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RESEARCH ARTICLE

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Quantifying the errors in animal contacts recorded by proximity loggers

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Abstract

Automated contact detection by means of proximity loggers permits the measurement of encounters between individuals (animal-animal contacts) and the time spent by individuals in the proximity of a focal resource of interest (animal-fixed logger contacts). The ecological inference derived from contact detection is intrinsically associated with the distance at which the contact occurred. But no proximity loggers currently exist that record this distance and therefore all distance estimations are associated with error. Here we applied a probabilistic approach to model the relationship between contact detection and inter-logger distance, and quantify the associated error, on free-ranging animals in semi-controlled settings. The probability of recording a contact declined with the distance between loggers, and this decline was steeper for weaker radio transmission powers.

Even when proximity loggers were adjacent, contact detection was not guaranteed, irrespective of the radio transmission power. Accordingly, the precision and sensitivity of the system varied as a function of inter-logger distance, radio transmission power, and experimental setting (e.g., depending on animal body mass and fine-scale movements). By accounting for these relationships, we were able to estimate the probability that a detected contact occurred at a certain distance, and the probability that contacts were missed (i.e., false negatives). These calibration exercises have the potential to improve the predictability of the study and enhance the applicability of proximity loggers to key wildlife management issues such as disease transmission rates or wildlife use of landscape features and resources.

KEYWORDS

bio-logging, error measurement, false negatives, false positives, focal resource use, proximity loggers, wildlife encounters, wireless sensor networks

In ecology, a contact is defined as the spatial and temporal proximity of 2 individuals at or below a threshold distance, within a defined interval of time (Cross et al. 2012). Contacts can be quantified through different methods based on the collection of data from an array of bio-logging sensors. Specifically, Global Positioning System (GPS) locations can be used to map areas of spatiotemporal overlap within animal home ranges (Long et al. 2015) and to infer co-location rates from which proximity patterns can be inferred (Pepin et al. 2016). When used in conjunction with on-board cameras, GPS-collars permit the observation and characterization of contacts between animals (Bombara et al. 2017). Research on proximity detection and inter-individual relationships has been spurred by the introduction of proximity loggers in animal ecology (Ji et al. 2005, Lavelle et al. 2014, Williams et al. 2020). These bio-logging devices, that in some systems can be combined with GPS to determine the location of a contact (Picco et al. 2015), detect proximity events by exchanging ultra high frequency radio beacons (usually 434–868 MHz, but higher in some systems [e.g., 2.4 GHz]; Picco et al. 2015), thus recording the identity of the connecting loggers, an index of the quality of the received radio signal (received signal strength indicator [RSSI]), and the duration of the contact.

The communication between these loggers forms a wireless sensor network (Picco et al. 2015, Whitford and Klimley 2019), where proximity loggers can be attached to free-ranging animals (mobile loggers), or deployed at specific focal resources (fixed loggers; Ossi et al. 2016), creating the basis for relevant ecological investigation (Kays et al. 2015). Animal-to-animal contact detection (mobile–mobile contacts) allows the exploration of social behavior and learning (Krause et al. 2013), for example through social network analysis (Farine and Whitehead 2015), disease transmission models (Böhm et al. 2009, Drewe et al. 2012), or the detection of predator-prey interactions and kill sites (Tambling and Belton 2009). Additionally, animal-to-focal-resource contact detection (mobile–fixed contacts) allows the monitoring of focal resource use by an individual (Hayward and Hayward 2012, Ossi et al. 2017) and the ability to record indirect contacts between wildlife species visiting the same resource, which can influence the transmission of diseases (Lavelle et al. 2016).

One of the most important parameters associated with contact detection is the distance at which the proximity events occur (Cross et al. 2012). For instance, an assessment of pathogen transmission via direct contact between domestic and wild animals might require, in some cases, the detection of a short distance (e.g., 1–2 m; Böhm et al. 2009, Drewe et al. 2012) whilst interactions involving social learning or territory defense do not necessarily occur within short distances (Rutz et al. 2012). Assessing the distance at which a given contact occurs is therefore a key step for properly inferring the underlying ecological interactions of the encounters measured by proximity loggers (Rutz et al. 2012, Krull et al. 2019).

