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Research Article

ProxLogs: Miniaturised proximity loggers for monitoring association behaviour in small animals

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Abstract

The ability to monitor associations between wild animals is essential for understanding the processes governing gene transfer, information transfer, competition, predation and disease transmission. Until recently, such insights have been confined to large, visible or captive animals. However, the rapid development of miniature sensors for consumer electronics is allowing ecologists to monitor the natural world in ways previously considered impossible. Here we describe miniature (<1 g) proximity loggers we have developed that use Bluetooth Low Energy transmission to register contacts between individuals. Our loggers are open source, low cost, rechargeable, able to store up to 2000 contacts, can be programmed in situ and can download data remotely or through a mobile phone application, increasing their utility in remote areas or with species which are challenging to recapture. We successfully trialled our loggers in a range of field realistic conditions, demonstrating that Bluetooth Low Energy is capable of logging associations in structurally complex habitats, and that changes in received signal strength can be equated to short range changes in distance between loggers. Furthermore, we tested the system on captive European starlings (*Sturnus vulgaris*) and captive multimammate mice (*Mastomys natalensis*). The ability to include other sensors is retained in our prototypes, allowing for the potential integration of physiological and behavioural inference into social networks derived from our approach. Due to its open source nature, small size, flexibility of use and the active research currently being undertaken with Bluetooth Low Energy, our approach is a valuable addition to the biologging toolkit.

Data accessibility
Logging data and the R code used to download and manipulate the data will be made available as example data for R functions / R package to manipulate logger data.

Introduction

Most animal social systems are heterogeneous with the extent to which animals are in contact with each other varying spatially and temporally (Vanderwaal et al., 2014) sometimes over relatively small time scales (Tentelier et al., 2016). In order to accurately determine how population level social structure emerges from highly dynamic individual behaviour, it is essential to gather robust, accurate, high resolution empirical evidence of association behavior (Krause et al., 2013). However, systematic, disturbance free observation, particularly of highly mobile, nocturnal or small species, can be extremely challenging (Krause et al., 2013).

Understanding intra-specific associations is hugely important for understanding the processes underpinning survival, reproduction and disease transmission. How individuals associate with each other may mediate the flow of information transfer within a group (Clair et al., 2015) or establish social hierarchies (Ilany and Akçay, 2016) with multi-generational consequences (Ilany and Akçay, 2016). The heterogeneous nature of social contacts also has consequences for understanding disease transmission, both within species of conservation concern (Galbraith et al., 2017; Hamede et al., 2009; Vanderwaal et al., 2014) and hosts of zoonotic diseases (Davis et al., 2015; Jones et al., 2008) or diseases of economic interest (Drewe et al., 2012; Ji et al., 2005).

Associations of interest may also be inter- rather than intra-specific; animal associations are often embedded within a complex network of different species. Pairwise associations between two species may be modified by pathogen or predator mediated apparent competition (Sheehy et al., 2018), resulting in complex outcomes (Sheehy et al., 2018). However, it can also be challenging to assess the nature and frequency of these associations, with consequences for understanding demography and designing successful conservation programs (Croft et al., 2016). A lack of a thorough understanding of contact processes can even have serious, unintended consequences with a substantial conservation or economic impact (Greenlees et al., 2007). Animals also interact with their environment, often in conflict with human activities (Leirs, 1994) or as a result of human behaviour, with potential consequences for survival or disease transmission (Galbraith et al., 2017; Jones et al., 2008).

Proximity loggers, small devices worn by a target animal which log when another device is within a certain distance, can provide unparalleled insights into individual behaviour and associations. For ex-

Author contributions
LK, HL, RB, WM, EM and IHO conceived the study design. LK, RB and IHO designed the methodology, LK, IHO, AM and CS participated in the fieldwork, LK and IHO analysed the data, LK and IHO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. LK and IHO contributed equally to the writing of this manuscript.

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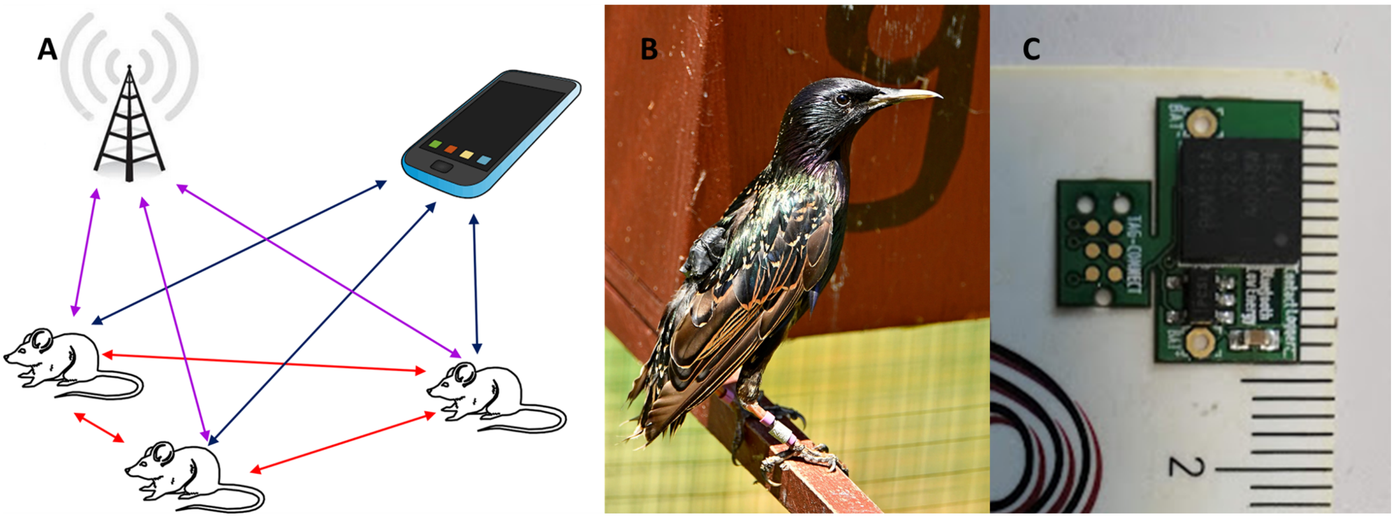

Figure 1 – A: Schematic showing system set up. Coloured arrows indicate communication between different parts of the system. Loggers communicate directly between themselves when mounted on a focal animal(red arrows), downloading the stored data to either a gateway once a user determined threshold is reached (purple arrows)or a mobile phone application, as and when a user desires (blue arrows). B: Picture of a starling wearing a logger sealed with plastidip and attached as a backpack. C: Picture of the mobile logger. The 6 pin TAG-Connect programming port is detachable to reduce logger weight and footprint further. The battery is attached to the back of the logger.

ample, such loggers have been used to identify inter-specific associations between cattle and badgers in relation to possible bovine tuberculosis transmission events (Drewe et al., 2012), how contact patterns in raccoons relate to rabies transmission (Reynolds et al., 2015),to monitor whole herd movements for improved livestock management (Maroto-Molina et al., 2018) or most recently to explore how sickness effects social encounters in wild vampire bats (Ripperger et al., 2020b).

Whilst the importance of accurately understanding contact behaviour is well established, limits have been imposed by technological capabilities. Classic approaches to determining contact between individuals often involve indirect approaches such as VHF transmitters (Böhm et al., 2008) or GPS loggers (Craft et al., 2010), and proximity loggers should provide a far more accurate picture (Krause et al., 2013). Unlike methods which use spatial positioning to estimate associations, proximity loggers directly record the contact between two or more individuals. Proximity collars, one of the earliest examples of this technology (e.g. Sirtrack, New Zealand) record the length of time that loggers are less than a user defined distance apart from each other (e.g. 40 cm; Ji et al., 2005), thereby providing a duration of presumed contact (Drewe et al., 2013), although this data is purely of a binary nature. While Sirtrack / Lotek proximity loggers have been instrumental in understanding the role of contact behaviour in a number of different systems (Drewe et al., 2012), they are prohibitively large for many mammal species (collar weight is between 30–450 g; Ji et al., 2005; Kays et al., 2015; Reynolds et al., 2015; Walrath et al., 2011), and require the recovery of the collar in order to access the data.

As the majority of animals are smaller than the weight of a proximity collar, a key focus has been on creating smaller proximity loggers. The first reduced size proximity logger was that of the Encounternet system. Originally 10 g, modifications of these loggers achieved an impressive miniaturisation, with the smallest loggers weighing 1.3 g (Levin et al., 2015), however this came with a significant reduction in battery life (only a number of hours) and they are no longer available for use. Another recent approach to proximity logging in mammals involves the use of low frequency radio waves and a system of loggers connected to ground nodes (Ripperger et al., 2016). The system is capable of efficiently and accurately monitoring associations between a number of individuals simultaneously, while also providing spatial information (Cassens et al., 2017; Ripperger et al., 2016, 2020b). In this system, mobile nodes are tracked by ground nodes providing spatial information, while encounter information is recorded by mobile nodes and stored until contact with a ground node (Dressler et al., 2019). While the encounter approach is comparable to the one we describe, ground nodes achieve contacts over a greater distance than Bluetooth Low Energy (BLE) alone is capable of and long range movements can also be recorded. However, this system is currently not available to researchers (Simon Ripperger, *pers. comm.*), and the costs of implementing the system are unclear, as is the size and power consumption of the ground nodes. Therefore, while the BATS (Broadly Applicable Tracking System; see Appendix for an index of all acronyms used in this paper) approach will answer questions concerning both proximity and long range movements of animals effectively, inaccessibility and potentially cost remains an key issue. Finally, a similar approach using a BLE mesh has been described by (Ayele et al., 2018; Maroto-Molina et al., 2018) where neighbour discovery using BLE is combined with LoRa (Long Range) technology to gather information on larger movements. Although the size of the proposed collar is not provided in either system, as a combination of BLE, LoRa and GPS (Global Positioning System) collars are used, it is highly likely that these approaches have not been miniaturised for use on small (>20 g) animals. Combining two radios (e.g. LoRa or NB-IoT; Narrow-Band Internet of Things) on the same chip will increase the weight while giving poor localisation accuracy ($\approx$300 m error; Aernouts et al., 2018; Lemic et al., 2019 and these systems have limited global coverage.

