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A location fingerprinting approach for the automated radio telemetry of wildlife and comparison to alternative methods

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Abstract

Background Automated radio telemetry (ART) systems enable high-temporal resolution data collection for species unsuited to satellite-based methods. A challenge of ART systems is estimating the location of radio tagged animals from the radio signals received on multiple antennas within an ART array. Localisation methods for ART systems with omni-directional receivers have undergone rapid development in recent years, with the inclusion of machine learning techniques. However, comparable machine learning methods for ART systems with directional antennas are unavailable, despite their potential for improved accuracy and greater versatility. To address this, we introduce an open-source machine learning-based location fingerprinting method for directional antenna-based ART systems. We compare this method to two alternative localisation approaches. Both alternatives use relative signal strengths recorded among multiple antennas to estimate the signal's angle of arrival at each receiver. In the 'biangulation' approach, the location is estimated by finding the intersection of these angles from two receivers. In contrast, the 'linear regression' approach uses a linear regression model to estimate the distance from the receiver along the angle of arrival, providing a location estimate. We evaluate these methods using an ART data set collected for the southern black-throated finch (*Poephila cincta cincta*), in the Desert Uplands Bioregion of Queensland, Australia.

Results The location fingerprinting method performed slightly better than the best performing alternative, the linear regression method, with mean positional errors of 308 m (SE = 17.7) and 335 m (SE = 18.5), respectively. The biangulation method performed substantially worse, with a mean positional error of 550 m (SE = 42.9, median = 540 m). Improved accuracy was observed with shorter distances between transmitters and receivers, higher signal strengths, and a greater number of detecting receivers, suggesting that increasing receiver density improves localisation accuracy, albeit with potential trade-offs in system coverage or cost. Furthermore, shorter pulse intervals of transmitters resulted in greater accuracy, highlighting the trade-offs among battery life, transmitter weight and radiative power.

Conclusions The open-source location fingerprinting method offers an improved and versatile localisation approach suitable for a wide variety of ART system designs, addressing the challenge of developing study-specific localisation methods using alternative approaches.

Keywords Automated radio towers, Movement ecology, Radio tracking, Positional error, Localization, Positioning, Wildlife tracking

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Background

The field of movement ecology has seen rapid growth, driven by the development of tracking technologies that enable the monitoring of animal movements across time and space in diverse environments [1]. These technologies encompass a range of methods including radio telemetry, satellite-based systems (e.g., GPS and Argos), accelerometry, and wireless sensor networks [2–4]. Each method has its inherent limitations, such as tag mass, cost, accuracy, frequency of location estimates, and data retrieval options, with no one-size-fits-all solution [2, 5, 6].

Among these technologies, Global Positioning Systems (GPS) stand out for their capacity to deliver location estimates with high spatio-temporal resolution [2, 6]. The ongoing miniaturisation of GPS transmitters has resulted in multiple manufacturers offering minimum tag weights between 2.6 g and 5 g. Despite this miniaturisation, GPS transmitters remain too large to affix to animals weighing less than approximately 100 g, assuming maximum transmitter weight of no more than 5% of an animal's weight [7]. In comparison, radio transmitters, with minimum weights of around 0.13 g (e.g. Lotek NanoPin), remain an important tool for the telemetry of smaller animals weighing less than 100 g [2, 8, 9].

Traditional manual radio telemetry techniques are often limited by the time and cost constraints of locating and resighting tracked animals [10]. Automated radio telemetry (ART) systems have emerged as a promising development, enabling high-temporal resolution data collection remotely from radio tagged animals [9, 11]. ART systems can use lightweight and low-cost radio transmitters, making them a versatile approach that has been used to track over 180 species of birds, bats and insects to date [9, 11].

Unlike satellite-based methods, ART systems do not directly receive transmitter locations. Instead, transmitter locations are estimated from the relative signal strength (RSS) of the transmitter's signal recorded by one or more receivers [9, 10, 12–15]. There is substantial variation in the design and objectives of ART systems that result in no versatile approach to localisation [16].

The design of ART systems can be broadly split into omni-directional and directional systems. Omni-directional systems typically use one isotropic antenna per receiver. The antenna receives signals in an approximately uniform pattern, 360 degrees around the antenna; however, little information is provided with regards to the angle of arrival (AOA), or bearing, of the signal to the receiver [15, 17]. In contrast, directional systems typically use multiple antennas (3–6) per receiver, with each antenna orientated in different directions to allow the AOA of the signal to be estimated [9, 11, 14]. In general,

directional systems often have a longer range than omni-directional systems but have a higher cost per receiver [9].

A variety of methods have been employed to localise transmitter position from omni-directional and directional ART systems. Lateralation techniques (Fig. 1A) are common for omni-direction systems [17]. Lateralation estimates the distance of a transmitter from multiple receivers using the decline in RSS with distance from transmitter. Lateralation requires simultaneous detections on at least three receivers in order to identify a point at which distances to the receivers overlap [16, 17]. Since lateralation does not require an AOA of the signal, it has been widely applied to omni-directional systems [18]. However, lateralation is generally not applied to ART designs with directional receivers as data pertaining to the AOA is wasted [16]. ART systems with directional receivers therefore employ methods that rely on angulation, which is where the AOA of the transmitter to the receiver is calculated using the relative signal strength recorded among the multiple directional antennas per receiver [16]. Once the AOA has been calculated, locations are estimated using biangulation or triangulation, which is the point at which the AOAs from multiple

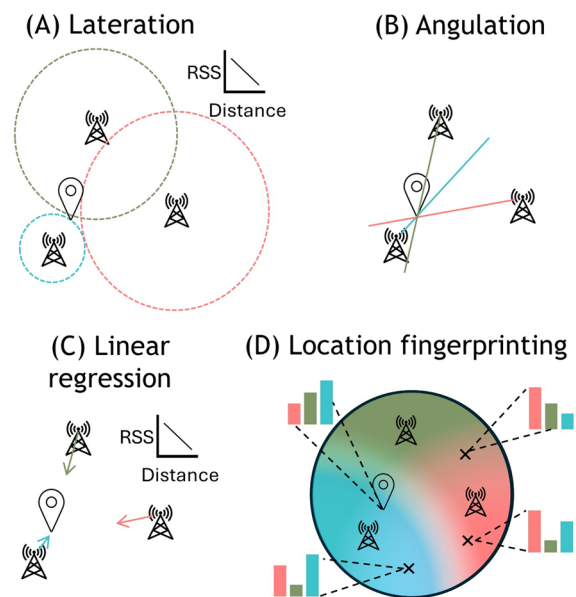


Fig. 1 Localisation methods for automated radio telemetry systems, which estimate location by: **A** finding the intersection of distance estimates that are inferred from relative signal strengths (RSSs) on omni-directional receivers; **B** finding the intersection of multiple angles of arrival (AOA) produced by directional receivers; **C** using the AOA and distance estimates inferred from the RSSs of directional receivers; and **D** developing a radio fingerprint map of each receivers' capture area (denoted by the colours red, green and blue), using ground-truthed RSS data

receivers intersect (Fig. 1B) [10, 12]. Alternatively, the distance between the transmitter and the receiver can be inferred from the RSS, typically based on the assumption of a linear decline in RSS with increasing distance (Fig. 1C) [14].