Proximity loggers do not directly measure contact detection distance (Williams et al. 2020). Radio signals attenuate with distance (Rutz et al. 2015) depending on the transmission power (Ossi et al. 2016), which is the factor that mainly affects the distance at which loggers detect each other. Several researchers have proposed the association between a certain radio transmission power and a determined inter-logger detection distance (Böhm et al. 2009, Drewe et al. 2012), but such relationships are complicated by the intrinsic variability of radio wave propagation (Ceriotti et al. 2010). This variability causes the relationship between contact detection and inter-logger distance to follow a probabilistic step-declining function, which is composed of 3 distinct zones: an area of maximum connectivity, or white zone, ranging between zero and distance *W*, yielding the best conditions for contact detection (i.e., theoretically close to 1, all contacts detected); a black zone, beyond the maximum range of contact detection *R*, where contact detection cannot occur; and a grey zone of gradual transition between *W* and *R*, where connectivity is not guaranteed but may occur (Zuniga and Krishnamachari 2007). Within the grey zone, errors in contact detection are likely to happen, which may bias the derived ecological inference. When calibrating proximity loggers, users should therefore focus on these errors and estimate the precision and sensitivity of the system under investigation (Burns and van Loon 2015). If overlooked, these errors may bias the estimation of connectivity rate between individuals (Boyland et al. 2013, Bettaney et al. 2015), with profound consequences on the ecological inference, and thus on the implementation of appropriate resource management action. For example, contact rate between individuals is one of the key parameters in modeling disease transmission dynamics (e.g., for chronic wasting disease [CWD]; Potapov et al. 2013). Similar considerations apply to the monitoring of animal focal resources (Mennill et al. 2012, Ossi et al. 2016) where the knowledge of contact detection error helps the user to correctly estimate the actual use of a given resource (e.g., water holes; Chamaillé-Jammes et al. 2016).

Calibration exercises have so far been rather limited and, when performed, have not fully accounted for the errors associated with contact detection. The first attempts mainly targeted estimation of the accuracy and precision of the RSSI as an indicator of the inter-logger distance (Rutz et al. 2015, Triguero-Ocaña et al. 2019), with contrasting results (Krull et al. 2019). Only in a few cases has contact detection been envisioned and modeled as a probabilistic rate of successes over a series of attempts (Ossi et al. 2016) that varies as a function of inter-logger distance (Krull et al. 2019) and other environmental factors (Triguero-Ocaña et al. 2019). The monotonically declining probabilistic relationship between contact success and inter-logger distance has been investigated (Krull et al. 2019, Triguero-Ocaña et al. 2019), but there remains a substantial knowledge gap as to the pattern of underlying errors: false negatives (expected contacts at a given distance that were not detected) and false positives (unexpected contacts that were detected at a given distance).

We characterized and modeled the structure of these error components in contact detection, thereby making them explicit and measurable. We thus evaluated the precision and sensitivity of the system (Table 1), ultimately obtaining an error profile at each inter-logger distance for different radio transmission powers. We performed this calibration exercise in 2 experimental settings where we could observe and record the 2 types of

TABLE 1 Double-entry matrix denoting the errors, and the associated metrics to measure them, based on combinations of expected and occurred contacts. Pr = precision; FNR = false negative rate; Se = sensitivity

	Expected contact	Not expected contact	Error metric
Detected contacts	True positives (TP)	False positives (FP)	Pr = TP/(TP + FP)
Not detected contacts	False negatives (FN)	True negatives (TN)	
Error metric	FNR = FN/(FN+TP) = 1 − Se		

proximity events: those between animals (mobile–mobile contacts) and those between animals and a mimicked focal resource (mobile–fixed contacts). We conducted the first experiment on domestic horses habituated to the presence of humans, to easily observe and record the proximity events between them. We then ran the second experiment on roe deer (*Capreolus capreolus*; deer) kept in semi-captivity, which were the ultimate target of our calibration assessment. We expected to observe a declining relationship between contact probability and distance between loggers for each tested radio transmission power, with consistent patterns between the 2 experimental settings.

STUDY AREA

We ran the first experiment on contacts between animals (mobile–mobile experiment) on 4 domestic horses in a fenced area (~3 ha) in Scorgiano village, central Italy, 200 m above sea level (coordinates: 43.349586, 11.159367) over 28 days, from 16 February to 17 April 2014 (Figure 1). The study area was characterized by gentle slopes without obstacles (trees, buildings) that could potentially hamper logger connectivity.

We performed the second experiment on contact detection between animals and a mimicked focal resource (mobile–fixed experiment) on 2 deer living in captivity in 2 separate sections of a fenced area (~1.5 ha) within Stelvio National Park in the Italian Alps (Pejo town, 1,500 m above sea level; coordinates: 46.358140, 10.667310). We ran the tests over 5 days, from 14–18 June 2014. We captured the deer using drive nets (López-Olvera et al. 2009), and fitted them with mobile loggers. We deployed a fixed logger in a waterproof box on a wooden pole at 1.5 m height from ground, within the section of the fenced area where one deer ranged but still close enough to the other section to guarantee contact detection with the other deer (Figure 1). The study site was characterized by a moderately steep meadow, with some trees interspersed in the lower part of the fenced area, mainly spruce (*Picea abies*), laburnum (*Laburnum anagyroides*), and birch (*Betula pendula*). In both experiments, weather conditions were sunny or cloudy, with neither rain nor severe winds, and comparable air temperature ranges; hence, we did not expect atmospheric conditions to bias the results of the experiments.

