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Understanding and geo-referencing animal contacts: proximity sensor networks integrated with GPS-based telemetry

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Abstract

Background: In animal ecology, inter-individual encounters are often investigated using automated proximity loggers. However, data acquired are typically spatially implicit, i.e. the question '*Where* did the contact occur?' remains unanswered. To resolve this issue, recent advancements in Wireless Sensor Network technology have facilitated the geo-referencing of animal contacts. Among these, WildScope devices integrate GPS-based telemetry within fully distributed networks, allowing contact-triggered GPS location acquisition. In this way, the ecological context in which contacts occur can be assessed. We evaluated the performance of WildScope in close-to-real settings, whilst controlling for movement of loggers and obstacles, performing field trials that simulated: (1) different scenarios of encounters between individuals (mobile–mobile contacts) and (2) patterns of individual focal resource use (mobile–fixed contacts). Each scenario involved one to three mobile and two fixed loggers and was replicated at two different radio transmission powers. For each scenario, we performed and repeated a script of actions that corresponded to expected contact events and contact-triggered GPS locations. By comparing expected and observed events, we obtained the success rate of: (1) contact detection and (2) contact-triggered GPS location acquisition. We modelled these in dependence on radio power and number of loggers by means of generalized linear mixed models.

Results: Overall we found a high success rate of both contact detection (88–87%: power 3 and 7) and contact-triggered GPS location acquisition (85–97%: power 3 and 7). The majority of errors in contact detection were false negatives (66–69%: power 3 and 7). Number of loggers was positively correlated with contact success rate, whereas radio power had little effect on either variable.

Conclusions: Our work provides an easily repeatable approach for exploring the potential and testing the performance of WildScope GPS-based geo-referencing proximity loggers, for studying both animal-to-animal encounters and animal use of focal resources. However, our finding that success rate did not equal 100%, and in particular that false negatives represent a non-negligible proportion, suggests that validation of proximity loggers should be undertaken in close-to-real settings prior to field deployment, as stochastic events affecting radio connectivity (e.g. obstacles, movement) can bias proximity patterns in real-life scenarios.

Keywords: Contact-triggered GPS, Fully distributed Wireless Sensor Networks (WSNs), Movement ecology, False positives and false negatives, Proximity loggers

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Background

Proximity loggers are increasingly used animal-borne devices [1] (see also Table 1), with great potential for behavioural ecology studies (e.g. predator–prey interactions [22]; intra-specific relationships [23]; social systems [24]) and wildlife epidemiology (i.e. by evaluating contact rate [10]). Proximity loggers contain a radio unit that is able to receive and transmit a low-power signal (ultra-high frequency, UHF, range 300 MHz–3 GHz) from/to other nearby loggers, thus forming a Wireless Sensor Network (WSN). In this way, loggers 'detect' the proximity of one another. A micro-controller and a power unit are essential complements to the radio sensor for deploying proximity loggers on animals, so that radio transmission and detection are self-powered, and recording and storing of information automated. Proximity loggers can be used as both biologging units, i.e. deployed on animals for subsequent data retrieval via recapture [5], and as biotelemetry devices, i.e. equipped with a remote data retrieval system, such as a GSM modem [9, 19], or a WSN comprised of mobile proximity loggers and fixed base stations (see Table 1 and [2, 9]). However, proximity loggers frequently provide only spatially implicit information, often processed with network-based analytical tools (e.g. Social Network Analysis [6, 12]), where the sampling units are the *contacts* between individuals (or 'edges') rather than the individuals wearing the devices. The value of proximity information can be further enhanced by making animal-to-animal contacts spatially explicit [25], providing ecologists with the added value of knowing *where* animal encounters occur. Thus, the ecological context of a given contact can be inferred (e.g. *which* habitat features characterize the contact site). Recent advancements in proximity logging technology have incorporated *indirect* geo-referencing of animal contacts (see Table 1). In particular, Encounternet [12] and BATS [20] are WSN systems that infer spatial contextualization of proximity patterns by post-processing, and specifically by estimating the distance between mobile loggers worn by individuals, and fixed loggers deployed in the study area. In this scenario, the geo-referencing of proximity patterns essentially depends on the spatial overlap between a network of fixed loggers and animal movements, i.e. ultimately on the range of the target species. Where monitored animals move over wide areas (as is typical of medium to large mammals), coverage with fixed loggers becomes unfeasible. In this case, geo-referencing of proximity patterns between individuals is possible via integration of a GPS sensor in the logger [13]. This capability is provided by those WSNs which integrate proximity detection with GPS-based telemetry to simultaneously provide GPS location acquisition with animal-to-animal contacts [19]. Two different configurations have been developed to date. One is a so-called master–slave configuration where *only* the 'master' logger has the capacity to communicate with other loggers (the 'slaves') and triggers GPS scheduling when contact occurs, but contacts and GPS locations between the 'slaves' are not recorded [26]. Another is a *fully distributed* configuration where *all* loggers communicate *equally* with each other, with both contacts and triggered GPS positions recorded by *all* loggers in the network [19]. The fully distributed configuration characterizes the prototype WildScope [19] and has recently also been proposed for some commercial loggers [27], although so far empirical applications in animal ecology remain limited.

Fully distributed configurations of WSNs somewhat parallel those of acoustic tags in the marine environment (e.g. detection of pelagic fish in harbours [28]), in that they combine a 'mixed' network of mobile and fixed loggers. Hence, they also provide new opportunities to simultaneously investigate both geo-referenced encounters between individuals (mobile–mobile contacts) and the use of specific habitat resources by individuals (mobile–fixed contacts). The latter has long been recognized as an important application of WSNs [5] but has thus far seldom been used in animal ecology studies (but see [10, 11] and Table 1). In this work, we explore the functionality and potential of WildScope WSN ([19] and Additional file 1) for animal ecology investigation.

