenges of any study of animal social dynamics is to map association patterns, that is, the physical proximity of two or more individuals. Biologging or biotelemetry systems offer two main conceptual approaches to achieving this: encounters can either be recorded 'directly', with technology that enables animal-to-animal data exchange (one piece of information produces an encounter record), or 'indirectly', with technology that charts the spatiotemporal positions and movements of individual animals (two pieces of information are combined to produce an encounter record; Table 1). Direct encounter mapping uses animal-borne proximity loggers (for a review of available systems, see footnotes to Table 1), which unlike conventional telemetry tags (terrestrial, VHF radio-telemetry [17]; aquatic, acoustic telemetry [12], Figure 1), have dual functionality, acting both as transmitters and receivers of coded signals (hence the synonym 'transceiver tag')[*]. Whenever two tagged animals come within reception range, their tags record the encounter in reciprocal date-, time- and ID-coded log files, a process some researchers have likened to the swapping of business cards when humans meet (hence, the second synonym 'business card tag'; [18]). In some (terrestrial) systems, tags record the strength of received radio pulses as 'received signal strength indicator' (RSSI) values, which are converted into an estimate of animal-to-animal distance at the data-analysis stage, using an appropriate calibration curve; this conversion is based on the basic premise that, all else being equal, animals in close proximity should exchange comparatively stronger radio signals than animals that are farther apart (Box 1). Logger data can be retrieved through field-deployed wireless sensor networks (Box 1; for a review of alternative methods, see Table 1).

Indirect encounter mapping, which is currently used more frequently, can be conducted (for details and further references, see Table 1) either with tags that enable the recording (with a specified sampling rate) of the unconstrained movement trajectories of animals (terrestrial, VHF radio-telemetry [17] or global positioning system (GPS) logging [19,20]; aquatic, mainly acoustic telemetry [21–24], Figure 1), or systems where fixed receivers detect the visits of animals to specific localities within a study area (coded radio tags [25–27], acoustic tags [21], and passive integrated transponder/radio-frequency identification (PIT/RFID) systems [28–32]). The former approach generates independent data sets that are integrated at the analysis stage, whereas the latter produces temporal records of co-location (Box 2).

The choice of biologging or biotelemetry technology is affected by a multitude of general trade-offs (Table 1), as well as by study-specific research priorities and constraints. Although under most circumstances, direct encounter mapping will generate richer and more accurate association data sets than will indirect approaches, this

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[*] The proximity-logging principles outlined here are not limited to radio or acoustic transmission, and future applications may use other communication technologies.

technology is not yet suitable for all study systems and research contexts. For example, even the smallest available proximity loggers (terrestrial: *ca.* 9 g [14]; aquatic: *ca.* 30 g in air [33]) are still considerably larger than passive transponders [28], and their long-term utility is severely constrained by their limited battery lifespan (several weeks to months, depending on battery size [14,33]). Furthermore, in its most basic form, direct encounter mapping does not provide geospatial referencing of association data, so in studies that seek high-resolution movement data (e.g., for hidden Markov models (HMMs); see below), other technologies (e.g., GPS logging in terrestrial applications) are preferable, unless a high-density grid of fixed receiver stations can be deployed for cross-triangulating roaming proximity loggers [14,34]. The latter approach illustrates that there are no absolute boundaries between the two major conceptual approaches (direct versus indirect encounter mapping) and that technologies can sometimes be combined effectively in a single application [34,35].

Table 1. Basic functionality, advantages, disadvantages, and deployment examples of different biologging and biotelemetry technologies for mapping animal associations

