

TELEMETRY CASE REPORT

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Performance of proximity loggers under controlled field conditions: an assessment from a wildlife ecological and epidemiological perspective

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Abstract

Background: Ecological sciences have, in recent decades, benefited from the ability of proximity loggers (PLs)—i.e. devices that transmit and receive radio signals (UHF)—to quantify intra- and inter-specific interactions. These are used to estimate the frequency of contacts according to a predefined distance between individuals or between individuals and environmental features. The performance of these devices may, however, be potentially affected by several factors, signifying that they require accurate calibration under field conditions in order to correctly interpret the information obtained. We assessed the effect of four relevant factors in ecological and epidemiological studies over the attenuation of radio waves in terms of the received signal strength indicator (RSSI) and contact success rate at a short (3 m) and medium distance (up to 20 m). The factors considered were: height above the ground (0–1 m), the presence/absence of vegetation, the presence/absence of live body mass around the devices, the distance between devices and the overlaid effects of all of them.

Results: The RSSI was found to be an accurate measure of distance, although its precision decreased over greater distances (up to 100 m), with the loss being sharper with vegetation, with body mass and when the devices were located on the ground. The success rate at up to 20 m decreased with distance and was also affected by body mass and vegetation. A probability of contact success of 81% was obtained in the best conditions (without vegetation and body mass) at a distance of 3 m, whereas it was of 56% in the worst conditions.

Conclusions: Our study shows the potential synergistic effects of external factors on the performance of PLs, even when they are used to infer near-contacts. We, therefore, highlight the importance of assessing, for each particular study, the combined effect of non-controllable external factors on the performance of PLs in order to estimate the minimum (best scenario) and maximum (worst scenario) level of underestimation in the field data. The sampling design described here is a cost-effective protocol suitable for this purpose.

Keywords: Biologging, Direct–indirect contacts, Ecology, Epidemiology, Proximity loggers, Received signal strength indicator, Contact success rate

Background

Proximity loggers (PLs) are devices that both transmit and receive ultra-high frequency (UHF) radio signals. PLs are connected to each other by means of the emission

of an identified pulse and the reception of other nearby signals. PLs have been employed, since the beginning of the twenty-first century, in ecological sciences to record proximity events between animals and/or animals and tagged points and to estimate their frequency. This has been done with the purpose of understanding processes such as behaviour during mating and that of predators (e.g. [1, 2]), the social structure of wildlife populations

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(e.g. [3, 4]) and the spread of pathogens within and among populations/species (e.g. [5, 6]). Thus, PLs are able to provide data informing about ecological and epidemiological processes that can be used for management and conservation.

Proximity loggers record the radio signal strength as a 'received signal strength indicator' (RSSI) value, which can be calibrated (i.e. check the effect of external factors over the attenuation of radio waves) against distance under controlled conditions. Subsequently, the distance obtained may correspond to a contact between individuals according to a specific definition of it. Therefore, a previous calibration of the RSSI parameter is necessary in order to study contacts. In addition, the reception between devices is far from perfect, since some of the potential contacts are not recorded owing to the internal malfunction of the devices and/or the effect of external factors (e.g. [7]). Under experimental conditions, the contact success rate measures the ratio among the contacts recorded regarding false negatives (contacts expected but not recorded). This information is essential when interpreting the accuracy of the contact rate obtained between devices under field conditions.

Several studies have assessed the effect of different factors over the radio transmission of each device individually. The distance between PLs has been adjusted according to the specific interests of the study, covering distances from less than 1 m [1, 8] up to approximately 50 m [9]. However, the potential of PLs to record contacts over longer distances has not been further evaluated, even when it may be relevant for ecology in, for instance, studies related to avoiding behaviours in prey-predator systems or in territoriality related behaviours (but see [2]). Prange et al. [10] noted that the orientation of the antenna on the PLs has an effect on the detection distance between devices. Under field conditions, this results in differences in the number and duration of pair-to-pair contacts depending on the distance between devices. The presence of some natural and artificial elements between the devices also affects the performance of PLs, since the waves may undergo modifications when they are reflected or attenuated by, for instance, vegetation, water or snow, or other individuals nearby [4, 11]. It has also been suggested that the mass of animals may have an effect on signal reception, and this has sometimes been simulated in PLs calibration tasks (e.g. [8, 12]). The height above the ground at which PLs are located is also relevant, because the soil attenuates the signal that they emit [10]; this is relevant in studies in which the species of interest are of markedly different sizes (see [5]). All these issues make it necessary to check the effect of external factors over the performance of PLs according to the species of interest and the geographical area in

which the study will be carried out [4, 13]. Researchers have mainly focused on studying the effect of some of the aforementioned factors; nevertheless, many aspects of their overlaid effects, which are the real situation when PLs are used in the field, are still unknown (but see [14]).