Proximity loggers—and GPS-based geo-referencing proximity loggers—should be carefully calibrated prior to use [13], as with all biologging devices. To this end, several authors have attempted to identify both the potential and the limitations of WSNs, including contact reciprocity [15], effect of antenna orientation [5] and RSSI/distance relationship ([11, 13]; see also Table 1). However, no published studies have been presented so far to investigate performance of GPS-based geo-referencing proximity loggers in animal ecology and in particular to describe (1) *how to design* field calibration studies based on GPS-based geo-referencing proximity loggers, (2) what *type of information* GPS-based geo-referencing proximity loggers collect and (3) *how reliable* they are at collecting it.

To address these issues, we developed and tested a protocol to derive data on the occurrence and location of animal encounters in semi-controlled conditions using WildScope GPS-based geo-referencing proximity loggers. The work represents an extension of a preliminary field calibration [19] that measured the average contact distance threshold of loggers at different radio transmission powers, in static and controlled open-air conditions [10]. Here, we introduced two well-recognized sources of stochasticity in contact detection, i.e. the movement of loggers [11] and the presence of obstacles in the network [29]. Specifically, in our calibration exercise we mimicked

Table 1 Review of proximity logger deployments

Study	Logger brand or project name	Logger weight (g)	Target species	Mobile loggers	Static loggers	Target detection range (m)[a]	Radio frequency	Geo-referencing of encounters	Remote data download	Calibration scenario	Power consumption analysis
[2]	Zebranet	Not reported	Zebra (*Equus burchellii*)	Yes (only for data retrieving)	Yes (base stations 'daily drive')	Not reported	900 MHz	No A GPS module is embedded in the logger to track zebra movements	Yes Via radio between mobile loggers and base stations	Not reported	Yes
[3]	Sirtrack Ltd.	30	Common brushtail possum (*Trichosurus vulpecula*)	Yes	No	0.3–0.5	160 MHz	No	No (recapture necessary)	Tests on captive Possums [4]	No
[5]	Sirtrack Ltd.	125	Racoon (*Procyon lotor*)	Yes	No	1–1.5	916.5 MHz	No	No (recapture necessary)	Laboratory test to assess (1) threshold contact distance in dependence of antenna orientation; (2) contact duration and robustness Field tests on raccoons to evaluate (1) inter-logger distance variation pre- and post-deployment; (2) contacts reciprocity between loggers	Yes
[6]	Sirtrack Ltd.	150 (badger); not reported the weight of the cattle logger	Eurasian badger (*Meles meles*)/domestic cattle (*Bos taurus*)	Yes	No	1.5–2.5	916.5 MHz	No	No (recapture necessary)	Laboratory test to assess threshold contact distance	No
[7]	Sirtrack Ltd.	120	Tasmanian devil (*Sarcophilus harrisii*)	Yes	No	0.3–0.5	916.5 MHz	No	No (recapture necessary)	Laboratory test to assess threshold contact distance Field test on captive Tasmanian devils to assess contact distance, using video camera as ground truth	No
[8]	Sirtrack Ltd.	Not reported	White tailed deer (*Odocoileus virginianus*)	Yes	No	0–1.0	916.5 MHz	No	No (recapture necessary)	Field test on captive white tailed deer to compare observed and recorded contacts Contacts reciprocity assessed	No

Table 1 continued

Study	Logger brand or project name	Logger weight (g)	Target species	Mobile loggers	Static loggers	Target detection range (m)[a]	Radio frequency	Geo-referencing of encounters	Remote data download	Calibration scenario	Power consumption analysis
[9]	CraneTracker	~100	Whooping crane (*Grus americana*)	Yes (only for data retrieving)	Yes (base stations)	Not reported	2.4 GHz	No A GPS is embedded in the logger to track long-range migratory movements	Yes Via radio between mobile loggers and base stations placed at wintering and breeding sites; via GSM modem during migration phase	Field test on wild turkeys (*Meleagris gallopavo*) and on crane species other than *Grus americana*, to evaluate logger functioning prior to deployment on target species	Yes
[10]	Sirtrack Ltd.	Not reported	Eurasian badger (*Meles meles*)/domestic cattle (*Bos taurus*)	Yes	Yes	0.5–2	916.5 MHz	No	No (recapture necessary)	Laboratory test to evaluate (1) inter-logger distances at different heights and combinations; (2) contacts reciprocity; (3) contacts duration Field test on cattle to compare observed and recorded contacts	No
[11]	Encounternet	1	Long-tailed manakin (*Chiroxiphia linearis*)	Yes	Yes	5–30	433 MHz	No	Yes Via radio between mobile loggers and base stations, then via radio to a PC by means of a masternode	Field test to evaluate (1) RSSI/distance relationship; (2) duration and robustness of contacts; (3) effect of antenna orientation on connectivity; (4) effect of movement on connectivity (simulation)	No
[12]	Encounternet	10	New Caledonian crow (*Corvus moneduloides*)	Yes	Yes (base stations)	20–40 for mobile loggers 100 for static loggers	433 MHz	Yes Via cross-triangulation between base stations and mobile loggers. RSSI values used to estimate inter-logger distance	Yes Via radio between mobile loggers and base stations, then via radio to a PC by means of a masternode	Field test on a fixed network made up of dead quails, to model the probabilistic relationship between RSSI and distance in function of height from ground, antenna orientation, habitat type. Details of calibration model are provided in [13, 14]	No
[15]	Sirtrack Ltd.	Not reported	Cattle (*Bos taurus*)	Yes	Yes (base stations)	2.0–3.5	916.5 MHz	No	No (recapture necessary)	Laboratory test to assess inter-logger distance (mobile–base station) Field test on dairy cows to measure loggers reciprocity in measuring contact duration	No

