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Ornithological Methods

Field methods to improve received signal strength (RSS)–based localization for tracking songbird movements in forests

Métodos de campo para mejorar la localización basada en la intensidad de la señal recibida (RSS) para el rastreo de movimientos de aves canoras en bosques

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ABSTRACT. Animal movement studies that provide information on a species' behavior, habitat use, dispersal, and migration are critical for making well-informed conservation and management decisions. Advancements in automated radio telemetry systems (ARTS) may improve our ability to monitor animal movements continuously and simultaneously but require further testing and development to maximize their benefits for wildlife research. We investigated the use of automated telemetry for tracking fine-scale songbird movements in a forested environment. We placed automated receiver units (or nodes) at 100-m spacing across our study site to automatically detect ultra high frequency (UHF) tags. We established a received signal strength (RSS)-to-distance relationship and used trilateration with data from ≥3 nodes to determine test tag locations. We estimated locations with a median accuracy ranging from 31 to 39 m and location loss (i.e., number of test tag locations that could not be estimated) ranging from 17% to 95%. RSS-based localization using automated telemetry can be a useful method for tracking fine-scale songbird movements in forests, where obstructions can reduce RSS values. However, extensive habitat-specific calibration tests in close proximity to each node may be necessary to reduce the effect of signal attenuation, better inform RSS-distance relationships, and minimize location error.

RESUMEN. Los estudios sobre el movimiento animal que proporcionan información sobre el comportamiento de una especie, el uso del hábitat, la dispersión y la migración son fundamentales para tomar decisiones de conservación y gestión bien fundamentadas. Los avances en los sistemas de radio telemetría automatizada (ARTS, por sus siglas en inglés) pueden mejorar nuestra capacidad para monitorear los movimientos de los animales de manera continua y simultánea, pero requieren más pruebas y desarrollo para maximizar sus beneficios en la investigación de la vida silvestre. Investigamos el uso de la telemetría automatizada para el rastreo a escala fina de los movimientos de aves canoras en un entorno forestal. Colocamos unidades receptoras automatizadas (o nodos) con un espaciamiento de 100 metros a través de nuestro sitio de estudio para detectar automáticamente etiquetas de frecuencia ultrahalta (UHF). Establecimos una relación entre la intensidad de la señal recibida (RSS) y la distancia, y utilizamos la trilateración con datos de ≥ 3 nodos para determinar las ubicaciones de las etiquetas de prueba. Estimamos las ubicaciones con una precisión mediana que osciló entre 31 y 39 metros, y una pérdida de localización (es decir, el número de ubicaciones de etiquetas de prueba que no pudieron estimarse) que varió del 17% al 95%. La localización basada en RSS mediante telemetría automatizada puede ser un método útil para rastrear los movimientos a escala fina de aves canoras en bosques, donde las obstrucciones pueden reducir los valores de RSS. Sin embargo, puede ser necesario realizar extensas pruebas de calibración específicas para el hábitat en estrecha proximidad a cada nodo para reducir el efecto de la atenuación de la señal, mejorar la precisión de las relaciones RSS-distancia y minimizar el error de localización.

Key Words: *automated radiotelemetry; automated receiver units; movement ecology; RSS-based localization; songbirds*

INTRODUCTION

Animal movement studies that provide information on a species' behavior, habitat use, dispersal, and migration are critical for making well-informed conservation and management decisions (Kays et al. 2015, Wierucka et al. 2016, Deuel et al. 2017, Karelus et al. 2021). However, it is challenging to track the movements of species that are small-bodied (Bridge et al. 2011), inconspicuous (Wallace et al. 2022), or exhibit protracted and long-distance dispersals (Rowcliffe et al. 2012, Cooper and Marra 2020) using traditional methods (e.g., field observations of marked individuals). In addition, the resulting data may not fully capture an individual's movements (Reynolds and Laundré 1990, Anich et al. 2009). Advancements in automated radio telemetry systems (ARTS) that utilize lightweight, very high frequency (VHF) or ultra high frequency (UHF) tags and stationary arrays of antennas to obtain location data could help overcome these challenges and improve our ability to monitor animal movements continuously and simultaneously. However, these technologies require further testing and development to maximize their benefits for wildlife research.

One application of ARTS to study the activity patterns (Ward et al. 2013, Mitchell et al. 2015, Schofield et al. 2018), timing of departures and arrivals (Cooper et al. 2023), and broad-scale movements (Lenske and Nocera 2018, Bégin-Marchand et al. 2022) of animals is the collaborative Motus Wildlife Tracking System (Birds Canada 2023). Motus is a global, automated radio telemetry network with >1426 receiver stations and >285 species (i.e., birds, bats, and insects) tagged worldwide (Birds Canada

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2023). The receivers record detections of VHF/UHF tagged animals that pass within approximately 15 km of a station and have provided important insight into how animals move across the landscape (Taylor et al. 2017, Griffin et al. 2020). When a project requires fine-scale movement data, wildlife biologists have placed multiple automated receiver units (ARUs or nodes) at regular intervals across their study sites to automatically detect tags (e.g., Ward et al. 2014, Celis-Murillo et al. 2017, Fisher et al. 2021). Each ARU stores detection data, which is transmitted to a base station, downloaded remotely, and processed post hoc (Kays et al. 2011, Mennill et al. 2012, Paxton et al. 2022, Wallace et al. 2022).