Location fingerprinting is a method that has been widely employed for indoor positioning systems and has recently been developed for ART systems [16]. This method uses machine learning based techniques to develop a model that relates the RSS of signals received to the locations of known reference points [19]. The model is then used to estimate the location of new signals (Fig. 1D). Tyson et al. [18] and Wallace et al. [17] have developed location fingerprinting methods for omnidirectional systems and achieved accuracies of approximately 10–30 m. However, there is no comparative open source system available for directional receiver systems, nor studies comparing the effectiveness of location fingerprinting to alternative localisation approaches.

Location fingerprinting offers a highly versatile approach with potential for improved accuracy compared to alternative methods. The method requires the development of study-specific radio fingerprinting models (Fig. 1D), which account for receiver specific variation in topography, vegetation density and radio tower design, as well as study-specific variation in species behaviour, radio transmitter power, receiver spacing and radio pulse interval [18]. All of these factors are difficult to factor into alternative approaches [10, 16]. Using study-specific location fingerprint models allows the location fingerprinting approach to generally achieve higher accuracies than alternative approaches [16, 18, 19]. Furthermore, this method offers a low-code approach to localising wildlife positions from ART data as site-specific training data are used to build location fingerprint models through machine learning techniques, rather than through coding bespoke solutions, which would be required to customise alternative approaches [10, 12, 14].

A key requirement of location fingerprinting is the collection of reference points, or ‘training data’, which are known coordinates where the RSS is measured to develop the fingerprint model. In their location fingerprinting systems for omnidirectional systems, Tyson et al. [18] and Wallace et al. [17] collected training data over 50 ha and 0.4 ha study areas, respectively, to create a whole-of-array radio fingerprint map. However, directional systems are often used to track animals over study areas one to three orders of magnitude larger [8, 12, 20, 21], which can make the collection of training data for whole-of array radio fingerprint maps time and cost prohibitive [16]. An alternative approach that has not been explored is to train a fingerprint model for each directional receiver and apply the same model to multiple receivers where they have the

same design and are in a similar environment (e.g., consistent topography and vegetation structure). While this would come at a cost of accuracy, it would proportionally reduce the training data required and enable the location fingerprinting method to be applied to large-scale ART systems.

In this study, we present an open-source location fingerprinting method to estimate radio transmitter positions from directional receiver-based ART systems. The method provides a versatile approach to location fingerprinting that allows the development of models that pool training data among similar receivers and thus allows the method to be applied to large-scale ART systems where collection of whole-of-array training data is time prohibitive. We demonstrate the application of this method across a 2680 ha ART array tracking a threatened Australian bird species, the southern black-throated finch (*Poephila cincta cincta*). We compare the performance of the location fingerprinting model (Fig. 1D) to two alternative localisation methods, namely: (1) finding the intersect between AOA from pairs of two receivers, hereafter ‘biangulation’ (Fig. 1B); and (2) using a linear regression model to estimate the distance that a transmitter is located along the AOA, given the RSS, hereafter ‘linear regression’ (Fig. 1C).

Methods

Case study species

The southern black-throated finch (SBTF), *Poephila cincta cincta*, is a small grassfinch (~15 g) in the family Estrildidae. The species is endemic to north-eastern Australia, with a current range that has contracted by over 80% from its historical extent [22]. The species inhabits grassy woodlands and feeds primarily on grass seeds, with movement across the landscape influenced by water and resource availability [23]. Movement patterns of SBTF may be characterised as sedentary with a large home range of approximately 319 ha [24]. On a daily basis, SBTF move through their home range between foraging, drinking and nest locations [24]. The SBTF also uses all structural layers of the woodlands in which they inhabit, ranging from the ground layer in which they feed, up to the canopy and subcanopy layers in which they perch and nest [23, 25].

Study area

The study was conducted in a 75,000 ha section of the Moray Downs property (Fig. 2), located within the Desert Uplands Bioregion of Queensland, Australia, which is one of the few remaining strongholds of SBTF [26]. Remnant vegetation occurs over 79% of the study area, which is dominated by *Eucalyptus melanophloia* and *Eucalyptus brownii* open woodland ecosystems [27]. Sub-canopy