In this context, we aimed to calibrate the RSSI as distance indicator controlling by different external factors and to evaluate the effects of these factors on the contact success rate. Among the factors, we considered: (i) the height above the ground of the transmitter and receiver; (ii) the presence of vegetation, and (iii) the body mass of individuals, as regards a gradient of distances (3–100 m).

Methods

Study area

The field experiments took place in Ciudad Real province (38° 48' 38.9" N, 3° 53' 24.5" W), in the region of Castilla-La Mancha, south-central Spain, which is 690 m a.s.l. The area is characterized by a Mediterranean climate, with an average temperature of 14.1 °C and an average precipitation of 598 mm. The typical vegetation consists of evergreen oak (*Quercus ilex*) scrublands with scattered pastures and small crops. The field trials were carried out on 27th December 2017, in favourable meteorological conditions (daylight, low humidity, 10 °C average temperature and 3.6 m/s average wind speed [Ciudad Real meteorological station, <https://opendata.aemet.es>]).

Configuration of proximity loggers

The equipment employed for the trials was manufactured by Microsensory S.L. (Microsensory S.L., Fernán Núñez, Spain). Proximity technology uses a MS3241-Prox radio chip (Microsensory Semiconductor) which operates in the 433.050–434.790 MHz band. Devices use a communication protocol of an ultra-low consumption and long-range (uLRuIP), with a transmission power from –20 to +10 dBm (decibels relative to one milliwatt). Two parameters can be set in PLs: the time receiving-window and the frequency of UHF beeps emission. Both parameters have a trade-off with the lifespan of the battery, so they must be assessed carefully as regards project objectives and the monitoring period. The time receiving-window consisted of 10 s each minute, during which the devices were able to receive the IDs of other nearby PLs, the date, time and RSSI of the contact. The frequency of UHF beeps emission was configured to send every 4 s. The beep includes the ID information of the transmitter. We choose this configuration in order to use the minute as a temporal reference in the trials. This configuration allows the PLs to register at least two contacts each minute once two devices are within the detection distance.

Distance, presence of vegetation, body mass of individuals and height above the ground of PLs

The effect of four external factors over the radio transmission was considered: distance, vegetation, body mass and transmitter/receiver height, and all possible combinations between them. The effect of these factors was measured on RSSI attenuation and contact success rate. To calibrate the relationship among RSSI and distance, we used the values of this parameter measured in dBm. The RSSI decreases with the distance, so the higher the dBm, the higher the intensity of the signal, the lower the distance between devices. For the contact success rate, we used “attempts” as unit of measure: an attempt is defined as a time period of 1 min in which the PLs were maintained in the same position.