The majority of extant species weigh around 50 g or less, particularly species in the order Chiroptera or Rodentia which are responsible for a large proportion of zoonotic diseases of interest, yet their average mass is 45 g (3–491 g; Pantheria dataset; https://ecologicaldata.org/wiki/pantheria). Current recommendations are that loggers do not exceed 5% of the animals body weight for rodents and birds and 8% body weight for bats, although recent studies have exceeded this limit for short term studies (Roeleke et al., 2016). Regardless, if loggers are too heavy, they will alter animal behaviour and provide inaccurate data. Therefore, our target was to miniaturise loggers capable of recording proximity data to 1 g (not including housing or collar weights) in order to use them on animals with a weight of 20 g or more, staying within the restrictions of a 5–8% of body mass weight limit. We do not include weights of housing (e.g. epoxy or sealant) or attachment method as these vary widely from species to species and will be subject to user experience with their study system.

Here, we present and validate the system we have developed using Bluetooth Low Energy (BLE). Bluetooth Low Energy is highly efficient, capable of operating in high interference environments and is supported by modern phones and laptops, which means that user configuration does not require complex hardware (Berkvens et al., 2018), particularly in areas where infrastructure can be lacking. Our system consists of three components (Fig. 1A):

1. Contact loggers, which record the time stamp and the received signal strength (RSSI) of the contact between individuals (Fig. 1B

shows an example *Sturnus vulgaris* wearing a logger as a backpack, Fig. 1C shows the dimensions of the mobile logger);
2. The gateways which store the logs downloaded from the contact loggers onto a microSD card;
3. A mobile phone application which allows real time programming, monitoring, and downloading of the loggers.

To begin with, we emphasise that the system is most appropriate for situations where users wish to investigate close contacts in a species where either the user can get close enough to download the data at some point (for example if the animal uses a nest) or gateways can be placed at strategic points for data download (e.g. known roost sites or within a closed grid), small scale spatial movements (up to 10 m from a logger) are being monitored or when animals can be reliably recaptured to download data logs. Mesocosm studies would be particularly appropriate for this kind of system, although, as long as sufficient knowledge already exists about the species specific behaviour, open systems can also be used. This system will not provide information on animal movements over long distances (e.g. several kilometers or outside of a grid of stationary loggers), if animals spend a long time in a location where data download is not possible, or in situations where many animals are within a very small distances (<1 m) of each other simultaneously; in these cases alternative approaches such as GPS loggers or the BATS system should be considered.

Below we describe how our system differs from other, similar systems which we feel makes it a valuable tool for answering specific questions.

1. Our system is completely open source, low cost and readily available as we have concentrated on only using "off the shelf" components that can be easily accessed. By designing a mobile phone app for both Android and iOS devices, real time programming and monitoring of the loggers is easy and does not require specialist knowledge or equipment.
2. Contacts are directly stored on the chip of the logger, and downloaded once a user determined value is reached. This substantially increases the operational time of the logger by limiting contact between the loggers and the gateways, and allows the user to be circumspect about placement of the gateways which will download the stored data. How the user decides to place gateways or set download limits will depend on their knowledge of their study system; for example if the user believes that they are unlikely to regularly see their target animal, the download threshold can be set lower than in situations where the gateway is likely to regularly detect the mobile loggers.
3. Unlike Sirtek proximity collars, the IDs and the RSSI of the received identification are recorded, allowing fine grained differences in the association to be quantified and related to the potential nature and quality of the association.
4. The gateways have been designed to also operate under very low power meaning that they can be deployed in the field for months using relatively small batteries. This also ensures that they can be easily camouflaged in areas where interference or theft could occur and users can focus on just replacing loggers, or gateways can be placed in less accessible areas.
5. Similar to the BATS approach, the loggers and gateways are powered by rechargeable batteries, so loggers can be reused if recovered.
6. Loggers can be fully manipulated to match data requirements. Loggers can be set as "hidden" where they do not broadcast their own ID but still scan for and record other IDs, "advertise only" where loggers broadcast their own ID but do not scan for other IDs, or "fully distributed" where they both scan for IDs and advertise their own ID. Setting loggers as hidden stops stationary loggers from detecting each other, focusing data acquisition on the mobile loggers, while setting loggers as advertise only can substantially increase battery life. Loggers can be switched between these options in the field by using the mobile phone application.
7. The system has been designed to give complete flexibility to the user. Therefore limits can be set on the hours of operation (forced sleep during certain hours) and on which loggers are recognised by other loggers, again through use of the mobile phone app.

We recognise that some of the previously described systems have some but not all of the aforementioned points, however the open source nature, accessibility and low cost of this approach, we believe, makes it a valuable addition to the ecologist tool box.

Methods

General functionality of the system

Development of BLE (carried out by the Bluetooth Special Interest Group) is focused towards increasing energy efficiency. BLE devices "advertise" their identification to their surroundings, the frequency of which is determined by the advertisement interval and a random back off interval which reduces potential collision risk between two loggers advertising at the same time. Advertisements are also capable of holding some information, meaning that the device is also able to publish data to its environment. Devices listen for advertisements by "scanning", the length of which is determined by the scan window. The frequency at which a device scans is therefore its scan or measurement interval. The range over which BLE can transmit is determined by line of sight and the nature of any interference. Due to the miniaturisation of our loggers, transmission distances are considerably lower than those achieved by standard BLE (standard BLE can transmit up to 200 m in open areas while our loggers transmit up to 10 m as the board of the logger acts as part of the antenna for the signal and has been reduced below the optimum BLE operating distance). Complex habitat structure (Drewe et al., 2012), particularly with a high water content, can substantially reduce the range over which the loggers can transmit (Qureshi et al., 2016); therefore users need to consider the habitat within which their study species is moving, what constitutes a contact within their system before use, and ensure that loggers are calibrated. For example, when loggers are placed at floor level in thick undergrowth, transmission distances were reduced to 5 m or less.

Our contact loggers scan and advertise within the default BLE schedule with user determined scan / advertisement parameters, storing any received IDs along with the RSSI and a time stamp. The loggers expose their unique identifier, amount of data logged and mode of operation in their advertisements, so other devices (e.g. the gateway, mobile phones, tablets etc.) can access this data without connecting to the logger. Once the chip connects with a gateway it will download the stored data. If the connection with the gateway is lost before the full data transfer is completed, the data is not saved and will have to be downloaded again when the connection is restored. Once all the data is downloaded to the gateway, the contact logger memory is wiped. If the connection to the gateway is lost before all the data is downloaded, then the contact logger memory is not wiped and the data downloaded to the gateway is not stored. The data on the gateway is written to a microSD card which can then be retrieved by users at a convenient time. Data is written to the microSD card as a comma delimited file (`.csv`) for ease of onward processing. Contact data can also be directly downloaded from the loggers through the mobile phone application, as can programming the contact loggers to set the measurement interval, the mode of operation and the loggers unique identifier (Berkvens et al., 2018). Loggers can be used in two different ways: as mobile nodes on moving animals which are restricted by weight, or as stationary nodes which are placed in the environment in a regular grid, do not have any weight restrictions and which provide spatial information, as well as inferring social contacts from proximity in space and time.

Contact loggers

The initial prototype was designed with a Silicon Labs BMG111 module[1], but subsequently we used BMG121[2] due to its smaller footprint[1,2]. The printed circuit board (0.3 mm flex PCB) includes a

[1] BGM111 Blue Gecko Bluetooth Module Data Sheet, Silicon Labs, 2018. Rev. 1.4.1.
[2] BGM121/BGM123 Blue Gecko Bluetooth SiP Module Data Sheet, Silicon Labs, 2018. Rev. 1.3.2.

detachable 6 pin TagConnect[3] connector which reduces the footprint required for programming and debugging, allowing us to maintain the small logger size. Battery terminals are at the bottom of the board. A voltage regulator is included to protect the chip from the high voltage from a fully charged battery. The PCB also contains a ground loop to tune the antenna and maximize transmit efficiency. A 47 µF X5R decoupling capacitor is used to accommodate for sudden spikes in current the module needs for radio activity when smaller batteries struggle to provide sufficient current. In total, the chip weighs 230 mg. Using the smallest prototype, the transmission distance is reduced compared to theoretical transmission distances as the length of the board is shorter[2]. Loggers can run as either scanning and advertising, where all loggers record the associations with other loggers, or as advertising only, where a network of stationary loggers can be used to infer contacts in space and time. After each advertisement, the module will listen for other devices to see if any other device wants to initiate a connection. If other devices in the area that are set to scanning want to connect, they wait for an advertisement, then immediately send a connection request within that scan window. Using the advertising only setting can increase operation times dependent on the schedule being used. For example, using the smallest battery (10 mA), when scanning and advertising on a 10 second scanning schedule (the highest time resolution we employ), battery life is 56 hours compared to 112 hours when advertising only. In comparison, logging on moderate accuracy (e.g. every minute) will result in a runtime of 274 hours when advertising only, or 137 hours if scanning is enabled. Berkvens et al. (2018) and Fig. 2A–C demonstrates in more detail the relationship between battery life and measurement interval when scanning is implemented compared to advertising. Most of the time the chip is in EM2 DeepSleep mode, where the timer continues to run but other parts of the chip are inactive. This can be supported by a 25 mA battery for 333 days, and is 0.03% of the power consumption required for scanning[2]. By limiting the hours during which the logger is operational, the battery life can be extended (for example covering hours of activity for nocturnal animals, see Fig. 2D).