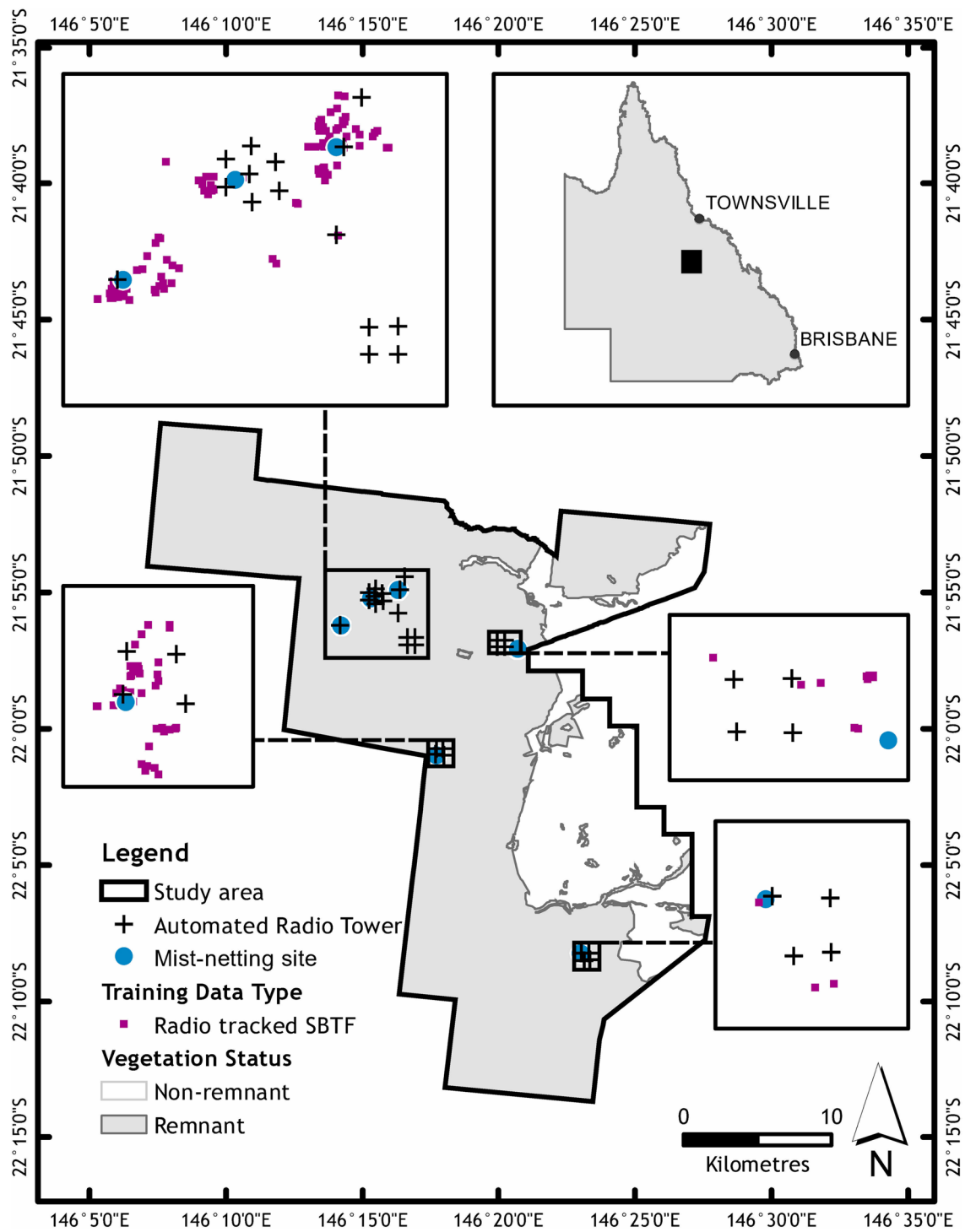


Fig. 2 Map of the study area showing the locations of automated radio towers ($n=27$) and radio tracked southern black-throated finch (SBTF) ($n=232$), which were used for training and testing the localisation methods

and shrub layers are generally sparse and commonly include *Acacia* spp. *Bursaria incana* and *Carissa lanceolata*. Other habitats include *Acacia* woodlands and

shrublands and cleared grazing pastures, which are typically not suitable habitat for SBTF [22].

Automated radio telemetry system

Twenty-seven (27) receiver stations were installed within remnant woodland within the study area in November 2020. Receiver stations were installed as four arrays of four towers, with an additional array of 7 towers surrounded by four individual towers (Fig. 2). Receivers within an array were separated by approximately 500 m. Site-based testing of the receivers found a typical detection distance of approximately 300–800 m depending on whether the SBTF was foraging on the ground or perching (typically 2–10 m above ground height). Thus, foraging SBTF could be reliably detected by at least one receiver when in an array and substantial overlap in the detection ranges among towers was achieved while SBTF were perching. The total area covered by the array after subtracting areas of overlapping coverage among receivers was approximately 2680 ha, assuming an 800 m detection range of each transmitter. The number of receivers and antennas that simultaneously detected each signal was recorded to model their impact on localisation error.

The receivers remotely and autonomously logged the radio signals received from nearby radio tagged birds. The design of radio telemetry receivers was similar to the Motus Wildlife Tracking System [11]. Each receiver comprised four 5-element Yagi-Uda antennas (TDJ-150B 150 MHz) mounted on a 4 m telescopic aluminium tripod (Fig. 3). The antennas were horizontally polarised and oriented to face north, east, south and west. Antennas were spaced $\frac{1}{4}$ wavelength apart (approximately 0.5 m at 150.6 MHz) and connected to a Lotek SRX800-D1 receiver. Antennas were scanned at 15 s intervals, resulting in a complete scan of all four antennas every minute. Receivers stored the transmitter ID, received signal strength (RSS) measured in decibels, antenna direction and GPS-synced time stamp of the detection. Transmitters were individually coded (Lotek Nanotag NTQB2-2) allowing multiple transmitters to be detected simultaneously while scanning antennas.

Radio transmitter attachment

We mist-netted SBTF over eight survey periods, each approximately 12 days in length, between February 2021 and May 2023. A total of 47 SBTF were fitted with Lotek NTQB2-2 transmitters (0.32 g, <2.5% of the bird's weight), across six mist-netting locations that were dispersed among the spatial extent of the ART system (Fig. 2). The number of transmitters attached at each mist-netting location ranged from one to 14. Transmitters were attached by trimming a small patch of feathers on the bird's back and attaching the transmitter to the skin using cyanoacrylate glue [23, 28, 29]. Transmitter function and signal detection were tested using a hand-held receiver (Lotek SRX1200 M2) prior to release. Two



Fig. 3 Automated radio telemetry receiver with four directional antennas installed within the study area

radio pulse intervals were used within this study, each below the 15 s receiver antenna scan windows used to ensure that at least one antenna would detect a tagged bird when within range of the receiver tower. Transmitters with a 13 s pulse interval ($n=21$) and 97 day battery life were initially used based on an estimated transmitter retention time [29]. Following initial field surveys and evaluation of tag retention times, we changed to a 3 s pulse interval and 29 day battery life ($n=26$) to better reflect the tag retention that was being achieved, which was on average 21.8 days (SD=22.5 days) and improve manual radio-tracking efficiency.

Collection of training and testing data

We collected ART receiver data when the transmitters were at known locations. These data were used to train the localisation models and evaluate the model's accuracy, referred to as 'training' and 'testing' data.

Training data were collected by manually radio tracking tagged SBTF with a 3-element Yagi-Uda antenna connected to a Lotek SRX1200-M2 receiver. We used a hand-held GPS (Trimble Nomad TDC100) to record the location of the bird and the start and end times (GPS-synchronised) of each sighting where the SBTF was in the same location for more than 3 min. We truncated records to a maximum of 20 min for balanced data representation among locations. In total, 232 unique locations were recorded across the 47 radio tagged birds, which ranged

from one to 27 locations per bird. The average duration of recording was 8.5 min (SD=5.0 min; range 3–20 min).

Following data collection, we randomly excised 20% ($n=47$) of the radio tracked SBTf locations to use as a testing data set. These testing data were not used for model training, which avoided the leakage of training data into the testing set [30]. The remaining 80% ($n=185$) of the radio tracked SBTf locations were used for the purposes of training the location fingerprinting model and in the linear regression method (described below).

Location fingerprinting method

Location fingerprinting overview

We developed a data processing pipeline to train a location fingerprinting model (Fig. 4A) and then predict locations of radio transmitters using the trained model (Fig. 4B).

Model training (Fig. 4A) is divided into two steps: (1) data pre-processing restructures the raw ART signal data

into a format suitable for input to a location fingerprinting model; (2) signals are mapped to their known locations in order to train a location fingerprinting model using an open source automated machine learning platform [31].

Inference (Fig. 4B) combines the signal pre-processing steps (as per the model training) and applies the location fingerprinting model to predict locations of new signal data. Transmitter location is estimated separately for each receiver on which the signal is received. A location averaging function is then applied when transmitters are recorded simultaneously across multiple receivers. The model training and inference methods are described below. All data processing was undertaken using Python (version 3.6.9, Python Foundation).