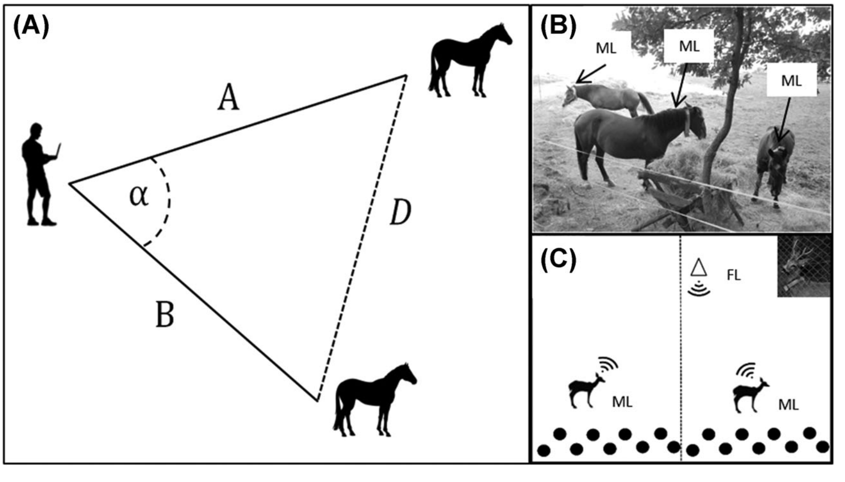

FIGURE 1 A) Scheme of the experimental protocol implemented to measure the inter-logger distance. B) The experimental setting of the mobile–mobile experiment on horses wearing mobile loggers (ML). The experiment was performed in Scorgiano village, central Italy, from 16 February to 17 April 2014. C) The mobile–fixed experiment on roe deer (1 roe deer is pictured in the upper box). The dashed line denotes the separation of the fence, the black circles represent the interspersed trees at the bottom of the fence, and the triangle indicates the position of the fixed logger (FL). The experiment was performed in Pejo town, Italy, from 14–18 June 2014

METHODS

Deployment of proximity loggers on free-ranging animals

We used a recently introduced proximity logger prototype that combines contact detection with GPS acquisition (WildScope, developed by a consortium of partners in Italy; Picco et al. 2015, Ossi et al. 2016). We tested contact detection among the 4 horses at 4 radio transmission powers (from weaker to stronger, with associated expected detection threshold distances when available from previous *in vitro* studies: 3 = −25 dBm (4 m), 7 = −15 dBm (10 m); 11 = −10 dBm (not available); 15 = −7 dBm (23 m). Picco et al. (2015) provide additional details. Deer loggers were set to power 7 only, to minimize the stress on the deer potentially induced by the multiple recaptures needed to change configuration settings. In their fenced areas, the horses and deer could move freely with no human disturbance. The experiments respected the ethical standards for animal welfare. In particular, in the experiment on horses, collars were fitted and removed from the animals in the presence of the owner, whilst the collaring of deer was performed during routine captures for deer health monitoring by the Stelvio Park team (veterinary doctor and chief wildlife biologist, with assistants) under Stelvio Park welfare regulations (official authorization: Autonomous Province of Trento: art. 36, law n. 24/1991 and successive Executive Regulation [art. 31-33 n. 16-69/1992]).

For both experiments, we measured the inter-logger distances and compared these to the contact data recorded by the WildScope proximity loggers (Figure 1). Specifically, from a fixed observation point, we first measured the distances A and B between the observer and focal dyads of loggers (pair of horses; deer and fixed logger) using a rangefinder (Bushnell, Overland Park, KS, USA), and the associated bearings using a compass. We then computed the inter-logger distance *D* as:

$$D = \sqrt{A^2 + B^2 - (2 \times A \times B \times \cos \alpha)}, \tag{1}$$

where α denotes the angle between the segments A and B. We rounded *D* to the closest meter (i.e., spatial resolution of the experiment equal to 1 m) and bounded it to 70 m, which was the maximum distance observable within the limits of the fenced areas.

While taking these measurements, we recorded the timestamp of each observation at the temporal scale of one minute, using a digital wristwatch synchronized with the logger internal clock. We considered as valid only those minutes of observations where the focal dyads did not change their mutual position. We then matched the timestamps of the empirical observations with those of the contacts detected by each logger.

For each experimental setting and observed *D*, we thus obtained a time series of observations at one-minute temporal scale, to which we associated an occurred (1) or missing (0) detection according to the data recorded by each logger at any minute of observation. For each distance *D*, we then derived the contact success (*CS*) as the rate between the minutes of detected contacts (*DC*) and the sum of minutes of detected and not detected (*NDC*) contacts:

$$CS = \frac{DC}{DC + NDC} \tag{2}$$

Estimation of error components in contact detection

We modeled contact success as a function of the inter-logger distance by means of generalized linear models with a binomial distribution and logit link function, for mobile–mobile and mobile–fixed experiments separately. For the former, we nested the inter-logger distance within radio transmission power (3, 7, 11, and 15), and tested the importance of fitting the observed dyads (i.e., dyad identification) as a random effect (Bolker et al. 2009). For each experimental setting, we thus obtained the predicted probability P(*x*) of detecting an expected contact at any given inter-logger distance *j* (true positives; Figure 2; Table 1). For each distance *j* spanning from zero to the maximum