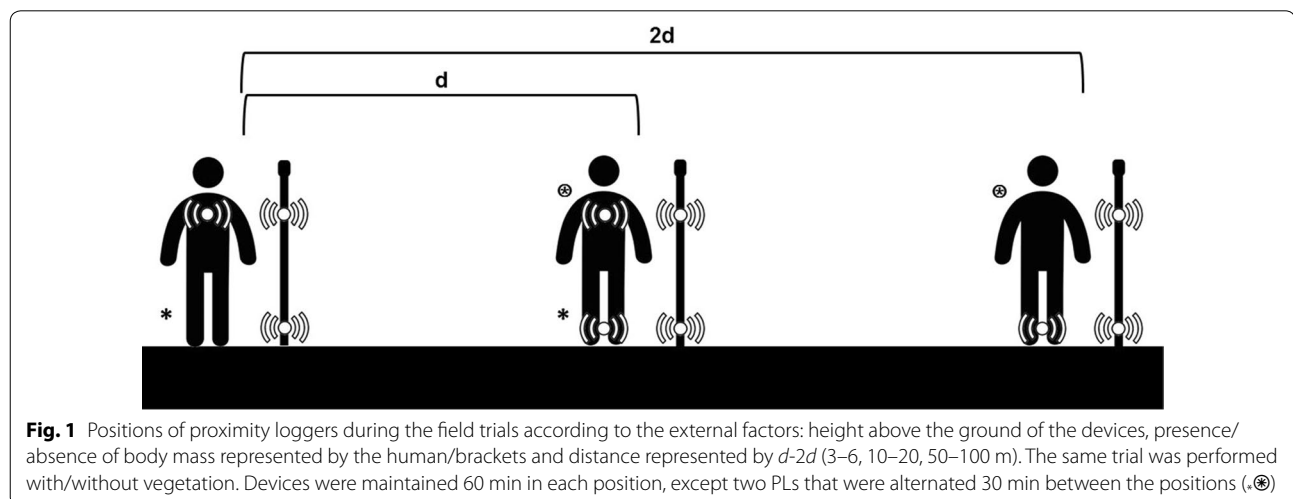
The effect of the factors was considered over the performance of 10 devices in pairwise trials (see the experimental design in Fig. 1 and the sampling effort in Additional file 1: Appendix S1). The PLs were set for 60 min at 3 m, 6 m, 10 m, 20 m, 50 m and 100 m. The devices had sufficient signal intensity to be recorded by nearby devices located at these distances. Body mass effect was tested by placing the PLs on stakes (no body mass) or carrying the PLs by the field staff (to simulate the body mass of an animal), at all heights above the ground and distances taken into account. With regard to height above the ground, the PLs were placed at ground level (0 m) in order to study the effects of an animal lying down, or at 1 m to test the effect that different heights of receivers or transmitters have on contact success and on the loss of the RSSI. We randomly selected the devices to be assigned to a given situation in the sampling design, namely distance, heights and body mass, in order to avoid possible biases due to specific malfunction of devices. Finally, this design was

applied in two areas, with and without dense scrubland vegetation.

Statistical analysis

Before the statistical analysis, we checked the collinearity between variables using the variance inflation factor (VIF). We first checked for reciprocity up to 20 m between the devices that would be recording contacts, i.e. the probability that if a device A registers a device B, then B also registers A. The reciprocity was modelled using a generalized linear mixed model (binomial distribution and logit link function) using all the external factors (see below) as fixed effects, and the ID of the PLs as random effects. In this model, a categorical variable containing reciprocity/no reciprocity (i.e. both PLs register the contact/only one device registers the contact) at attempt level was used as a response variable. The results showed a low reciprocity (0.4) between PLs at up to 20 m (see Additional file 1: Appendix S2—Fig. S1). Thus, according to this result and to the fact that PLs cannot obtain directionality in the contact, we considered in the subsequent analysis all the contacts recorded, regardless of the device recording the contact and of the reciprocity between devices recording the same contact, i.e. in a dyad both devices were considered to have recorded the contact if at least one of the devices in the dyad did it.

Three different statistical models were developed to assess and quantify the effect of external factors on the performance of the PLs in terms of RSSI intensity and contact success rate. In order to assess the effect of external factors on the loss of the RSSI of the devices, we applied a linear mixed model (Gaussian distribution and identity link function), using the value of RSSI as the response variable, the IDs of the PLs involved in the contact as two random effect factors and the external factors



(see below) as fixed effects (model i). The marginal and conditional R squared (R^2c and R^2m) were obtained for this model. We also modelled the contact success rate at 3 m (model ii) and for up to 20 m (model iii) in order to check the effect of external factors at short and medium distances, using generalized linear mixed models (binomial distribution and logit link function). In both the short and the medium distance models, a categorical variable containing reception/no reception (1/0) at attempt level was used as a response variable, the IDs of the PLs were employed as random effects and the external factors as fixed effects. All possible two-way interactions between the four external factors were considered in the reciprocity and the success rate models, whereas only those interactions in which distance was involved were checked in the RSSI model (i.e. distance*vegetation, distance*height and distance*body mass). In addition, in order to estimate the range of potential error of the data recorded under field conditions, from the model parameterized up to 20 m (model iii) we checked the probability of contact success in the worst (presence of vegetation and body mass) and the best (no vegetation and no body mass) conditions.

In all the models, predictors were selected from a null model following a forward stepwise selection procedure using the corrected Akaike's Information Criterion (AICc) [15]. All the statistical analyses were conducted using R software 3.3.2 [16]. Mixed models were employed using the 'lme4' R package [17] and their validation was carried out following the protocol established by Zuur and Ieno [18]. Finally, fitted values for all the significant factors and interactions were plotted using the 'effects' R package [19] and 'ggplot2' [20].

