J. Field Ornithol. 89(2):173–187, 2018 DOI: 10.1111/jofo.12254

Field test of an automated radio-telemetry system: tracking local space use of aerial insectivores

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Received 10 January 2018; accepted 8 May 2018

ABSTRACT. Documenting local space use of birds that move rapidly, but are too small to carry GPS tags, such as swallows and swifts, can be challenging. For these species, tracking methods such as manual radio-telemetry and visual observation are either inadequate or labor- and time-intensive. Another option is use of an automated telemetry system, but equipment for such systems can be costly when many receivers are used. Our objective, therefore, was to determine if an automated radio-telemetry system, consisting of just two receivers, could provide an alternative to manual tracking for gathering data on local space use of six individuals of three species of aerial insectivores, including one Cliff Swallow (*Petrochelidon pyrrhonota*), one Eastern Phoebe (*Sayornis phoebe*), and four Barn Swallows (*Hirundo rustica*). We established automated radio-telemetry systems at three sites near the city of Peterborough in eastern Ontario, Canada, from May to August 2015. We evaluated the location error of our two-receiver system using data from moving and stationary test transmitters at known locations, and used telemetry data from the aerial insectivores as a test of the system's ability to track rapidly moving birds under field conditions. Median location error was ~250 m for automated telemetry test locations after filtering. More than 90% of estimated locations had large location errors and were removed from analysis, including all locations > 1 km from receiver stations. Our automated telemetry receivers recorded 17,634 detections of the six radio-tagged birds. However, filtering removed an average of 89% of bird location estimates, leaving only the Cliff Swallow with enough locations for analysis of space use. Our results demonstrate that a minimal automated radio-telemetry system can be used to assess local space use by small, highly mobile birds, but the resolution of the data collected using only two receiver stations was coarse and had a limited range. To improve both location accuracy and increase the percentage of usable location estimates collected, we suggest that, in future studies, investigators use receivers that simultaneously record signals detected by all antennas, and use of a minimum of three receiver stations with more antennas at each station.

RESUMEN. **Prueba de campo de un sistema automatizado de radio-telemetría: rastrear el uso del espacio local de insectívoros aéreos**
Documentar el uso del espacio local de aves que se mueven rápidamente, pero son demasiado pequeñas para llevar un GPS, como las golondrinas y los vencejos, puede ser un desafío. Para estas especies, los métodos de seguimiento como la radio-telemetría manual y la observación visual son inadecuados o requieren mucho tiempo y trabajo. Otra opción es el uso de un sistema de telemetría automatizado, pero el equipo para estos sistemas puede ser costoso cuando se usan muchos receptores. Nuestro objetivo, por lo tanto, fue determinar si un sistema automatizado de radio telemetría, que consta de solo dos receptores, podría proporcionar una alternativa al seguimiento manual para recopilar datos sobre el uso espacial local de seis individuos de tres especies de insectívoros aéreos, incluido un individuo de *Petrochelidon pyrrhonota*, uno de *Sayornis phoebe* y cuatro de *Hirundo rustica*. Establecimos sistemas automatizados de radio-telemetría en tres sitios cerca de la ciudad de Peterborough en el este de Ontario, Canadá, de mayo a agosto de 2015. Evaluamos el error de ubicación de nuestro sistema de dos receptores utilizando datos de transmisores de prueba móviles y estacionarios en ubicaciones conocidas, y usamos datos de telemetría de los insectívoros aéreos como una prueba de la capacidad del sistema de rastrear aves que se mueven rápidamente en condiciones de campo. El error medio de ubicación fue ~250 m para las ubicaciones de prueba de telemetría automatizada después del filtrado. Más del 90% de las ubicaciones estimadas tenían grandes errores de ubicación y se eliminaron del análisis, incluidas todas las ubicaciones > 1 km de las estaciones receptoras. Nuestros receptores automáticos de telemetría registraron 17,634 detecciones de las seis aves radiomarcadas. Sin embargo, el filtrado eliminó un promedio del 89% de las estimaciones de ubicación de aves, dejando solo datos de *P. pyrrhonota* con ubicaciones suficientes para el análisis del uso del espacio. Nuestros resultados demuestran que se puede usar un sistema de radio-telemetría automatizado mínimo para evaluar el uso del espacio local por aves pequeñas y muy móviles, pero la resolución de los datos recolectados usando solo dos estaciones receptoras era muy general y tenía un rango limitado. Para mejorar la precisión de ubicación y aumentar el porcentaje de

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estimaciones de ubicaciones recopiladas que se puedan utilizar, sugerimos que, en futuros estudios, los investigadores utilicen receptores que graben simultáneamente las señales detectadas por todas las antenas, y el uso de un mínimo de tres estaciones receptoras con más antenas en cada estación.