Receiver groups

The data pipeline uses a receiver-centric fingerprinting approach, whereby a fingerprinting model is trained for each receiver. Fingerprinting models may be grouped

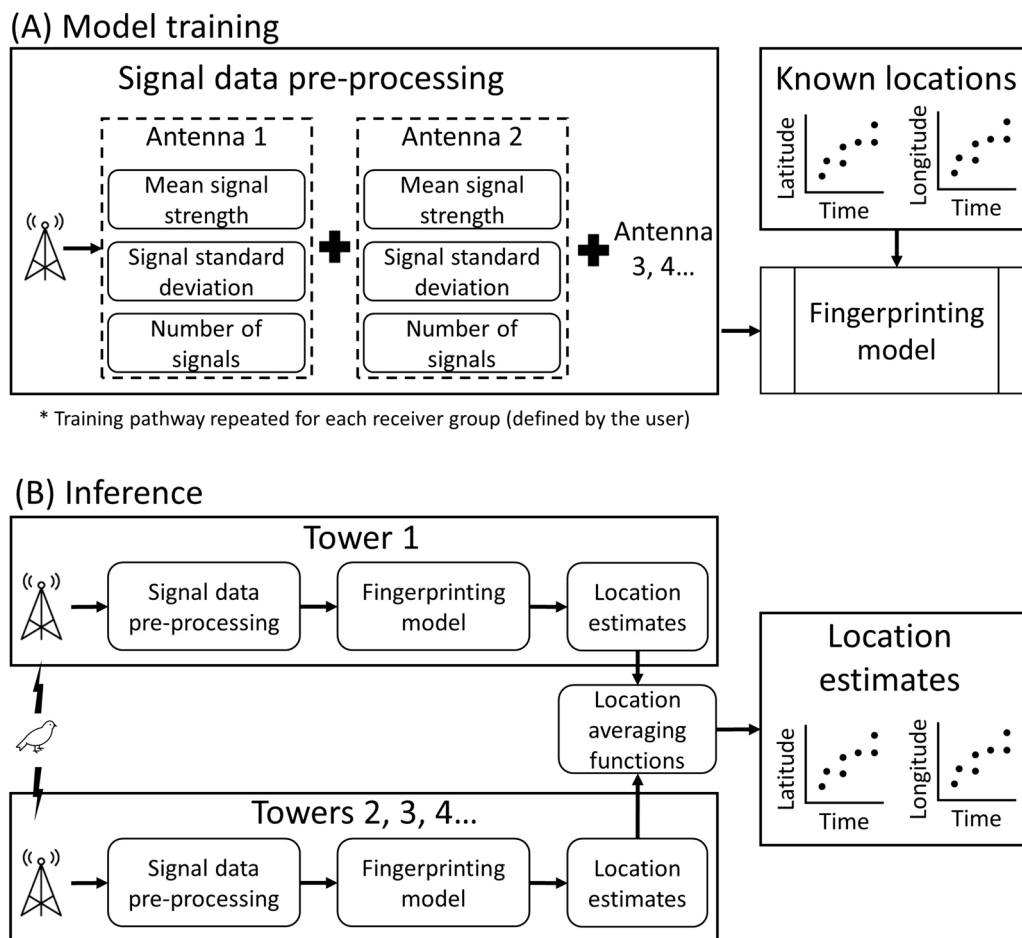


Fig. 4 Data pipelines for the training of the location fingerprinting model (A) and inference of transmitter location (B)

among receivers that have similar properties, such as antenna design, topography and vegetation structure. This receiver-centric approach allows users to train and deploy location fingerprinting models for receivers that have limited training data available by pooling training data among receivers [32, 33]. It also provides the versatility to allow receiver-specific fingerprinting models, should sufficient training data be available [33]. The amount of training data required will be study-specific; however, we provide an assessment of training data requirements in the ‘model evaluation’ section of the methods.

For this study, we chose to train one location fingerprinting model that was shared among all of the receivers. We did this as no single receiver had training data locations from the breadth of its area of coverage, which was approximately 800 m from the receiver (Fig. 2). In addition, all receivers within our study used the same design and were located in similar vegetation (eucalypt open woodland) with flat topography.

Data pre-processing

Manually radio tracked SBTF locations were time-matched to ART receiver data to create a labelled data set of ART signals received when transmitters were at known locations. Example training data used as input into the data pipeline are provided in the Supplementary Information.

To prepare training data for input to the location fingerprinting model, we calculated the average RSS for each transmitter detection at each antenna within a specified period (t). We selected a t value of 3 min, as the base duration for creating training and testing samples. This time frame was chosen because it corresponds to three complete cycles of the antennas connected to each receiver, balancing the accumulation of more signal data from a SBTF location with the potential of the tracked animal moving. While we used a 3-min period in this study, the data pipeline accepts any other value of t , which may be adjusted based on the frequency and speed of animal movements and pulse interval.

For each period of t , the data pipeline creates three variables for each antenna of each receiver. These variables include the mean RSS, a count of the number of signals received and the standard deviation of the signal strength. Thus, for our ART system, which had four antennas per receiver, the data pre-processing produced 12 predictor variables in total. These 12 predictor variables were then used to train the location fingerprinting model to predict the transmitter’s easting and northing position, which were the response variables.

To construct the response variables, we normalised the transmitter locations to an X–Y grid, where the origin (0,0) was the location of each receiver and X–Y axes represented the east–west (x) and north–south (y) distance from the receiver. To do this, we converted GPS locations from their geographic coordinate system (represented by latitudes and longitudes) to a projected coordinate system (represented by eastings and northings) using the `utm` package (version 0.7.0) in Python. We then subtracted the easting and northing coordinate of the receiver from each GPS recorded location to obtain the X and Y distances of the transmitter relative to the receiver. This step was undertaken for each receiver within the ART array independently, allowing one transmitter location to be simultaneously associated with multiple receivers that received the signal within the period t . Example data obtained after the post-processing steps are provided in the Supplementary Information.

Machine learning model

Predictor and response variables were input into the H2O AutoML algorithm (version 3.40.0.4), which is an open source platform to automate the training and optimisation of a wide variety of supervised machine learning models [31]. H2O AutoML was chosen due to its open source design, the general high performance of the platform in automated machine learning tests [34] and its ability to integrate into our broader automated data processing pipeline.

Separate models were trained to independently predict the x -axis (east–west) and y -axis (north–south) distances of the transmitter from each receiver, resulting in two models per receiver group.

Location averaging

Location estimates produced for each receiver were an X–Y offset from the centre of the receiver. These locations estimates were converted to an easting-northing Universal Transverse Mercator grid reference by offsetting the known location of each receiver by the estimated X–Y offset determined by the H2O AutoML model.

Where two or more receivers produced a location estimate for the same transmitter within the same time-period (t), we calculated the geographic midpoint by averaging the easting and northing estimates.