The ARU designs and analytical approaches used for tracking fine-scale animal movements are similar to what is used in indoor positioning systems, which can determine the locations of targets within buildings, such as stores, stadiums, and parking garages (Bembenik and Falcman 2020). Indoor positioning systems use received signal strength (RSS) from Bluetooth low energy (BLE) beacons or wireless local area networks (hereafter nodes) to determine the distance from a node to a mobile device (Ilci et al. 2015, Bembenik and Falcman 2020). This is accomplished by establishing an RSS-distance relationship, filtering uninformative (i.e., weak) RSS values, and using trilateration with data from ≥3 nodes to determine the location of a signal. RSS-based localization has broad-scale applications because it is low-cost and can be very accurate (e.g., <1 m accuracy); however, RSS is easily reduced or blocked by obstructions (Shi et al. 2020, Rueda-Uribe et al. 2024, Tyson et al. 2024). In indoor environments, Bembenik and Falcman (2020) recorded weak signals that required filtering to improve location estimates, especially when nodes were behind walls. Because of the instability of RSS values, extensive tests are necessary to minimize the error in location estimates and reduce data uncertainty (Krull et al. 2018, Wallace et al. 2022). With line-of-sight to nodes in indoor environments (e.g., small, open spaces), Javaid et al. (2015) and Shi et al. (2020) produced minimal localization errors of 0.126 m and <1.46 m, respectively.

Similar to indoor positioning systems, researchers who utilize ARU designs to detect fine-scale animal movements commonly calculate an RSS-distance relationship to estimate the location of tagged animals that occur within the range of their receivers (Krull et al. 2018, Paxton et al. 2022, Wallace et al. 2022). However, many factors influence the accuracy of RSS-based localizations in outdoor environments, including weather conditions (e.g., rain, humidity), shadowing (i.e., object blocking a signal), and reflection (i.e., signals bouncing off an object) (Rutz et al. 2015, Shafer et al. 2019, Tran et al. 2024). For example, Rutz et al. (2015), Rueda-Uribe et al. (2024), and Tyson et al. (2024) found that distance estimates based on RSS values tended to decrease in reliability as habitat variability increased. Studies have also shown a range of errors associated with estimated animal locations within node networks depending on node spacing and field site calibration, which stresses the importance of study-specific calibrations to reduce error before performing localization analysis (Krull et al. 2018, Paxton et al. 2022, Tran et al. 2024). For example, Wallace et al. (2022) calculated a median location error of 4.3–32.8 m but the nodes were distributed within an open, small spatial area (0.4 ha; antenna density of 80 antennas/ha). Paxton et al. (2022) used filters (RSS, distance) to mitigate the effect poor signals had on location estimates and estimated a location error of 28–73 m in an urban environment. Similarly, Tran et al. (2024) used Paxton et al.'s (2022) methods to test localization error within a managed pine barren and estimated a location error of 46–65 m. However, this approach is still relatively new, and RSS-based localization has not been thoroughly tested in structurally complex environments (e.g., forests), where the height of vegetation is consistently ≥5 m.

Our goal was to explore the use of automated telemetry for tracking fine-scale movements of forest-dwelling songbirds and provide methods that could be used to improve RSS-based location estimates from automated telemetry networks in similarly complex outdoor environments. We built upon methods presented by Paxton et al. (2022) and used their analytical framework to determine field methods that can be used to increase data transfer and mitigate error in RSS-based localization within node networks in forests. Our specific objectives were to (1) determine whether increasing the height of nodes improved RSS values and increased the transfer of data from nodes to a base station, and (2) compare how different field calibration methods and filters (RSS, distance) affected the accuracy of localization estimates.

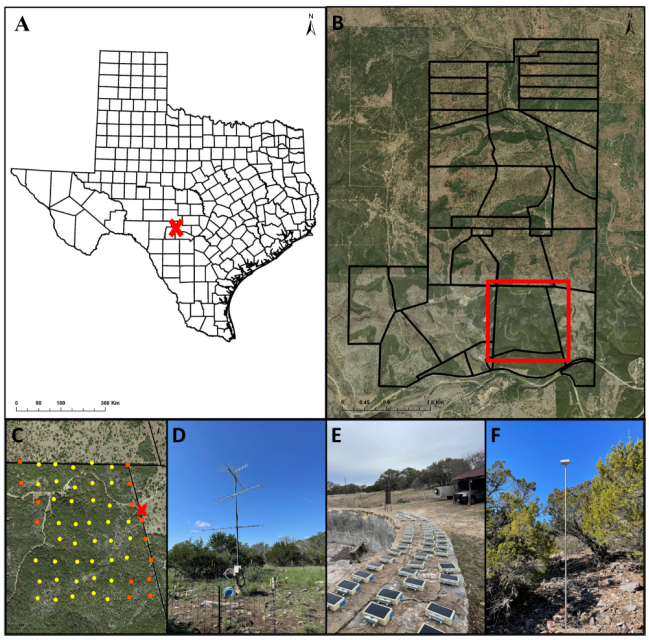
We expected that increasing the height of nodes to reduce the amount of vegetation obstructing line-of-sight to the base station would improve both RSS values and data transfer to the base station, as study sites with fewer obstructions tend to have stronger signals and higher detection probability between receivers (Heupel et al. 2006, Taylor et al. 2017, Shi et al. 2020). We expected that the accuracy of the location estimates we obtained in a forested environment would be lower than what was previously observed in more open, less complex field sites (e.g., Paxton et al. 2022, Wallace et al. 2022), and that the strict RSS and distance filters we applied would significantly reduce the amount of usable data for localization analysis (Paxton et al. 2022, Tran et al. 2024). However, we expected that test locations at closer distances to nodes would provide us with more informative RSS values and, as a result, decrease the error in location estimates. Because we used the results from year one of our study to update our methods for year two, we presented the methods and results for each year separately below.

