Associations on land and at sea? A pilot study on the utility of proximity loggers to assess inter-individual relationships in colonial seabirds

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Conflict of Interest

The authors declare that they received a rebate from TechnoSmart for the proximity loggers to conduct this pilot study. TechnoSmart did not see a draft of the manuscript prior to submission, nor did they participate in the study or in the writing of the manuscript. The authors did not receive any compensation for using the proximity loggers.

Data accessibility: Data, including analysis, are available in an open-access public repository, accessible via this **link**.

Author Contributions

Antoine Morel and Pierre-Paul Bitton together conceived the ideas and designed the methodology. Antoine Morel led the data collection, the analysis and the writing of the manuscript. Pierre-Paul significantly contributed to the analysis and editing the manuscript. All authors contributed to the drafts and gave final approval for publication.

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Abstract

Accurate and extensive data collection is essential for understanding animal sociality, but collecting associations between individuals remains challenging. Animals often associate and interact outside of the range of an observer, especially in environments such as underwater or underground. However, the development of proximity loggers using Bluetooth and radio frequency to detect associations allows scientists to access behavioural information that would otherwise be impossible to collect. Here we examined the use of a logger with a proximity feature to capture associations between Atlantic puffin individuals and assessed how it could complement observations social network studies. To understand the capabilities of the logger, we tested the effect of distance on signal strength and proportion of associations detected, as well as the proportion of contacts recorded by each logger in a dyad, in lab-based and field environments. Thereafter, we tested the loggers on live Atlantic puffins and compared their performance against visual observations. As expected, signal strength decreased with distance, and lab-based values were more consistent than in the field. The proportion of contacts successfully processed decreased with distance, but our experiment in the field was more reliable, probably because we used a lower logger density, limiting opportunities for interference among units. More importantly, the loggers identified more putative associations than detected by observations, including many when and where individuals were not under observation. We also demonstrate that Atlantic puffins that associate frequently on land also associate frequently at sea. Our results bring new insight into the understanding of Atlantic puffin social behaviours, particularly at times and in locations challenging to monitor.

Keywords: Associations, Atlantic puffin, Dyad, Focal sampling, Social behaviour, Social network, Visual observation

Introduction

Social behaviours, defined as interactions between two or more individuals, are likely to be better described in abundant and easy-to-detect species (Webber & Vander Wal, 2019). Furthermore, our understanding of inter-individual relationships is biased by when and where animals are observable, especially for those that spend much time in areas that are challenging to sample (e.g., open sea, dense forest, at night, or during migration). Therefore, it can be difficult to accurately assess social processes without methods that comprehensively sample associations (Farine & Whitehead, 2015; Hoppitt & Farine, 2018). By combining remote sensing with observational data collection, we explored the potential for proximity loggers to replace and/or complement observational data collection in the detection of on-land and at-sea associations in the Atlantic puffin.

The quantification of social relationships is often used by researchers to measure sociality between individuals. However, the reliability of this measure is dependent on the accuracy of the data collection (Farine & Whitehead, 2015; Hoppitt & Farine, 2018). Focal observations, involving an observer recording associations or interactions between known individuals, are commonly used in network sampling (Webber & Vander Wal, 2019). To increase the chance of encountering individuals, scientists often target locations where certain species come back regularly, such as breeding sites (e.g., Nomano et al., 2014) or artificial feeding sites (e.g., Firth et al., 2017, Heinen et al., 2022). While free-range living animals such as birds or mammals are among the most studied taxonomic groups in social networks (Webber & Vander Wal, 2019), they are likely to be challenging to sample when away from their breeding site, and their behaviours may be influenced by human disturbance produced by the presence of the observer. The resulting observational biases can skew data collection toward specific biological mechanisms, periods, and locations (Hoppitt & Farine, 2018). A general example is one of seabird species that migrate broadly and breed on remote protected islands. Targeting individuals at their breeding site is the easiest way to collect social behaviour information. However, sampling on those islands is likely to generate disturbances (Brown et al., 2013) and bias sampling toward specific inland associations. To address these limitations, there is a growing need for new methods that ensure reliable data collection with limited human intervention.

Remote technology is gaining popularity in the study of animal behaviour, particularly in collecting associations when and where observations are challenging or not possible (Webber & Vander Wal, 2019; Smith & Pinter-Wollman, 2021). Radiotelemetry and Global Positioning Systems (GPS) have been used in attempts to assess proximity between individuals (Ramsey et al., 2002; Atwood & Weeks, Jr., 2003; Wallace et al., 2022; Davis et al., 2018), but the detection of social relationships often require a high temporal and spatial resolution that these methods lack, particularly when changes in vegetation and topography occur (D'eon & Delparte, 2005; Frair et al., 2010). Miniaturised proximity loggers for association detection on small animals such as birds were initially introduced by Rutz et al. (2015) using radio frequency and later developed with Bluetooth (Kirkpatrick et al., 2021; Huels et al., 2025). These loggers are now often packaged with other functionality, such as GPS and accelerometer and are mounted on a collar, backpack, or leg band. They are powered by batteries, sometimes complemented with solar panels to increase battery life span. While their use remains uncommon (3.6 % of the social network studies reviewed by Webber & Vander Wal (2019) used proximity loggers), they have returned very good results on large and mid-sized mammals such as white-tailed deer (*Odocoileus virginianus*; Walrath et al., 2011), brushtail possums (*Trichosurus vulpecula*; Ji et al., 2005) and domestic cattle (*Bos taurus*; Swain & Bishop-Hurley, 2007). Recently, due to the advances in technology, and often at the cost of battery lifespan, miniaturised proximity loggers have been used on birds such as New Caledonian crow (*Corvus moneduloides*; Bettaney et al., 2015), European starlings (*Sturnidae vulgaris*; Kirkpatrick et al., 2021), wire-tailed manakin (*Pipra filicauda*; Ryder et al., 2012) and small mammals such as prairie voles (*Microtus ochrogaster*; Gaidica et al., 2024). However, these systems are limited to a few days in duration, which makes them inconvenient for studying animals over longer periods. Still, proximity loggers with battery life-saving performance and integrated solar panels present a solution for short-term data collection on species that are challenging to observe, and their use on smaller species requiring technology adaptation has received little attention.