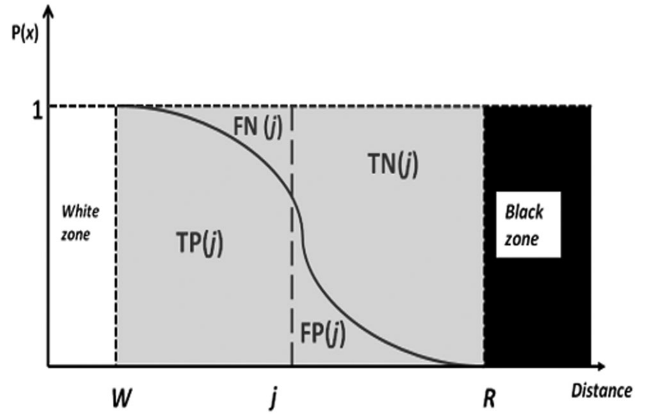

FIGURE 2 The theoretical distribution of contact probability P(*x*) as a function of inter-logger distance. For distances shorter than *W*, the area under the curve indicates maximum connectivity (white zone). For distances greater than *R*, no contacts are detected (black zone). For distances between *W* and *R*, the contact detection probability varies (grey zone). Given a generic distance *j* of interest, the curve delimits 4 regions within the grey zone: the cumulative probability of detecting an expected contact within distance *j* (i.e., the true positives [$TP_{(j)}$]); the cumulative probability of missing an expected contact within distance *j* (i.e., false negatives [$FN_{(j)}$]); the cumulative probability of detecting an unexpected contact beyond distance *j* (false positives [$FP_{(j)}$]); and the cumulative probability of missing an unexpected contact beyond distance *j* (true negatives [$TN_{(j)}$])

range of transmission *R*, defined as the distance where P(*x*) = 10^{-5} (Figure 2), we also computed the precision of the system Pr(*x*), which is the probability that a recorded contact occurs within the given distance *j* and not beyond (Table 1). Specifically, at each distance *j*, we computed the precision as the ratio between the cumulative true positives (expected and occurred contacts within the distance *j*) and all the cumulative detected contacts, including true positives and false positives (i.e., contacts occurring beyond the distance *j*; Figure 2):

$$\mathrm{Pr}(x) = \frac{\sum_{i=0}^{j} p(x)}{\sum_{i=0}^{R} p(x)} \tag{3}$$

Next, we computed the false negative rate (FNR), which is the probability of missing a contact within *j* and the complementary to 1 of the sensitivity (Table 1). We computed the false negative rate at each distance *j* as the ratio between the cumulative false negatives (contacts expected but not occurred within *j*) and all the expected contacts within *j* (false negatives + true positives; Figure 2):

$$\mathrm{FNR}(x) = \frac{\sum_{i=0}^{j} (1 - p(x))}{\sum_{i=0}^{j} p(x)} \tag{4}$$

Finally, we computed the receiving operating characteristic (ROC) curves to evaluate the performance of the empirical predictive models (Steyerberg et al. 2010).

RESULTS

We recorded 429 observations between horse dyads across the 4 tested radio transmission powers, and 68 observations between roe deer and the fixed logger. The monitoring time lasted overall 2,355 minutes (1,719 minutes for mobile–mobile experiment; 636 minutes for mobile–fixed experiment). The duration of the observations spanned from

TABLE 2 Summary of empirical predictive models of contact detection as a function of inter- logger distance, for all studied settings. We report the intercept (with SE) and the β coefficient estimate (with SE and *P*-value [Student's *t* test]) of the predicted curves and the number of observations they were based on (*n*). The area under the curve (AUC) indicates the goodness of fit of the curves (for random curve: AUC = 0.5). One minus the intercept provides the estimate of false negative rate at a distance of 0. We present the difference with random curve (DR) and its significance (**P* < 0.05; ***P* < 0.01; ****P* < 0.001)

Setting	Intercept ± SE	β ± SE	*P*	*n*	AUC	DR
3, horses	0.78 ± 0.08	−0.44 ± 0.03	<0.01	207	0.88	2,418.5***
7, horses	0.77 ± 0.09	−0.11 ± 0.01	<0.01	106	0.86	987.6***
11, horses	0.76 ± 0.11	−0.07 ± 0.01	<0.01	60	0.82	332.6***
15, horses	0.72 ± 0.16	−0.02 ± 0.01	<0.01	54	0.62	18.9***
7, deer	0.90 ± 0.16	−0.26 ± 0.03	<0.01	68	0.92	581.8***