Results

In the analysis performed to study the external factors that could affect the reciprocity, 5961 attempts were used. To study the effect of external factors over RSSI, we recorded 14,742 contacts between devices, so this same number of RSSI values was employed in the calibration model (model i). In the model performed for the contact success at 3 m (model ii), 2282 attempts were used. Finally, for the model up to 20 m (model iii), 7725 attempts were used. For more information about sampling effort see Additional file 1: Appendix S1.

All predictors had VIF values lower than 3 and therefore, none of them was excluded from the models. The model for reciprocity included all the external factors (distance, height above the ground, vegetation and body mass) and the interaction between vegetation and body mass (see Additional file 1: Appendix S2—Table S1).

The most parsimonious lineal model fitted to the RSSI parameter (model i) included the interactions

between the distance and all the other factors (see Table 1; see also model selection in Additional file 1: Appendix S3—Table S1). The RSSI decreased with the distance through a logarithmic distribution ($R^2c = 0.66$, $R^2m = 0.84$), signifying a loss in the intensity of the signal with distance (Fig. 2a). The decrease of RSSI was more evident with vegetation and when the devices were located on the ground (Fig. 2b, d). The presence of body mass significantly affected the intensity of the RSSI. Note that when body mass is absent, the RSSI values increase (Table 1 and Fig. 2c).

The presence of vegetation increased the contact success rate of the model parameterized with data at 3 m (model ii, see Table 2; model selection summary in Additional file 1: Appendix 3—Table S2). On the other hand, distance and the interaction between vegetation and the presence of body mass were retained in the most parsimonious model, explaining the success rate up to 20 m (model iii, see Table 3 and Fig. 3; model selection summary in Additional file 1: Appendix 3—Table S3). Specifically, in the model up to 20 m (model iii), distance yielded slightly lower success rates for the worst scenario (i.e. presence of vegetation and body mass around the devices) when compared to the best scenario (without vegetation and without mass around the devices) (Fig. 4).

Table 1 Results of the final linear mixed model used to explain the RSSI values (intensity of proximity loggers signal) according to external factors and their interactions

| | Estimate | Std. error | t value | p values |
|--------------|----------|------------|---------|----------|
| (intercept) | -50.82 | 3.24 | -15.67 | *** |
| DIST | -12.29 | 0.14 | -85.91 | *** |
| HEIGHT1 | 6.79 | 0.44 | 15.40 | *** |
| HEIGHT2 | 3.96 | 0.39 | 10.18 | *** |
| VEG1 | 9.31 | 0.31 | 29.64 | *** |
| BMASS1 | -5.45 | 5.01 | -1.09 | ns |
| BMASS2 | -2.69 | 2.51 | -1.07 | ns |
| DIST:VEG1 | -3.20 | 0.11 | -29.31 | *** |
| DIST:BMASS1 | 1.83 | 0.18 | 10.17 | *** |
| DIST:BMASS2 | 1.28 | 0.12 | 10.97 | *** |
| DIST:HEIGHT1 | 0.33 | 0.15 | 2.16 | * |
| DIST:HEIGHT2 | -0.42 | 0.14 | -3.07 | ** |

VEG: presence (1) vs. absence of vegetation; DIST: distance; HEIGHT: height of the receiver and transmitter (reference class 0 [both devices located at ground level]: 0-0; 1 [both devices located at 1 m]: 1-1 and 2 [receiver located at 0 m and transmitter at 1 m, or vice versa]: 0-1); BMASS: presence of body mass around the receiver and transmitter (reference class 0 [without body mass]: 0-0; 1 [body mass around both the receiver and the transmitter]: 1-1 and 2 [body mass around only one device, receiver or transmitter]: 0-1)

p values: $p \geq 0.1$ "ns"; $p < 0.1$ "."; $p < 0.05$ "**"; $p < 0.01$ "***"; $p < 0.001$ "****"