METHODS

Study site

We conducted our research from March to July of 2022 and 2023. Our study site was located at the Kerr Wildlife Management Area (KWMA) in Kerr County, Texas (Fig. 1). This wildlife management area is in the Edwards Plateau ecological region and contains 2627 ha of oak-juniper woodlands and savanna (TPWD 2021). Ground elevation at the KWMA varies between 640 and 661 m a.s.l. and vegetation is predominated by Ashe juniper (*Juniperus ashei*), post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), and live oak (*Q. fusiformis*) (Diamond 1997). We conducted our research in the Spring management unit on the south end of the KWMA (Fig. 1), where percent canopy cover is 30−100%, tree height is 4.5−11.3 m, and percent shrub cover is <20% (Long et al. 2021a, 2021b).

Fig. 1. (a) Red X identifying the location of our study site at Kerr Wildlife Management Area in Kerr County, Texas. (b) Map of study site (red box) and management units (black lines) at Kerr Wildlife Management Area. (c) Map of Motus station (red X), 2022 grid of automated telemetry nodes (yellow dots), and nodes added in 2023 (orange squares) in northeast corner of Spring management unit. (d) Motus tower. (e) Nodes charging prior to installation. (f) Node at a grid point.



2022 field methods

We installed a Motus tower equipped with a SensorStation (version 2.0) and 40 solar powered automated telemetry units called nodes (version 2.0) at KWMA to localize battery-powered radio transmitters (PowerTag-80; SensorStation, nodes, and PowerTags developed by Cellular Tracking Technologies [CTT]). We installed the nodes along an ~5 x 8 grid (30 ha), with each node spaced 100.05 ±13.05 m apart in the northeast corner of the Spring management unit in a location that would maximize the elevation of the Motus tower, minimize distances from the nodes to the tower, and minimize potential interference from topographic obstructions (Fig. 1). We attached each node to the top of a 3-m tall, 19 mm stainless steel pole in a location with no canopy cover to ensure that vegetation did not obstruct the solar panel (Fig. 1). We installed the Motus tower and SensorStation <800 m from the farthest node so that the data could be transmitted from the nodes to the station (Fig. 1). As recommended by CTT, we attached an omnidirectional antenna (manufactured by Data Alliance) to the Motus station to receive the node data; this antenna had a radius of 360° with a range of 1 to 1.5 km. The data transfer (check-ins) from the nodes to the station occurred every 5 minutes (12x per hour); however, transfer depended on signal attenuation and nodes did not send backlogged data. Although we did not use this feature, each node also has an SD card to store detection data, which can be downloaded if there are issues with data transfer from the nodes to the station. We deployed and tested this node grid before tagging and tracking Golden-cheeked Warblers (*Setophaga chrysoparia*) for a concurrent study (Gamble et al., *unpublished manuscript*).

After we deployed the nodes, we accessed the SensorStation interface daily using an ethernet cable and laptop. We examined the data from each node and recorded the locations of nodes that did not check in and submit data for ≥1 hr, which included 30% of nodes (n = 12) during the first week of the field season. To improve signal to the base station for nodes that did not submit data, we increased the height of nodes to 4.5 m using a 19 mm EMT conduit coupling and a 1.5 m pole; 92% of these nodes (n = 11) submitted data within the hour after the height change. Then, after 8 d, approximately half of the nodes (some we had previously raised and others we had not) simultaneously stopped submitting data to the station. As recommended by CTT, we increased the power output of all nodes by 10 dB, and they resumed regular check-ins with the station. On 9 April, the same issue with data submission occurred; other researchers reported similar issues attributed to faulty Data Alliance omnidirectional antennas that reduced the range of the antenna (D. A. LaPuma, 2022, personal communication), so we removed the omnidirectional antenna from the SensorStation and added three 6-element 434 MHz Yagi antennas to receive the data. The 6-element Yagi has a detection range of approximately 10 km depending on topography and vegetation (Birds Canada 2023). After replacing the antennas, all nodes reliably transmitted data to the base station for the remainder of the 2022 study period.