Table 1 continued

Study	Logger brand or project name	Logger weight (g)	Target species	Mobile loggers	Static loggers	Target detection range (m)[a]	Radio frequency	Geo-referencing of encounters	Remote data download	Calibration scenario	Power consumption analysis
[16]	Encounternet	65–70	Galapagos sea lion (*Zalophus wollebaeki*)	Yes	Yes (base stations)	10	433 MHz	No	Yes Via radio between mobile loggers and base stations, then via radio to a PC by means of a masternode	Laboratory test to assess (1) RSSI/distance relationship; (2) effect of antenna orientation on connectivity; (3) duration and robustness of contacts Field test (1) to measure loggers reciprocity; (2) to compare observed and recorded contacts; (3) to assess RSSI/distance relationship in outdoor conditions	No
[17]	Bat Monitoring Project	30–50	Flying fox family (Pteropodidae)	Yes	Yes (base stations)	Not reported	< 1 GHz	No A GPS is embedded in the logger to track bats movements	Yes Via radio between mobile loggers and base stations, then via GSM modem to the central database	Not reported	Yes
[18]	Encounternet	1.3	Barn swallow (*Hirundo rustica*)	Yes	Yes (base stations)	0–40 for mobile loggers 100 for static loggers	433 MHz	No	Yes Via radio between mobile loggers and base stations, then via radio to a PC by means of a masternode	Field tests to evaluate (1) body effect, antenna orientation and environment effect on RSSI/distance relationship; (2) inter-logger variability; (3) contacts reciprocity	No
[19]	WildScope	440	Roe deer (*Capreolus capreolus*)/domestic horse (*Equus caballus*)	Yes	Yes	5–30	2.4 GHz	Yes A GPS is triggered in case of contact between proximity loggers	Yes Via GSM modem from mobile loggers to the central database	Field test 'in vitro' to evaluate effect of height from ground, casing and radio power on contact distance Field test on horses to compare observed versus recorded contacts in relation to distance and radio power Field test on roe deer to evaluate functioning of contact-triggered GPS acquisition in case of contact	Yes

Table 1 continued

Study	Logger brand or project name	Logger weight (g)	Target species	Mobile loggers	Static loggers	Target detection range (m)[a]	Radio frequency	Geo-referencing of encounters	Remote data download	Calibration scenario	Power consumption analysis
[20]	BATS	2	Mouse-eared bat (*Myotis myotis*)	Yes	Yes (base stations)	50	868 MHz	Yes Via cross-triangulation between base stations and mobile loggers. RSSI values used to estimate inter-logger distance	Yes Via radio between mobile loggers and base stations	Not reported	Yes
[21]	BATS	2	Fringe-lipped bat (*Trachops cirrhosis*)	Yes	Yes (base stations)	10	868 MHz	No	Yes Via radio between mobile loggers and base stations	Field test 'in vitro' to model relationship RSSI/distance, also in function of antenna orientation Field test 'in vivo' on mouse-eared bats to link RSSI variation to individual movement, using video camera as ground truth	No

The table collects information on some of the most well-known proximity logger deployments. Details on target species, proximity logging features, calibration attempts and geo-referencing functionalities are provided

[a] We report the detection range of interest for the specific study, which does not necessarily pair the maximum distance potentially covered by the loggers of any given brand

stereotyped individual encounters and individual use of focal resources [11], designing and performing field trials in semi-controlled conditions. During the trials we described and predicted logger performance (in terms of contact detection and contact-triggered GPS locations acquisition) based on the results provided in Picco et al. [19] (objective 1). Eventually, we compared the predicted and observed data to derive estimates of contact success rate and contact-triggered GPS location success rate, thus testing the reliability of WildScope GPS-based geo-referencing proximity loggers (objective 2).

Methods

WildScope proximity sensor network

WildScope GPS-based geo-referencing proximity loggers are designed to be deployed in a network of mobile and fixed sensors (Fig. 1). Mobile loggers are commonly deployed on animals, whilst fixed loggers are deployed at static stations. The mobile devices include, among other components, a radio unit for contact detection that can be set at different transmission powers, a Global Positioning System component for individual localization and a quadriband GSM/GPRS modem for remote data download. The fixed loggers are equipped solely with a radio unit, to allow contact detection with mobile loggers (see Additional file 1 and Picco et al. [19] for further details).

WildScope adopts a fully distributed configuration of the WSN: in contrast to the master–slave configuration, all loggers transmit and receive a radio signal on the same channel, so that connectivity is allowed throughout the network (see Additional file 1). A contact between two mobile loggers (i.e. a dyad) denotes an event of animal proximity, representing an animal encounter [13]. When a contact occurs between two mobile loggers, WildScope triggers the acquisition of a GPS location (i.e. 'contact-triggered GPS location acquisition') that is independent from the scheduling of periodic GPS acquisition, which happens in parallel (see Additional file 1 and Picco et al. [19] for details). Finally, a contact occurring between a mobile and a fixed logger represents the interaction of an individual with a static feature, e.g. use of a focal resource [19].

Lifetime properties, details on power settings, data storage and data processing of WildScope are described extensively in Picco et al. [19] (see also Additional file 1).