Technology	Habitat[a]	Concept	Pros[b]	Cons[b]	Application examples
Direct encounter mapping					
Proximity logging (radio)[c]	T	Animal-borne transceiver loggers; tag-to-tag communication during social encounters; data retrieval through tag recovery, or wireless transfer to field-deployed receivers (fixed or handheld)	Very high sampling rates; reliable recording of ‘zero’ edges in social networks; spatially unconstrained; reciprocity (each encounter is recorded independently by each participating tag); basic loggers can be adapted to relay additional sensor information (e.g., video or audio); no or minimal human disturbance during data collection	Expensive; depending on size, tags can be severely battery and/or memory limited; laborious field calibration for robust conversion of RSSI values into estimates of animal-to-animal distance; in most basic configuration, no geospatial information	Social dynamics in zebras [79]; mating in cattle [34]; potential for disease transmission in possums [80], Tasmanian devils [81], badgers/cattle [55,82,83], and rabbits [84]; detection of lion kills [85]; and social networks in crows [14]
Proximity logging (acoustic)[d]	A	As for terrestrial proximity logging	As for terrestrial proximity logging	As for terrestrial proximity logging	Social dynamics in sharks [18,33]
Indirect encounter mapping					
VHF radio-telemetry	T	Animal-borne radio-tags (transmit only); mapping of spatiotemporal animal movements with handheld receivers or fixed receiver towers (for automated cross-triangulation)	Small tags with good battery lifetime; in some study systems, opportunities to collect behavioural data for social encounters (through ‘homing in’ and direct observation of tagged animals)	Very low sampling rates; labour intense (manual tracking) or costly and logistically challenging (fixed receiver towers); in case of manual tracking, risk of disturbing tagged subjects; comparatively large location error (often several tens of meters)	Potential for disease transmission in rodents [86]
Ultrasonic acoustic telemetry	A	Animal-borne acoustic tags (transmit only); mapping of spatiotemporal animal movements with fixed hydrophones arrays (for automated cross-triangulation)	Comparatively small tags; no or minimal human disturbance during data collection; very high burst rates of few seconds	Expensive and logistically demanding hydrophone array; requires sophisticated data processing; macrophytes and noise environments limit data quality; in some commercial systems, code collisions limit the number of animals that can be tracked	Positional telemetry, habitat association, and movements in fish [22–24,56,57]
Coded VHF radio-tags (fixed receivers)	T	Animal-borne radio-tags (transmit-only); fixed receiver stations record the presence of tagged animals at selected locations	Small tags with good battery lifetime; reliable data collection at sites of research interest (e.g., nests, leks, or foraging sites); no or minimal human disturbance during data collection	Data collection spatially constrained (i.e., only at receiver stations); laborious field calibration	Lekking in manakins [25,26][e]
GPS tracking	T[f]	Animal-borne GPS loggers; satellite-based mapping of spatiotemporal animal movements; data retrieval through logger recovery, satellite uplink, or wireless transfer to field-deployed receivers (handheld or fixed)	High-resolution spatiotemporal mapping; spatially unconstrained; no or minimal human disturbance during data collection	Expensive; depending on size, tags can be severely battery and/or memory limited; not suitable for densely vegetated habitats (loggers require clear ‘view’ of the sky, and can sometimes have surprisingly large location errors)	Social dynamics in sheep [87]

Table 1 (*Continued*)

Technology	Habitat[a]	Concept	Pros[b]	Cons[b]	Application examples
PIT/RFID technology	T and A	Animal-borne (or implanted) tags; fixed readers record the presence of tagged animals at selected locations	Very small tags (<<1 g); inexpensive and, therefore, suitable for large-scale studies; excellent tag lifetime (theoretically unlimited for passive tags); no or minimal human disturbance during data collection	Very short reading distances (usually <1 m); relatively high rate of missed detections (e.g., when two or more individuals are present at the same time only one gets registered); data collection spatially constrained (only at reader locations)	Social dynamics in cattle [88] and badgers [89]; pair formation [28] and food-patch discovery [29] in great tits; and boldness in fish [90]

[a] Abbreviations: A, aquatic; T, terrestrial.

[b] Advantages and disadvantages of certain technologies inevitably vary with study-specific constraints, including: (i) size of the study species (and, hence, permissible tag mass; large tags are usually less battery and memory limited); (ii) behaviour of the study species, and topography and/or habitat of the study site; and (iii) project budget.

[c] Independently developed systems: *MateID* [91,92], *ZebraNet* [79,93], *encounter* from Sirtrack Ltd. [94], *EcoLocate* [35], and *Encounternet* [14].

[d] Commercially available systems: 'businesscard tags' from Vemco [18] and *ARX* from Sonotronics Inc. [33].

[e] Ryder *et al.* [26] used animal-borne coded VHF radio-tags that are detected by field-deployed fixed receiver stations. Although they referred to their system as 'proximity logging' technology, we suggest that this term remains strictly reserved for applications with tag-to-tag communication and (temporary) data storage in on-board tag memory.

[f] GPS devices have been used on aquatic species [10], but require animals to 'surface' for the generation of fixes. For this reason, they can be used for mapping movements, but are generally unsuitable for mapping social associations.