1 minute in both experiments, to 47 minutes for the mobile–mobile experiment and 85 minutes for the mobile–fixed experiment. In all experimental settings, the probability of contact detection decreased significantly with inter-logger distance, but not abruptly, as expected from the theoretical scenario (Table 2; Figures 2 and 3). Conversely, because some contacts also occurred in the tail of the distribution, the probability of a contact being detected within distance *j* (i.e., the precision) increased with inter-logger distance until the maximum range value *R* (Figure 4). In the mobile–mobile experiment on horses, the contact probability decreased more sharply for power 3, with almost no contacts beyond 15 m (i.e., *R* = 15 m), whereas for powers 7 and 11, contact probability decreased less abruptly, with *R* = 50 m and *R* = 70 m, respectively. For power 15, *R* could not be estimated because it exceeded the maximum observation distance possible within the fenced area (70 m). In the mobile-fixed experiment on deer (power = 7), contact probability decreased more sharply than in the mobile–mobile experiment on horses with the same power (*R* = 25 m). In the mobile–mobile experiment, where multiple dyads could occur, we observed a non-negligible variability between them, as the random effect was always significant. We were interested in general predictions on contact detection probability, but we provide the output for the population-level average (Appendix A).

In all settings, even when 2 loggers were very close to each other (*j* = 0), contact probability was not 100% (Table 2, Figure 3). Accordingly, because contacts could also be missed when loggers were very close, the intercept of the false negative rate curve with the y-axis was not zero (Table 2, Figure 5). For the mobile–mobile experiment on horses, where loggers were set up with different radio transmission powers, the precision and false negative rates were greater at the same inter-logger distance for contact detection with lower powers (Figures 4 and 5). The proximity loggers yielded a greater precision in the mobile–fixed experiment than in the mobile–mobile experiment (power = 7) at all distances, and a lower false negative rate for distances <10 m (Figures 4 and 5). The area under the curve values of the ROC of all curves supported the high reliability of the predictive models that differed significantly from the random model (Table 2), although power 15 performed poorly compared to the other settings.

DISCUSSION

We performed a calibration exercise on real animals in semi-controlled environments to model the errors associated with contact detection by proximity loggers, demonstrating their relevance for a robust assessment of encounters. We have accounted for false negatives (existing but undetected contacts) in modeling the probability of contact detection. We concluded that in animal deployments of proximity loggers, there is no certainty of detecting an occurring contact even when the animals are very close to each other. Further, we modeled the occurrence of false negatives so that, at any inter-logger distance in a specific scenario, it would be possible to estimate the probability of a certain contact occurring and to

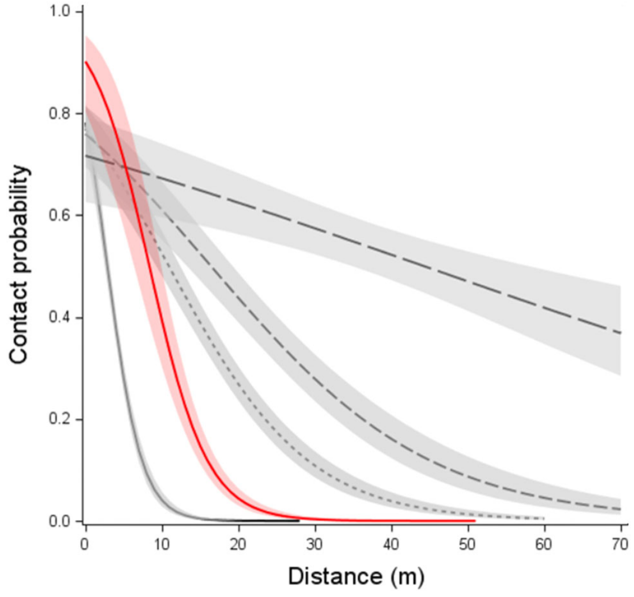

FIGURE 3 Predictive curve denoting contact detection probability as a function of inter-logger distance, for all experimental settings. We plotted the predictive plot referring to the population-level average. The colored areas around the curves represent the 95% confidence intervals. Black continuous line = power 3 for mobile–mobile experiment on horses; red continuous line = power 7 for mobile–fixed experiment on deer; black short dashes = power 7 for mobile–mobile experiment on horses; black medium dashes = power 11 for mobile–mobile experiment on horses; long dashes = power 15 for mobile–mobile experiment on horses

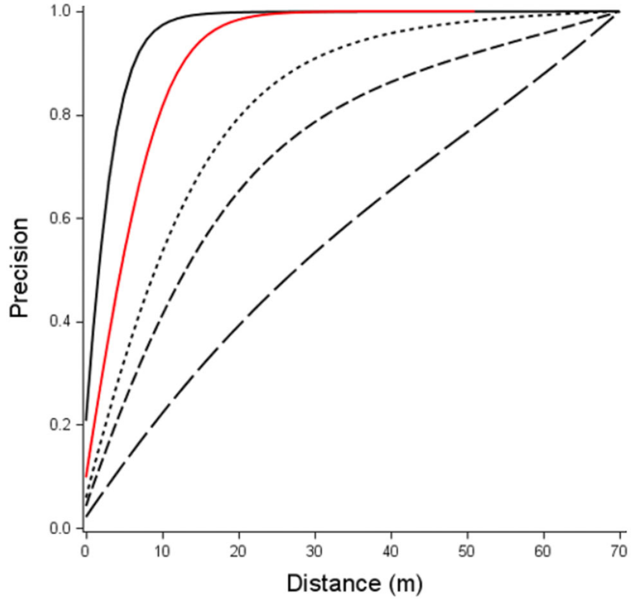

FIGURE 4 Predictive curve of precision as a function of inter-logger distance, for all experimental settings. The curves are truncated at the maximum range of contact *R*. Black continuous line = power 3 for mobile–mobile experiment on horses; red continuous line = power 7 for mobile–fixed experiment on deer; black short dashes = power 7 for mobile–mobile experiment on horses; black medium dashes = power 11 for mobile–mobile experiment on horses; long dashes = power 15 for mobile–mobile experiment on horses