2022 calibration and localization methods

We conducted all analysis in R statistical software (V. 4.2.2; R Core Team 2022). We used an RSS-based trilateration method to estimate test tag locations, which requires data from ≥3 nodes to estimate a location (Krull et al. 2018, Paxton et al. 2022, Wallace et al. 2022). This method is based on the relationship between RSS values (i.e., signal strength received by each node when a tag is detected) and the distance from each node to the signal (i.e., tag location). In 2022, we followed the field methods presented by Paxton et al. (2022) to calibrate the RSS-distance relationship at our study site. We first attached a 0.4 g PowerTag with a 2-min pulse interval to a small bottle (similar weight to a Golden-cheeked Warbler) to simulate a small bird, attached the bottle to the top of a 3-m nonconductive pole, and oriented the transmitter antenna horizontal to the ground to mimic the position of a transmitter on a perched bird. We then walked to approximately half the nodes in the grid and tested signal strength from the transmitter to each node at set distances of 1, 10, 20, 50, 75, 100, and 125 m to cover the range of vegetative and topographic conditions found across our study site, resulting in 7 test locations per node. For each test, we placed the bottom of the pole on the ground and oriented the transmitter at a right angle from the node. We held the pole stationary for 10 min to ensure multiple tag detections per test location, and we recorded the start and end time of each test as well as the GPS coordinates of each test location.

We then downloaded the calibration data from the SensorStation and, as described by Paxton et al. (2022), we averaged the RSS values of each node over the 10-min field test period and calculated the Euclidean distance between each node and test

location. We used a non-linear least square approach to run a negative exponential decay model that represented the relationship between the average RSS values and distance of the nodes from each test location. The model formula for this analysis was RSS ~ $a \times \exp(-S \times \text{distance}) + K$, where K = horizontal asymptote of RSS values, a = intercept, and S = decay factor.

We also applied RSS and distance filters to the dataset to limit the number of nodes used in trilateration because Paxton et al. (2022) found that including all nodes during analysis pulled location estimates to the center of a node network. We filtered the data with RSS cutoff values of −80, −85, −90, −95, −100, and −105 dB (i.e., we only used nodes that received RSS signals above these values in trilateration analysis) to examine location accuracy and data loss. Additionally, we tested distance filters that were multiples of the average grid spacing (i.e., times 1.25, 2, 3, and 4) to examine location accuracy. The average spacing in our grid was 100 m, which resulted in distance filters of 125, 200, 300, and 400 m. For this analysis, we took the node with the strongest signal and then selected all other nodes that were within the filtered distances of the node receiving the strongest signal to use in trilateration. This allowed for only nodes with the strongest signal to be used in trilateration. More stringent RSS filters are expected to result in less location error but increased data loss (Paxton et al. 2022, Tran et al. 2024). After filtering, using the RSS-based trilateration method, we estimated the test locations based on the average RSS-to-distance relationship and compared the difference in distance (m) between the estimated test locations and the known test locations to determine location error for the study site based on each signal and distance filter (Paxton et al. 2022).

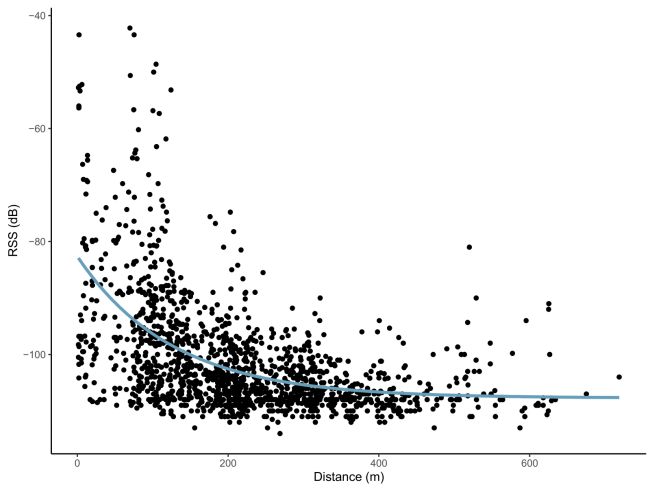
2022 results

We conducted 112 known radio transmitter location tests across 55% (n = 22) of the node grid, which produced a test dataset of 1440 data points with RSS values and associated known distances to all the nodes in the grid. Applying the negative exponential decay model to the dataset resulted in a decline in RSS values as distance from the nodes increased (Fig. 2), which was expressed as $\text{RSS} = 25.07 \times \exp(-0.008 \times \text{distance}) - 107.71$. Without filters, the median localization error (difference between known and estimated locations) was 110.50 m (Table 1). Because we required ≥3 nodes with RSS values above the filter cutoff for trilateration, the most stringent RSS filters (i.e., RSS −80, −85) resulted in no estimated locations. The next most stringent filters (i.e., Distance 1.25x, RSS −90) provided estimates with a median localization error that ranged from 82.77 to 96.62 m (Table 1). However, an RSS −95 filter provided estimates with a median localization error of 70.66 m and the most stringent filters had a location loss that ranged from 13% to 90% (Table 1).