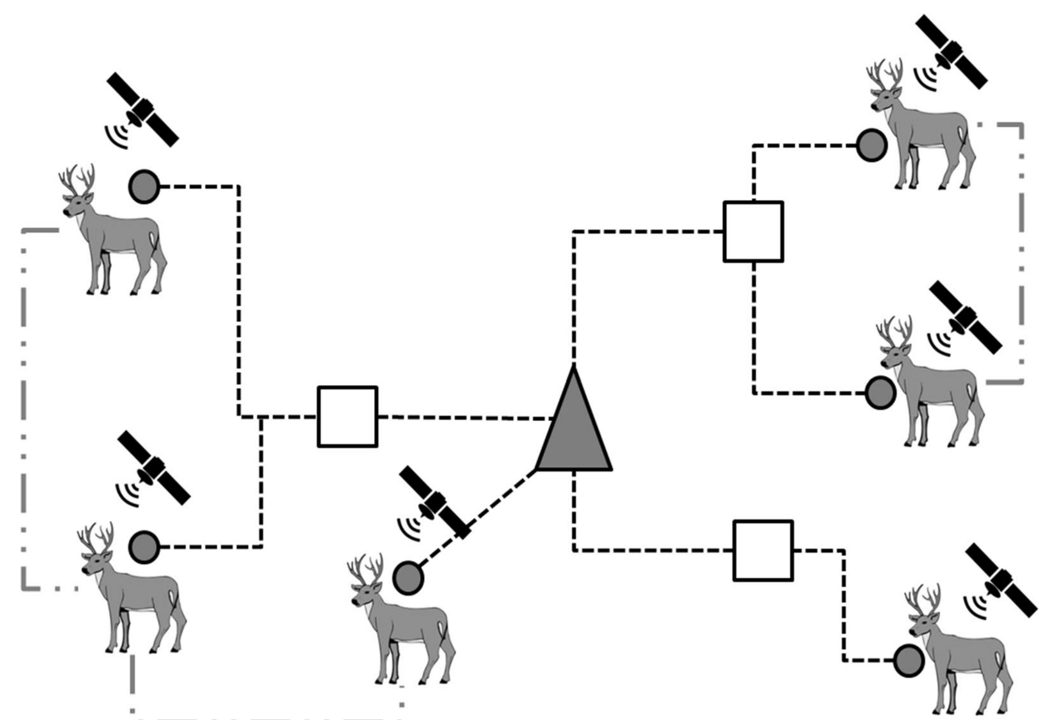

Fig. 1 Conceptual scheme of a mixed Wireless Sensor Network. The network is composed of mobile loggers deployed on animals (*circles*), equipped with GPS unit for localization, fixed loggers deployed on focal resources (*squares*) and a base station (*triangle*). *Grey-filled forms* denote the presence of a modem on the unit for remote data retrieval. Mobile loggers can be in contact via radio with each other (*dash-dot line*). Data download can also happen via radio through contact detection (*dotted lines*), either between mobile and fixed loggers (and from here to the base station) or directly from the mobile loggers to the base station

Wireless Sensor Networks at work: network design and data recording (objective 1)

The primary goal of our experiments was to design field trials in close-to-real settings that simulated stereotyped encounter patterns between individuals and between an individual and a focal resource [11], and to describe logger performance. In particular, we designed three different behavioural scenarios (Fig. 2). The first simulated use of focal resources by one individual (mobile–fixed loggers) and the others additionally mimicked behavioural modes that imply proximity between individuals (mobile–mobile loggers; Fig. 3), specifically: encounter and avoidance (e.g. territory defence); paired movement in parallel directions (e.g. mother–calves); and random, independent movement of individuals in the same surroundings (e.g. for feeding purposes).

Fig. 3 Photograph of deployment scenarios. Two people move the mobile loggers on an established path to simulate a pair of individuals moving side by side

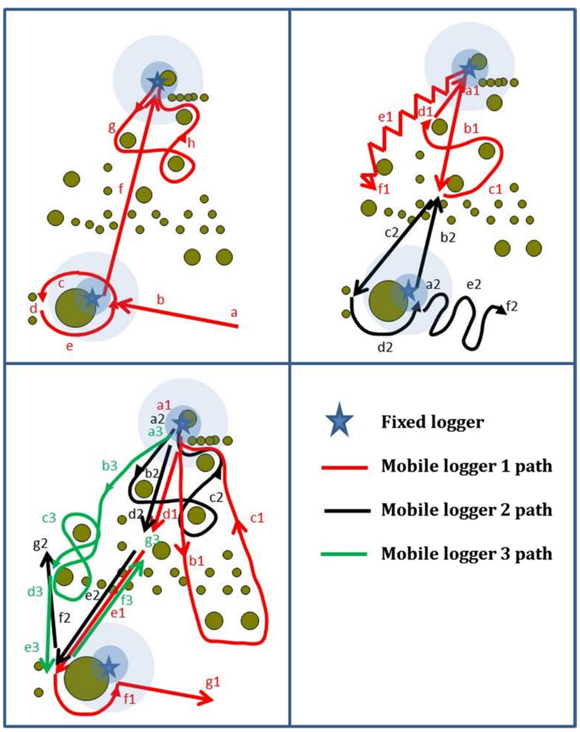

Fig. 2 Graphical description of the three deployed scenarios to test WildScope. The path followed by each mobile logger is described by a line of a different *colour*. The sequence of contemporary actions is represented by *letters*, whereas *numbers* indicate different loggers. Scenario 1: one mobile logger moving towards two fixed loggers (mimic of focal resource use) (*box 1*, *upper left*); scenario 2: two mobile loggers (mimic of encounter and avoidance movements) and two fixed loggers (*box 2*, *upper right*); scenario 3: three mobile loggers (mimic of parallel and random movements) and two fixed loggers (*box 3*, *bottom left*). The *shaded circles* represent the expected range of contact detection for the fixed loggers (*stars*) at the two power settings (*dark-shaded small circle*: power 3; *light-shaded large circle*: power 7). The radii of these *circles*, which are not reported here on the proper scale, were derived from the outcome of previous tests [8]. The *dark green circles* represent trees and bushes of various sizes in the arena where we performed the experiments

The experiment took place in San Michele all'Adige, Italy, from 14 May 2014 to 20 May 2014, in dry and windless conditions, for a total of 7 days. The study site encompassed a regular and flat terrain with some trees and bushes (Fig. 3). We intentionally included these environmental obstacles in our trials to account for the generic noise of connectivity typical of the environments in which loggers are deployed on animals [10, 29, 30]. We set the loggers to two radio transmission powers: 3 and 7, since they corresponded to average contact distances appropriate to studying the type of stereotypical encounters described above (see Additional file 1 for details on the power settings; Picco et al. [19] for average contact distances).