In all cases we use a Lithium polymer (LiPo) battery to run both mobile and stationary nodes. Stationary nodes are a similar footprint to the mobile nodes, but are not restricted to 0.3 mm boards and include a battery connector for ease of use. The smallest batteries currently available are 10 mA and weigh 0.4 g. The choice of battery size for the logger will depend on the species being investigated and the time over which data is to be collected. Loggers can also be recharged and reused, extending the usability of a single logger. In total, the logger plus 10 mAh battery and some additional housing such as heat shrink material weighs ≈1 g. However, heat shrink housing alone may not be sufficient for all species and additional coatings such as an epoxy resin may be required which will increase logger weight.

Gateway

The prototype of the gateway is built upon the Nordic Development Kit for the nRF52840[4] which has full BLE5 support, an Adrafruit MicroSD card module is connected by soldering jump wires to the slot and inserting the wires in the appropriate connectors. An Adafruit GPS unit is also included to maintain an accurate time stamp. To facilitate power in the field, a 6600 mAh Li-Po battery-pack is attached to a voltage-regulator module with its output wires soldered to the external power-input pins on the development kit. Alternatively the gateway can be powered with any rechargeable lithium battery with a micro-usb connector. The gateway will continuously scan for nearby loggers. When a logger is detected which holds data that exceeds the download-threshold, a connection is made and data is transferred to a temporary buffer. After the end of data is successfully detected, the gateway updates the clock on the logger to its own clock to ensure the timestamps on all loggers are synchronized. Both the nRF52 development board and the loggers have a 32 kHz crystal at 20 ppm, with a drift rate of 2 seconds per day. The frequency at which the GPS unit updates the gateway is user determined, but an update every 4–8 h maintains 1 second accuracy across the whole system. Once the clock is successfully set, the gateway sends the erase-command which clears the data off the logger, after which the connection is closed and the data in the buffer gets written to the microSD card. When the connection is lost before the end of data is detected, the buffer gets cleared and no data is written to the microSD card. The data is also not wiped from the contact logger.

[3]C.N. Ltd., Tag-connect,llc, http://www.tag-connect.com, 2018.
[4]Nordic Semiconductors, nrf52 development kit product brief, http://infocenter.nordicsemi.com/pdf/nRF52_DK_PB_v2.0.pdf, 2018. Rev. 2.0.4

Mobile phone application

The mobile phone application is written in Dart using Flutter. The application uses the Bluetooth Low Energy capability supported on modern mobile phones to directly interface with the contact loggers. The app publishes a list of nearby contact loggers along with all the data that is in their advertisements (unique identifier, amount of data logged and operation mode). After a logger has been detected, a connection can be made allowing the user to edit parameters and directly download the data. The binary data is automatically parsed into a `csv` file. The application can also emulate a gateway by automatically downloading and storing the data off nearby loggers, though this is less efficient than using the gateway which is optimised for speed, with a download rate of 1.8 seconds per 100 logs. The unique ID for each logger is set through the app, as is the scanning frequency. The app also allows users to select whether loggers are visible or hidden, whether they are advertising only, whether logs are limited to certain time periods and clears logs from loggers. The app also displays information such as the timestamp of the logger and the number of contacts stored on the logger. The app also displays the gateway when the gateway is functioning.

Trials

Battery life: We can estimate the average current draw of a logger by adding the charge consumed by all advertisements and the scan in a single cycle and dividing that by the length of the cycle. Sleep current has not been taken into account due to these currents being so small they become insignificant.

$$I_{adv} = \text{Average advertising current} \tag{1}$$
$$I_{scan} = \text{Average scanning current} \tag{2}$$
$$T_{adv} = \text{Advertisement length} \tag{3}$$
$$T_{scanInterval} = \text{Scan interval} \tag{4}$$
$$T_{advInterval} = \frac{\text{Advertisement interval}}{\text{Scan length}} \tag{5}$$
$$N_{adv/cycle} = \frac{T_{scanInterval}}{T_{advInterval}} \tag{6}$$
$$I_{Average} = \frac{I_{scan}T_{scanLength} + I_{adv}T_{adv}N_{adv/cycle}}{T_{scanInterval}} \tag{7}$$

Multiple power measurements were carried out in the Simplicity Energy Profiler to evaluate the accuracy of the model. Figure S1 (Supplemental Materials) shows the model applied on the BGM111 BLE-module, accompanied with actual measurements at set intervals.

Collision rates: Depending on the amount of Bluetooth Low Energy (BLE) devices in the immediate area, packet-collisions will occur. When two Bluetooth devices advertise simultaneously on a channel, both messages will render corrupt. This results in a chance that two or more loggers will not detect each other. The BLE-specification has measures in place to minimize these collisions but it is impossible to fully eliminate them. Following Ghamari et al. (2018), we derived a model (Eq. 1) to estimate collision rates depending on the advertisement interval, amount of nearby BLE-devices and the time it takes to completely transmit an advertisement (see Appendix S2 in Supplemental Materials for details and Fig 2D for predicted collision risk for a range of nodes and advertisement intervals).

Contact logger tests: Initial tests were carried out to establish the range over which contact loggers could send and receive signals in a variety of different environments. First trials were carried out in Belgium to ensure that the tags were functioning as expected in open environments (Berkvens et al., 2018), with all following tests carried out at the field site in Morogoro, Tanzania (6°51′11.8″ S, 37°38′20.5″ E) during August 2018. We originally designed the loggers for use on *Mastomys natalensis*, a small rodent (≈20–60 g) that is widespread throughout sub-Saharan Africa. A prolific breeder (Leirs, 1994), *M. natalensis* undergoes extreme population fluctuations in response to food availability and is a significant agricultural pest (Leirs, 1994). In addition, *M. natalensis* is the host for a range of zoonotic diseases including Lassa fever and plague (Borremans et al., 2014), therefore understanding how social association behaviour influences disease transmission is of considerable interest for this species. Calibration tests were carried out in enclosed experimental mesocosms within which the preferred habitat of *M. natalensis* is maintained (Borremans et al., 2014). Tested habitats included thick grass (<30 cm high) which had been cut and had all cuttings removed, thick grass had been cut, with cuttings left in situ and very long grass >2 m (see Supplemental Materials Fig. S3 for images depicting the different habitats we trialled).

Initial calibration tests were carried out with and without an epoxy sealant. We found no evidence of epoxy application affecting the functioning of the Bluetooth chip, so continued all tests with loggers which had been coated in a thin layer of epoxy resin as deployment in the field will always require coating of some kind to ensure waterproofing of the loggers.

First validations: Two contact loggers were placed next to each other alongside tape measuring two metres with separate IDs and a scan interval of 10 seconds. Contact loggers were left for 1 minute 30 seconds to record contacts. The data was downloaded to a central `.csv` file stored on the mobile phone by selecting each logger in turn and downloading the data. The timestamp at which the data was downloaded is recorded in the data file. One contact logger was then moved ten centimetres along the measuring tape, the loggers were reset and the process was repeated. Each time the data is downloaded from the logger it is appended to a single `.csv` file for ease of management, as well as creating separate logger specific download files. The logger was moved ten cm for one metre, then 20 cm for the next metre. This process was repeated for loggers without epoxy, loggers with epoxy and loggers mounted on laboratory gloves filled with 48 ml of water to mimic one of our focal animals.

Grid validations: Rutz et al. (2015) described a detailed approach to calibrating animal borne proximity sensors which combines a thorough documentation of the distance signal strength relationship across the three-dimensional environment the focus animal will move through (Ripperger et al., 2016; Rutz et al., 2015) with statistical models and computer simulations (Rutz et al., 2015). Furthermore, the size and behaviour of the tagged animal will also influence the relationship between signal strength and distance. Loggers attached to arboreal mammals will detect each other over increased distances when ascending a tree compared to when moving terrestrially in long grass, and the water content of the animal itself may also influence the range of BLE transmission (Qureshi et al., 2016). Due to these considerations, accurate calibration, tailored to the specifics of both the focal species and the habitat in which the focal species move is vital. We designed a calibration routine which was suitable for our specific habitat (see Supplemental Materials Appendix S4 for a detailed description), allows the simultaneous testing of five loggers, and would be appropriate for any terrestrial, non-arboreal species. Two measuring tapes were laid out in a cross, with distances marked on them as described in Supplemental Materials Fig. S5. . One logger was placed at the centre of the cross and remained there for the duration of the test, while the four other loggers were placed on each arm of the cross. As each logger was moved along the arm of the cross, it moved a set distance from the other four loggers (see Supplemental Materials Fig. S5). The same protocol was used as described above; loggers were set to advertise every 10 seconds, and loggers were moved after one minute 30 seconds again. The data was downloaded from all five loggers to the mobile phone application between each movement. This was repeated twice in two different representative habitats in our study area (thick grass without cuttings and thick grass with cuttings).

Statistical analysis: Theoretical models for battery life and collision rate were carried out in Matlab. All statistical analysis was carried out in R (R core Develpoment Team, 2020). The relationship between RSSI and distance was validated using a linear model (mounted logger trials), as was the relationship between distance moved and average contacts recorded. The relationship between RSSI and distance for the grid validation was modeled using an additive model with a gaussian distribution, including a smoothed term for distance and habitat type and logger ID as fixed effects. Residuals were checked visually for normality.