2023 field methods

In 2023, we deployed 14 additional nodes for a total of 54 nodes, which expanded the size of our grid from 30 ha to 42 ha (Fig. 1), and we continued to use three 6-element 434 MHz Yagi antennas connected to the Motus station to receive node data. We kept all nodes at the 10 dB increased power output because of the weak tag signals (RSS < −95 dB) shown in the model output from 2022 (Fig. 2). However, when we redeployed the nodes, we returned them to the 3 m height to test whether the 6-element Yagi antennas could consistently receive node data across the network. We

Fig. 2. The relationship between received signal strength (RSS) and known distances of a radio transmitter derived from 112 test locations within a network of 40 nodes on the Kerr Wildlife Management Area in 2022. This relationship is represented by the negative exponential decay equation $\text{RSS} = 25.07 \times \exp(-0.008 \times \text{distance}) - 107.71$.



moved three nodes at least once during the field season that would not check in to the base station to improve the signal, so we excluded these from the 2023 node analysis.

2023 calibration and localization methods

In 2023, we attached a PowerTag with a 1 min and 15 sec pulse interval to the top of a 3-m nonconductive pole and tested signal strength from transmitter to nodes at set distances of 1, 10, 20, 30, 40, 50, 75, 100, and 125 m (9 test locations per node). We used a different tag from what was used in 2022, but we used the same nodes. The tag pulse interval was different in 2023 from 2022 (2 min pulse interval) because the tags were manufactured with a larger battery in 2023, which allowed for a more frequent ping rate. We added distance tests at 30 and 40 m from each node, which we did not conduct in 2022. We increased the number of test locations in 2023 because our model results from 2022 showed poor signals (i.e., RSS < −95 dB) for most test locations, especially at ≥50 m (Fig. 2). We then downloaded the calibration data from the SensorStation and conducted the same localization methods as in 2022.

2023 statistical analysis

We downloaded the node data weekly from the SensorStation and plotted the RSS value of each check-in per node and the number of check-ins per node per hour. After each download, we visually inspected the plots and subsequently raised 33% (n = 17) of the nodes to 4.5 m that consistently had an RSS < −95 dB (i.e., weak and contributing to signal loss) and ≤7 check-ins/hr (≤58%). Consistent check-ins of <60% per hour in combination with the first season's location loss results (~60%; Table 1) from applying filters reduced our location sample size. We attempted, through raising the nodes, to improve the amount of detection data received to ≥60% to increase the number of locations that could be estimated. To test whether raising the nodes improved the

Table 1. Summary of localization error (difference in meters between the known and estimated location) of trilateration location estimates for a node network on the Kerr Wildlife Management Area with uniform spacing among nodes (100 m) in 2022.

Filter	Location loss (%)	Mean nodes (n)	Mean error	Lower 95% CI	Upper 95% CI	Median error	Min error	Max error
No filter	1	9.43	128.68	111.89	145.47	110.50	21.33	637.41
Distance 1.25x (125 m)	13	4.12	108.14	92.57	123.72	96.62	6.53	487.07
Distance 2x (200 m)	7	6.05	111.92	97.27	126.57	103.25	7.27	472.07
Distance 3x (300 m)	3	8.61	119.74	105.44	134.05	104.59	4.38	431.73
Distance 4x (400 m)	2	9.11	124.38	107.03	141.73	101.18	6.17	637.41
RSS −90 dB	90	3.00	93.03	60.44	125.62	82.77	24.89	165.58
RSS −95 dB	55	3.35	79.93	64.89	94.97	70.66	12.93	258.03
RSS −100 dB	18	4.75	87.32	74.46	100.18	84.30	5.33	388.95
RSS −105 dB	5	7.36	95.76	82.73	108.80	85.57	5.33	455.53

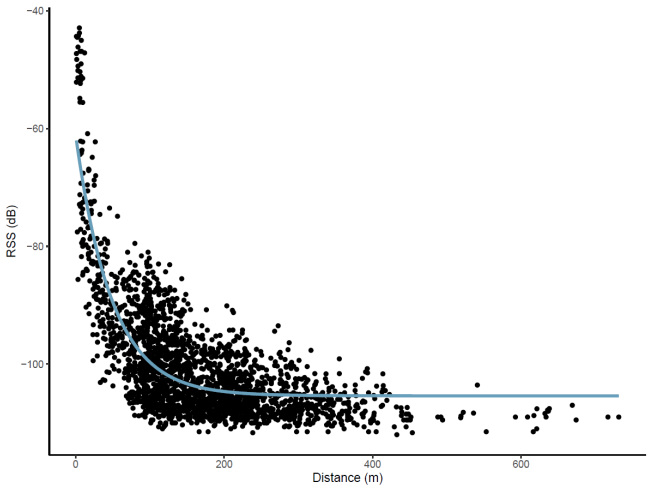
signal strength and the number of check-ins, we performed paired *t*-tests (a = 0.05) to compare the average signal strength and percent check-ins before and after we raised the nodes (Boslaugh 2012). We also calculated the average signal strength and percent check-ins for the nodes we did not raise during the 2023 season.