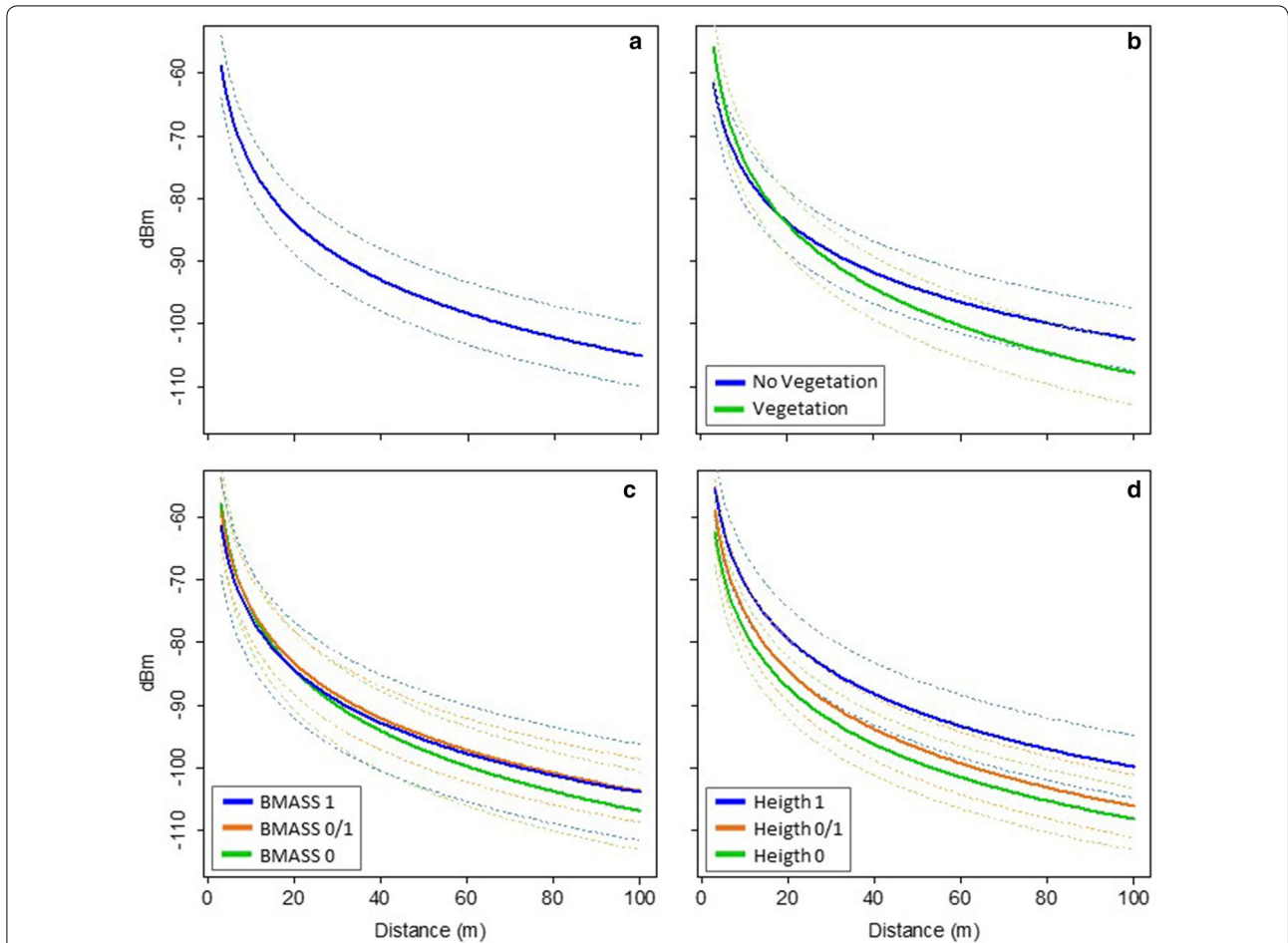


Fig. 2 Statistically significant factors and interactions of the linear mixed model (intensity of proximity logger signal, in dBm) parameterized to explain RSSI values. **a** RSSI vs. distance relationship; **b** RSSI vs. vegetation (blue = no vegetation, green = presence of vegetation); **c** RSSI vs. presence of body mass (blue = presence of body mass around both PLs; orange = body mass around receiver or transmitter; green = absence of body mass); and **d** RSSI vs. height of receiver or transmitter (blue = both PLs at 1 m; orange = receiver 1 m, transmitter 0 m, or vice versa; green = both PLs at 0 m)

Table 2 Results of the final generalized linear mixed model (binomial distribution and logit link function) to explain the probability of contact success according to external factors and their interactions at 3 m

| | Estimate | Std. error | z value | p values |
|-------------|----------|------------|---------|----------|
| (intercept) | 1.28 | 0.30 | 4.24 | *** |
| VEG1 | 0.22 | 0.11 | 1.96 | * |

VEG: presence (1) vs. absence vegetation

p values: $p \geq 0.1$ "ns"; $p < 0.1$ ". "; $p < 0.05$ "***"; $p < 0.01$ "****"; $p < 0.001$ "*****"