This study was conducted on the Atlantic puffin, a central-place forager species that returns to the colony after foraging at sea, offering a good contrast between observable and non-visible associations. We tested the Gipsy 6© (TechnoSmArt Europe, Colleverde, Italy), a miniaturised solar-powered GPS with an embedded proximity logger and evaluated its performance in the detection of associations in Atlantic puffins, at sea and on land. Specifically, we tested its performance and repeatability in lab-based and field environments and compared its detection rate with observational methods to test for detection when and where observations were not possible.

Materials and methods

Study site and species

We collected data on Great Island, located in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada (47.1855N, 52.8121W). The reserve comprises the largest Atlantic puffin population in North America (~590,000 breeding individuals; Wilhelm, unpublished data, Great Island hosting around 350,000; Wilhelm et al., 2015). The Atlantic puffin is a monogamous colonial seabird with a long life span (up to 45 years in the wild; Fransson et al., 2023) that forms densely populated breeding colonies (~1.6 burrows/m² in Great Island; Belenguer, 2023). They display daily and seasonal colony attendance cycles with individuals generally gathering more on land in the evening (Calvert & Robertson, 2002). It has also been suggested that individuals on land prefer to be surrounded by conspecifics and will give signs of nervousness in low density (Calvert & Robertson, 2002). Atlantic puffins are highly social and associate more with close nesting conspecifics (Morel et al., 2025). At sea, they often stay in groups (i.e., rafts) that are likely to be used as information centres (Weimerskirch et al., 2010).

Data collection

Logger testing

Logger description

We used the Gipsy 6© (TechnoSmArt Europe, Colleverde; Figure S1), a remote detection device that combines GPS, accelerometer, and radio frequency to detect proximity between devices. We set the time of activity, signal strength and scanning interval frequency before deployment. The device was shaped to limit frontal surface area and drag (11 x 6 x 4 millimetres), was waterproof to 60 metres and was black to better match the mantle of the puffins. The units were powered by a lithium battery connected to a solar panel, weighed six grams, and were attached using Tesa® tape. The data were downloaded using a base station with a range of 500 metres and a short antenna with a range of 10 metres.

Lab-based environment

We evaluated the performance and repeatability of the proximity loggers in optimal conditions by testing them in a lab-based environment. We deployed 12 loggers on an asphalt-shingled rooftop, as it provided a flat high ground away from physical barriers. Each logger had a unique ID and was placed along a circle 0.5 metres away from the centre (Figure S2). The distribution in a circle aimed to reproduce a high-density aggregation of individuals as observed in nature. The scanning interval frequency was set for one minute, and each trial was 20 minutes long, at the end of which loggers were moved an extra 0.5 metres away from the centre. The procedure was repeated until a maximum distance of five metres between the farthest loggers was reached (each 2.5 metres away from the centre).

Field environment

We evaluated the performance and repeatability of proximity loggers under field conditions by deploying them on an established study plot on Great Island, Witless Bay Ecological Reserve. We deployed the same 12 loggers on a 168 square metres (14 x 12 metres) plot. The plot had a consistent 40-degree angle slope facing West. Its surface was irregularly covered by tall grass, branches, and shallow, solitary boulders. The density of burrows was estimated at 1.6 burrows/m^2 (Belenguer, 2023). The loggers were set at 0.5 metres intervals on a diagonal following a 45-degree angle to the bottom ledge (Figure S3). All loggers but the three farthest were programmed to send their signal once every five minutes for 350 minutes. The loggers at distances of 5.5, 5, and 4.5 metres did not implement the new schedule between trials and were scanning every minute.

Comparison with observational data

To compare the data collected by the loggers with observational data and assess associations potentially missed by scan sampling, we attached proximity loggers to 6 individuals in 2023, as part of a long-term study that included an additional 131 colour-banded individuals (50 in 2021, 74 in 2022, and 13 in 2023). To avoid increasing risks of breeding failure by tagging both parents, we only equipped one individual of any given pair. Because breeding adult seabirds are likely to abandon their nest if disturbed early in the breeding season (Yorio & Boersma, 1994; Rodway et al., 1996; Blackmer et al., 2004), we captured adults only after their chicks had hatched. To evaluate the best capture period, we assessed burrow occupancy regularly and captured birds after 80 % of the eggs had hatched, and we sampled only the burrows in which chicks were present. To maximise the capture rate and minimise disturbance, experienced banders and their assistants operated at night when the birds were usually in the burrow. We trapped the adults in their burrows by hand grubbing before taking them to a banding station set a few metres away. Banders fitted each individual with a unique combination of three Darvic plain colour bands custom-made from *Avian ID* (9.53 mm ID X 7.93 mm HT, Red, White, Green, Black, Grey, Yellow, Light blue and Dark blue), and a Canadian Wildlife Service stainless steel grey band with a unique identifier. Six individuals were tagged with a proximity logger using the methods presented in Wilson and Wilson (1989), with four strips of Tesa® tape and one zip tie. The loggers were set on the lower back, just above the uropygial gland, with an expected retention of 15 days. Each bird was handled for no more than 15 minutes before being released in its original burrow.

To capture associations using proximity detection, we set the loggers to scan every two minutes during periods when birds are the most visible on land (from 5:00 a.m. to 10:00 p.m.; Calvert & Robertson, 2002). To save battery, we had them turn off from 10:00 p.m. to 5:00 a.m., when individuals are often found inside their burrow (Calvert & Robertson, 2002). To assess individual presence on the plot, we set one extra logger in the centre of the study area, scanning every two minutes. Data were collected using a long-range base station and, alternatively, a short-range antenna when birds with loggers were observed (Figure S1). The long-range antenna was fixed on the blind used for scan sampling, five metres away and facing the plot.