2023 results

For nodes we raised, we found no significant difference (t_{31} = 1.33, P = 0.19) between RSS values (dB) before and after they were raised (before: −98.64 ± 3.47, range = −91.50 to −103.81; after: −96.90 ± 4.12, range = −85.87 to −100.90). We also found no significant difference (t_{19} = 0.79, P = 0.44) between percent check-ins before and after nodes were raised (before: 80.05 ± 0.30, range = 5.56 to 98.68; after: = 86.09 ± 0.096, range = 61.30 to 95.20). For 67% (n = 34) of the nodes we did not raise, the mean RSS value (dB) was −86.67 ± 7.89 (range = −65.01 to −96.91), and the mean percent check-in was 93.29 ± 0.021 (range = 84.55 to 95.79). There were 3 nodes that checked in <45% of the time before we raised them but when raised, the check-in rate increased to >60%.

We conducted 217 known radio transmitter location tests across 50% of the node grid (27 nodes), which produced a test dataset of 2746 data points with RSS values and associated known distances to all the nodes in the grid. Applying the negative exponential decay model to the dataset resulted in a decline in RSS values as distance from the nodes increased (Fig. 3), which was expressed as RSS = 44.81 × exp(−0.0199 × distance) − 106.12. Without filters, the median localization error was 50.18 m (Table 2). The most stringent RSS filters (i.e., RSS −80, −85) resulted in no estimated locations. The next-most stringent filters (i.e., Distance 1.25x, RSS −90) provided location estimates with a median localization error that ranged from 31.28 to 38.63 m (Table 2). However, the most stringent filters had a location loss that ranged from 17% to 95% (Table 2).

Fig. 3. The relationship between received signal strength (RSS) and known distances of a radio transmitter derived from 217 test locations within a network of 54 nodes on the Kerr Wildlife Management Area in 2023. This relationship is represented by the negative exponential decay equation RSS = 44.81 × exp(−0.0199 × distance) − 106.12.



DISCUSSION

Many factors can influence the signal strength of receivers or radio transmitters, including weather (e.g., humidity, rain, temperature; Thelen et al. 2005, Bannister et al. 2008), habitat conditions (e.g., vegetation; Marfievici et al. 2013, Rutz et al. 2015), and interference from concurrent transmissions (Haenggi and Ganti 2009, Kessel et al. 2015). Increasing line-of-sight and limiting obstructions between receivers can improve signal strength and detection probability (Heupel et al. 2006, Shi et al. 2020). Typically, increasing the height of a receiver can improve signal strength and detection probability, as well as the range of the receiver (Taylor et al. 2017). Withey et al. (2001) and Grovenburg et al. (2013) documented reduced signal transmission rates for receivers that were closer to the ground. We found reduced signals and decreased data transmission from nodes to the SensorStation even after we increased the power output of each node by 10 dB, likely because of canopy cover and topography.

Although we did not test the signal and check-in rate of each node before and after boosting the power output, previous studies suggested that increasing the power output of receivers improves signals and communication between antennas and receivers (Kessel et al. 2015, Wallace et al. 2022). Reduced data transmission affected approximately one third of the node grid, and raising the nodes by 1.5 m slightly improved signal strength and check-in rate, but this effect was not significant. The lack of significant improvement was likely due to the high variability in RSS values (Koubâa et al. 2012), potentially exacerbated at our study site by canopy cover and topography. In addition, raising the nodes 1.5 m may not have significantly changed the effect

Table 2. Summary of localization error (difference in meters between the known and estimated location) of trilateration location estimates for a node network on the Kerr Wildlife Management Area with uniform spacing among nodes (100 m) in 2023.

Filter	Location loss (%)	Mean nodes (n)	Mean error	Lower 95% CI	Upper 95% CI	Median error	Min error	Max error
No filter	0	7.36	57.53	52.87	62.20	50.18	4.00	266.00
Distance 1.25x (125 m)	17	3.95	47.14	42.13	52.15	38.63	2.38	189.28
Distance 2x (200 m)	2	5.38	48.43	43.66	53.19	40.14	0.67	266.00
Distance 3x (300 m)	1	7.00	52.24	47.78	56.69	45.63	0.67	266.00
Distance 4x (400 m)	0	7.33	55.85	51.28	60.43	48.81	4.00	266.00
RSS −90 dB	95	3.09	32.93	25.55	40.31	31.28	18.09	60.61
RSS −95 dB	66	3.51	39.16	33.48	44.84	34.68	3.12	113.41
RSS −100 dB	25	4.50	44.95	40.61	49.28	39.97	2.72	161.60
RSS −105 dB	2	6.67	53.42	49.12	57.72	45.53	6.63	140.36

obstructions surrounding each node had on signal strength or check-in rate because raised nodes still sat below the canopy. Raising nodes higher, above the canopy, could further improve signal strength and data transmission rates. There were three nodes that had very low (<45%) check-in rates and raising the nodes increased the check-in rate to >60%; however, more study is needed to determine how node positioning can mitigate data transmission in forested habitats. These findings suggest that researchers should consider amplifying the signal for receivers, particularly in structurally complex environments. Researchers could also access the data on each node's SD card if they still have frequent data transmission problems.