A major limitation of both direct and indirect encounter-mapping technologies is that they can only detect the physical proximity of tagged animals, but provide no contextual information for these encounters. In other words, it remains unknown whether the animals 'interacted' with each other (rather than passing by passively) and, if so, what the nature (i.e., affective or antagonistic) and biological context (e.g., allogrooming, mating, fighting over resources, or observing foraging behaviour) of these interactions was. Rapid technological progress means that tags will soon become available that can record such information with a multitude of additional on-board sensors [10]. For example, basic proximity loggers could be fitted with miniature video cameras [36–41] or microphones that directly record the behaviour of animals during social encounters [42], or with accelerometers that provide proxy measures of behavioural states [43–45]; other sensors could enable the real-time measurement of physiological processes [8], such as hormone levels or even brain activity [46]. Obtaining these additional data layers will contribute considerably to the productive implementation of some of the analytical approaches outlined below (HMM; see below and Box 3).

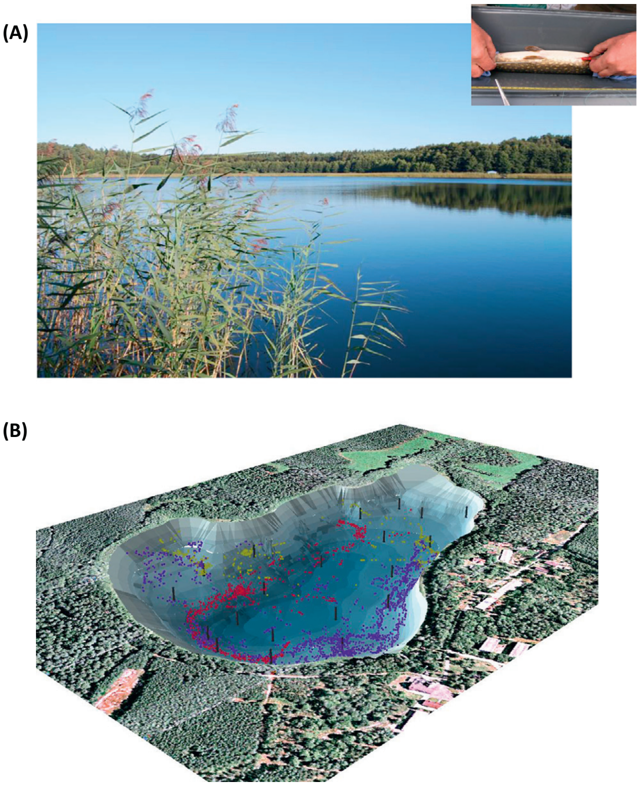

Figure 1. Whole-lake acoustic array. **(A)** The Kleiner Döllnsee, a natural lake in Brandenburg, Germany, was equipped in 2009 with a whole-lake acoustic array that enabled high-resolution positional telemetry by hyperbolic triangulation; surgery was used to insert tags into the body cavity of northern pike (*Esox lucius*). **(B)** A series of 20 hydrophones (black vertical symbols) enabled the 3D tracking of a large number of individual fish (visualised by coloured data points). Reproduced, with permission, from David March Morla (B).

For the following reasons, proximity logging is likely to become the method of choice for reality mining in wild animals (cf. Table 1; Box 1): (i) high quality of association data; (ii) recent advances in tag miniaturisation (and likely further improvements of tag lifespan); (iii) high tag functionality; (iv) effective automated data collection; and (v) scope for integrating complementary sensors (e.g., GPS for detailed movement information in terrestrial systems, and/or video or accelerometers for behavioural context). Proximity logging is a cutting-edge methodology that requires commitment of considerable financial and other resources for successful calibration and field deployment, but it has the potential to change fundamentally the way in which social associations in free-ranging animals can be quantified.

Data analysis and modelling

Although enormous tracking data sets can accumulate with relative ease (Box 1), detecting biological signals of interest

Box 1. Reality-mining studies in birds

The first study to achieve direct encounter mapping in a wild bird population examined social network dynamics in New Caledonian crows (Figure IA [14]), a species renowned for its use of complex foraging tools [95]. The researchers were particularly interested in social interactions between nonfamily birds, because horizontal or oblique transmission processes could have an important role in the 'cultural' accumulation of tool-related information. In total, 41 crows, a large proportion of the study population, were fitted with miniature proximity loggers ('Encounternet'; contact: John Burt, Washington University, Seattle, USA), which emitted ID-coded radio pulses every 20 s while continuously 'listening' for other nearby tags. Using 45 tree-mounted fixed receiver stations, data were harvested remotely from roaming loggers, enabling near real-time charting of association patterns [14]. Importantly, because loggers recorded uncensored RSSI values, the researchers were able to subsample their data set at the analysis stage according to estimated animal-to-animal distances, producing 'close-range' (birds within *ca.* 5 m of each other) and 'wide-range' (within *ca.* 20 m) networks that correspond to distances over which different social-learning mechanisms would operate (e.g., direct observational learning versus local enhancement). Analysis of approximately 28 000 encounter logs for 34 individuals over the first 7 days of a 2-month data-collection period revealed a substantial degree of close-range association between nonfamily birds as well as potential for rapid information flow in the network.