To capture associations based on visual observation, we conducted 210 hours of scan sampling from June 06th to August 07th 2023, on the 137colour-banded individuals. From a blind facing the plot, we usually conducted two observation sessions of four hours each in a day, regardless of weather conditions. We started the first session at civil twilight and the second session four hours before sunset, the evening session lasting until the visibility was too low to identify colour bands correctly. Each session consisted of two observers equipped with binoculars (Swarovski EL 10x42 WB), observing the plot and the areas peripheral to the limits of the plot, searching for social associations. The observers were trained to accurately assess distance using flags and natural features. To optimise detections, we ensured that the area was scanned from top to bottom, and right to left when the slope was crowded, and we followed specific individuals when in low density. For this study, we defined an association as any known individuals (i.e., identified with colour bands) within a two-metre radius of another. Observers created an event each time a new association occurred or when the association was still ongoing after two minutes. All events were time-stamped and given unique sequential record numbers.

Analyses

Logger testing

For all data management and analyses performed, we used R statistical Software v.4.2.3 (R core Team, 2025). To evaluate the performance and repeatability of the loggers in lab-based and field environments, we assessed two metrics: the Received Signal Strength Indicator (RSSI; hereafter signal strength), within and between distances and the proportion of total contacts recorded by each logger in a dyad. Signal strength is expressed in decibel-milliwatts (dBm) and generally ranges between zero and -

120 with values close to zero indicating a strong signal. We applied a general linear mixed model to test the significance of the relationships between signal strength and distance between loggers using the glmmTMB package (Brooks et al., 2017). We used strength as the dependent variable and treatment with the logarithmic values of distance as the independent variable. We used logger ID as a random factor, and allowed slopes to vary by Treatment (i.e., Lab-based and Field-based trials as categorical variables). The assumptions were validated by evaluating the analytical plots from the DHARMa package (Hartig & Lohse, 2022), and we found that the t-family returned the best assumptions. The repeatability of the signal strength was tested using the *rptR* package (Stoffel et al., 2017). We calculated the repeatability estimation using the linear mixed model method by setting signal strength as the response variable and distance as the grouping variable. We obtained the repeatability estimate R, p-value and the confidence interval estimates after bootstrapping the procedure 1000 times. We tested the relationship between the proportion of detection, distance and treatment using a generalised linear mixed model. For this model, the square root of distance was used, and logger ID was included as a random factor. Using diagnostic plots, we validated our assumptions and found that the beta-family was returning a better model fit.

To compare the use of loggers against traditional observations, we evaluated three metrics. We 1) compared the number of associations concurrently captured by field observations and loggers, 2) assessed the proportion of associations detected by the loggers occurring outside of observation hours, and 3) assessed the proportion of associations detected by the loggers away from the plot. To compare the proportion of associations captured by both methods, we cross-referenced the associations captured during observation from the blind and the data automatically collected from the loggers. We filtered the associations automatically detected in the plot, during observational hours, and for which signal strength was more than -95dBm. The -95dBm threshold was selected as it is the minimum signal strength detected by loggers for which association within 2 metres distance was visually validated. We excluded associations occurring out of the reach of the visual observation method by including only associations that were also detected by the plot logger. Because loggers can sometimes miss the signals sent every two minutes, we applied a four-minute buffer (i.e., two interval lengths duration). We assumed all individuals on the plot would be detected because they often stay for an extended period on land to rest, which would have been detected by the stationary logger's frequent screening. To select the associations automatically captured at the same time as visual observation, we kept a record of the observation period and selected associations within these time windows. By dividing the number of contacts within the plot but outside of the observation time window, we calculated the proportion of contacts missed by the observation method.

To evaluate the pattern of dyadic association on the plot or not (presumably at sea), we first attributed a location to each dyadic association detected by the loggers using the time window built with the stationary logger. Then we represented the distribution of contacts by location and expressed its strength using a Pearson correlation.

Ethical Note

This study was performed on a protected Atlantic puffin colony within the natural reserve of Witless Bay Ecological Reserve. Animal ethics were covered by an Animal Use Permit (23-01-PB) issued by XXX University Animal Care Committee. All research activities, including trapping, banding and the construction of a non-permanent structure, were allowed under a Province of Newfoundland and Labrador scientific research permit (wepr2021-23atpucolouration), a Banding permit (10926) and a Migratory Bird Research permit (SC4061) issued by Environment and Climate Change Canada.

Results

Logger function in lab-based and field environments

In this study, we tested 12 loggers in lab-based and field environments to determine whether signal detection warranted deployment on live animals. When testing the effects of distance and environmental conditions on strength and proportion of contact we found that signal strength decreased with distance ($\chi2 = 71054.809$, df = 1, $p < .001$; Figures 1 and 2), and decreased more in the lab-based environment than in the field setting (coefficient estimate lab-based environment = 18.1402, field setting = 16.1834; $\chi2 = 23.089$, df = 1, $p < .001$). Most of the variance was explained by the logger ID (R^2 conditional = 0.963, R^2 marginal = 0.846). We also found that signal strength was moderately repeatable among distances (R = 0.661). Similarly, we found a significant effect of distance on the proportion of contact ($\chi2$ (1) = 58.297, df = 1, $p < .001$; Figure 3), with a difference between treatments ($\chi2 = 228.532$, df = 1, $p < .001$). The loggers performed better in the field environment (coefficient estimate lab-based environment = -1.5858, field setting = -0.0954). Additionally, we found a difference in the proportion of contacts recorded by each logger in a dyad (Figure 4). Particularly, for both environments, more than 50 % of the dyads did not record equal logs. (i.e., an equal number of contacts received by a logger and detected by the emitting logger).