Comparative methods

We compared the results of our location fingerprinting method against two commonly used approaches to localise transmitters from directional ART data (Fig. 1), which

are described below. In addition, the code for these methods is accessible in the Supplementary Information.

Biangulation

For each period of t and for each receiver, we identified the pair of orthogonal antennas with the highest combined RSS. Given that our receivers each had four antennas orientated towards the cardinal directions, this step effectively determined the quadrant where the transmitter was expected to be located relative to the receiver. We then calculated the AOA using the equation:

$$\text{AOA} = \frac{90}{\pi} \times \arccos(\Delta g)$$

where Δg was the difference in RSS between the two antennas ($s_l - s_r$) normalised by the maximum signal strength difference Δm , using the equation [10, 35]:

$$\Delta g = \frac{(s_l - s_r)}{\Delta m}$$

The transmitter's location was calculated by biangulating two lines generated from this approach from each pair of receivers that detected the signal [10, 35]. This method therefore requires at least two receivers to estimate a position. If more than two receivers detected the signal in period t , each pair of receivers was biangulated separately and the geographic midpoint of the resulting location estimates was calculated. We excluded any location estimates falling outside of the study area, as these would be beyond the ART receivers' potential detection range.

Linear regression

The linear regression method followed two steps. Firstly, the AOA was calculated following the biangulation method as above. Secondly, the distance between the transmitter and receiver was estimated using a linear regression model that estimated the decline in RSS relative to the increasing distance between the transmitter and receiver. We then calculated the transmitter position by using the distance from the receiver placed along the line of the AOA, with the known receiver position serving as the reference point.

To develop the linear regression model, we calculated the Euclidean distance of each recorded location in the training data set to the respective receivers. We then fitted a linear regression using the sklearn package version 1.4.1 [36] to model the relationship between the RSS and the distance to the receiver [14]. Where transmitters were recorded on multiple antennas in the same period of t , we used a linear regression model that averaged the RSS–distance relationship among all antennas [14]. If the transmitter was recorded on only one antenna, we used a

linear regression that had been fitted only to training data for that antenna and estimated distance from the receiver using the average signal strength for that antenna in period t along the cardinal bearing of the antenna. Where two or more receivers detected the signal in period t , the geographic average of the resulting location estimates was calculated.

Model evaluation

We evaluated the performance of the three localisation methods using a test data set that comprised 47 radio tracked SBTF locations. The error of location predictions for each method was calculated as the Euclidian distance between the predicted and the actual locations, herein referred to as 'positional error'. Four additional variables were calculated for each SBTF location, which were factors that we identified a priori as having potential to affect the positional error of localisations. These were the: (1) mean distance of the transmitter to the receivers on which the signal was detected; (2) number of receivers that detected the signal; (3) pulse interval of the radio transmitter; and (4) mean RSS of the detections.

We examined the effects of localisation method, mean distance to the receiver, number of receivers, mean RSS and pulse interval using a generalised linear mixed effects model with the glmmTMB package version 1.1.7 [37]. A gamma distribution with a log link function was selected to fit the response variable, positional error, which was in the form of continuous data with a positively skewed distribution. Continuous fixed factors were standardised using the sjPlot package version 2.8.15 [38]. A unique identifier of test data set location was included as a random effect, to account for test data set locations that spanned longer than the period of t (3 min) having multiple location estimates. All model fits and the distribution of residuals were tested using the DHARMA package version 0.4.6 [39] (Supplementary Information).

We developed five candidate generalised linear mixed effects models and used an information theoretic approach to select the best performing model [40, 41]. We used Akaike Information Criterion corrected for small sample size (AIC_c) to select the best performing model. The six candidate models were developed based on an a priori understanding of potential factors and interaction effects likely to impact positional error (Table 1). All candidate models used the unique identifier of the test data set location as a random effect.

We estimated the impact of sample size on positional error for each of the two methods that required site-specific training data (location fingerprinting and linear regression). To do this, we iteratively performed each method using randomly chosen subsets of the training data, varying the subset size from 5 to the total number

Table 1 Candidate models evaluating the effects of localisation method, mean distance to the receiver, number of receivers, pulse interval and mean relative signal strength (RSS) on the positional error of location estimates

Model	K	AIC _c	ΔAIC _c	w _i
Localisation method * (Receiver count + Pulse interval + Mean distance to receiver + Mean RSS)	17	5190.4	0.0	1
Localisation method + Receiver count + Pulse interval + Mean distance to receiver + Mean RSS	9	5214.5	24.1	0
Receiver count + Pulse interval + Mean distance to receiver + Mean RSS	7	5256.3	65.9	0
Localisation method	5	5267.6	77.2	0
Intercept only model	3	5303.0	112.6	0

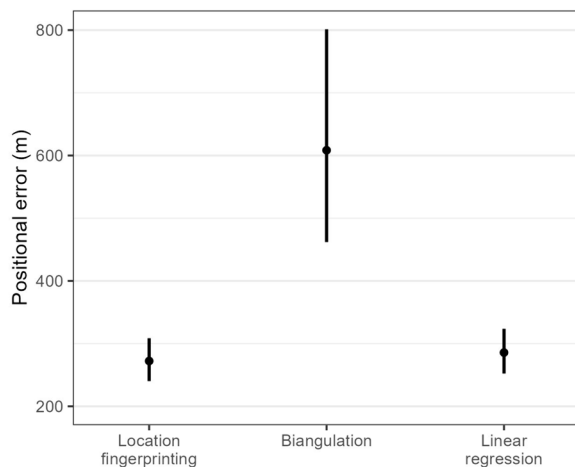


Fig. 5 Comparison of the mean positional errors of each localisation method. Bars show 95% confidence intervals

of samples ($n = 185$) and increasing the number of training data samples by 5 in each iteration. The positional error of these models was then calculated using the complete testing data set. This process was repeated 10 times to account for bias in positional errors introduced by chance, which was particularly relevant to small sample sizes. All data analyses were undertaken using R statistical language version 4.3.0 [42].

Results

Positional error

The average positional errors were: 308 m for the location fingerprinting method (SE = 17.7, median = 230 m, Fig. 5), 335 m for the linear regression method (SE = 18.5, median = 280 m, Fig. 5), and 550 m for the biangulation method (SE = 42.9, median = 540 m). Both the location fingerprinting and linear regression methods were able to estimate locations for all of the 47 test locations, while the biangulation method was only able to estimate a location for 19 of the 47 test locations (40%). Of the 28 test locations that could not be estimated using the biangulation method, 23 locations (82%) failed as the transmitter

was recorded on only a single receiver for each period of t , while 5 locations (18%) failed due to non-intersecting AOA estimates.

Positional error was best predicted by the model that included all main effects and the first order interactions between localisation method and the other fixed effects (Table 1). The next best performing model had an AIC_c that was 24.1 higher than the best model and as such we solely used the best performing model for interpretations [40].