Indirect encounter mapping was implemented on a scale that fits our definition of reality mining by a study on social dynamics in great tits and other woodland passerines in Oxfordshire, UK (Figure IB [28,29,96]). Using ID-coded PIT tags attached to the rings of hundreds of birds, and a dense grid of RFID readers mounted near experimental bird feeders, the researchers amassed many thousands of time-stamped bird location records. Using techniques explained in Box 2, dyadic association metrics were derived from co-occurrence patterns at readers and subsequently used to conduct a range of analyses within a social network framework. Even during its early stages, this ongoing study has shed light on processes that had hitherto remained difficult to study in small birds, such as the formation of pair bonds [28], the discovery of novel food patches [29], and the structure and dynamics of mixed species flocks [96].

These two studies, as well as pioneering work using coded radio-tags in conjunction with stationary receivers (for the automated investigation of lekking in manakins [25,26]), illustrate the potential of a reality-mining approach for advancing understanding of social dynamics in wild bird populations, especially when combined with experimental manipulations [29].

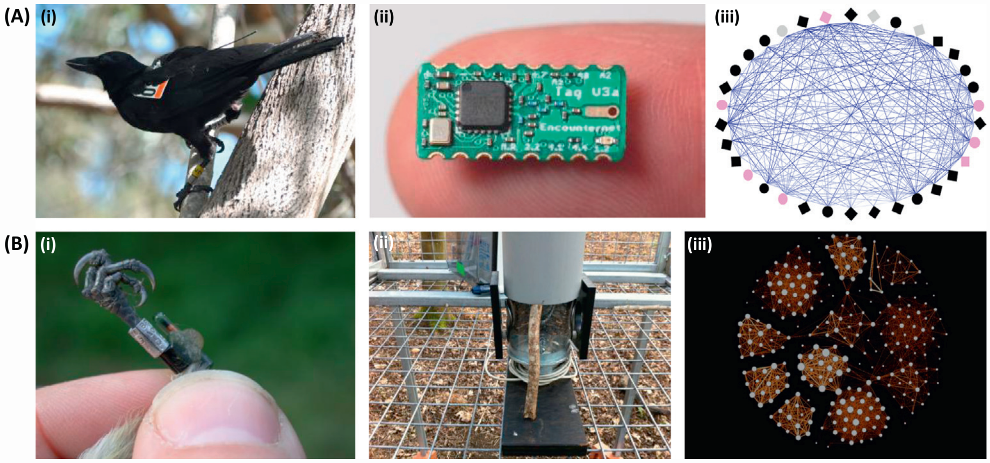

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Figure I. Social networks in birds. **(A)** A New Caledonian crow [14] fitted with a harness-mounted miniature proximity logger (i), the miniature transceiver board of a crow proximity logger (on finger tip for scale) (ii), and a sample network generated by the tracking system (iii). **(B)** A great tit with a PIT tag [28] fitted to its leg ring (i), an RFID reader at an experimental feeding site, and a sample network from the feeding site (Box 2) (iii).

in machine-sensed information can be challenging. Here, we review two main approaches that have been used successfully in reality-mining studies and that are likely to prove useful in future applications: social network analysis and HMMs. Readers who are primarily interested in modelling spatial data for movement analyses are referred to more specialised reviews [47–49], because our focus is on the social fine structure of animal groups and populations.

Social network analysis

Social networks are quickly becoming the method of choice for visualising, describing, analysing, and predicting social-association patterns in human and animal populations [15,50,51]. Networks comprise nodes (individuals) and edges (associations between individuals) where the latter can be weighted (depending on the frequency or duration of contact between two individuals) and/or directed (denoting an asymmetric relationship, for example, due to dominance hierarchies). One of the key strengths of the network approach is that it enables measurement of individual characteristics as well as of global (network) properties, thereby providing a convenient tool to span the range of social complexity from individuals to social group, to population [15,50]. Another advantage is that networks put the individual in the context of the population without neglecting the social fine structure of the latter. For example, game theoretic approaches tend to assume that all individuals in a population freely admix, whereas empirical studies show that this is not usually the case. Thus, game theory played on networks produced some novel predictions regarding the evolution and maintenance of behavioural strategies, such as cooperation [52,53].