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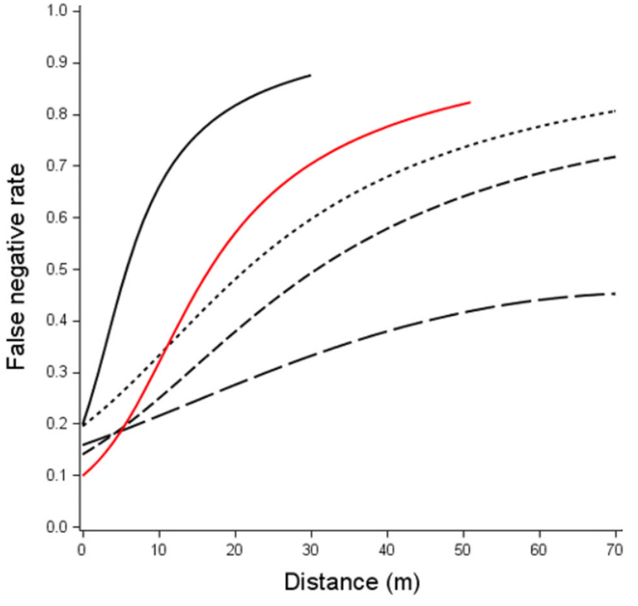

FIGURE 5 Predictive curve of false negative rate as a function of inter-logger distance, for all experimental settings. The curves are truncated at the maximum range of contact *R*. Black continuous line = power 3 for mobile–mobile experiment on horses; red continuous line = power 7 for mobile–fixed experiment on deer; black short dashes = power 7 for mobile–mobile experiment on horses; black medium dashes = power 11 for mobile–mobile experiment on horses; long dashes = power 15 for mobile–mobile experiment on horses

determine the percentage of missed contacts. Lastly, we systematically introduced the concept of false positives into contact detection research, by defining the concept of maximum range distance, and modeling the precision of the system. The users of proximity loggers should be aware that the association between a certain radio transmission power and a determined inter-logger detection distance, proposed earlier (Böhm et al. 2009, Drewe et al. 2012), is not realistically applicable in proximity detection studies (Krull et al. 2019), especially in real settings. Relying on radio transmission power as a proxy measurement of inter-logger distance when using proximity loggers can lead to incorrect interpretation of the output of these bio-logging devices. Instead, detected contacts are empirical observations that are subject to device measurement error and the ambient context of measurement (Rutz et al. 2015).

The occurrence of errors in contact detection is likely more evident when deploying the proximity loggers on animals than when testing them in controlled scenarios where loggers are moved around by personnel (Ossi et al. 2016, Krull et al. 2019, Triguero-Ocaña et al. 2019). Further, these errors are likely to vary among different observed dyads of proximity loggers (Wilber et al. 2019), and accordingly the random effect of the observed dyad was significant for each tested power setting in the mobile–mobile experiment on horses. With our innovative experimental protocol, we have been able to account for such noise typically generated, among other environmental factors (Marfievici et al. 2013, Triguero-Ocaña et al. 2019), by body encumbrance (Krull et al. 2019) and fine-scale movements of animals. For instance, 2 loggers attached to animals within contact detection distance may unexpectedly interrupt radio transmission if the individuals move in a back-to-back position, thus interposing their bodies between loggers. These behaviors may explain the missed contacts observed for adjacent loggers, irrespective of radio transmission power. As such, the white zone with maximum connectivity described in theoretical models of radio transmission (i.e., the area between zero and the distance *W*; Figure 2) seems not to apply in real scenarios of contact detection due to environmental noise. The maximum range of contact detection we calculated exceeds that reported in controlled *in vitro* scenarios (Picco et al. 2015, Ossi et al. 2016). Possibly, this is another consequence of the environmental effects introduced by deploying the proximity loggers on animals, which can lead to the recording of contacts beyond the desired detection distance threshold (i.e., the generation of false positives). The combined effects of body encumbrance and fine-scale movements possibly also explain the higher sensitivity and precision in the mobile–fixed experiment on deer relative to the mobile–mobile experiment on horses at the same radio transmission power. We speculate that these differences were due to a lower body mass of deer and a proportionally reduced effect of fine-scale movements in a mobile–fixed setting with respect to animal-to-animal encounters. Conversely, the greater maximum range of transmission *R* observed for the mobile–mobile experiment (50 m; i.e., double that of the mobile–fixed experiment when set at the same power), is possibly explained by a combination of terrain topography and logger height from the ground, both of which differed between these experimental settings. Indeed, the maximum range of connectivity increases with logger height from the ground (Ceriotti et al. 2010, Picco et al. 2015, Rutz et al. 2015), as is the case for relatively larger and taller animals (e.g., horses vs. deer). Further, the steep alpine terrain where the experiment on deer was conducted might have contributed to reduced radio wave connectivity (Anastasi et al. 2004), in contrast to the gentle hilly slopes characterizing the setting of the experiment that we ran on horses.