After adjusting the nodes, researchers need to calibrate their node network to determine their habitat-specific RSS-distance relationship. This allows researchers to calculate an accurate error estimate for their locations based on their node network design. In our first field season, we followed Paxton et al.'s (2022) calibration field methods as they used the same node technology; however, we conducted 10-min tag tests across the node network instead of 3-min tests. A longer tag test is not necessary if the radio transmitter has a frequent pulse interval (Krull et al. 2018, Paxton et al. 2022). Researchers can set the duration of their tag tests as long as test duration is consistent and provides multiple tag RSS readings that researchers can average for each distance to each node to limit the effect of outlier RSS values. The distances Paxton et al. (2022) used in an urban environment for their tag tests produced reduced signal strength results at our forested study site, likely because of signal attenuation caused by canopy cover and topography (Whitehouse et al. 2007, Shi et al. 2020, Rueda-Uribe et al. 2024). As expected, in our second field season, conducting tag tests closer to each node (increments of 10 m up to 50 m) and doubling the number of tests provided more usable RSS values (≥ −95 dB). These signal results indicate that it is important for researchers to extensively test the RSS-distance relationship within a node network to determine whether they need to make adjustments to better inform the relationship within a study site. To optimize calibration, researchers should allocate additional time prior to the start of data collection to conduct field tests and understand how habitat conditions affect signal strength. It took approximately one week to conduct the field tests, but testing could take more or less time depending on environmental conditions and the size of the grid.

Like previous studies (Bembenik and Falcman 2020, Paxton et al. 2022, Tran et al. 2024), applying RSS and distance filters to the calibration data decreased location error compared to unfiltered data. Unlike Paxton et al. (2022), RSS filters had less location error than distance filters within our node network. Distance filters may not have performed as well because of the thick canopy cover and hilly terrain of our study site. A node that is significantly higher than surrounding nodes or has increased line-of-sight to a tag could receive a better signal than a node that is closer to a tag but is obstructed or at a lower elevation (Bembenik and Falcman 2020, Rueda-Uribe et al. 2024). Because distance filters selected the node with the strongest signal, location estimates could potentially get pulled toward nodes that are not near the tag location. Paxton et al. (2022) found that RSS filters performed better in node networks that had uneven node spacing; although our network was on average spaced at 100 m, there was variation in node spacing because node placement was limited to locations where canopy cover would not obstruct the solar panel on top of the node. In addition, the most stringent RSS filters (−80, −85 dB) resulted in no location estimates because there were never ≥3 nodes per test location that recorded RSS values at these levels that could be used for trilateration. However, Paxton et al. (2022) were able to use an RSS filter of −80 dB, likely because of the more open landscape of their study site, and Bembenik and Falcman (2020) used a minimal signal strength threshold of −78 dB inside a building at close distances. We could only use RSS filters ≤ −90 dB, and RSS values < −95 dB are unreliable for location estimation (Paxton et al. 2022, CTT 2024), which limited the RSS filters we could apply to our dataset. Similarly, Tran et al. (2024) were only able to use RSS filters ≤ −102 dB for detection data received from nodes within hardwood and pitch pine forests. This demonstrates the importance of testing multiple filters for habitat-specific calibration data to determine the filter that provides the least localization error.

After localization, we found that the most stringent RSS filter (−90 dB) and increasing the number of calibration tests at closer distances to nodes improved median localization error from approximately 71 m to 31 m. In 2022, after applying the most stringent RSS filter, a majority of the RSS values recorded at locations >50 m from each node were removed. Without additional calibration tests closer to each node (<50 m), we were limited in the number of RSS values we could use for our RSS-distance relationship, which negatively affected our location error. In 2023, conducting calibration tests in 10 m increments up to 50 m improved RSS values within our node grid, which better informed our RSS-distance relationship and decreased our location error. In forested habitats (i.e., hardwood, pitch pine), Tran et al. (2024) estimated a localization error of approximately

60 m. However, they spaced nodes 200 m apart and used calibration data from only four nodes to calculate the localization error within the forested area of their study site. Rueda-Uribe et al. (2024) estimated a median localization error of 105 m at a study site in the Columbian high Andes with heterogenous vegetation cover and more topographic relief than our study location.

Other studies in less complex environments have calculated various estimates using RSS-based localization. In indoor environments, node and signal tests in small grids (4 x 4 m or 6 x 4 m) produced location error <1.46 m (Javaid et al. 2015, Shi et al. 2020). Wallace et al. (2022) used a similarly spaced node grid within a 0.4 ha study site in an open, outdoor environment and calculated a location error of approximately 4 to 33 m. However, these node designs are not feasible for tracking species that cover large areas. Paxton et al. (2022) simulated node configurations that varied in the spacing of nodes (100, 175, and 250 m) and calculated an error of approximately 28 to 73 m. The 28 m error was with the most stringent RSS filter (−80 dB) and in the same node grid spacing as our study (~100 m). Node networks spaced further than 100 m and unevenly had decreased location accuracy, highlighting the importance of node spacing in location error estimates (Paxton et al. 2022, Tran et al. 2024). It is important to note that we used CTT Node version 2.0 for our study, which was discontinued for version 3.0 that quadruples battery capacity and allows researchers to mount the solar panel separately from the node (CTT 2024). This will improve the use of node technology in forests by optimizing recharging capabilities and retaining node grid symmetry when breaks in the canopy are not evenly spaced throughout a study area. With that said, version 3.0 would provide limited benefit at field sites with a dense forest canopy where there are not many openings in the canopy to place the solar panel.