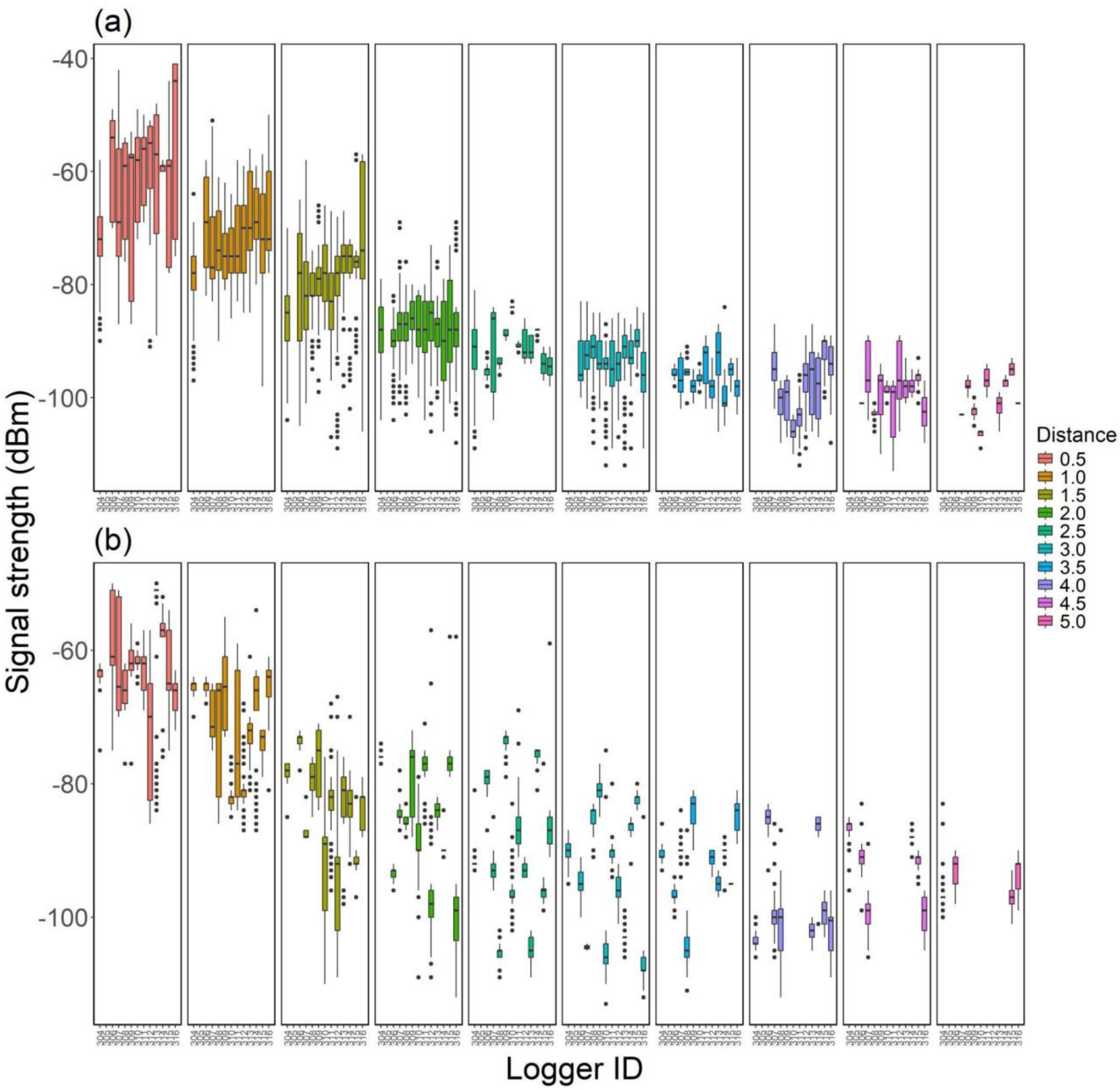

Figure 1. Among and within logger variations in signal strength in relation to distances between units. Data were collected on 12 loggers in a (a) lab-based environment and (b) field environment. Values of signal strength (in decibel-milliwatts) closer to zero indicate a strong signal strength.