Field realistic trial: Loggers were tested in two field realistic trials, once on a captive colony of European starlings *Sturnus vulgaris* enclosed in a large aviary (50×10 m) at the campus of the University of Antwerp and once on a captive colony of *Mastomys natalensis* (the multimammate mouse), the species for which we originally designed ProxLogs. A small indoor arena was constructed at the University of Antwerp measuring 2×4 m (see Supplemental Materials Fig. S6). The arena was provided with enrichment in the form of sleeping places, shredded paper, peanuts and other foods to encourage foraging as well as water and standard rodent food. Overhead cameras allow monitoring of the mice but identifying to individual is not possible due to the picture quality. Cameras were set to record at hourly intervals. Loggers were attached to mice as collars. The logger was sealed in epoxy resin then braided steel wire coated in heat shrink tubing was used to construct the collar itself (Supplemental Material Fig. S7). Loggers were set to record a contact every 120 seconds. After 3 full days of logging mice were recaptured, loggers removed and mice checked for any sign of injury. Mice were weighed before and after they were added to the arena. Mice were added to the arena for 4 days before the collars were added to give them time to adjust to the new surroundings and establish dominance hierarchies. All work was carried out under ethical approval (licence no. 2021–26).

The European starling, the most studied non-domesticated passerine, is a highly social species (Eens, 1997; Bateson and Feenders, 2010), and is therefore appropriate for investigating contact behaviour. We chose to test the loggers inside an aviary as that way we would identify periods with missing logs as a consequence of system malfunction rather than missing animals. We tagged 15 birds (8 males and 7 females) with Proxlogs attached as backpacks sealed in epoxy resin in November 2020 (outside of the reproductive season). All work undertaken in this study complied with ethical guidelines of the University of Antwerp and Flemish and European laws regarding animal welfare, and adheres to the ASAB/ABS guidelines for the use of animals in behavioural research and teaching. Specifically, permission to capture starlings from the wild and house them in captivity (in approved facilities) was granted by the Flemish administration (Agentschap voor Natuur en Bos, ID number ANB/BL-FF/ V20-00142). Loggers were all below 5% of the birds' body weight. Eight nest boxes were placed in the aviary, with stationary loggers placed underneath the box (Fig. S9 in Supplemental Materials) and a Bushnell wildlife camera placed in front of each box. Cameras were set to record for 30 seconds after being triggered, allowing contacts between birds and stationary loggers placed at nest boxes to be verified (Fig. S10 in Supplemental Materials). It is not possible to observe the birds directly as the presence of an observer is too disturbing for the birds, and this way we were able to observe for 24 hours a day. Birds were provided with clean water for bathing and a feeding station which also had a stationary logger. Mobile loggers on the birds were set to "scan" every 120 seconds for the full 24 hour period. Stationary loggers were set to "hidden" so they were able to record contacts with the mobile loggers but did not record other stationary loggers, and were set on the same scanning schedule as mobile loggers. Data was downloaded automatically through the gateway which was placed outside the aviary in the centre. This is adjacent to the feeding station so likely to detect all birds regularly, but was able to download from all stationary loggers in this position. The birds were checked every day for signs of problems, after 3 full days of logging birds were recaptured, loggers removed and birds checked for any sign of injury.

Acquiring the loggers: Users interested in discussing whether the loggers are appropriate for their study system or question can contact the authors on `proxlogs@gmail.com` for more information on accessing and using the system.

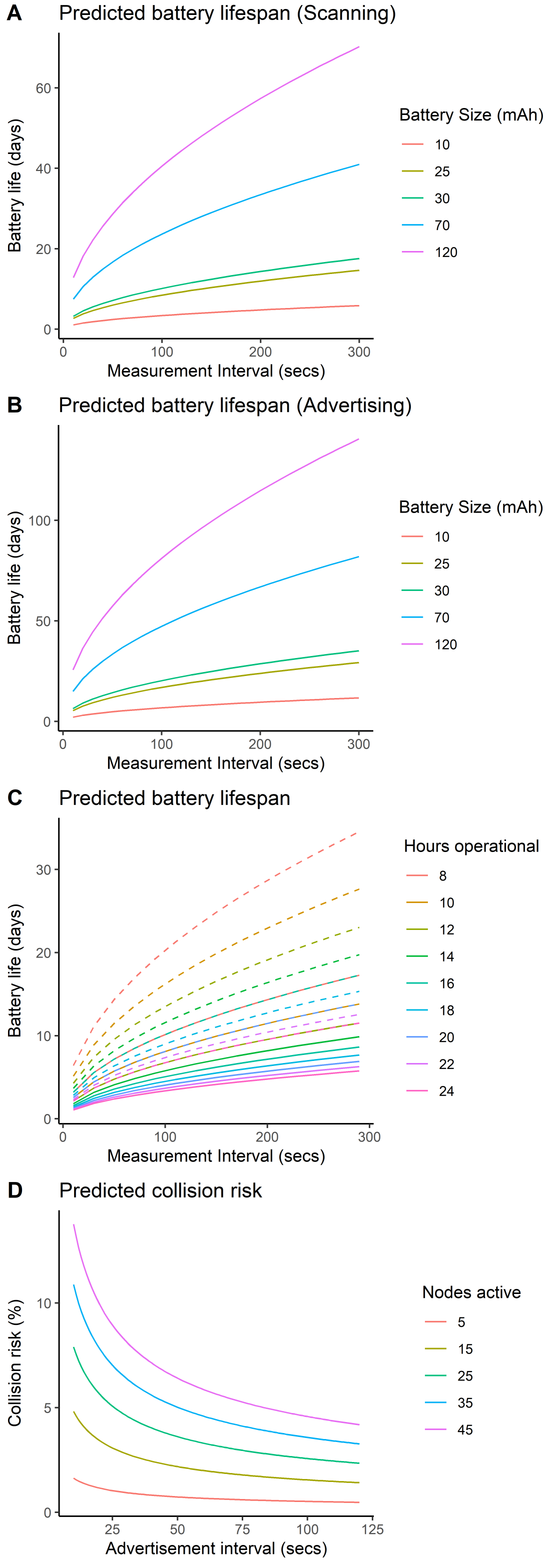

Figure 2 – A: Predicted battery operating lifespan for a range of different battery sizes when scanning is enabled. B: Predicted battery operating lifespan for a range of different battery sizes when scanning is disabled. C: Predicted battery operating lifespan changes with hours operational. Loggers can be set to sleep for given periods which will increase battery lifespan. Solid lines show predicted lifespan when scanning is enabled, dashed lines show predicted lifespan when scanning is disabled. D: Predicted collision risk for given numbers of active nodes over a range of different scanning schedules.

Table 1 – Estimates and standard error (SE) from additive model including distance as a smoothed term. Distances were calculated using the grid calibration validation.

Model	Estimate	SE
Uncut grass + cuttings	−54.5	0.12
Uncut grass - cuttings	−4.9	0.10
Logger 1	−2.6	0.16
Logger 2	−0.7	0.16
Logger 3	−4.5	0.16
Logger 4	−0.3	0.16
Logger 5	−1.3	0.16

Results

Tag functionality

Battery life and collision rates: The choice of battery size is constrained by the size of the focal animal. With the smallest batteries (10 mAh, 0.4 g), and a measurement interval of 10 seconds, we predict a battery life of 2.3 days. This can be extended by either increasing the measurement interval (e.g. a measurement interval of five minutes will extend battery life to 12.8 days) or by only logging associations during the period of known activity (Fig. 2C), which will increase the predicted lifespan. Our theoretical predictions of battery life were similar to those we experienced in the field during our trials and matched actual measurements (see Supplemental Materials Fig. S1) Berkvens et al., 2018).

Figure 2D plots expected collision rates based on the model from Ghamari et al. (2018). We observed an elevated amount of collisions when enforcing a low scan-interval and a large number of nodes (high data-resolution). This is expected as more advertisement-transmissions are required when scanning frequently, thus resulting in a higher congestion of the air-space. This extreme example highlights that collision risk will be higher if you are expecting a large number of animals (e.g. more than 30) to be within a few metres of each other and you have a high scanning rate (e.g. every 10 seconds). In these situations we would suggest that another system may be more appropriate.

Logger function in field realistic conditions: Loggers were tested in field realistic settings to determine whether using Bluetooth Low Energy would be suitable for animal borne proximity loggers. Encouragingly, we found that our system was able to detect advertisements in a range of habitats representative of our focal species' preferred habitats. The range over which we were able to detect contacts differed with habitat type and between loggers (Tab. 1), reinforcing the importance of calibration for effective logger use.

Validations: The relationship between distance and received signal strength (RSSI) is variable depending on both the logger itself and the habitat within which the logger is moving. Adding the loggers to gloves

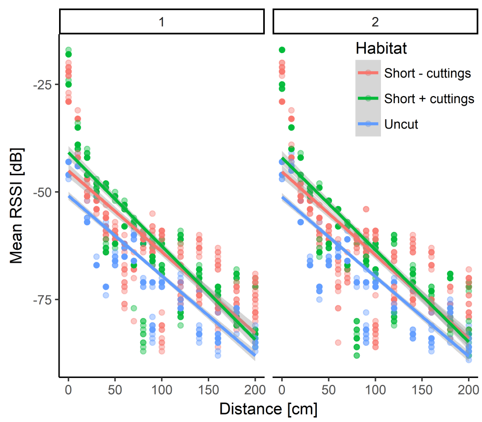

Figure 3 – Relationship between RSSI and distance for two habitat types and 5 loggers (all with epoxy applied). Points indicate raw measurements in different habitats, ribbons indicate predicted relationship between RSSI and distance returned from the model, pale ribbon indicates the 95% simultaneous confidence intervals.