We set up the experimental network of fixed and mobile loggers as follows. Two fixed loggers were fitted on trees at 1 m height, within plastic water-proof boxes; mobile loggers (one to three, according to the scenario) were fitted onto two-litre bottles filled with a saline solution to mimic the body effect of an animal [10, 19] and then fixed to rigid wooden supports, with the antenna oriented upwards (Fig. 3). For consistency, we chose the same site and logger support used for the field calibration described in Picco et al. [19] that we expanded to 'noisier' settings.

In each of the three scenarios described above, one or more experimenters moved the mobile logger(s) on a predetermined path for a period of 17 min, which represented the *trial* (Fig. 3). Each trial comprised a 'script' of actions controlling the position of every logger in space and time (Table 2), at 1-min intervals (i.e. the temporal resolution of contact detection chosen or '*epoch*'; see

Table 2 Example of scenario for testing contact detection and contact-triggered GPS location

Minute	Action	Expected event	Reason for expectation
1	Stop	No contact	Distance M1–L1 and M1–L2 > 2.38 m
2	Stop	No contact	Distance M1–L1 and M1–L2 > 2.38 m
3	Stop	No contact	Distance M1–L1 and M1–L2 > 2.38 m
4	Stop	No contact	Distance M1–L1 and M1–L2 > 2.38 m
5	Movement	Start contact with L1	Distance M1–L1 < 2.38 m
		GPS triggered	Detection of a contact
6	Movement	In contact with L1	Distance M1–L1 < 2.38 m
7	Movement	In contact with L1	Distance M1–L1 < 2.38 m
8	Stop	End of contact with L1	Distance M1–L1 > 2.38 m
9	Movement	Start contact with L1	Distance M1–L1 < 2.38 m
		GPS triggered	Detection of a contact
10	Movement	End of contact with L1	Distance M1–L1 > 2.38 m
11	Movement	Start contact with L2	Distance M1–L2 < 2.38 m
		GPS triggered	Detection of a contact
12	Movement	End of contact with L2	Distance M1–L2 > 2.38 m
13	Movement	No contact	Distance M1–L2 > 2.38 m
14	Movement	Start contact with L2	Distance M1–L2 < 2.38 m
		GPS triggered	Detection of a contact
15	Stop	In contact with L2	Distance M1–L2 < 2.38 m
16	Stop	In contact with L2	Distance M1–L2 < 2.38 m

Example of a 17-min trial 'script' for testing contact detection and contact-triggered GPS location acquisition with WildScope loggers, deployed in a mixed network (mobile and fixed loggers). The script refers to the first scenario (Fig. 2, one mobile logger M1 and two fixed ones, L1 and L2), with loggers set at power 3 where the expected contact detection threshold is 2.38 m [19]. The table refers only to the actions taken by the mobile logger. Both expected contact detection and contact-triggered GPS location expected events are reported, with the associated reason for expectation

Additional file 1). Thus, for each minute, we knew the respective position (and distance) of loggers from each other. We were able to express the 'expected' connectivity between loggers based on the findings of Picco et al. [19], who determined the average contact distance in baseline conditions (static loggers, open-air, no obstacles; see also [10]). Notably, Picco et al. [19] determined an average contact distance of 2.38 ± 1.65 m for power 3 and 7.31 ± 2.97 m for power 7. Thus, we expected loggers to be in contact if they were at or below the linear distance of 2.38 m for power 3 and 7.31 m for power 7 (see also Fig. 2: such threshold distances are represented as buffers around the loggers). Similarly, every *observed* contact leads to the acquisition of an expected contact-triggered GPS location. For each trial, we were thus able to express all expected events (Table 2), that we then cross-referenced with the observed ones, based on the timestamp (Table 3).

Table 3 Example of match between expectations and observations

Minute	Expected event	Observed event	Typology event
1	No contact	No contact	True positive (TP)
2	No contact	No contact	True positive (TP)
3	No contact	No contact	True positive (TP)
4	No contact	No contact	True positive (TP)
5	Start contact with L1	Contact with L1	True positive (TP)
	GPS triggered	GPS location	True positive (TP)
6	In contact with L1	Contact with L1	True positive (TP)
7	In contact with L1	No contact with L1	False negative (FN)
8	End of contact with L1	No contact with L1	True positive (TP)
9	Start contact with L1	Contact with L1	True positive (TP)
	GPS triggered	GPS location	True positive (TP)
10	End of contact with L1	No contact with L1	True positive (TP)
11	Start contact with L2	Contact with L2	True positive (TP)
	GPS triggered	GPS location	True positive (TP)
12	End of contact with L2	Contact with L2	False positive (FP)
13	No contact	Contact with L2	False positive (FP)
14	Start contact with L2	Contact with L2	True positive (TP)
	GPS triggered	No GPS location	True positive (TP)
15	In contact with L2	Contact with L2	True positive (TP)
16	In contact with L2	Contact with L2	True positive (TP)

Example of matching the expected and observed data in terms of contact detection and contact-triggered GPS location acquisition. The results refer to the first scenario, as for Table 2 (one mobile logger M1 and two fixed loggers L1 and L2, power 3, see also Fig. 2), and specifically to the results obtained for the mobile logger. The recorded events depend on the comparison of expected and observed events

We performed three replicates of the trials for each experimental setting and power, for a total of 18 trials. We used three to five loggers to perform the trials, depending on the scenario mimicked, and reused the same loggers across replicates to avoid biases arising from a single-logger malfunctioning.