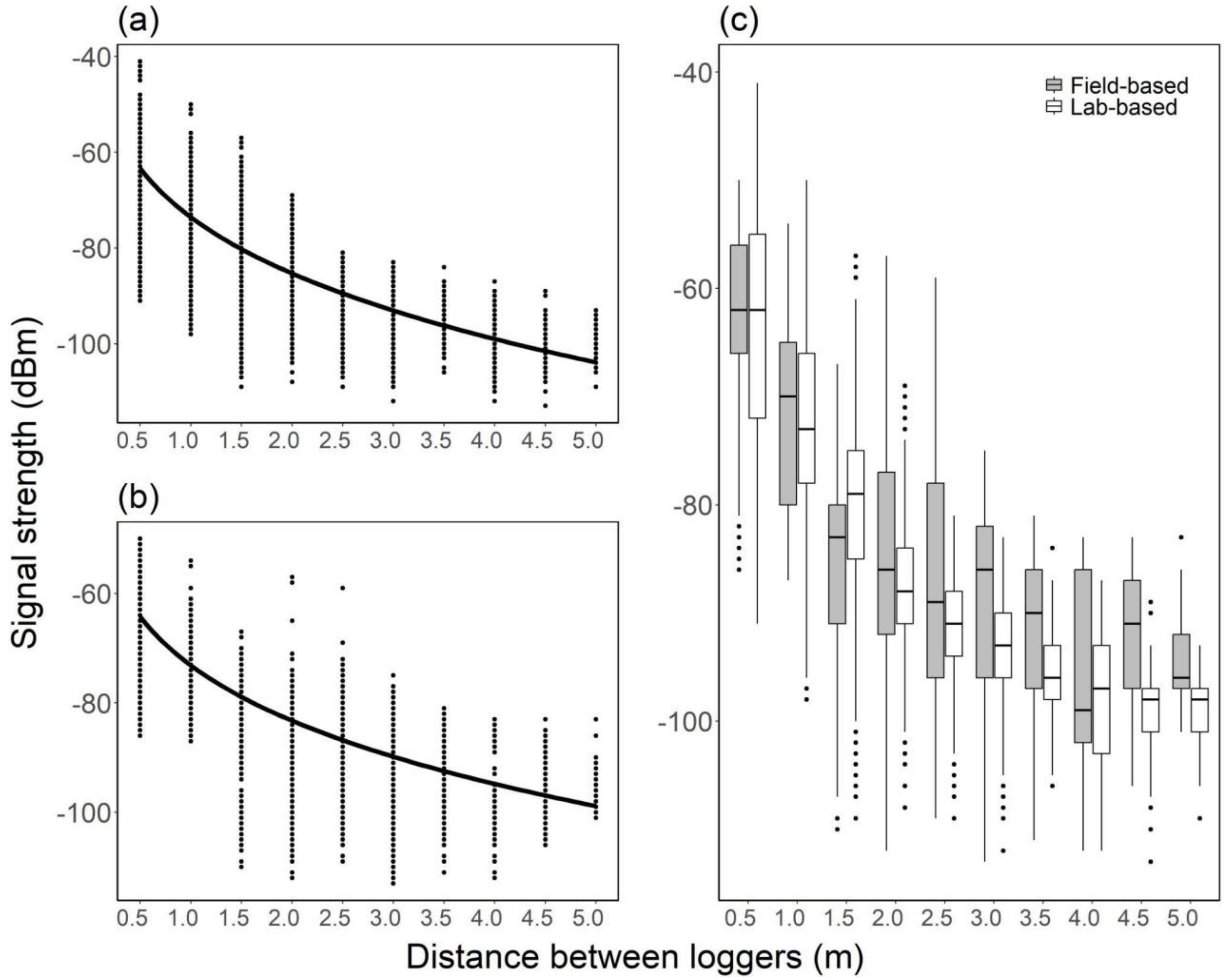

Figure 2. Relationship between logger signal strength and distance for 12 loggers tested in (a, c) a lab-based environment and (b, c) in a field-based environment. The trendlines represent the exponential decay equation of the line of best fit.

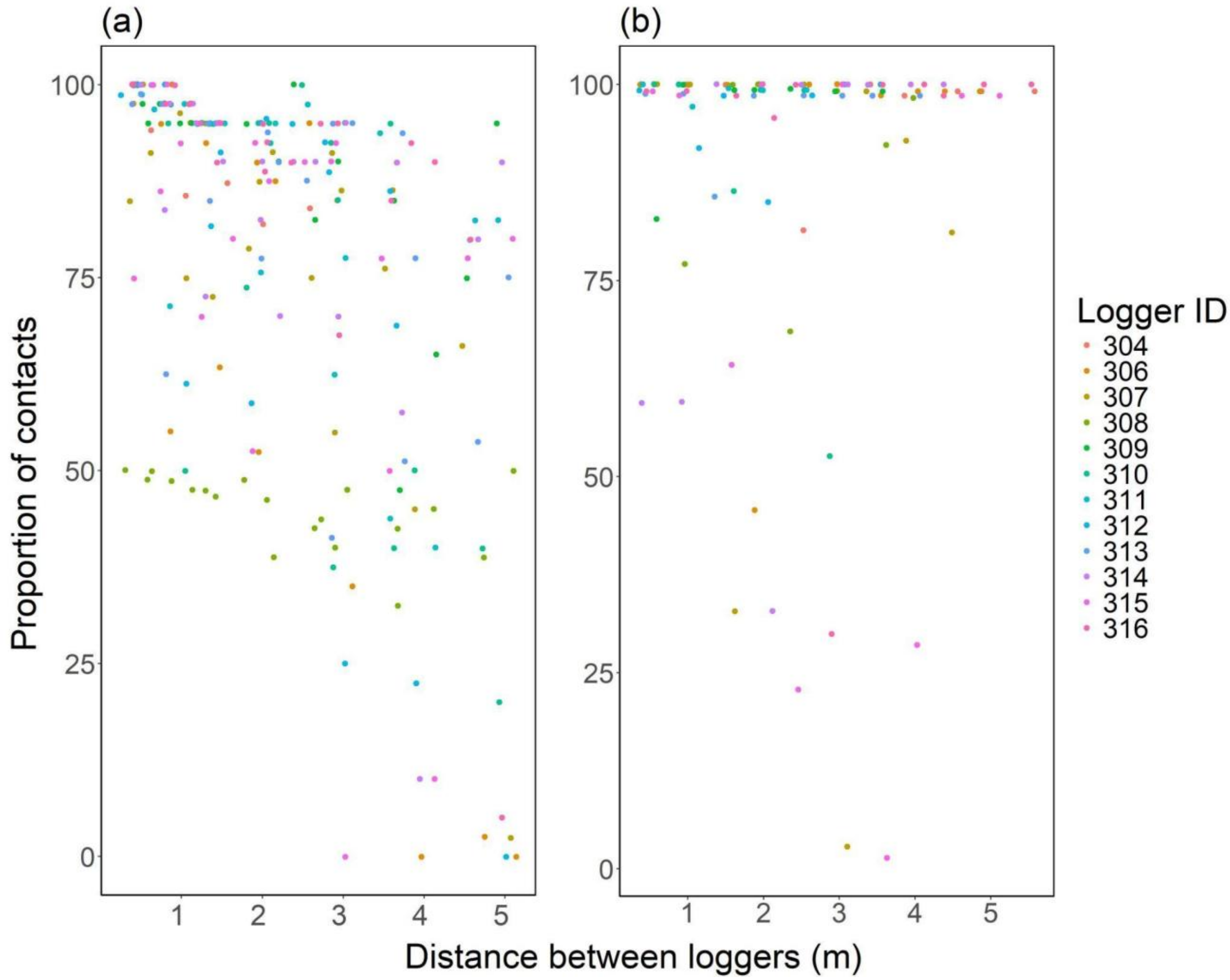

Figure 3. Relationship between the proportion of expected contacts correctly processed and distance for 12 loggers tested in (a) a lab-based environment and in (b) a field environment. The values are jittered on the x-axis for better representation.