Discussion

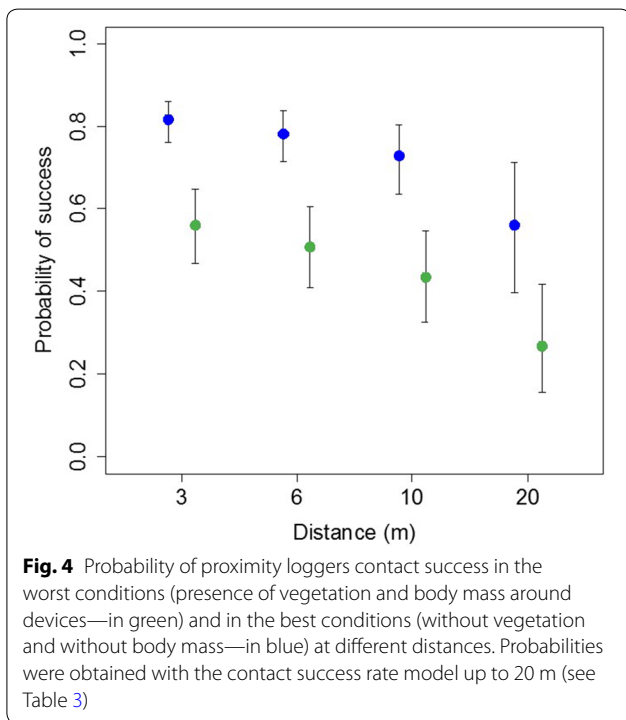
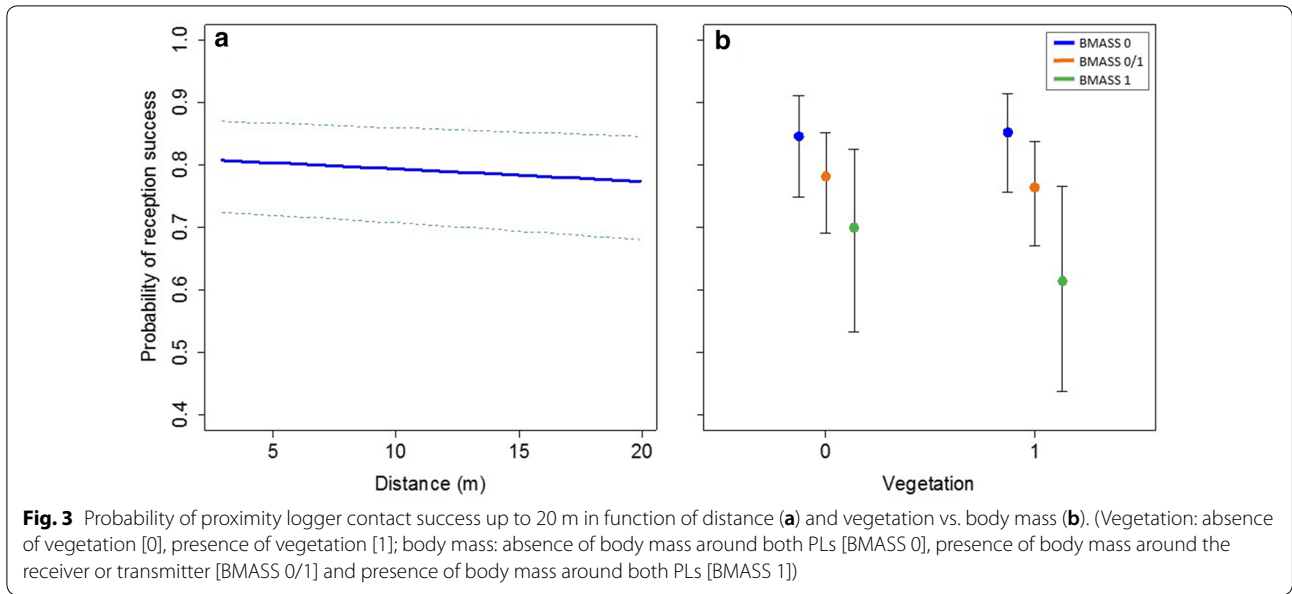
Proximity loggers have traditionally been employed in ecology in general, and in epidemiology in particular, to detect contacts between individuals at short distances with high accuracy and precision [1, 10, 21]; however,