Our results suggest that users should be aware of potential bias in the application of proximity loggers, as with any bio-logging device (Bettaney et al. 2015, Burns and van Loon 2015). The general principles of error structure in contact detection presented in this work have a wide applicability, but the measurement of the parameters of contact detection (e.g., the maximum range of contact detection *R*) are highly specific to a given experimental setting. We therefore emphasize the need to adequately calibrate proximity loggers in conditions as similar as possible to those of their intended deployment (e.g., by testing some units on captive individuals of the target species). We acknowledge that sometimes this is not feasible because of the difficulty of finding a setting that allows the observation of dyadic interactions among groups of individuals of the target species (as it was the case here for deer). In this case, we still encourage the users of these tools to test the proximity loggers in a controlled scenario (e.g., on domestic animals) to assess the probabilistic relationship between contact detection and inter-logger distance. Then, if feasible, the users could perform a targeted experiment on the focal species, even when settings are not optimal (e.g., on a very limited sample size). For instance, in our mobile–fixed experiment on 2 individual deer, we limited the test to the radio transmission power that, based on previous results from the mobile–mobile experiment on horses, was of major interest for further ecological investigation. In our case, although we acknowledge the potential limitation of the results of the mobile–fixed experiment, the overall comparable predicted pattern of contact detection between the 2 experimental settings demonstrates the validity of this calibration protocol.

MANAGEMENT IMPLICATIONS

Our proposed experimental protocol provides practical and repeatable guidelines for choosing the settings of proximity loggers matching the desired study objectives, with particular attention to the pattern of false positives and negatives. To this end, we propose a decision tree to guide the user's choice (Figure 6). First, the user should identify the desired distance of contact that better matches the ecological process under investigation. For example, studies on direct disease transmission typically focus on short distance contacts (e.g., small values of *R*), whereas social interactions such as territoriality or mate choice may rely on relatively large distances to define an encounter. Based on this, the user should evaluate the trade-off between the desired precision and sensitivity of the system. If the user is mainly interested in not missing any contacts within a given distance (i.e., minimizing the false negatives), they should set the proximity loggers to a power with maximum range *R* greater than the inter-logger distance of interest *D*. The user will accept, as a trade-off, that a certain proportion of the observed contacts will happen in a range between *D* and *R* (i.e., that the precision of its assessment will be suboptimal). Vice versa, the user may decide to maximize the precision of the system to avoid the occurrence of false positives. In this case, the user will set the system so that *D* is close to *R*, with the understanding that some contacts may be overlooked, especially when occurring at relatively large distances (i.e., close to *R*).

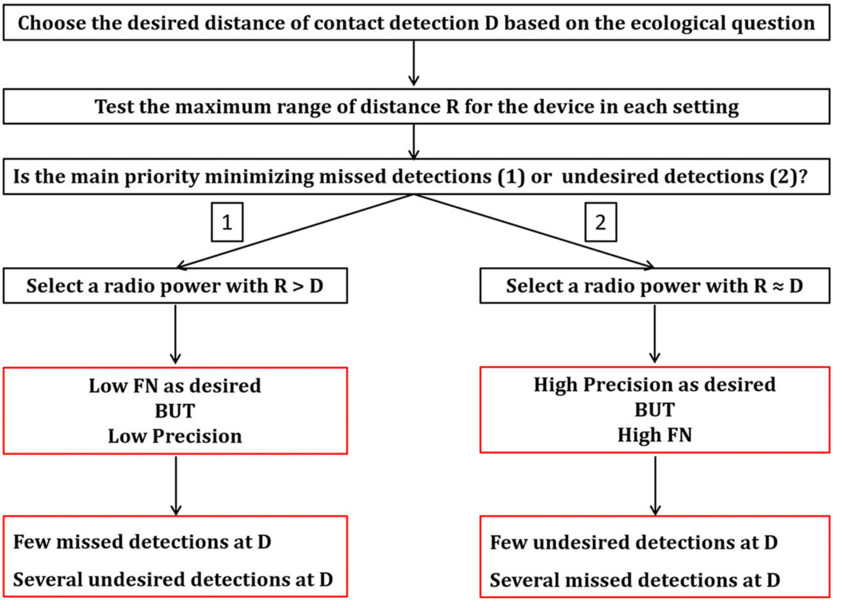

FIGURE 6 Decision tree to guide the user on optimal setting choice for proximity loggers. Black boxes denote the actions that the user may undertake, while the red boxes indicate consequences of such actions. In the decision tree, D denotes the desired contact detection distance, R indicates the maximum range of detection distance, and FN defines the false negatives

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DATA AVAILABILITY STATEMENT

Data will be made available upon reasonable request.