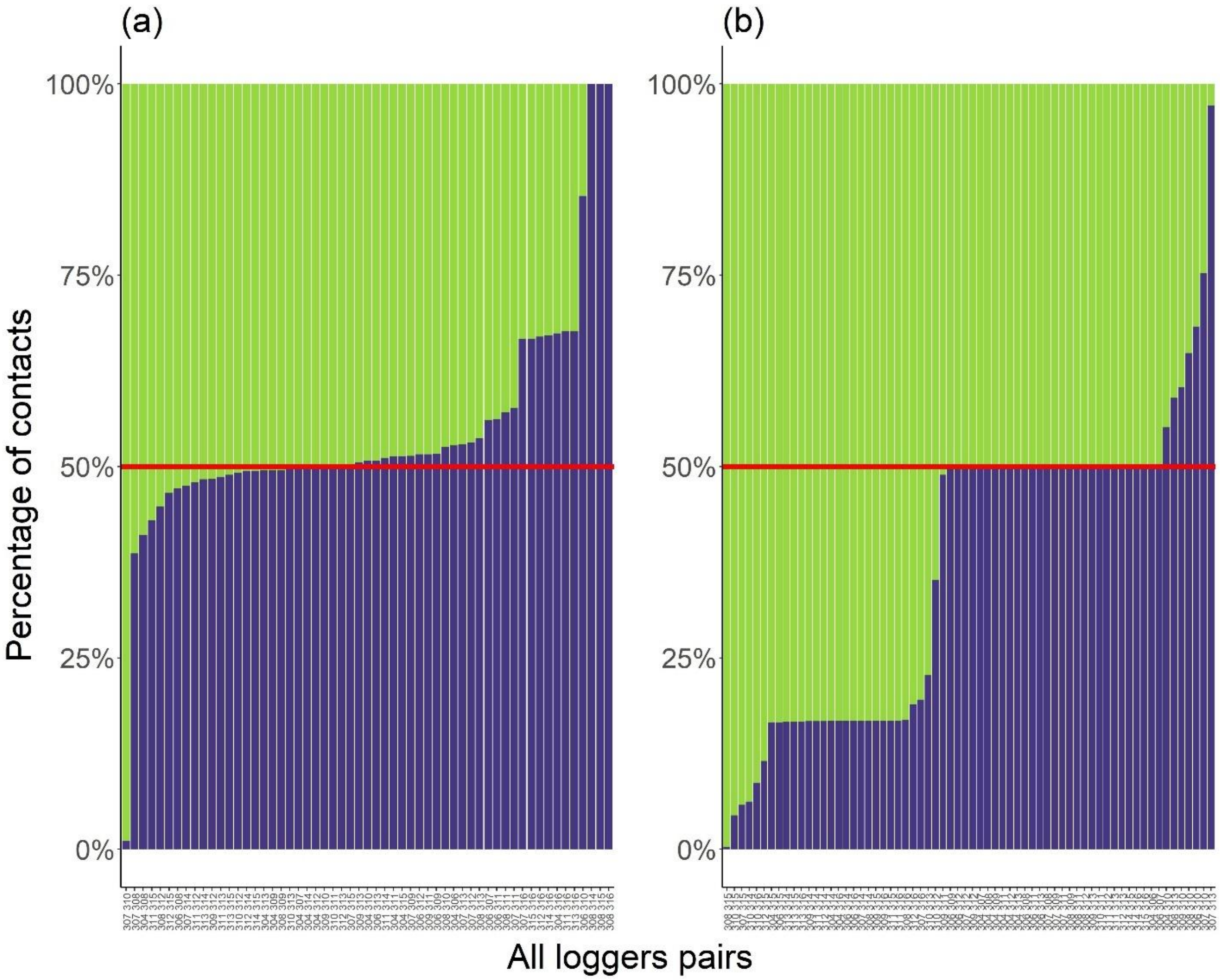

Figure 4. Percentage of contacts recorded by loggers for each dyad formed by 12 loggers tested in (a) a lab-based environment and in (b) a field environment. The horizontal red line represents an equal proportion of contacts received within the dyad.

Logger function on live animals

To determine if the use of the Gipsy 6© proximity feature could be used instead of scan observations, we tested six devices on live animals and evaluated whether they were detected at the same time by visual observations and their proximity loggers. We found that all six visual occurrences of associations between logger carrying birds made by an observer were confirmed at the same time by contact detection. However, only 6.5 % of the associations captured by loggers were confirmed by visual observation. By looking at the contact detection outside of the plot and between observation periods, we found that 20.26 % of loggers' contacts occurred outside the plot (number of contacts outside the plot = 338, number of contacts within the plot = 1330) and 19.92 % of loggers' contacts within the plot happened outside of observation hours (number of contacts outside hours = 265, number of contacts within hours = 1065 contacts).

To test whether individuals associated with the same conspecific on land and at sea, we compared the count of association in and outside of the plot, for each dyad (Figure 5). We found that the counts of association on land and outside the plot (presumably at sea) were strongly correlated (r(17) = 0.93, p < 0.01).