Table 3 Results of the final generalized linear mixed model (binomial distribution and logit link function) to explain the probability of contact success according to external factors and their interactions up to 20 m

| | Estimate | Std. error | z value | p values |
|-------------|----------|------------|---------|----------|
| (intercept) | 1.71 | 0.32 | 5.40 | *** |
| DIST | -0.07 | 0.03 | -2.52 | * |
| BMASS1 | -0.87 | 0.48 | -1.81 | . |
| BMASS2 | -0.44 | 0.25 | -1.78 | . |
| VEG1 | 0.05 | 0.10 | 0.50 | ns |
| VEG1:BMASS1 | -0.43 | 0.17 | -2.46 | * |
| VEG1:BMASS2 | -0.14 | 0.12 | -1.14 | ns |

DIST: distance; VEG: presence (1) vs. absence vegetation; BMASS: presence of body mass around the receiver and the transmitter (reference class 0 [without body mass]: 0-0; 1 [body mass around both the receiver and the transmitter]: 1-1 and 2 [body mass around only one device, receiver or transmitter]: 0-1.)

p values: $p \geq 0.1$ "ns"; $p < 0.1$ ". "; $p < 0.05$ "***"; $p < 0.01$ "****"; $p < 0.001$ "*****"



the information collected with these devices should be calibrated under local field conditions for a correct interpretation. When the distance between devices is crucial for a precise ecological inference (e.g. the transmission of information and/or the transmission of pathogens), then the conversion of the RSSI measure into a distance estimation (or a contact, after we have defined it) should be

as accurate as possible. Tambling and Belton [2] observed a strong and significant relationship between a distance of up to 400 m and signal intensity ($R^2=0.9$). Similarly, our statistical model showed a strong significant relationship between the distance (up to 100 m) and the RSSI ($R^2=0.84$; Fig. 2a), and that the RSSI values were more variable at greater distances, which is also consistent with previous studies [14]. Apart from distance, we observed a significant decrease in the signal intensity when the devices were located at ground level, possibly owing to the capacity of the soil to absorb the UHF waves [10]. Moreover, we noticed that the effect of the height was greater when the contacts took place over long distances, which could have implications for the study of, for instance, contacts between small species. According to Böhm et al. [5], the height of both the receiver and the transmitter must be taken into account when estimating the distance of a contact between individuals from the same species or between species of different heights. With regard to other interfering factors, previous studies have registered a decrease in RSSI intensity of 20% in areas with vegetation [22]. In this study, we registered a significant effect of vegetation decreasing the signal intensity, but we also observed that this effect was more noticeable at greater distances. This is of great importance as regards assessing the different types of contacts, depending not only on the environment and its different signal attenuation properties [2, 8], but also on combining the effect of the habitat with the distance at which the contact occurred. Finally, although in previous studies the body mass around both the receiver and transmitter devices was thought to absorb UHF waves [11, 12],

we observed that this factor interacted with the distance, decreasing the loss of signal at greater distances when body mass was present. This result suggests that the mass of a collared animal probably acts as a directional antenna to receive the signal (but see below). In spite of these external factors, the intrinsic differences in the performance of PLs are also known [23] and the estimation of the distance through the use of the RSSI parameter must be necessarily probabilistic [8]. Our results, therefore, showed that although PLs are efficient at detecting contacts at short distances with high spatial accuracy, their use could also be recommended to detect contacts that are further away, by using specific emission frequencies and controlling for external factors.

The performance of PLs has normally been studied by comparing the contact rates registered with PLs and direct observations of these contacts [4] or by using the reciprocity between PLs registering contacts [11, 12, 23]. Although there is no preferred method to assess this rate under field conditions, it is always necessary to consider the possible sources of bias that may interfere with the correct performance between devices. In our study, reciprocity was explained by almost the same factors than contact success up to 20 m. Thus, reciprocity is suggested to be just a matter of success rate and no other processes. Our PLs achieved a low probability of reciprocity (0.4), similar to the registered by Drewe et al. [12]. Although previous studies selected only reciprocally recorded contacts [24], we considered contacts independently of the device registering the contact. Considering all the contacts, and under optimal conditions, the probability of reception increased up to 81%. This result is consistent with those of recent works in which contact success rate was 89% [7]. In spite of the high probability of success, the ideal conditions used here are not frequent in the field (e.g. two animals sufficiently close for 1 min) and the real probability of success could be lower than that reported in this field experiment, and near-contacts among animals could be lost. The configuration of beep emission and reception could improve the accuracy of the monitoring system by increasing the frequency of emission and, principally, expanding the receiving-window. However, this configuration has a trade-off with the lifespan of batteries (e.g. [25]) and therefore researchers must use the parameters (i.e. frequency of emission and receiving-window) that better fit with the aim of the study.