Social networks can be generated using field data from different tracking technologies, as described in the section on data collection above. In the case of PIT/RFID technology, time-stamped records of the presence of

Box 2. Analysis of spatiotemporal data streams

Some indirect encounter mapping technologies, such as PIT/RFID systems, generate time-stamped records whenever tagged individuals visit field-deployed receivers (see main text; Box 1 and Figure IB). When analysing such temporal visitation data, it is reasonable to assume that, the smaller the time between the visits of two subjects to the same location, the higher the likelihood of them being 'associated' in a biologically meaningful way. For example, individuals that are observed at the same site within 2 s are likely to be associated, whereas individuals that appear 2 h apart may have no social bond. Here, we discuss two methods for extracting such association information from (co-)occurrence data streams.

The first approach [97–100] involves partitioning the raw data stream into a series of segments of fixed size Δt and placing ties between individuals that fall within the same time window (Figure IA); the association strength, or weight, is simply the total number of pairwise co-occurrences across all time windows. An alternative approach is based on exploiting the observation density profile of data streams where visits may not be uniformly spread across time, but appear in 'bursts' [28] (i.e., lots of visits clustered together) interspersed by long observation-free periods (Figure IB). Using appropriate statistical methods, it is possible to identify such increased data density, which can be viewed as 'gathering events' of socially affiliated individuals [28]. The social associations between animals can then be reconstructed from their coparticipation in such gatherings (the more events two individuals co-occur in, the stronger the tie between them). Method choice depends on the problem setting. Time-slicing approaches are usually simpler to implement but require some prior knowledge of the system to determine an appropriate sampling window size. Gathering event identification overcomes this problem, but may fail in cases where observations are spread uniformly across the data stream.

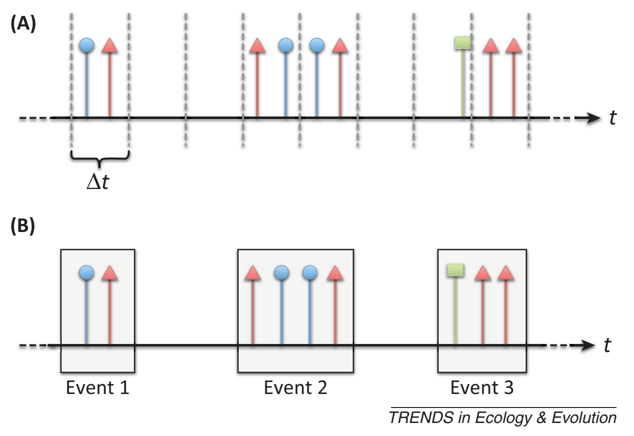

Figure I. Illustration of a hypothetical visitation sequence. **(A)** Data stream segmented based on a fixed time window of size Δt. Individuals that fall within Δt are assumed to be associated, as for example, the blue ○ and the red △ (with a weight of 3). **(B)** Gathering events, as identified by applying a clustering algorithm on the data stream. Individuals within such events are assumed to be associated.

animals are produced by readers positioned at strategic locations with high animal activity (Boxes 1 and 2), for example at preferred foraging, courtship, or roosting sites (if different behaviours are reliably expressed in different locations within the study site, this can be exploited for inferring behavioural activity for more detailed HMM analyses; see next section). This can lead to the rapid accumulation of hundreds of thousands of tag reads. The challenge, then, is to extract social ties from (co-)occurrence records, by examining the extent to which potential encounters at a reader location signify social affiliation (for a case study, see Box 1; for a possible analytical approach, see Box 2). If proximity loggers are used instead, direct records of animal-to-animal distances are produced (see above), but analysis will require careful data-quality checking [14,54] and hardware calibration [14,25,55]. In terms of data screening of proximity logger data, essential steps include: (i) *post-hoc* synchronisation of internal logger clocks, to 'align' encounter logs from different loggers; (ii) filtering out of corrupt encounter logs and data duplications; and (iii) verification of the symmetry of dyadic encounters, by examining the raw association matrix (if individual A was associated with individual B, then B should have also been associated with A). Once the final data sets have been obtained, robust biological interpretation is dependent on results from adequate calibration