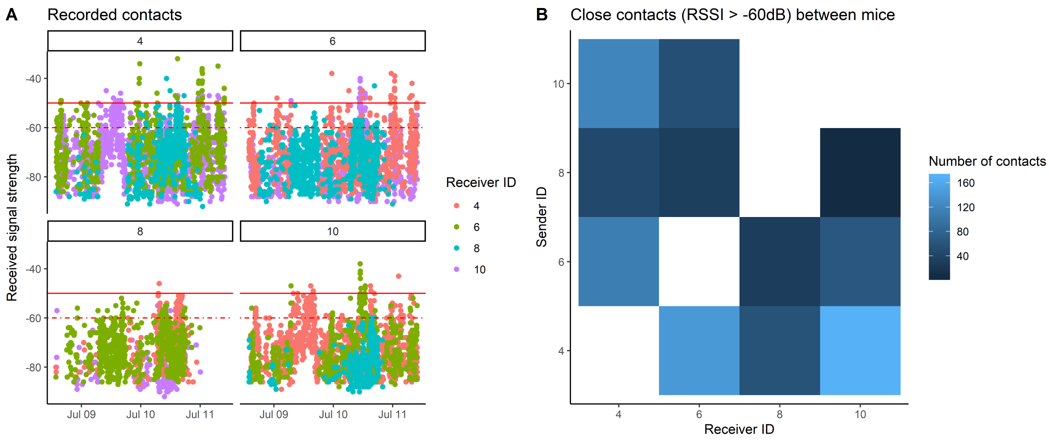

Figure 4 – Contacts recorded between collared rodents. A: Contacts recorded between collared rodents for the duration of the experiment. Coloured points indicate a contact between two individuals, horizontal dashed red line shows -60 dB, the cut off in received signal strength for a close contact (within 50 cm), horizontal solid red line shows -50 dB, the cut off in received signal strength for a very close contact (within 10 cm). B: Distribution of contacts between individuals showing that loggers mostly recorded similar numbers of contacts.

filled with water to mimic a rodent body did not cause any change to signal transmission in the three different habitats. Signal transmission declined more steeply with distance in the very long grass than in either the cut grass with cuttings removed or the cut grass with cuttings retained (F_{2468}=39140; short grass no cuttings: -44.7±0.4; short grass + cuttings: -43.0±0.4; uncut grass: -50.1±0.3, adjusted R^2=0.98; Fig. 3).

Grid validation: The additive model accounted for 73% of the variation in received signal strength. We found significant variation between loggers (Tab. 1), with logger 4, for example, consistently recording lower RSSI values than other loggers. Distances below 30 cm, which could constitute a "contact" in our system, were predicted by RSSI values of an average of -27 (95% CI -10.8–43.6) dB (Fig. 3). However, we did find occasions where dyads of associations were not registered (i.e. contacts were recorded on one logger but not the other logger). The extent to which this occurred increased with distance (F_{478}=25.8, change in position: -0.03±0.007); at the shortest distance loggers had an average of 3.5 (95% CI 2.3–4.0) contacts compared to 3.0 (95% CI 1.5–4.0) as distance increased.

Gateway: Increasing the height of the gateway increased the distances at which the gateway was able to connect with the loggers. If the gateway was moved from 15 cm off the ground to 1 m off the ground, the distance at which it could receive loggers increased from 5.5 m to 11.7 m. Raising it a further metre from the ground increased the distance to 18.2 m due to improved line of sight. It is therefore advised to consider the distance over which tag download is required when placing gateways. Signal strength at the gateways can be increased by the addition of an antenna, increasing the potential coverage of the gateway. However, this is beyond the scope of what is currently developed for the system, and has not yet been tested.

Field realistic trial results

Multimammate mouse trials: We tested the loggers on our multimammate mice in an indoor arena. Because the arena was indoor and very small, we would expect loggers to be in near constant range of eachother. In total 8076 logs were recorded between the four individuals out of an expected 8195, missing 1.5% of possible logs, likely due to signals colliding with each other. Loggers recorded a total of 833 close contacts (10% of all logs, RSSI greater than -60 dB; Fig. 4A) and 90 very close contacts (1% of all logs; RSSI greater than -50 dB, Fig. 4A). Very close contacts coincided with animals huddled together during the "day", which was visually confirmed from inspecting video

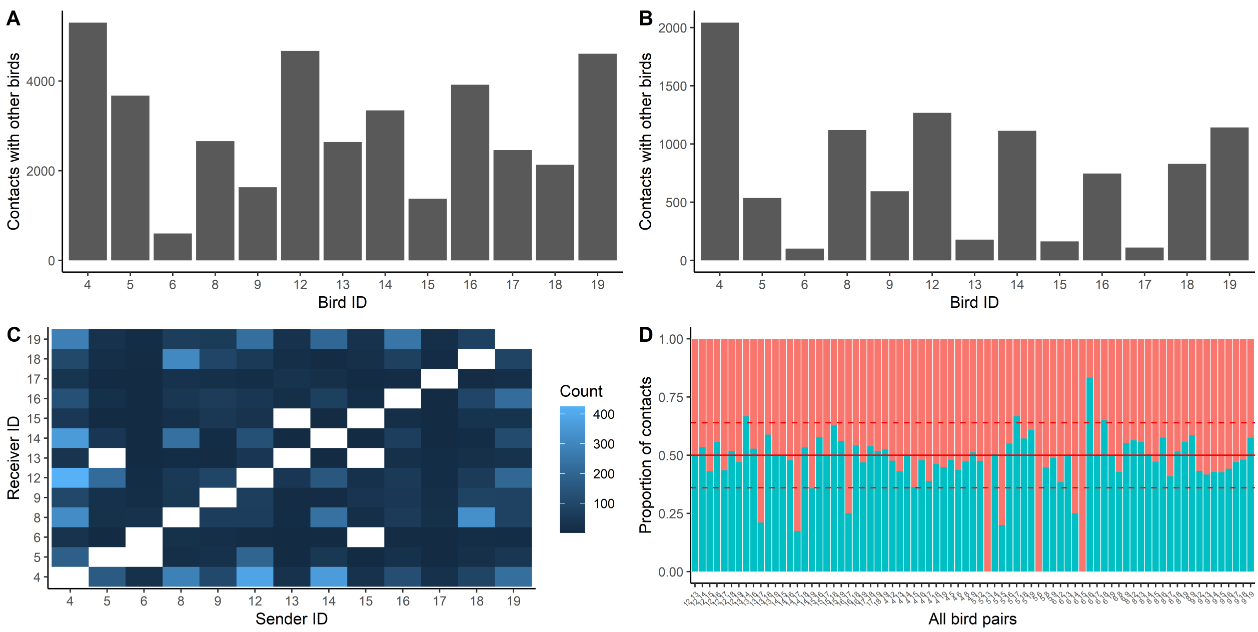

Figure 5 – Contacts recorded with other birds for each bird for A: Contacts (RSSI >-60) where birds are within half a meter of each other and B: Close contacts (RSSI >-50) where birds are within a few centimeters of each other. C: Plot showing registers on each pair of loggers, fill shows the count of logs recorded by each logger in the pair; D: Proportion of total contacts recorded by each logger in a pair. Solid red line indicates 0.5 where both loggers have recorded equal logs of each other, dashed lines represent the standard deviation. Logger pairings which fall outside of the standard deviation indicate where one logger in the pair recorded more / less logs than the other logger.

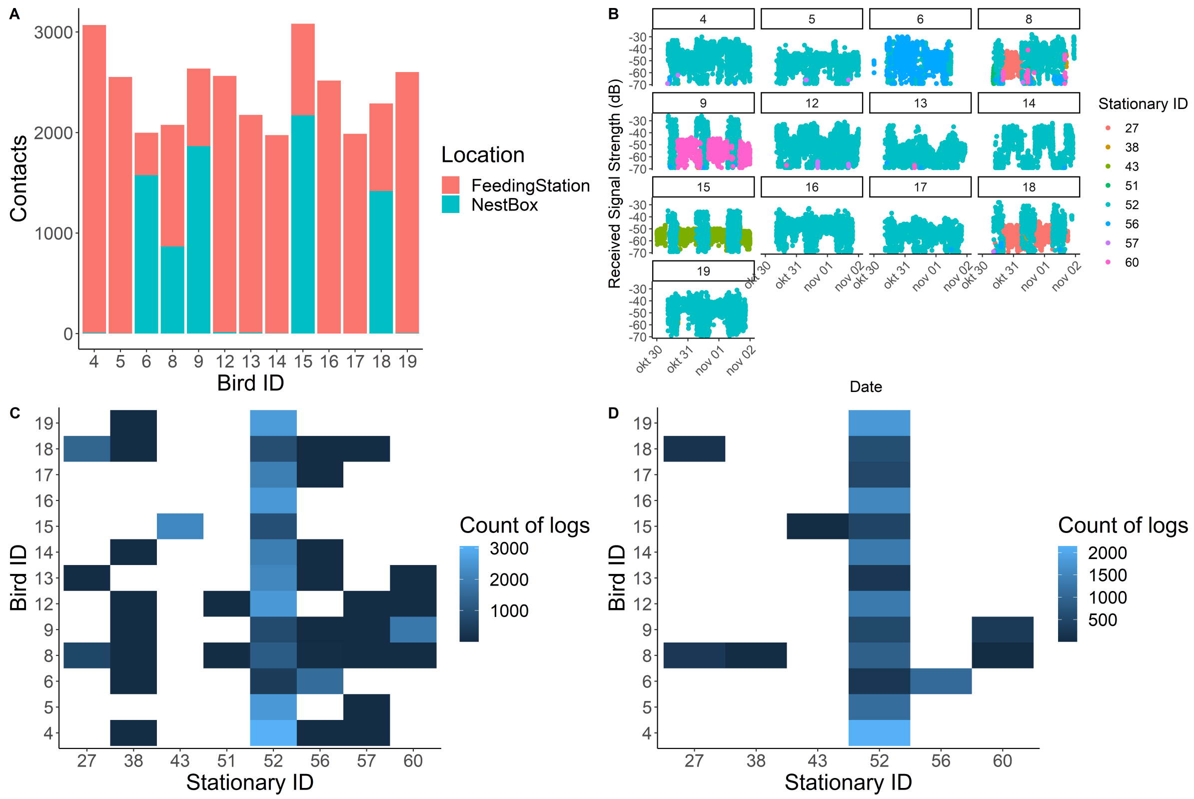

Figure 6 – A: Number of logs recorded on stationary loggers for each bird separated by whether the stationary logger was placed at the feeding station or a nest box. B: Temporal fluctuations in contacts between stationary and mobile loggers during the course of the experiment. Logs are filtered to only consider contacts with an RSSI of -70 dB or more. C: Heatmap showing logs by nest box and feeders for each bird when considering contacts (RSSI >-70dB). D: Heatmap showing very close (>-50dB) contacts between birds and stationary loggers.

footage. Because of the quality of the camera footage and the size of the indoor arena it was not possible to relate associations between individuals on the camera footage to associations detected by the loggers. However, individuals differed in the number of contacts that were recorded, with three individuals having similar numbers of contacts and one individual recording far fewer close contacts and very close contacts (see Fig. 6). Individual 8 had fewer close and very close contact associations than the other individuals (Fig. 4B). She was also the heaviest individual (15 g heavier than the other individuals) and increased in weight during the experiment while all others lost weight (see Supplemental Materials Table S8). The low number of close and very close contacts recorded suggests that mice spent the majority of time apart from each other, even given the small space of the arena. This is also visible in the video footage where mice are seen to be very active during the “night” with few associations between individuals but do spend some time sleeping together in very close proximity (e.g. two mice were seen on video footage sleeping together in a tube for 5 hours, which was revealed to be mice 6 and 10 from the logger data).