Compared to the location fingerprinting method, the linear regression method achieved a similar positional error ($\beta = 1.08$, 95% CI 0.97–1.21, Table 2, Fig. 5), while the positional error of the biangulation method was substantially greater ($\beta = 2.44$, 95% CI 1.82–3.28). Model accuracy was affected by all fixed factors assessed (Table 2, Fig. 6). Signals detected on more receivers and signals with a higher average RSS both decreased positional error ($\beta = 0.89$, 95% CI 0.80–0.99; $\beta = 0.72$, 95% CI 0.65–0.80, respectively). In contrast, tags with a longer pulse interval and tags located further from receivers had a higher positional error ($\beta = 1.45$, 95% CI 1.01–2.06; $\beta = 1.16$, 95% CI 1.02–1.32, respectively).

While positional error increased with both increasing distance to the receivers and decreasing signal strength, the effect was less for the location fingerprinting method than the other methods. The result of this effect was that location fingerprinting achieved a lower positional error than both alternative methods where transmitters were far from the receivers (Fig. 7). This is demonstrated by small but significant interaction effects between the mean distance to the receiver and the linear regression method ($\beta = 1.28$, 95% CI 1.13–1.44) as well as between the mean signal strength and both the linear regression and biangulation methods ($\beta = 1.11$, 95% CI 1.00–1.24; $\beta = 1.59$, 95% CI 1.12–2.272, respectively Table 2).

Sample size requirements

The relationship between positional error and training data size showed an approximately exponential decay distribution, with an initial rapid decrease in positional error with additional training samples, plateauing as more

Table 2 Relationships between positional error and fixed factors for the top performing model identified in Table 1

Predictor	Estimate (β)	95% CI	<i>p</i>
(Intercept)	256.19	223.87–293.17	< 0.001
Biangulation	2.44	1.82–3.28	< 0.001
Linear regression	1.08	0.97–1.21	0.162
Receiver count	0.89	0.80–0.99	0.04
Pulse interval (13 s)	1.45	1.01–2.06	0.041
Mean distance to receiver (km)	1.16	1.02–1.32	0.02
Mean received signal strength	0.72	0.65–0.80	< 0.001
Biangulation x Receiver count	0.94	0.75–1.18	0.596
Linear regression x Receiver count	1.09	0.97–1.23	0.143
Biangulation x Pulse interval (13 s)	0.58	0.36–0.93	0.023
Linear regression x Pulse interval (13 s)	0.83	0.62–1.10	0.195
Biangulation x Mean distance to receiver (km)	1.07	0.84–1.35	0.598
Linear regression x Mean distance to receiver (km)	1.28	1.13–1.44	< 0.001
Biangulation x Mean received signal strength	1.59	1.12–2.27	0.01
Linear regression x Mean received signal strength	1.11	1.00–1.24	0.05
Observations	406		
R2 marginal/R2 conditional	0.408/0.614		

Methods were compared using a generalised linear mixed effects model with a log-link gamma distribution. Model estimates (β and 95% confidence intervals [CIs]) have been scaled

samples were included. The linear regression method required relatively few training data samples to plateau in performance, achieving a plateau after approximately 25 training locations. In contrast, the location fingerprinting method required over 100 training locations for a plateau to be reached (Fig. 8).

Discussion

We compared the performance of three localisation methods for ART systems with directional receivers. We found that the location fingerprinting and linear regression methods demonstrated comparable accuracy for estimating transmitter locations, with mean errors of 308 m and 335 m, respectively. Previous studies that have used similar methods to localise ART data have substantially differed in their ART design, which makes direct comparisons of accuracy among studies challenging. Nonetheless, previous studies have included: Harbicht et al. [43], who achieved sub-meter accuracy using a location fingerprinting method that used six receivers to track Atlantic salmon (*Salmo salar*) along a 295 m linear waterway; Fisher et al. [14], employed a linear regression method and achieved a median error of 72 m tracking monarch butterflies (*Danaus plexippus*) in the centre of an array of four receivers located 250 m apart, with limited vegetation or topographic variation; and Scardamaglia et al. [44] who used a location fingerprinting method with relatively few receivers over a 500 ha study area to achieve a mean positional error of 488 m.

The biangulation method was the worst performing method in this study, with an average positional error nearly double that of the best performing methods. Angulation methods, which include biangulation, are the most widely applied localisation method [8, 10, 12, 35, 45]. Accuracies achieved in previous studies have been wide ranging and include a median error of 250 m for aerial insectivorous birds [45] down to 21 m in an environmentally uniform and short-range trial [10], albeit noting the aforementioned challenge of directly comparing accuracy estimates among studies. Regardless of the accuracy of the biangulation method, the method is limited by its inability to estimate locations from signals detected on only a single receiver or where the estimated AOAs do not intersect [10]. In our study, which had receivers that were sparsely distributed compared to previous studies, biangulation could localise only 40% of the test data locations. While using triangulation or multiangulation (more than three receivers) may improve accuracy [10], it is likely to come at a cost of fewer localisations. For many studies, including our SBTF study, reducing the number of location estimates is a key disadvantage of the biangulation method.

The wide range of positional errors achieved in our study and previous studies [13, 21, 46, 47] highlights the practical trade-offs that must be considered when designing an ART system and subsequent localisation methodology. We found that across all methods that we employed, positional error was affected by four fixed