Box 3. Applications of hidden Markov models

HMMs have proven to be useful for modelling systems that can be thought of as passing through states that cannot be directly observed or that are uncertain, but that have some observable effect. A state can be anything that has a duration and that can be distinguished from other states. For example, an individual might be regarded as being in the state 'social' after it has joined a group and in the state 'alone' after it has left the group, the kind of information that is readily obtainable with current tracking technology (see main text and Table 1). A particular strength of HMMs is that they are capable of modelling simultaneously the variability of both the durations and the observable effects of the states. The durations are modelled by state-transition probabilities and the observable effects by state-specific probability distributions that specify the possible outputs of each state. For constructing a basic HMM, the empirical data set is usually split into at least two parts, the training set and the test set. The training set is used for probability estimation and the test set for model evaluation.

A good example of a reality-mining application of HMMs is a study that developed behavioural models of honeybees, based on data generated by automated video tracking [72]. The models described behaviours such as performing a waggle dance, following a dancer, or accomplishing some work inside the hive. The states of these models corresponded to elementary movements (e.g., arcing left, arcing right, moving straight, or waggling), such that each behaviour could be modelled by a Markov chain specifying the characteristic transition probabilities between these states. Given that it was practically impossible to identify uniquely and correctly these states in their large data set, the researchers used HMMs to deal with uncertainty, by additionally attaching probabilities to observed movements, that is, by regarding the observed movements as observable effects produced by the 'real' states of the HMMs. The video-tracking system produced time series of x- and y-coordinates for individually marked bees, from which features such as changes in speed and heading could be extracted, which were further processed to yield sequences of information about the movement of bees. The resulting models were used to recognize automatically the behaviour of honeybees in data not used for model construction. However, model outputs could have also been used for comparisons between hives or time periods, as outlined more generally in the main text.

experiments that characterise tag-to-tag signal transmission within the full envelope of recording conditions experienced by the field-deployed system (including variation in relative antenna angles, habitat composition, and tag height above ground). Similar demands exist for high-resolution positional data generated by indirect positional biotelemetry systems, where raw data have to be post processed to remove erroneous fixes ([22–24,56,57]; for an example of a whole-lake array, see Figure 1).

To explore the structural properties of networks, a large number of local and global network descriptors and tests have been devised [50]; in the context of this review, we only highlight a few, referring the interested reader to specialised reviews on this topic for further information [16,50,58]. One of the most frequently used metrics is the 'degree' or 'connectivity' of individuals, which is defined as the number of edges that a given individual has in the network [16]. Node degree is likely to be a good predictor of transmission processes on networks, as recently highlighted in a population of tool-using New Caledonian crows ([14] Box 1), and is relatively robust against missing observations and/or recording errors [16]. Unlike most other data-collection techniques, proximity logging can also indicate the absence of edges (so-called 'zero' edges) with high confidence [14], enabling researchers to study which animals may actively avoid each other. Another useful analytical approach is to search for 'substructures' (i.e., communities or subgroups) within networks. For example, in a human reality-mining study investigating mobile-phone use at societal level, 'strong' ties were found to be important for within-community connections, whereas 'weak' ties created links between communities and, therefore, were crucial for the global flow of information in the population [6]. The study used aggregated call duration as a measure of tie strength between nodes, but very little is currently known about the relation between the frequency and duration of encounters in social networks, in either human or animal systems. Reality mining holds the potential to elucidate whether preferential associations are characterised by particularly frequent and/or long associations (and whether these two parameters are correlated), with important implications for our understanding of information transmission and social-learning processes.

In captive or semi-captive settings, loggers or tags can potentially be deployed on all individuals in a group, unless they are so numerous that this becomes prohibitively expensive (e.g., thousands of chickens in a poultry farm). By contrast, in free-ranging animals, often only a certain proportion of a local population can be fitted with devices, because of logistical constraints. Therefore, social network analyses will have to deal with missing data (which can also result from device malfunction), a problem that is increasingly receiving attention [59,60].

Several programs are available for automated network visualisation (e.g., Gephi and Netdraw) and analysis (e.g., UCINET [61] and SocProg [62]), which provide an excellent starting point for any investigation.