Starling trials: Of 15 birds fitted with a logger, 13 retained the logger in working order for the full 3 days of the experiment while two loggers failed, apparently due to moisture ingress.

Mobile loggers mounted on birds recorded a total of 103029 contacts, of which 39132 (37%) signified actual contacts (RSSI greater than -80 dB), and 9966 (10% of the total logs and 25% of the contact logs) would be considered close contacts (RSSI greater than -50 dB implying that the two loggers are within ≈10 cm to each other). Contacts were fairly evenly distributed between birds (Fig. 5A) but when concentrating on close contacts it is clear that some birds had a lot more close contacts than others (Fig. 5B). Contacts should be logged twice, by both individuals involved in the association. When considering close contacts, in the majority of cases logs on each member of a pair match each other (Fig. 5C), although there are some cases where one bird logged contacts and another didn’t. For example, bird 5 did not log any contacts with bird 6, but bird 6 did log one contact with bird 5. Birds logged each other more similarly when considering individuals with more logs (Fig. 5D); bird pairings with very uneven logs were all those which had a very small number of logs (less than 10 logs in total between both birds). Stationary loggers recorded a total of 31629 logs, of which 14368 could be considered very close contacts and would indicate the bird is on the feeder or in the nest box. The vast majority of logs were recorded by the logger placed at the feeding station (23602 logs, 12587 close contact logs; Fig. 6A). Loggers were placed at the 8 nest boxes distributed in the aviary; while all nest box loggers recorded some associations, not all boxes recorded close associations suggesting that birds did not use all boxes (Fig. 6A). Associations with the feeder and nest boxes varies between birds, with some birds staying in the vicinity of the feeding station at all times, while others split their time between the feeding station and nest boxes (Fig. 6B, 6C). Some nest boxes were also more popular than others, with boxes 57 and 51 appearing to have few contacts and no close contacts (Fig. 6C, 6D). Combining stationary and mobile logger data revealed that birds were sharing nest boxes overnight (e.g birds 8 and 18).

Comparison with camera footage: Comparing logs with the camera trap footage revealed that logs of RSSI -60 dB and greater corresponded to a bird interacting with the box (sitting on the perch, being inside the box, or sitting inside the box looking out). An RSSI of -50 dB or greater corresponded with a bird being inside the box. Nestbox loggers recorded 7094 associations at -60 dB or greater, of which 6 (0.08%) could not be matched with either direct camera trap footage of a bird entering or leaving a box, or with periods between which birds were seen entering or leaving a nest box. Camera trap footage can be associated directly with 46 (0.7%) of logs, indicating birds either sitting on the perch outside the box or entering and leaving the nest box. In some cases the camera was clearly triggered by a bird entering or leaving the box, but the bird was either not visible (but box shaking and a close contact log recorded) or was just visible. In 30 cases (0.42%), logs show associations with the boxes that are not detected at all by the camera trap. It was rare that camera trap picture quality was sufficient to ID a bird, but the ID of the bird could be determined by cross referencing the logger ID with the camera trap footage. Logger data gave additional data that would not be possible to retrieve from camera traps alone. The camera traps often missed an entry or an exit, or the ID of the bird was not visible so the duration and ID of any birds association with the nest box would be unknown; 80% of the logs between nest boxes and birds occurred over night or when a camera had missed a bird enter or leave. After removing camera trap footage involving a bird with a broken logger, there were 8 occasions (0.01% of associations) where birds were caught by the camera trap at a box without any corresponding logger data. While camera traps do record interactions and behaviour that would not be inferred from logger data (for example antagonistic interactions between two birds at a nest box), loggers also captured behaviour that was missed by cameras, such as birds sharing a box when the entry of one bird was not captured on the camera traps. Furthermore, the loggers provide reliable information about the ID of the animal involved in the associations which very rarely occurred from camera trap data. Comparison of the stationary, mobile and camera trap data shows that the majority of bird associations took place away from nest boxes. Of nearly 10000 close contact logs that were recorded, 40% were in close proximity of the feeder, 0.8% were in close proximity with nest boxes and the other 59% were elsewhere in the aviary. Such associations away from a focal point would be missed in a system where a ground antenna is required to record presence, such as a passive RFID (Radio Frequency Identification) system.

Discussion

Common analytical tools used to explore animal contact networks, such as graph theory, are known to be highly sensitive to the sampling effort carried out to define the network (Tentelier et al., 2016). Missing associations can have significant consequences for some topographical statistics (James et al., 2009), therefore accurately quantifying associations is vital for parameterizing many network analysis approaches (James et al., 2009). Furthermore, the ability to record the behaviour of the most species-rich body weight classes in birds and mammals depends on either battery miniaturisation or reduced energy consumption of such tags (Kays et al., 2015). Here we present a novel approach to determine contacts between wild animals using extensive miniaturisation and Bluetooth Low Energy, a form of wireless communication which is currently under active development. To date, weighted automated social network data on small animals derived from proximity loggers are sparse due to the size constraints imposed by the loggers themselves (Levin et al., 2015). While approaches using RFID readers have become more popular in recent years, these can only record associations within the presence of a reader, which may involve altering animal behaviour to record the association (for example providing feeders or nest boxes to record associations). While these experiments can reveal fascinating insights into animal behaviour, our live experiment showed that the majority of associations actually took place away from the feeder or a nest box, showing the utility of proximity detection systems for providing a continuous log of animal association behavior (Ripperger et al., 2020a).

We experimentally tested our system performance with two experiments, one in which we tagged 15 European starlings (*Sturnus vulgaris*) in a large, outdoor aviary, with stationary loggers placed at a feeding station and eight nest boxes and another in which we tagged four multimammate mice in a small, indoor arena. This experiment was a trial for a larger experiment collaring wild *M. natalensis* and was used to verify collars fitted mice without causing any damage. For the starlings, two loggers failed shortly after attachment but the others collected data for the full period of the experiment. Coverage was very consistent throughout both experiments, with data collected at a high temporal resolution. We found little evidence of substantial data loss due to collisions in either trial, with most logs mirrored on both loggers particularly when considering close contacts only. Logs deviated from being very similar when very few logs were recorded, which may suggest that these associations were only fleeting rather than data loss due to collision risk. For the starling experiment we were able to compare the camera trap and logger data, which showed a high accordance between the two. Logger data and camera trap data was able to be matched 99% of the time, although both forms of surveillance provided different forms of additional data. While bird interactions with each other and the nest boxes were observed on the camera traps, the bird ID was often hard to identify from rings due to the picture quality or the time of the photo (after dark and therefore not in colour), and had to be inferred from the loggers. Furthermore, camera traps missed key moments like birds swiftly entering and leaving the boxes while loggers provided a consistent record of bird presence in the boxes and with each other. In contrast a very small number of associations were recorded at nest boxes that were missed by the loggers (less than 1% of the total associations).

We were not able to use the video footage to identify individuals in the multimammate mouse experiment, but the loggers did reveal evidence of a dominance hierarchy that was substantiated by the video footage. For example, one individual had very few close and very close contacts and two individuals were often seen sleeping together which was also reflected in a large number of very close contacts recorded by the loggers during the same time period.

Such insights into small mammal behaviour are extremely challenging to gather from other means yet may play in important role in a wide range of different population level processes, from disease transmission to mate selection. For example, sickness is known to induce avoidance behaviour in mice (Kavaliers et al., 2019) as well as alterations to individual behaviour that reduce social contacts (Lopes et al., 2016; Ripperger et al., 2020b). Animal association behaviour can also change with environmental context; ground squirrel associations can differ depending on whether they are above ground or below ground (Smith et al., 2018) with consequences for both disease and information transmission. Such proximity loggers can also provide insights into mate choice through the creation of sexual networks (Tentelier et al., 2016) which will have potential consequences for population growth and control. Indeed, standard proximity or GPS loggers have revealed complexities in the social lives of large mammals such as giraffe (Vanderwaal et al., 2014), elk (Vander Wal et al., 2013) and tasmanian devils (Hamede et al., 2009) and new developments such as ICARUS (https://www.icarus.mpg.de/en) and miniaturised GPS systems are increasing the range of vertebrate species which can be tracked. However, for the majority of extant vertebrate species, the spatial scale and accuracy of GPS based approaches is too coarse, particularly in structurally complex environments such as under forest canopy cover (Ripperger et al., 2020a). In such cases, alternative small scale and lightweight tracking devices such as described here hold great promise in uncovering the role behaviour may play in driving various demographic processes such as reproduction, disease transmission or information transfer.