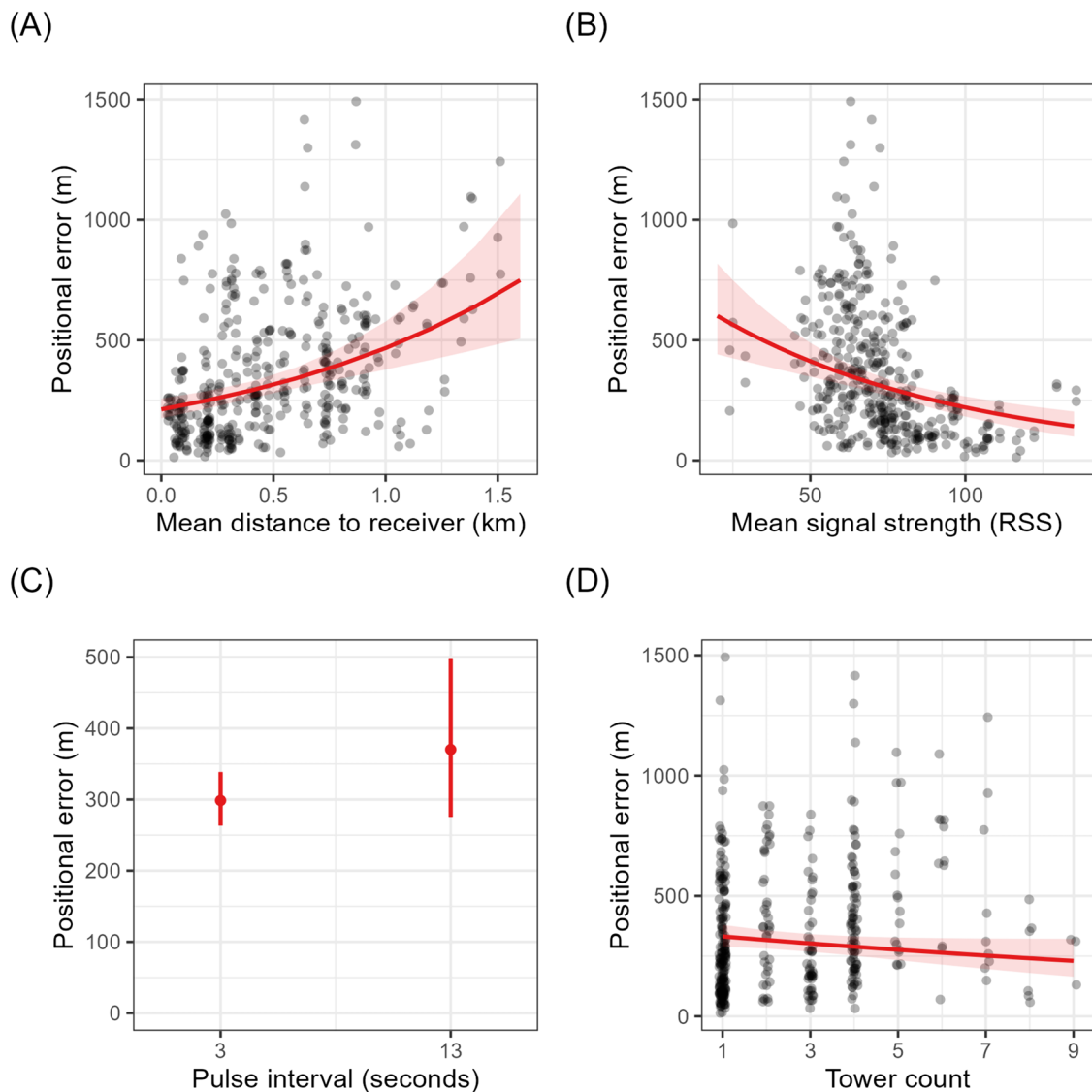


Fig. 6 Effect of four covariates on the positional error of localisations. The relationships depicted include the: **A** mean distance to the receiver; **B** mean relative signal strength (RSS) of the detections; **C** pulse interval of the transmitter; and **D** number of receivers on which the signal was recorded. All figures show the mean estimate with 95% confidence intervals. A random jitter has been applied to the points of (D) to aid data visualisation

factors, all of which may be considered within ART system design. Accuracy was increased when the mean distance to the receiver was lower, signal strengths were higher and the number of receivers that simultaneously detected the signal was higher. Increasing receiver density and having transmitters located inside of an array area, instead of on the periphery, are likely to improve localisation accuracy through changes to these three factors. However, it comes at the cost of either reduced coverage or greater cost to install more receivers [35]. Accuracy was also greater for tags with a shorter pulse interval, demonstrating a common trade-off in radio telemetry,

which is that among the battery size, battery life, transmitter weight and radiative power of the transmitter [46, 47]. Positional error is also impacted by animal mobility and behaviour, with species that move quickly, irregularly and among a range of habitats (e.g. height above ground level) producing a more inconsistent signal and result in greater localisation error [14, 21, 48].

The trade-off between spatial coverage, accuracy and cost is an important consideration for researchers implementing ART systems. Griffin et al. [9] estimated that a network of 85 ART receivers would cost approximately USD \$500,000 and Birds Canada [49] suggests a cost per

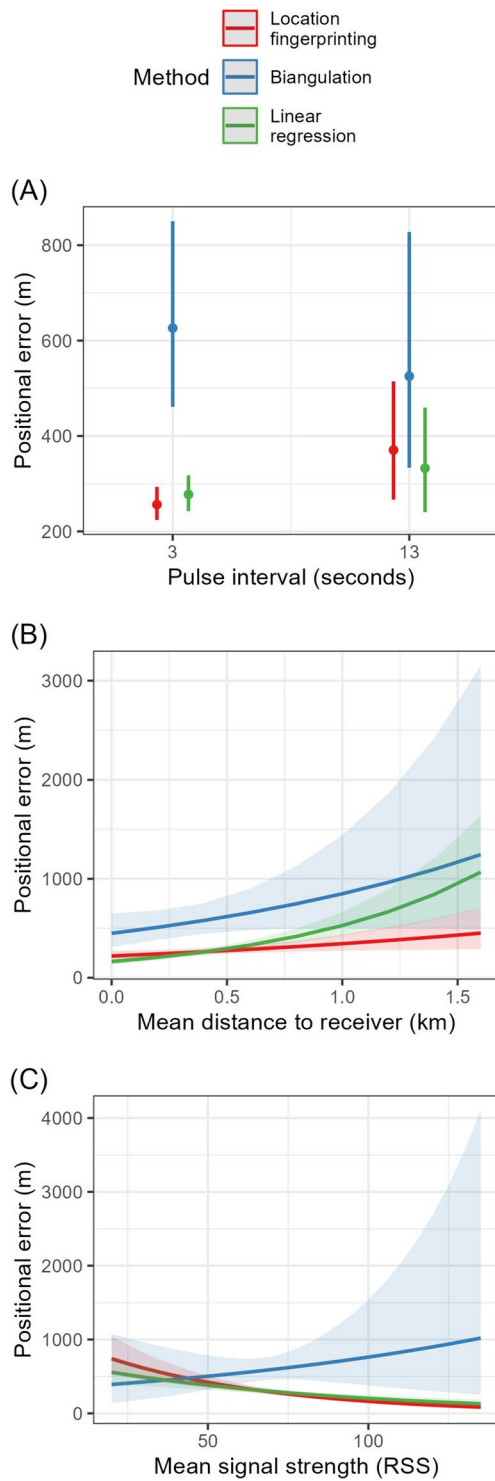


Fig. 7 Interaction effects between localisation method and the: **A** pulse interval; **B** mean distance to the receiver; and **C** mean relative signal strength (RSS) of the detections. All figures show the mean estimate with 95% confidence intervals