Hidden Markov models in animal behaviour

Hidden Markov modelling is a well-established stochastic modelling tool that has been applied successfully in a wide range of contexts, including speech recognition in humans, pattern recognition, and the analysis of genetic sequences [63], as well as first reality-mining studies [2,13,64]. HMMs are based on simple Markov chains where the future state of a system is only dependent on its current state, the so-called 'Markov property' [63]. In a simple Markov chain model, each observed data sequence corresponds to a unique sequence of states. This means that a model can be constructed based on a sequence of given states of a system (e.g., 'being asleep', 'foraging', or 'mating'). In many systems, the states can be observed directly, and transition probabilities between states (e.g., the probabilities of other states following 'being asleep') can be estimated to construct a Markov chain model. Examples include studies on grooming behaviour in flies [65], mother–infant interactions in monkeys [66], and stress-related behavioural changes in animal-welfare projects [67]. However, in a typical reality-mining scenario with remotely collected data, it is often impossible to map the data to a unique sequence of states; usually, a sequence of data can have multiple explanations in terms of state sequences. In an HMM, we assume that we cannot directly observe the states but only the variable outputs they produce. This makes HMMs suitable models of processes where the identification of states is part of the problem. HMMs then enable the identification of the state sequence that, given the reality-mining output, has the greatest probability (Box 3).

As mentioned above, HMMs are limited by the Markov property. Although simple Markov chains can easily be generalised to higher-order chains that take a finite sequence of previous states into consideration, this is more difficult for HMMs. However, it is possible to construct compound models, where, for example, HMMs form the states of a simple, higher-order Markov chain. Such a compound model would then simultaneously take into consideration the probabilities of the HMMs producing the observed data sequence and the probability of the high-level state sequence modelled by the simple Markov chain. Of course, other possibilities exist for combining HMMs with other modelling approaches that can keep track of a longer history (e.g., Eigenbehaviors [13]).

Most applications of HMMs to social dynamics of entire groups or populations have been conducted with human subjects, presumably because suitable animal tracking technologies had not been available. In humans, such data usually provide information about the location of an individual at a specific time, which enables inferences about its behavioural state. If, for example, an individual is at home at 3.00 am, the probability is high that its state is 'asleep in her bed'. However, if the same individual were in the office at 3.00 am, then the state would likely be 'awake working at her desk'. Based on this time and location data, and perhaps the presence of other individuals, it is possible to reconstruct daily routines of humans with certain probabilities [13]. Similar reasoning can be applied to animal data sets. Here, HMMs can be used to detect behavioural routines of individuals and to link these to possible drivers, such as time of day, or environmental factors. In some cases, it may be possible to go beyond a descriptive, correlative approach, by experimentally manipulating the factor(s) of interest (such as food availability) and measuring the response of the system. In this sense, HMMs provide a more sophisticated version of ethograms [64,68], with behavioural state changes being modelled according to environmental contexts. This approach puts social behaviour into the wider context of other behaviours and can provide important information on when and where social interactions are likely to take place.

Another advantage of HMMs is that they are generative models. They can be used to produce state sequences and output typical of the modelled system. This means that HMMs can also be used to generate social networks. Most studies of social networks focus on patterns using data that were accumulated over time. This means that little is known about the social dynamics that generated these patterns [69]. HMMs can fill this gap because they provide information on behavioural dynamics. Importantly, the discrete time intervals at which states are inferred by some tracking systems (Table 1) can be matched to the temporal dynamics of the activities of interest. Furthermore, information from HMMs can be used to parameterise individual-based models that simulate social dynamics and, thus, produce testable predictions, which can then be confronted with field manipulations to add ecological validity (e.g., to fish a lake that had previously been unexploited, and to study consequent changes in fish behaviour). A nice example of a dynamic change in network structure is provided by a study that examined how a research group behaved in response to an approaching deadline [2]. Initially, contacts of all group members with the group leader were frequent and strong. As the project got closer to the deadline, however, research group members became more interdependent, resulting in a different network architecture.

Many network measures are sensitive to the number of nodes (individuals) and edges (social connections between the nodes) and to missing observations [16] and, therefore, are only of limited use for network and/or population comparisons. By contrast, HMMs are usually less affected by these issues because they are aimed at providing general models of social behaviour for the whole group or population. Therefore, HMMs may provide a more promising approach for population comparisons, because they focus on differences in social processes, by comparing the transition probabilities between states rather than the resultant patterns.

Several software packages are available for the implementation of HMMs, such as HMMER (http://hmmer.janelia.org/) and ESMERALDA (http://esmeralda.sourceforge.net/) (reviewed in [63]).

Concluding remarks

In conclusion, reality mining involves the collection and analysis of machine-sensed data sets, to investigate social dynamics across scales, from the fine structure of individual behaviour to population-level processes. Originally conceived to study human social behaviour, pioneering studies illustrate how this basic conceptual approach can be applied productively to animal systems [14,28,29,70], through the effective combination of powerful data-harvesting techniques (such as animal-borne proximity loggers) and innovative analytical tools (such as social network analyses and HMMs).