Our approach includes a range of battery options which will allow the development of loggers with a minimum weight of <1 g depending on mounting options. However, while such small loggers increase both the species and individuals within species in which proximity behaviour can be explored, it should be noted that, as with all these systems, we are still only able to monitor a subset of the population due to trapping biases and individuals which do not meet the minimum weight requirements (James et al., 2009), and when monitoring such small animals, powered systems will always have some limitation to runtime. By incorporating different energy management regimes, we have increased the potential runtimes that can be achieved, therefore increasing the data which can be gathered. Nevertheless, miniature proximity sensors, produced with off-the-shelf components such as we have used here provide an inexpensive and lightweight approach to monitoring association behaviour between wild animals. As currently described, our system would be most appropriate for monitoring proximity behaviour of species which are either enclosed within a space that can be easily monitored with gateways (e.g. mesocosm experiments), or regularly pass or return to known points in order to download contact data. Our chips were able to consistently communicate with each other, the gateway and the mobile phone application in the field, validating the approach. The addition of epoxy did not change the effectiveness of the approach, suggesting that sealing to ensure that loggers are safe from damage will not adversely affect the system. As the antenna is contained within the PCB, we do not expect to see changes in RSSI in response to antenna manipulation as has been described from other systems (Ripperger et al., 2016; Rutz and Burns, 2012).

We predict a longer battery life than that described for the Encounternet system (Levin et al., 2015), with a similar temporal resolution. However, our system has additional flexibility built in that can be used to extend the battery life, such as by setting the logger to sleep during certain periods of known inactivity, or by deactivating scanning. Due to our configuration of data storage on the chip, our loggers are able to store up to 2000 contacts before becoming full, increasing the period during which focal animals can be away from the gateways before data loss occurs and allowing for contacts to be recorded when animals are in unknown locations. Alternatively, in systems where a relatively low number of encounters are expected, gateways can be set to download data from loggers when a lower number of contacts are stored, reducing the risk of losing data due to tag malfunction or loss of a focal animal (Rutz and Burns, 2012). Collision risk increases when a large number of loggers are in close proximity to each other; in systems where this is likely it may be preferable to increase the measurement interval to reduce the likelihood of collisions. While we recognise that this is not ideal, using the loggers within an enclosed aviary with 13 birds and 9 stationary loggers still resulted in high resolution social and spatial information. We have also made the system as simple to use as possible, the mobile phone application makes it straightforward to monitor and adjust detection settings in real time, including after loggers have been attached to focal animals while data is directly downloaded as a .csv file which can easily be manipulated for analysis.

The greatest challenge with analyzing proximity data is the conversion from RSSI to distances between animals (Ripperger et al., 2016; Rutz et al., 2015). When moved at ground level in structurally complex habitats, loggers were able to detect the presence of other loggers over a range of distances below one meter. Between two to three meters, this relationship was less clear and differentiating distances was no longer possible, although loggers were still able to make contact. This is lower than distances reported from the Encounternet system (Levin et al., 2015) and Ripperger et al. (2016), but our tests only considered movement for terrestrial rather than aerial species in structurally complex habitats. In our live tests, comparison of logging data and camera trap data revealed that RSSI's of -50 dB or greater were consistently aligned with very close associations (within 10 centimeters) in line with our tests and could therefore confidently be assigned to a contact. Detection distances between loggers will increase substantially in open space, if animals move vertically as well as horizontally, or with the addition of an antenna, which may be appropriate for other study systems. In our live test we also found that the gateway was able to reliably download loggers that were up to 30 m distant, reflecting the increase in transmission distance when both loggers and the gateway are placed at least 1m from the floor. In situations where users may want a larger gateway coverage, additional gateways can be used to download data. Although our system showed fairly stable declines in RSSI over short (<1 m) distance within different habitat types, there was considerable variation between the different loggers and this needs to be accounted for in the calibration. We present an approach, derived from Berkvens et al. (2018), which allows users to easily and relatively swiftly calibrate a number of loggers at one time; this is essential to estimate distance categories which reflect reality in the focal system (Clair et al., 2015; Ripperger et al., 2016; Rutz and Burns, 2012).

The miniaturisation of biologgers is an exciting development for researchers who want to understand how association behaviour influences a range of different processes. How animals interact with each other is fundamental to understanding both the biology and behaviour of animals (Krause et al., 2013), with consequences for disease transmission (Hamede et al., 2009), gene flow (Tentelier et al., 2016), information transfer (Clair et al., 2015) and resource exploitation (Marsh et al., 2011). The utility of proximity loggers is not restricted to mammalian or avian species; with sufficient miniaturisation loggers can also be applied to large invertebrate species, and current logger sizes would not preclude the use of these loggers on many reptilian species. Automated processes with remote access availability will increase the range of species such information can be collected on as the majority of vertebrate species are either small, cryptic or impossible to observe directly in the field (Croft et al., 2016; Kays et al., 2015).

Future directions

In recent years tracking technology has passed important thresholds in both the size of the logger and the resolution of the data being collected (Kays et al., 2015); miniaturised proximity loggers will not only allow an increased quantity and quality of data to be collected, but also allow the addition of other sensors to augment the proximity data being collected (Wilmers et sl., 2015), providing an integrated view of the animal and its environment (Kays et al., 2015; Wilmers et sl., 2015). For example, Cassens et al. (2017) demonstrated how including an accelerometer provides insight into the behaviour of tagged bats during monitoring with proximity sensors as well as incorporating an elegant way of restricting energy use to periods of activity. Temperature loggers may be useful to indicate arousal from torpor, or to equate association behaviour to environmental conditions (Cassens et al., 2017). The addition of other sensors to our loggers is easily achieved, although the energy requirements and additional weight of any sensors needs to be taken into account. Gateway development is currently underway to include the ability to download data remotely by accessing mobile data networks as well as creating a meshed "network" of gateways, extending the range over which loggers can be reliably downloaded. This approach would allow gateways to communicate between each other, offloading data to a single "master" gateway. Finally, recent improvements in range for BLE transmission means that data may now be collected over a larger spatial area or for a greater range of research questions. Our approach complements the similar approaches designed by Cassens et al. (2017); Duda et al. (2018); Ripperger et al. (2016), and adds another method to the growing toolbox of biologging approaches, particularly because the open source, low cost nature of our approach means accessing our system should be more achievable for a range of different users.

References

Aernouts M., Berkvens R., Van Vlaenderen K., Weyn, M., 2018. Sigfox and LoRaWAN Datasets for Fingerprint Localization in Large Urban and Rural Areas. Data: 1–15. 10.3390/data3020013

Ayele E.D., Meratnia N., Havinga P.J., 2018. Towards a new opportunistic IoT network architecture for wildlife monitoring system. In: 2018 9th IFIP International Conference on New Technologies, Mobility and Security (NTMS), IEEE. 1–5.

Bateson M., Feenders G., 2010. The use of passerine bird species in laboratory research: implications of basic biology for husbandry and welfare. ILAR Journal 51(4): 394–408.

Berkvens R., Olivares I.H., Mercelis S., Kirkpatrick L., Weyn M., 2018. Contact detection for social networking of small animals. In: International Conference on P2P, Parallel, Grid, Cloud and Internet Computing. Springer, Cham. 405–414.

Böhm M., Palphramand K.L., Newton Cross G., Hutchings M.R., White P.C.L., 2008. Dynamic interactions among badgers: implications for sociality and disease transmission. Journal of Animal Ecology: 77(4): 735–745.

Borremans B., Hughes N.K., Reijniers J., Sluydts V., Katakweba A.aS., Mulungu L.S., Leirs H., 2014. Happily together forever: Temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. Population Ecology 56(1): 109–118. 10.1007/s10144-013-0393-2

Cassens B., Ripperger S., Hierold M., Mayer F., Kapitza R., 2017. Automated Encounter Detection for Animal-Borne Sensor Nodes. EWSN '17 Proceedings of the 2017 International Conference on Embedded Wireless Systems and Networks. EWSN 17: 20–22.

Clair J.J.H.S., Burns Z.T., Bettaney E.M., Morrissey M.B., Otis B., Ryder T.B., Rutz C., 2015. Experimental resource pulses influence social-network dynamics and the potential for information flow in tool using crows. Nature Communications 6: 1–8. 10.1038/ncomms8197

Craft M.E., Volz E., Packer C., Meyers L.A., 2010. Disease transmission in territorial populations: the small-world network of Serengeti lions. Journal of the Royal Society Interface. 8(59): 776–786.

Croft D.P., Darden S.K., Wey T.W, 2016. Current directions in animal social networks. Current Opinion in Behavioral Sciences, 12: 52–58. 10.1016/j.cobeha.2016.09.001

Davis S., Abbasi B., Shah S., Telfer S., Begon M., Davis S., 2015. Spatial analyses of wildlife contact networks. Royal Society Interface, 12.

Dressler F., Mutschlechner M., Nabeel M., Blobel J., 2019. Ultra Low-Power Sensor Networks for Next Generation Wildlife Monitoring. 11th International Conference on Communication Systems & Networks (COMSNETS) 2061: 44–48.

Drewe J.A., O'Connor H.M., Weber N., McDonald R.A., Delahay R.J., 2013. Patterns of direct and indirect contact between cattle and badgers naturally infected with tuberculosis. Epidemiology and Infection 141(7): 1467–1475. 10.1017/S0950268813000691

Drewe J.A., Weber N., Carter S.P., Bearhop S., Harrison X.A., 2012. Performance of Proximity Loggers in Recording Intra- and Inter-Species Interactions: A Laboratory and Field-Based Validation Study. PLoS ONE 7(6): 0039068. 10.1371/journal.pone.0039068

Duda N., Nowak T., Hartmann M., Schadhauser M., Cassens B., Wägemann P., Kölpin A., 2018. BATS: Adaptive Ultra Low Power Sensor Network for Animal Tracking. Sensors 18(10): 3343. 10.3390/s18103343

Eens M., 1997. Understanding the complex song of the European starling: an integrated ethological approach. Advances in the Study of Behaviour 26: 355–434.