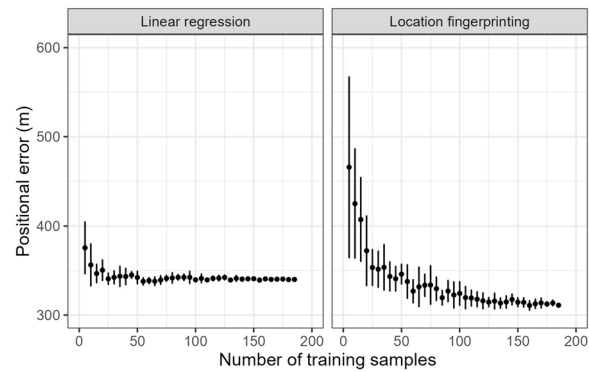


Fig. 8 Positional error of localisation estimates compared to the number of samples used to train the model. Bars show the standard deviation around the mean positional error. The y-axis scale is the same for both plots and does not start at zero

receiver ranging from USD \$2200 to \$7300. Our experience indicates a similar cost of approximately USD \$3500 to \$5000 per receiver. The benefits of ART systems must also be weighed against alternative radio telemetry methods, such as manual radio tracking [7] and drone-based methods [50–52]. Although there is no one-size-fits all solution, ART systems are likely to be most beneficial for studies requiring a high temporal resolution of data capture, as they allow for continuous radio signal detection. Due to their fixed nature, ART systems will also be most applicable to species that remain within the array’s coverage area or where regular movements through the array are of research importance, such as studying migration patterns [11, 21]. In contrast, manual radio tracking and drone-based systems are advantaged by their flexibility of spatial coverage [7, 51]. Finally, localising animal positions using ART systems has inherent inaccuracies. While small-scale controlled trials have reported accuracies less than 100 m [10, 14, 18], most applied field studies, including our own, have reported accuracies in the range of 100–500 m [13, 20, 44, 45]. Although positional accuracy can be improved by increasing tower density, it is unlikely to achieve the sub-20 m accuracy available through manual radio-tracking with a hand-held GPS [2]. Therefore, ART systems may not be suitable for studies requiring highly accurate position estimates for radio-tagged wildlife.

In our study, both top performing methods required the collection of training data. While collecting site-specific training data is labour-intensive, the results of our study and the indoor localisation literature [16] suggest that the most accurate localisation methods require

these site specific training data. However, in our study, the location fingerprinting and linear regression methods substantially differed in their training data requirements. The linear regression method required approximately 25 training data locations to achieve maximum performance for our data set. In contrast, the location fingerprinting method required over 100 training locations before the accuracy plateaued. The linear regression method uses site specific training data to train a simple linear regression model that relates the distance between the transmitter and receiver to the RSS. In contrast, the location fingerprinting method maps locations directly to the signal strengths from multiple antenna on each receiver [16]. As such, location fingerprinting requires training data from a broad area around the receiver, indicative of the spatial coverage of the receiver. For ART applications with limited training data, we therefore recommend the use of the linear regression approach; however, where sufficient training data can be collected then either the location fingerprinting or linear regression methods may achieve similar performance.

While we collected training data by manually radio tracking SBTf within the range of an ART array, this method is not feasible for all studies. Manual radio-tracking may be constrained by inaccessible terrain, limited resources and time, or species behaviour (e.g., highly vagile species) [50]. An alternative to manual radio-tracking is to use an artificial simulation of the tracked animal to collect training data. Methods include holding the antenna in the air with a low-conductivity medium such as PVC tubing [14, 18], attaching the transmitter to a drone [53], or using an artificial surrogate of the species, such as a glove filled with saline water [13, 47]. To train either a location fingerprinting or linear regression model, the simulation method should replicate the target species' signal properties as closely as possible to maximise the model's accuracy when applied to ART data from the target species [30]. In a small-scale experiment on the effective radiative power from different radio transmitter attachment methods, Naef-Daenzer et al. [47] found that the transmitter attachment technique and radiative coupling between the transmitter and the animal's body resulted in an almost three-fold difference in effective radiative power. Furthermore, Ward et al. [13] found that postural changes in radio tagged ratsnakes (*Pantherophis* spp.) resulted in significant variation in received signal strength. The design of an artificial surrogate of the species must therefore be considerate of the species behaviour, transmitter orientation and attachment, body mass and movement patterns [13, 14].

The location fingerprinting method, though more data-intensive, offers greater versatility across different ART designs with directional receivers. It accommodates

receivers with any number of antennas at any combination of orientation, two elements of ART design that would currently require custom code development to implement a linear regression method. An alternative location fingerprinting approach, which was employed by Tyson et al. [18] for omni-directional receivers and Harbicht et al. [43] for an aquatic environment, is to create a whole-of-array radio fingerprinting map, rather than the receiver-centric approach used in this study. The indoor positioning literature suggests that these whole-of-array approaches would provide the highest level of accuracy [16]; however, collecting training data for such whole-of-array models would be challenging, potentially prohibitive, in many large scale ART arrays. Nonetheless, should such training data be available, a whole-of-array location fingerprinting method would likely outperform the receiver-centric method we have applied [16]. Further research could improve our location fingerprinting method by incorporating time information associated with the RSS data and testing alternative approaches for location averaging to increase the weighting of receivers closer to the SBTf that record a higher RSS [54]. In addition, future extensions may integrate activity classification into the location fingerprinting method. Gottwald et al. [48] and Schofield et al. [55] demonstrated that machine learning methods can classify activity states of microchiropteran bats and songbirds by extracting features such as variation in received signal strength from ART data. Leveraging these techniques could improve insights into animal behaviour that are gained from ART systems.

The difficulties of comparing localisation performance among methods and studies underscores the importance of like-for-like methodological comparisons. While literature that compare localisation methods for omni-directional antennas have progressed in recent years [15, 18], our study is the first methodological comparison for ART systems with directional receivers. There remain methodological variations not included in this study, and likely future developments that will benefit from having their performance benchmarked to alternative methods. To this end, we have made our training and testing data sets and methods open access.

Conclusions

In this study, we introduced a novel machine learning based localisation method for ART systems that use directional receivers and compared it to two alternative approaches. We found that the location fingerprinting method provided a highly versatile approach to localisation for these systems that achieved comparable accuracy to the best performing alternative approach that we

tested. The location fingerprinting method can be applied to a wide variety of ART system designs; however, it requires the collection of site-specific training data, an important consideration in designing ART systems using this approach. In addition, our findings provide insights into the practical trade-offs in ART system design, especially among localisation accuracy, receiver density and cost.

Abbreviations

AOA	Angle of arrival
ART	Automated radio telemetry
GPS	Global Positioning Systems
SBTF	Southern black-throated finch
RSS	Received signal strength

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-024-00379-w>.

Supplementary Material 1.

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Author contributions

JVO, BD and GC conceptualized the study. JVO collected field data, developed the localisation code, performed analyses and wrote the initial manuscript. BD secured funding and contributed to project administration. All authors contributed critically to drafts of the manuscript and approved the final manuscript.

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Availability of data and materials

The code to perform the methods developed here as well as the data generated and analysed during this study are available on Github at: <https://github.com/johnvanosta/ml4rt>

Declarations

Ethics approval and consent to participate

Mist-netting, radio tag attachment and radio tracking were conducted under the animal ethics permit CA 2020/07/1392, issued by the Queensland Department of Agriculture and Fisheries, research permit WA0025814, issued by the Queensland Department of Environment and Science and Australian Bird and Bat Banding Scheme authority 2832-01, issued by the Australian Government Department of the Environment.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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