In humans, reality mining can capitalise on existing, self-generated data sets (e.g., mobile phone calls [6]), but may encounter problems of data confidentiality that severely limit data exploration and publication. Animal studies are free from these constraints, but require investment of considerable resources into data generation, in terms of money to buy hardware and time to calibrate, deploy, and operate a system in the field. Furthermore, data-handling procedures need to be in place to address problems that arise, for example, when incomplete or nonrepresentative samples of individuals are studied, tag performance varies across different habitats, or logger batteries fail (for strengths and weaknesses of different tracking technologies, see Table 1).

A major concern in traditional studies of animal social dynamics is the quantity and quality of field data, and the question of whether small samples adequately describe population-level phenomena [16]. Notwithstanding the challenges mentioned above, reality mining addresses these issues, both with regards to the number of subjects that can be simultaneously studied and the quality of the data generated per individual. Studies that track association patterns of large numbers of individuals with multi- or even subsecond sampling rates have the potential to converge, within obvious limits, on the ultimate goal of mapping biological ‘reality’. Social network studies, for example, routinely suffer from the problem that weak links and zero associations between pairs of individuals, and sparse networks in general, cannot be trusted, because they may simply be due to undersampling [16]. In proximity-logging applications, such zero associations become robust and meaningful data, because we can be relatively confident that all associations were recorded by the system and that those individuals that appear unconnected in the inferred network indeed had no encounters during the observation period [14].

Most conventional social network studies identify patterns from cumulative data, collected over days, weeks, months or even longer, through repeated observation or recapture of marked, or otherwise identifiable, subjects [16], an approach that ignores underlying short-term (transitional) dynamics. Current tracking technology can provide data sensing at time intervals small enough (e.g., the fish tracked in the study lake in Figure 1 were tracked for 3 years with a 9-s burst interval) to enable investigation of dynamic processes [71], for example, of how network topology tracks environmental conditions or responds to major natural or anthropogenic perturbations [2]. An understanding of behavioural dynamics is also an important prerequisite for the study of disease- or information-transmission processes in animal populations. With the help of HMMs, for example, it might become possible to detect state changes in animals that enable effective, real-time monitoring of the spread of diseases, highlighting a potential role of reality mining for population management. In domestic settings, high-resolution data could be valuable for animal welfare studies that aim to design environments for livestock where competition for resources and stress levels are minimised [67].

With basic association data no longer a limiting factor, researchers' attention can focus on generating, and interpreting, information on the behavioural context of encounters. In terms of data collection, additional sensors (video cameras or accelerometers) will soon be integrated into existing systems (such as 'Encounternet'), producing robust data on behavioural states. As in human studies [4], these data can then be analysed with HMMs, to help identify patterns and routines that individuals have in common, or that differ between groups, populations, or time periods, providing a more comprehensive description of fundamental biological processes than was previously possible for wild animals.

Even with current battery technologies, reality-mining projects can run over ecologically relevant time scales of weeks or months, which would cover a breeding period in many species. Therefore, data on mate choice [28] and mating behaviour, or relative positioning within social networks, can be collected and subsequently related to reproductive success and other components of fitness. This means that reality mining can contribute to efforts of modelling ecological phenomena from the bottom up, from individual interactions to population-level patterns, with an assessment of the fitness consequences of different behavioural strategies. The latter then joins ecology and evolution, resulting in the potential for modelling behaviour-mediated eco-evolutionary feedback.

We restricted our review to technologies that generate data using animal-attached devices, but note that other forms of machine sensing are conceivable. In the laboratory, it is already possible to perform tracking of individuals and their encounters using computer vision (Box 3 [64,72–75]), and we anticipate that similar automated approaches will soon be implemented in field studies, where grids of video cameras could monitor individually identifiable subjects. In some species, individual recognition is easily possible, based on natural patterns and markings [16], potentially rendering the laborious process of tag deployment obsolete.

Until now, conducting population or species comparisons of social network topology has been exceptionally difficult, because most network descriptors are sensitive to undersampling [16,76]. Rich biologging or biotelemetry data sets, in conjunction with innovative analytical techniques such as HMMs, will help biologists overcome these problems. Over the years, reality-mining studies will provide data and models on the social fine structure and dynamics of animal populations across a wide range of species, facilitating major new insights through broad evolutionary comparisons [77,78].

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