Estimation of contact detection and contact-triggered GPS location success rate (objective 2)

We used the proximity and contact-triggered GPS location data collected during the trials to measure the reliability of contact detection and acquisition of contact-triggered GPS locations by WildScope in close-to-real settings. We did this by comparing expected and observed contact events and acquisitions of contact-triggered GPS locations during the trials, to eventually determine the success rate both for contact detection and for acquisition of contact-triggered GPS locations. Specifically, we transposed contacts and contact-triggered GPS locations into a list of true positives (TP; expected and occurred contact detection events or expected and occurred contact-triggered GPS locations), false negatives (FN; expected events which were not recorded by the loggers) and false positives (FP; unexpected but observed events). In this way we derived estimates of contact success rate ($RTP_{contact}$) by computing the ratio of true positives to the total expected and unexpected events ($RTP_{contact} = TP/[TP + FP + FN]$). We also computed the false-negative rate of contact detection ($RFN_{contact}$) as the ratio of false negatives to total unexpected events ($RFN_{contact} = FN/[FN + FP]$). For the analysis on success rate of contact-triggered GPS locations, we did not include false-positive events, i.e. records acquired out of the expected contact-triggered GPS locations, because these represented spurious information that would not bias the analyses. Thus, we computed the success rate of contact-triggered GPS locations (RTP_{GPS}) as the ratio of true positives to the sum of true-positives and false-negative events ($RTP_{GPS} = TP/[TP + FN]$).

We used $RTP_{contact}$, $RFN_{contact}$ and RTP_{GPS} to evaluate the effect of radio transmission power on the performance of WildScope whilst controlling for the number of loggers in the network. Specifically, we fitted a generalized linear mixed model (GLMM) to evaluate the dependence of $RTP_{contact}$, RTP_{GPS} and $RFN_{contact}$ on power level (two levels, 3 and 7) and number of loggers (three levels: 1, 2 and 3). We used the 3 replicates within each combination of power per number of loggers in the network to estimate the variance. Since the dependent variable is binary (i.e. contact recorded or not, 1 and 0, respectively), we fitted a binomial distribution with a logit link function. For all the three analyses, we prepared a list of candidate models including all the potential combinations of the two covariates, fitted either as fixed or random effects. We adopted this procedure to evaluate whether the fitted covariates contributed to explain the variance of the intercept only, or whether they were significant predictors of the model (see also Additional file 2).

We then applied a model selection procedure based on AIC scores to determine the model of best fit [31]. We further evaluated the importance of each of the terms retained in the best-fit model to contribute to the goodness-of-fit of the model by means of an ANOVA based on deviance procedure (see Additional file 2). We applied an *F* test to account for overall differences within the variances of the covariates levels retained in the best-fit model. Lastly, we tested the significance of β-coefficients with respect to the reference level by means of a Student's *t* test.

All the statistical analyses were programmed in SAS software 9.3 [32].

Results

Contact detection and contact-triggered GPS location acquisition in simulated scenarios of encounters and movement (objective 1)

For each combination of number of loggers per power, we matched the observed and expected events for both contact detection and contact-triggered GPS location acquisition. Hereafter we provide a description of the mobile logger performance, as a guideline for users who wish to repeat this validation exercise (see Tables 2, 3 for the described example and Fig. 2 for the corresponding scenario). From the beginning until minute 6 we classified only true-positive events, i.e. M1 performed as expected (no contact from minute 1 to minute 4; contact detection with L1 at minutes 5 and 6, with consequent acquisition of contact-triggered GPS location). At minute 7, M1 was moved away, but still within the expected range of contact detection with L1. Contrary to expectations, M1 broke the contact with L1. We classified this unexpected end of contact as a false-negative event. From minute 8 until minute 11, the expected and observed events matched. At minute 12 and 13, contrary to our expectations, M1 kept the contact with L2. We classified this unexpected duration of the contact as a false-positive event. At minute 14, the scenario predicted a new contact between M1 and L2, with the consequent acquisition of a contact-triggered GPS location. Since the contact between M1 and L2 had not been interrupted during minutes 12–13, M1 kept the contact with L2 at minute 14 (true-positive event), but did not acquire a contact-triggered GPS location. This was correct, since the contact had been never interrupted. We thus classified the lack of acquisition of a contact-triggered GPS location as a true-positive event. In the last 2 min of the trial M1 performed as expected.

We adopted a similar approach for each combination of power and number of loggers involved in the scenarios.

Estimation of contact detection and contact-triggered GPS location success rate (objective 2)

We derived estimates of contact success rate based on 3095 total expected contact events, of which 2757 were true-positive events. We computed the false-negative rate from 231 false-negative and 108 false-positive events. We based our assessment of contact-triggered GPS location success rate on 104 realized contact-triggered GPS locations out of 113 expected locations (Table 4).

We found a high success rate of contact detection $RTP_{contact}$ with respect to the expected events that we described for the simulated scenarios, for both powers tested (89% for power 3; 89% for power 7) and across the number of loggers involved in the trials (86% for one logger; 87% for two loggers; 91% for three loggers).