In our study, contact success rate data were modelled at 3 and up to 20 m in order to dilute the effect of the distance on the other factors and in order to simulate studies in which PLs devices are used to record both close and distant contacts. As expected, at 3 m the effect of external factors affecting contact success was lower than at greater distances. However, some factors had a significant effect,

even at this short distance. Contrary to expectations, the presence of vegetation increased the probability of contact success at 3 m. This could respond to a low absorption of radio waves by vegetation at short distances that could even produce a rebound of the waves, increasing in this way the contact success. The effect of this factor differed in the up to 20 m model, signifying that the probability of contact success decreased with distance and with the interaction of vegetation and presence of body mass. When devices are located at close distances, a significant decrease in the contact success rate with the presence of vegetation can be interpreted as the potential barrier effect that vegetation cover may have on the transmission of the signal [10]. The presence of vegetation magnified the loss of contact success that the mass of an individual could cause. In fact, some authors have suggested the need to check the effect of the mass of collared animals [12, 23]. However, no studies have analysed this factor in detail. Although the effect of factors such as vegetation have also been taken into account [22, 26, 27], to the best of our knowledge, there are no previous studies that assess the overlaid effect of these factors at medium ranges of distance.

Interestingly, although the body mass had a negative effect on the contact success rate up to 20 m, this factor had a positive effect on the RSSI parameter by decreasing the loss of signal intensity. Although the mass of individuals has been simulated in previous experiments owing to its potential effect on the performance of PLs [8, 12, 27], this finding has not, to the best of our knowledge, been previously reported in the literature. We hypothesize that body mass may help the emission of the PLs signal in a determined direction, thus reducing the loss of the RSSI. However, body mass could also attenuate the signal received, thus reducing the reception capabilities of PLs. More studies should be designed in order to carry out a more detailed exploration of the effect of this relevant factor when PLs are used in ecology.

Conclusions

Proximity loggers (PLs) are becoming popular in ecological studies due to their capacity to detect contacts between individuals. However, a misinterpretation of PLs-derived data could lead to an underestimation of the contact rate between individuals or the recording of false positives, thus misvaluing the role that certain individuals may play in the ecological process under study, for example, pathogen transmission. Although multiple sources of error (namely presence of vegetation between devices, height, etc.) have been deeply studied with other technologies commonly employed to study animal behaviour (e.g. GPS technology [28]), only few studies have delved into the error caused by external factors in PLs devices.

Our results showed a relevant effect of external factors (pure and overlaid effects) on PLs performance in both the intensity of signal and the contact success. We, therefore, recommend the use of a sampling protocol, such as that described here, to quantify the effect of non-controllable factors that may interfere with the performance of PLs according to three practical considerations: (i) the specific definition of interaction (distance and duration); (ii) the characteristics of the target species (height, weight and behaviour), and (iii) the characteristics of the habitat (topography, canopy). Employing this method would make it possible to report a range of interaction frequencies, taking into account the uncertainty as regards the real effect of the factors on the performance of PLs in the field. This range is more accurate and honest than only the underestimated value directly registered by the PLs.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s40317-019-0186-2>.

Additional file 1. This additional file includes 3 appendices: (i) scheme of sampling design and sampling effort; (ii) analysis of reciprocity between devices; (iii) summary of model selection.

Additional file 2. This additional file includes the information recorded during the field experiment regarding intensity of the signal (RSSI) against different external factors.

Additional file 3. Contact success data. This additional file includes the information recorded during the field experiment regarding contact success rate against different external factors.

Abbreviations

PLs: proximity loggers; UHF: ultra-high frequency; RSSI: received signal strength indicator; a.s.l.: above sea level; dBm: decibels relative to one milliwatt; VIF: variance inflation factor; AICc: corrected Akaike's Information Criterion; VEG: presence/absence of vegetation; DIST: distance; HEIGHT: height of the receiver and transmitter; BMASS: presence of body mass around the receiver and transmitter.

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Authors' contributions

RTO, JV and PA conceived the ideas and designed the methodology; RTO and PA analysed the data and led the writing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analysed during this study are included in this published article and the Additional files 2 and 3.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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