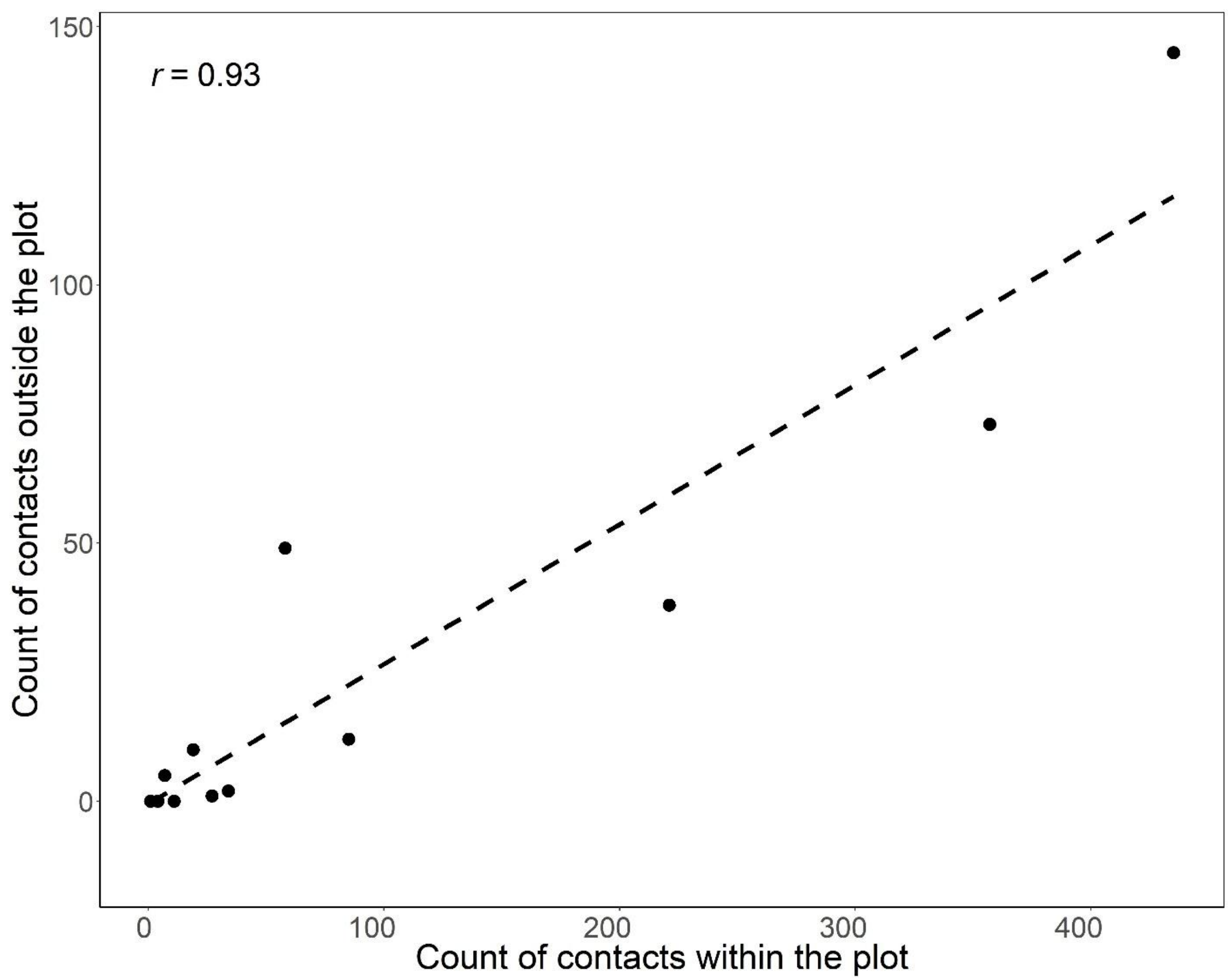

Figure 5. Relationship between the count of contacts within and outside of the plot for 13 dyadic combinations formed by six individuals. Each dot represents a dyad, and the dashed black line represents the trend.

Discussion

Remote sensing data collection has become increasingly popular to gather information when and where in-person observations are constrained. However, the use of proximity loggers for the collection of association data in small species is fairly limited. In this study, we tested Gipsy 6© loggers, a device with proximity functions, in a lab-based and field environment to evaluate their performance in contexts similar to our deployment condition, and on live animals to test their potential to replace human observers, particularly when individuals are not visible.

When testing the loggers in lab-based and field environments, we found a loss in signal strength with distance. We also found that signal strength was only moderately repeatable and that the identity of the logger was responsible for most of the variance in the model. Existing literature suggests three main explanations for the loss in signal strength in these types of devices. The dilution of the signal with distance (Ripperger et al., 2016; Kirkpatrick et al., 2021; Huels et al., 2025), the technical differences between devices as well as their settings (Prange et al., 2006; Huels et al., 2025) and the natural obstacles such as tall grass or reflecting materials disturbing the signal (Rutz et al., 2015; Triguero-Ocaña et al., 2019; Kirkpatrick et al., 2021). Our results align with those statements, and as expected, we reason that signal strength was affected by all three factors. As a consequence, signal strength should be used cautiously when attempting to evaluate the distance between individuals. In the context of social network analysis, they would be best used to assess group membership in flocking/herding species, or as in this study, to evaluate if conspecifics that nest near one another also travel or forage together. Nonetheless, using arbitrary thresholds of detections with minimum signal strength could be used to approximate the distance between individuals, which could still be sufficiently precise for studies that are interested in near-contact occurrence (Hamede et al., 2009).