Table 4 Contingencies to estimate contact success rate, false-negative rate and contact-triggered GPS location success rate

Trial	Contact success rate		False-negative rate		Contact-triggered GPS location success rate	
	Tot. events	True pos.	False neg.	False pos.	Tot. events	True pos.
1L-P3	204	184	20	0	14	14
1L-P7	204	167	29	8	8	8
2L-P3	480	414	46	20	17	11
2L-P7	480	423	40	17	15	13
3L-P3	864	774	52	38	29	28
3L-P7	864	795	44	25	30	30

The table summarizes the contingency data used to estimate contact success rate, false-negative rate and contact-triggered GPS location success rate. 'Tot. events', 'True pos.', 'False neg.' and 'False pos.' denote, respectively, the total events, true positives, false negatives and false positives used to estimate the rates. 1L-P3 = trials with one logger set at power 3; 1L-P7 = trials with one logger set at power 7; 2L-P3 = trials with two loggers set at power 3; 2L-P7 = trials with two loggers set at power 7; 3L-P3 = trials with three loggers set at power 3; 3L-P7 = trials with three logger set at power 7

The model selection and the ANOVA based on deviance procedure indicated that the number of loggers in the network positively affected the contact success rate (Table 5a), whilst the effect of power was negligible (see Additional file 2). The *F* test confirmed the significance of the number of loggers in predicting the pattern of contact success rate ($F_{2,15} = 6.11$; $P < 0.05$).

The analysis of false-negative rate $RFN_{contact}$ indicated that the false negatives constituted the majority of total failures for both powers (67% of total failures for power 3; 69% of total failures for power 7) and across the number of loggers in the trials (86% of total failures for one logger; 70% of total failures for two loggers; 60% of total failures for three loggers). The false-negative rate was negatively correlated with the number of loggers in the network, and this relationship approached significance ($F_{2,15} = 3.57$; $P = 0.0538$; Table 5b, see also Additional file 2).

Table 5 Summary of the best model accounting for the observed patterns of contact success rate (a), false-negative rate (b) and contact-triggered GPS location success rate (c)

	β-Coefficient	SE	*df*	*t*	*P*
(a) Model contact success rate					
Intercept	2.2893	0.08323	15	27.51	<.0001
1 logger	−0.4716	0.1653	15	−2.85	0.0121
2 loggers	−0.3635	0.1277	15	−2.85	0.0123
3 loggers	–	–	–	–	–
(b) Model false-negative rate					
Intercept	0.6931	0.1768	15	3.92	0.0014
1 logger	1.1192	0.4203	15	2.66	0.0177
2 loggers	0.1386	0.2647	15	0.52	0.6082
3 loggers	–	–	–	–	–
(c) Model contact-triggered GPS location success rate					
Intercept	4.0604	1.0086	15	4.03	0.0011
1 logger	11.2386	4.4765	15	0.03	0.9803
2 loggers	−2.9618	1.0881	15	−2.72	0.0157
3 loggers	–	–	–	–	–

β-Coefficients, standard errors and significance for each level of the number of loggers in the network, for the model of contact success rate (a), false-negative rate (b) and contact-triggered GPS location success rate. Since the number of loggers was fitted as a categorical variable in the models, the β-coefficients refer to the difference with respect to the reference level (three loggers)

The success rate of contact-triggered GPS location RTP_{GPS} was high at both powers (power 3: 88%; power 7: 96%) and across the number of loggers in the trials (100% for one logger; 75% for two loggers; 98% for three loggers). The *F* test indicated a marginal significance of the number of loggers in predicting the pattern of contact-triggered GPS location success rate ($F_{2,15} = 3.71$; $P = 0.0492$). In particular, RTP_{GPS} was significantly lower when two loggers were deployed, whilst there were no differences between trials with one and three loggers (Table 5c and Additional file 2).

Discussion

In this paper we describe contact detection by WildScope, a fully distributed proximity logging Wireless Sensor Network that allows GPS-based geo-referencing proximity detection, which we tested within a semi-controlled set-up. Previous studies have performed validation exercises of proximity loggers in order to evaluate the effect of body obstruction on radio connectivity (e.g. [9]) or to measure the relationship between logger distance and radio connectivity (e.g. [13]). The final goal of the majority of these calibrations was to measure the average threshold distances of contact detection (e.g. [6]) in order to choose the correct transmission setting that corresponds to the distance of biological interest (e.g. 1.5–2.0 m for perpetuation of bovine tuberculosis (bTB) in cattle herds [10]). Here, we also used average contact threshold distance, as derived from Picco et al. [19] and made the assumption that contacts should occur at such a distance, within defined error bounds, i.e. we calculated expected events of contact detection. However, Picco et al. [19] did not take into account the influence of factors such as the presence of obstacles [29] and the movement of loggers [11] on contact detection based on radio connectivity. Here, we built our experiments to control for movement and obstacles and demonstrated that, despite the loggers being generally reliable, there was a noticeable rate of failures in contact detection.

Furthermore, in our study the majority of failures were caused by false-negative events, i.e. expected contacts that did not occur. This is consistent with the increased noise arising from movement of loggers (as proposed by Rutz et al. [13]) and presence of obstacles [29]. Had the effect of movement and obstacles been negligible, we would have detected similar rates of false negatives and false positives arising as a consequence of equal distribution of errors within the variance of contact distance threshold determined by Picco et al. [19]. In contrast, the majority of failures due to false negatives might be due to a reduced connectivity compared with controlled settings, caused by logger movement and presence of obstacles in the network, i.e. an actual 'lower' threshold value in the 'noisier' conditions compared with the baseline ones of Picco et al. [19]. We also found that contact success rate increased with the number of loggers, and false-negative rate decreased. This can be explained by the hypothesized stochasticity of the 'noise' of the system, which is characteristic of radio transmission and thus of WSN deployments [29, 30]. In particular, the noise caused by the environmental conditions [30] in addition to the presence of obstacles and fine movements [29] is likely to exert stochastic variation in connectivity that leads to the occurrence of errors (either false positives or false negatives) in contact detection. Given the stochastic nature of this 'noise', its overall effect on connectivity should be less than proportional to the number of loggers included in the network. In other words, it should not strictly depend on the number of loggers deployed in the network. Conversely, the number of contacts between sensors (i.e. the true positives) increases proportionally with the number of loggers deployed in the network. Therefore, if the number of contact events increases beyond the number of associated errors, so too does the success rate. Further research in this direction should disentangle the overall stochasticity of the system with the variability linked to specific deployment features (but see [29, 30]). In particular, future studies should address the physics of transmission of WSN (but see [13]). Radio transmission power had a negligible effect on contact success rate and false-negative rate, demonstrating that observed patterns are robust to the power adopted.