As predicted, the location error at our study site was greater than in more open, less complex sites (e.g., fields) (Paxton et al. 2022, Wallace et al. 2022), but differences in location error between our study site and previous studies were minimal. However, we did have greater location loss compared to Paxton et al. (2022) for both distance and RSS filters, likely because of signal shadowing and reflection caused by canopy cover and topography (Rutz et al. 2015) with a 95% and 17% location loss for the most stringent RSS and distance filters, respectively. Using a RSS −95 dB filter, Tran et al. (2024) had a 100% location loss within their forested study areas, whereas we had a 66% location loss when we applied the same filter to our detection data. Our improved location loss estimate was likely due to our more extensive calibration dataset, shorter node spacing within our grid, and less canopy cover directly above our nodes. Despite less location loss with the distance filters, the distance filters produced less accurate locations than the RSS filters; as such, weighing location loss and accuracy is important in determining what filter researchers should apply to their data.

Since our study, there have been improvements and modifications to Paxton et al.'s (2022) RSS localization through trilateration. Tyson et al. (2024) developed a new method called radio fingerprinting, an alternative to RSS localization, that characterizes RSS patterns to create a radio map of the study site that is then used to estimate the location of new RSS patterns. For this method, Tyson et al. (2024) created a 25 x 25 m grid and tested three tags (5 s pulse interval) for 2 to 3 min at each calibration point. From the calibration tests, they calculated an average RSS value per test location that made up the RSS fingerprints of their radio map and then used a classification algorithm to predict locations of new RSS fingerprints. Compared to trilateration, radio fingerprinting had similar median localization error (~30 m) but it reduced error in forested habitats that were structurally similar to our study site. Radio fingerprinting limited the bias in trilateration estimates where error increases as the distance from a receiver increases or when there were missed detections within the network. Unlike trilateration approaches, it also allowed researchers to space nodes irregularly and farther apart (>100 m) without significantly affecting the localization accuracy. Radio fingerprinting may be a more robust method to use in structurally complex environments; however, this method may not be appropriate for all applications. Conducting field tests to create the radio map is more time-intensive than trilateration methods, and field tests would need to be conducted again if there are substantial changes in the vegetation or receiver network. Habitat structure, receiver network design, location accuracy, and time need to be considered when determining whether to use trilateration or radio fingerprinting.

CONCLUSION

Overall, our results showed that RSS-based localization using automated telemetry is a reliable method for ascertaining location estimates that are suitably fine-scale for tracking songbird movements within forests. However, forest canopy cover and topography likely limited the transfer of data from nodes to the receiver and reduced signal strength values throughout the node network. Raising nodes may slightly improve the transfer of data, which might capture animal movements in locations that are lacking data, but more study is needed to determine useful methods to increase the transfer of data in forested habitats. If needed, missing detection data not transferred to the station can be downloaded directly from nodes to limit gaps in location data. Further, researchers should conduct transmitter tests closer to each node to reduce the effect of signal attenuation, better inform the RSS-distance relationship, and minimize localization error. To achieve low location error (~30 m) in complex environments, we recommend conducting transmitter tests every 10 m up to 50 m from a subset of nodes. Depending on site-specific characteristics, it may be beneficial to continue transmitter tests at 10 m increments at distances >50 m. Additionally, our results demonstrated that location estimates in structurally complex environments can have similar accuracy estimates to those in open environments with extensive field testing and the application of stringent filters. For studies on species with limited space use data, and if resources allow, researchers could deploy nodes closer together, which would also improve signals and location accuracy. Even with these mitigation efforts, extensive location loss remains an issue; as such, analytical methods or research objectives may need to be adjusted to account for missing or reduced data. Researchers can also decide which filters to apply to their data to prioritize location accuracy or the required number of locations to answer research questions. However, for species that have larger space use requirements, researchers will need to deploy more nodes, which will increase costs and the time required to manage the node grid and process the detection data. Combined, our results emphasized the importance of conducting extensive calibration tests prior to localization to ensure the accuracy of

the data and provided information on the effectiveness of automated telemetry in forests, which can be used in various environments to obtain fine-scale animal movement data critical for science-based conservation and management decisions (e.g., land allocation, habitat restoration, timing of presence/absence at a location).

Author Contributions:

Ashley Long acquired funding; Michael Gamble, Nancy Raginski, and Ashley Long conceived the ideas and designed methodology; Michael Gamble and Nancy Raginski collected the data; Michael Gamble and Nancy Raginski analyzed the data; Michael Gamble led the writing of the manuscript. All authors contributed to review and editing of the drafts and gave final approval for publication.

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Data Availability:

The data that support the findings of this study are openly available in GitHub at https://github.com/mdgamble/ARTS_FieldTests.

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