Galbraith J.A., Stanley M.C., Jones D.N., Beggs J.R. 2017. Experimental feeding regime influences urban bird disease dynamics. Journal of Avian Biology 48: 700–713. 10.1111/jav.01076

Ghamari M., Villeneuve E., Soltanpur C., Khangosstar J., Janko B., Sherratt R.S., 2018. Detailed Examination of a Packet Collision Model for Bluetooth Low Energy Advertising Mode. IEEE Access 6: 46066–46073. 10.1109/ACCESS.2018.2866323

Greenlees M.J., Brown G.P., Webb J.K., Phillips B.L., Shine R., 2007. Do invasive cane toads (*Chaunus marinus*) compete with Australian frogs (*Cyclorana australis*)? Austral Ecology 32: 900–907. 10.1111/j.1442-9993.2007.01778.x

Hamede R.K., Bashford J., McCallum H., Jones M., 2009. Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecology Letters 12: 1147–1157. 10.1111/j.1461-0248.2009.01370.x

Ilany A., Akçay E., 2016. Social inheritance can explain the structure of animal social networks. Nature Communications 7(1): 1–10. 10.1038/ncomms12084

James R., Croft D.P., Krause J., 2009. Potential banana skins in animal social network analysis. Behavioural Ecology and Sociobiology 63: 989–997. 10.1007/s00265-009-0742-5

Ji W., White P.C.L., Clout M.N., 2005. Contact rates between possums revealed by proximity data loggers. Journal of Applied Ecology 42(3): 595–604. 10.1111/j.1365-2664.2005.01026.x

Jones K.E., Patel N.G., Levy M.A., Storeygard A., Balk D., Gittleman J.L., Daszak P., 2008. Global trends in emerging infectious diseases. Nature 451(7181): 990–993.

Kavaliers M., Colwell D.D., Wah D.T.O., Bishnoi I.R., Ossenkopp K.P., Choleris E., 2019. Conspecific infection threat rapidly biases the social responses of female mice: Involvement of oxytocin. Hormones and Behavior 113: 67–75. 10.1016/j.yhbeh.2019.04.016

Kays R., Crofoot M., Jetz W., Wikelski M., 2015. Terrestrial animal tracking as an eye on life and planet. Science 348(6240): aaa2478. 10.1126/science.aaa2478

Krause J., Krause S., Arlinghaus R., Psorakis I., Roberts S., Rutz C., 2013. Reality mining of animal social systems. Trends in Ecology & Evolution 28(9): 541–551. https://doi.org/10.1016/j.tree.2013.06.002

Leirs H., 1994. Population ecology of *Mastomys natalensis* (Smith, 1834). Implications for rodent control in Africa. PhD Thesis, University of Antwerp.

Lemic F., Handziski V., Aernouts M., Janssen T., Berkvens R., Wolisz A., Famaey J., 2019. Regression-Based Estimation of Individual Errors in Fingerprinting Localization. IEEE Access 7: 33652–33664. 10.1109/ACCESS.2019.2903880

Levin I.I., Zonana D.M., Burt J.M., Safran R.J., 2015. Performance of Encounternet Tags: Field Tests of Miniaturized Proximity Loggers for Use on Small Birds. PLoS ONE 9: 1–18. 10.1371/journal.pone.0137242

Lopes P.C., Block P., König B., 2016. Infection-induced behavioural changes reduce connectivity and the potential for disease spread in wild mice contact networks. Scientific Reports 6: 1–10. 10.1038/srep31790

Maroto-Molina F., Navarro-Garcìa J., Principe-Aguirre K., Gomez-Maqueda I., Guerrero-Ginel J., Garrido-Varo A., Perez-Marin D., 2018. A Low-Cost IoT-Based System to Monitor the Location of a Whole Herd. Sensors 19(10): 2298.

Marsh M.K., McLeod S.R., Hutchings M.R., White P.C.L., 2011. Use of proximity loggers and network analysis to quantify social interactions in free-ranging wild rabbit populations. Wildlife Research 38(1): 1–12. 10.1071/WR10150

Qureshi U.M., Shaikh F.K., Aziz Z., Shah Z., Sheikh A., Felemban E., Qaisar S., 2016. RF Path and Absorption Loss Estimation for Underwater Wireless Sensor Networks in Different Water Environments. Sensors 16(890): **missing page numbers**. 10.3390/s16060890

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reynolds J.J.H., Hirsch B.T., Gehrt S.D., Craft M.E., 2015. Raccoon contact networks predict seasonal susceptibility to rabies outbreaks and limitations of vaccination. Journal of Animal Ecology 84(6): 1720-1731. 10.1111/1365-2656.12422

Ripperger S., Josic D., Hierold M., Koelpin A., Weigel R., Hartmann M., Mayer F., 2016. Automated proximity sensing in small vertebrates: design of miniaturized sensor nodes and first field tests in bats. Ecology and Evolution 6(7): 2179–2189. 10.1002/ece3.2040

Ripperger S.P., Carter G.G., Page R.A., Duda N., Koelpin A., Weigel R., Mayer F., 2020. Thinking small: next-generation sensor networks close the size gap in vertebrate biologging. PLoS biology 18(4): e3000655. 10.1371/journal.pbio.3000655

Ripperger S.P., Stockmaier S., Carter G.G., 2020b. Tracking sickness effects on social encounters via continuous proximity sensing in wild vampire bats. Behavioral Ecology 31(6): 1296–1302. 10.1093/beheco/araa111

Roeleke M., Blohm T., Kramer-Schadt S., Yovel Y., Voigt C.C., 2016. Habitat use of bats in relation to wind turbines revealed by GPS tracking. Scientific Reports 6(1): 1–9. 10.1038/srep28961

Rutz C., Burns Z.T., 2012. Automated mapping of social networks in wild birds. Current Biology 22(17): 669–671. 10.1016/j.cub.2012.06.037

Rutz C., Morrissey M.B., Burns Z.T., Burt J., Otis B., Clair J.J.H.S., James R., 2015. Calibrating animal-borne proximity loggers. Methods in Ecology and Evolution 6: 656–667. 10.1111/2041-210X.12370

Sheehy E., Sutherland C., O'Reilly C., Lambin X., 2018. The enemy of my enemy is my friend: Native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. Proceedings of the Royal Society B: Biological Sciences 285(1874): 20172603. 10.1098/rspb.2017.2603

Smith J.E., Gamboa D.A., Spencer J.M., Travenick S.J., Ortiz C.A., Hunter R.D., Sih A., 2018. Split between two worlds: Automated sensing reveals links between above- and belowground social networks in a free-living mammal. Philosophical Transactions of the Royal Society B: Biological Sciences 373(1753): 20170249. 10.1098/rstb.2017.0249

Tentelier C., Aymes J., Spitz B., Rives J., 2016. Using proximity loggers to describe the sexual network of a freshwater fish. Environmental Biology of Fishes 99(8): 621–631. 10.1007/s10641-016-0504-y

Vander Wal E., Laforge M.P., Mcloughlin P.D., 2013. Density dependence in social behaviour: home range overlap and density interacts to aff(3): ect conspecific encounter rates in a gregarious ungulate. Behavioural Ecology & Sociobiology 68(3): 383–390. 10.1007/s00265-013-1652-0

Vanderwaal K.L., Wang H., McCowan B., Fushing H., Isbell L.A., 2014. Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). Behavioural Ecology 25(1): 17–26. 10.1093/beheco/art061

Walrath R., Van Deelen T., Vercauteren K., 2011. Efficacy of Proximity Loggers for Detection of Contacts Between Maternal Pairs of White-Tailed Deer. Wildlife Society Bulletin 35(4): 452–460. 10.1002/wsb.76

Wilmers C.C., Nickel B., Bryce C.M., Smith J.A., Wheat R.E., Yovovich V., 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology 96(7): 1741–1753. 10.1890/14-1401.1

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Acronyms

BLE *Bluetooth Low Energy* – Low energy form of Bluetooth wireless communication. Supported as standard by most mobile and computing operating systems.

RSSI *Received Signal Strength Indicator* – Estimate of the power that a radio frequency device is receiving from another device. Can be broadly equated to changes in distance, with the RSSI decreasing as distance between devices increases.

LoRa *Long Range* – Proprietary low power wide area network modulation technique. Enables long range transmission with low power consumption, but lacks accuracy over smaller ranges.

NB-IoT *Narrow Band Internet of Things* – Low power wide area network radio technology standard. Concentrates on low power, low cost indoor localisation

BATS *Broadly Applicable Tracking System* – Low power, wide band network developed by Ripperger and colleagues. Proximity detection is carried out using BLE, additional spatial localisation and long range downloading possible.

GPS *Global Positioning System* – Satellite based radionavigation system that provides geolocation and timestamp data to specific devices. Needs a consistent signal to at least 4 satellites for accurate positioning, and is not low power.

RFID *Radio Frequency Identification* – Passive system that uses electromagnetic fields at a reader that are triggered by the logger to register a contact. No battery is required on the animal as the tag is passive. The range at which a tag can activate the reader are relatively limited ($\approx$60 cm or less)

Supplemental information

- Additional Supplemental Information may be found in the online version of this article:

Figure S1 Comparison between modeled and actual power consumption.
Appendix S2 Collision rates statistical model.
Figure S3 Habitat in which trials were carried out and prototype loggers used.
Appendix S4 Calibration routine.
Table S5 Grid layout used for performing calibrations.
Figure S6 Setup of the indoor arena.
Figure S7 Picture of an example collar and a multimammate mouse wearing a collar.
Table S8 Details of the tagged multimammate mice.
Figure S9 Picture of starling with a logger attached as a backpack.
Figure S10 Layout of the starling aviary for the field trial.