Although mixed networks of fixed and mobile loggers represent the typical case for testing contact detection, they have rarely been included in animal-borne studies (but see [10, 11]). In this paper we propose a simple mixed network and provide a description of its functioning in the presence of moving subjects that mimic common animal behaviours. We propose this exercise as a convenient way for users to understand how proximity loggers might work in typical deployment scenarios and to easily test the reliability of a given proximity detection system whilst accounting for stochastic bias. Moreover, mixed networks have a much greater potential than being 'just' a technical tool to remotely download data acquired by mobile devices (e.g. [2, 9]). The integration of mobile and fixed loggers in a fully distributed WSN can help address a variety of important themes in animal ecology, including focal resource use in a given habitat by an individual [11]; identification of crucial corridors for animal movement or cross-road sites [33]; and consequences of resource distribution on animal social networks [14].

In this work, we also demonstrate the reliability of a relatively new function of GPS sensors—that is, contact-triggered GPS location acquisition, in application to animal ecology. Aside from our anomalous finding that contact-triggered GPS location success rate was reduced using two loggers, the overall performance of this GPS-based geo-referencing proximity logger system was highly satisfactory. Furthermore, the fully distributed (peer-to-peer) capability of WildScope and other logging systems with a fully distributed configuration considerably extends the type of ecological question that can be addressed in comparison with master–slave configurations. All loggers in the network can exchange proximity information with all others, whilst contacts and contact-triggered GPS locations are recorded in parallel by all loggers involved in the contact, thus permitting 'encounter direct mapping' (sensu [23]). This has the potential to elucidate previously little-known ecological and behavioural processes. For example, social interactions in a group of individuals can be detected and geo-referenced, as well as movement patterns of a group of individuals approaching or abandoning a point resource (e.g. feeding stations).

Finally, contact-triggered GPS locations are additional to periodic GPS acquisition for all individuals equipped with loggers. In this way, studies on spatially explicit contact detection can be combined with 'traditional' movement research [25]. The flexible scheduling of both contact-triggered and independent (periodic) GPS location acquisition allows the user to adjust the tool in accordance with study-specific requirements. For instance, mother–calf interactions can last a long time, so the investigator of parental care might decrease the scheduling frequency of the GPS device after the first

30 min of contact, to save battery lifetime. Conversely, the spatial contextualization of aggressive encounters between individuals, which can be instantaneous, might require an intense but brief GPS sampling regime. Indeed, we should note that when animal GPS detection is possible at a very high rate, i.e. when battery consumption constraints are irrelevant (e.g. large marine birds provided with solar-powered GPS units) high-frequency animal trajectories can provide identical information on animal-to-animal contacts as proximity detection sensors [34]. However, GPS frequency trades-off with battery lifetime (e.g. [19, 35]), with constraints including the length of the monitoring period for each individual, and recapture feasibility. If recapture is a viable option and/or the monitoring period required is short, then GPS frequency can be kept at a maximum, thus guaranteeing semi-continuous monitoring from which it is possible to extrapolate proximity patterns between individuals.

Notwithstanding study-specific trade-offs, the spatial information associated with contacts can remarkably increase the robustness of inference on animal encounters [36], enhancing a process-based interpretation of these observations [37]. This may prompt a completely new set of questions in behavioural ecology (e.g. do aggregation patterns in winter depend on resource distribution? Is provision of maternal care altered by habitat composition?), which could not be addressed with previous technology.

Conclusions

We tested a novel biotelemetry tool that integrates proximity detection and contact-triggered GPS location acquisition, in a fully distributed mixed wireless network. This technological advancement has the potential to bring together two branches of ecology thus far kept relatively distinct, namely movement ecology [37] and animal encounters [23]. Moreover, we suggest further enhancements of the application of mixed proximity logger networks to more comprehensively understand animal use of specific focal resources within a habitat. However, these wide-reaching and innovative applications of a novel GPS-based geo-referencing proximity logger must take into account the limitations of their use. We present a simple and repeatable series of scenarios to test the functioning and reliability of GPS-based geo-referencing proximity loggers, prior to deployment in field conditions. We foresee further steps for calibrating these tools, including probabilistic modelling of error rates associated with contact detection as a function of the distance between loggers, in conditions as close as possible to final deployment [13], i.e. on wild animals.

Additional files

Additional file 1. WildScope proximity loggers. This additional file describes in detail the technical components (hardware and software) of WildScope GPS-based geo-referencing proximity loggers.

Additional file 2. Model selection procedure. This additional file describes in detail the procedure to select the best model describing contact detection success rate, false negative rate and contact-triggered GPS location success rate).

Abbreviations

TP: true positive; FP: false positive; FN: false negative; $RTP_{contact}$: ratio of true-positive events of contact detection; RTP_{GPS}: ratio of true-positive events of contact-triggered GPS location acquisition.

Authors' contributions

FO, SF, GP, AM, DM, FC designed the experiments. FO, SF, DM, FC designed and carried out the analysis. FO, DM, NG carried out the experiments. FO, FC wrote the paper, with all other authors' contribution. All authors read and approved the final manuscript.

Authors' information

Our team is mainly constituted by academic researchers belonging to different fields. FO, SF, FC, NG, JG and BT are animal ecologists, whilst GP, AM and DM are information engineers with long experience in Wireless Sensor Network applications. These two components of the team worked side by side to assess the potential of WSN for animal ecology investigation and wildlife management.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The data set supporting the conclusions of this article is available in the Dryad repository.

Consent for publication

The subjects represented in Fig. 3 give their consent for publication of the image.

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