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APPENDIX A: COMPARISON OF THE MODELS WITH AND WITHOUT A RANDOM EFFECT

We tested the importance of fitting a random effect of the observed dyad solely in the mobile–mobile experiment on horses because in the mobile–fixed experiment on deer the number of observed dyads was too limited to permit the estimate of any effect in the model. For the mobile–mobile experiment on horses, we fitted the same fixed-effect model with and without a random effect (dyad identification) to assess the relevance of this component in the model through a comparison based on Akaike's Information Criterion scores corrected for small sample size (AIC_c; Burnham and Anderson 2002). For each power, the model with the random effect had a lower AIC_c score than the model without the random effect (Table A1). The empirical predictive plot denoting the relationship between contact detection probability and inter-logger distance evidenced rather wide confidence intervals, for each radio transmission power (Figure A1), probably because of the relatively small number of dyads. For the purpose of generality, we illustrated the predictions for the population-level average because the predictor's effect size did not change with respect to the random model (Table A2).

TABLE A1 Comparison based on Akaike's Information Criterion scores corrected for small sample size (AIC_c) scores of the models with or without a random effect (dyad identification), for the 4 different power settings of the mobile–mobile experiment on horses

Power	AIC_c with random effect	AIC_c without random effect
3	773.285	803.936
7	454.883	516.309
11	367.363	379.669
15	420.392	478.653

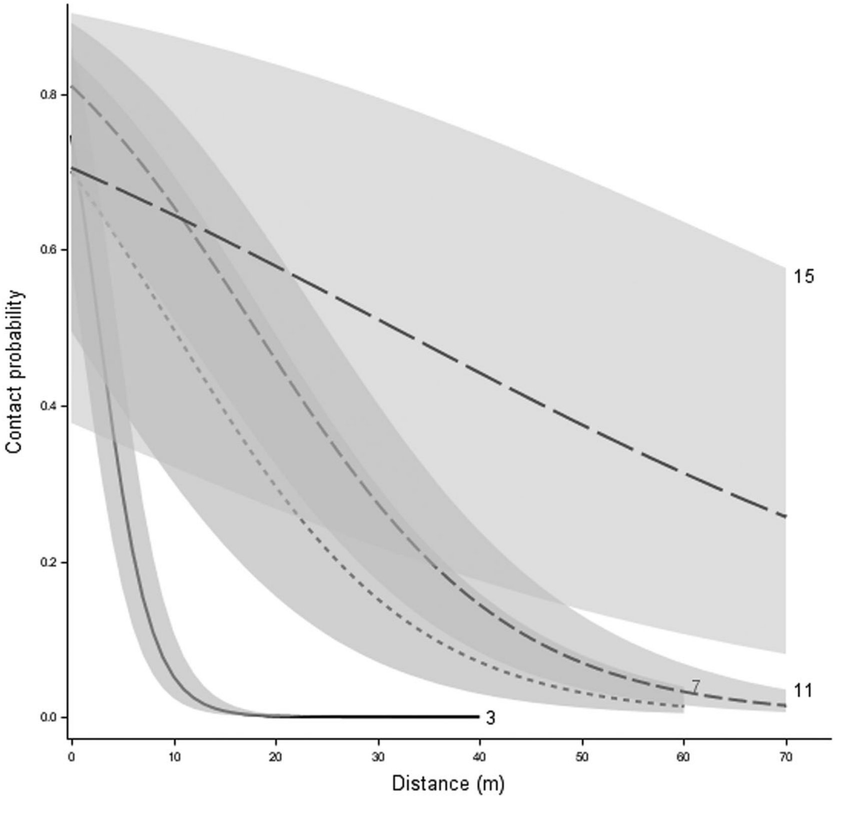

FIGURE A1 Plot denoting the relationship between contact detection probability and inter-logger distance for all the experimental settings on the mobile–mobile experiment on horses, for the models with a random effect. The colored areas around the curves represent the 95% confidence interval. Continuous line = power 3; short dashes = power 7; medium dashes = power 11; long dashes = power 15

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TABLE A2 Comparison of the model summary with and without a random effect (dyad identification) for the mobile–mobile experiment on horses, on each tested power setting. For each power, we report the predicted β coefficient estimate with standard error and significance at the 95% level of the Student's *t* test (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$)

Power	Random model β ± SE	Not random model β ± SE
3	−0.40 ± 0.03***	−0.44 ± 0.03***
7	−0.09 ± 0.01***	−0.11 ± 0.01***
11	−0.08 ± 0.01***	−0.07 ± 0.01***
15	−0.03 ± 0.01***	−0.02 ± 0.01***