The loss of signal strength with distance ultimately leads to a decrease in successful contacts as it becomes harder for a device to capture a weak signal. However, it is not the only reason driving loggers to miss contacts. Here, we found that only 50 % of the devices accurately detected the associations from their dyad both ways, regardless of the environments tested or their distance. Missing contacts have already been observed in other loggers (Drewe et al., 2012; Kirkpatrick et al., 2021; Huels et al., 2025), alongside extended-duration contact interpreted as multiple events (Prange et al., 2006). Missing contact often comes from weak signal strength from loggers at the edge of range detection (Prange et al., 2006), when the battery has diminished power (Drewe et al., 2012) or when the collision rate increases due to a locally saturated device emission environment (Kirkpatrick et al., 2021). Collisions prevent the proper detection of emitted signals and are generated when two or more loggers advertise simultaneously (Ghamari et al., 2018). We suspect that missing contacts in our study were the result of collision, as we deployed the loggers in high density, and with a relatively high sampling rate. As noted elsewhere, relatively high collision rates are one of the main limitations to the use of proximity loggers regardless of their use of Bluetooth signals (Kirkpatrick et al., 2021) or radio frequency signals (Drewe et al., 2012). The collision risk between loggers advertising at the same time is impossible to fully eliminate. However, it can be reduced by limiting the number of devices and the emissions interval to locally reduce congestion. Adding a small interval to gradually trigger the advertisement signal can also reduce collisions (Kirkpatrick et al., 2021). Those issues express the need to carefully review the dataset and apply corrective factors based on false-negative probability if necessary. Data sets with missing observations can, for example, be calibrated using corrective factors such as a simple ratio index or half-weight index (Hoppitt & Farine, 2018). However, adding statistical manipulations might limit the benefits of using proximity loggers compared to traditional methods.

By testing the effect of distance with two treatments (field and laboratory), we found that signal strength was more affected by distance in the lab setting than in the field environment. However, the number of contacts in the lab setting was more consistent than in the field. We suggest that these differences are explained by the topography and the deployment setting of the different locations. The loggers in the lab environment were deployed in a circle, only a few centimetres apart from each other, sending a signal every minute. In addition, the loggers were deployed on an asphalt-shingled rooftop with radio frequency reverberation properties different from regular soil (Omusonga et al., 2015). This configuration, in close proximity, with a high signal rate and in a reflective environment, might have increased the collision rate. In contrast, the loggers in the field environment were deployed diagonally, on a heterogeneous landscape with a 40-degree angle slope. Together with a lower frequency of signals, this configuration might have generated fewer signal collisions, but also higher variability in the number of contacts.

To investigate the potential of the Gipsy 6© proximity logger in replacing visual observation methods, we tested if observational data matched logger detections. Because loggers were set to turn off at night to save battery life, we did not record nocturnal social activities. Atlantic puffins have limited activity at night, either because they are sleeping in their burrow or resting at sea. Additionally, no pairs have been tagged with loggers and between-mate activity was not recorded. Thus, if some associations may have been missed, mainly individuals rafting at sea, we do not expect those associations to change the nature of their social network. We found that all tagged individuals observed on the plot were also confirmed by a contact made by loggers, but that the loggers detected more potential associations. Only 6.5 % of associations captured by loggers were confirmed by visual observation, while all visual observations of birds with loggers were remotely detected. While it is possible that observers missed a large number of associations, it is more likely that the number of associations within two meters detected by loggers was overestimated. As argued above, signal strength cannot be reliably used to estimate distance and many of the contacts identified by loggers could be the result of birds identified by the observer, but not included in an association because they were not close enough. Nonetheless, this finding suggests that, despite the unequal proportion of contacts recorded by each logger within a dyad and the decreasing signal strength with distance, the automatic detection not only matches but has the potential to outperform visual observation. Thorough ground truthing of the loggers in different contexts would be needed every time. Our results are similar to other studies testing observational methods and proximity logger (Drewe et al., 2012; Ripperger et al., 2016; Kirkpatrick et al., 2021; Huels et al., 2025), and can be explained by the limited number of individuals an observer can simultaneously keep track of. However, Drewe et al. (2012) detected decreasing battery and logger performance over time, an aspect that we did not cover due to the low retention time of the device on birds. While we cannot predict with certainty the consequences of low battery level on the Gipsy 6© performance, the presence of a solar panel, little battery consumption and the setting modularity of this model should limit such problems.

During the trial on animals, associations were detected by the loggers outside of the observation time (19.92 % of the observations) and plot (20.26 % of the observations). Indeed, those results highlight the benefit of having automatic detection to increase the quantity of data collected, but they also reflect the important proportion of data collected using a traditional scanning method. Knowledge of an animal's behaviour, in this case the aggregation of individuals at higher density at dawn and dusk, optimised the opportunities to observe near-contact between individuals. Of all associations, over 20 % were detected outside of the plot, which would never have been visible to observers. In themselves, these data are useful as they suggest that individuals in the study area probably raft or forage together. Furthermore, by comparing the number of contacts each dyad had on land and at sea, we found that individuals were often associated with the same social partners, suggesting that associations on land are maintained at sea. While leaving the colony (e.g., because of predation), Atlantic puffins take off in groups that circle above the ground or land on the water to form rafts. These aggregations on water are probably complemented by individuals from nearby parts of the colony, which could be expected to randomly mix. However, previous research has found that Atlantic Puffins not only associate on land with close conspecifics but can move to seek potentially familiar individuals (Morel et al., 2025). Because tagged individuals mainly associate away from the colony with the same conspecifics as on land, we suggest that familiar individuals may also seek each other at sea.

The development of miniaturised devices encourages the use of remote sensing to replace traditional observation techniques. The overall performance of the Gipsy 6© allowed us to determine that scan observations timed with the highest density of birds on land captured a majority of true associations, but also suggested that associations were likely missed. Furthermore, we were able to confirm that associations in our study area were maintained away from the plot, probably at sea. Broader use of these devices would certain help answer questions pertaining to the social structure of high-density colonial animals such as seabirds, but only after extensive consideration of the impact of signal collision rates, and in context where the actual distance between the individuals of interest is not as important as the fact that they are near one another.

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