Key words: habitat use, location error, movement, small birds, swallows

Satellite and GPS transmitters have increased our ability to track the fine-scale movements of animals (Cagnacci et al. 2010, Hebblewhite and Haydon 2010). However, the weight of such transmitters generally limits their use to larger animals, leaving visual observations and VHF radio-telemetry as the primary methods for tracking the movements of smaller animals, including many species of birds (Wikelski et al. 2007). Although costing less, visual observation requires significant effort and can result in small sample sizes and biased views of habitat use (Anich et al. 2009, Streby et al. 2012). Radio-telemetry can increase samples size and reduce bias, but fast-moving birds, such as swallows and swifts, present additional challenges because homing in on locations or obtaining accurate bearings for triangulation before they move to a new location is usually not possible with manually operated receivers. Assessment of local habitat use by an aerial insectivore has been accomplished with manual radio-telemetry, using a presence–absence approach where an observer stands at set locations and records detections of radio-tagged birds (Saldanha 2016). This method provides location data accurate to within several hundred meters, but manual radio-telemetry tracking still requires much time and effort to obtain a sufficient number of fixes, and access to areas used by the birds may also be a problem (Larkin et al. 1996). Use of automated radio-telemetry addresses both of these problems, numerous fixes can be obtained without additional effort and locations can still be recorded when birds spend time in areas with restricted access. Currently, the main obstacles to use of automated telemetry are the cost of equipment (Ward et al. 2013) and obtaining permission to set up receiver stations, especially in areas where most land is privately owned.

Automated radio-telemetry was first used to collect data on local movements of animals in the 1960s (Cochran et al. 1965), but most telemetry studies have continued to use manual radio-tracking (Ward et al. 2013). Recently, however, the results of several studies have demonstrated the effectiveness of automated radio-telemetry systems for obtaining animal locations (Kays et al. 2011, Ward et al. 2013, 2014, Celis-Murillo et al. 2017). Unfortunately, setting up such systems can be expensive ($3000 USD for a single SensorGnome receiver with three 9-element yagi antennas, and $7500 USD for a Lotek SRX800 receiver station with four 9-element yagi antennas). Tests with arrays consisting of fewer receiver stations would therefore be useful in determining if similar, but reduced, set-ups can still collect useful data on animal locations. Additionally, assessments of location error of automated radio-telemetry systems have so far been restricted to stationary transmitters (Ward et al. 2013, 2014, Celis-Murillo et al. 2017), transmitters moving at a walking pace (Kays et al. 2011), or ground-truthing the location of relatively slow-moving animals (Ward et al. 2013). In contrast, typical flight speeds of swallows and swifts can range from 30 to 45 km/h (Schnell and Hellack 1978, Brown and Brown 1999, Winkler et al. 2011, Brown et al. 2017). Transmitters can be programmed to emit signals frequently (high burst rates), decreasing the distance traveled by an animal between successive detections and reducing the error in recorded locations. However, when tracking rapidly moving animals that change direction frequently, such as foraging swallows, the angle of the transmitter's antenna relative to receiver stations will likely have changed between hits even when a high burst rate is used. These changes in antenna position alter the signal strength recorded by receivers, increasing the difficulty of determining the location of a transmitter (Mennill et al. 2012, Ward et al. 2013). In addition, high burst rates are often impractical because of the trade-off between battery life and frequent detections. Receivers that simultaneously detect transmitter signals on all antennas have recently become available (Taylor et al. 2017) and should solve the problem of variation in signal strength due to variable transmitter antenna angles, but older systems that require cycling through each antenna are still in common use and, therefore, a test of their abilities is relevant.

Our objective was to determine if data concerning local space use by aerial insectivores could be collected using minimal automated telemetry equipment (i.e., only two receiver stations) with an accuracy greater than or equal to manual telemetry. We measured the accuracy of our system using both moving and stationary transmitters in known locations, examined sources of location error, and tested custom filters designed to remove unreliable locations. We also collected data from three species of free-living aerial insectivores fit with transmitters, including Barn Swallows (*Hirundo rustica erythrogaster*), Cliff Swallows (*Petrochelidon pyrrhonota*) and Eastern Phoebes (*Sayornis phoebe*), as a test of performance under field conditions. When sufficient data were collected, we built a kernel home range and modeled space use as a function of proximity to a bird's nest site. Because aerial insectivores are central place foragers during the breeding season (Turner 2006), we predicted greater use of space closer to nest sites. Finally, we describe several improvements that should be considered for use in future studies using similar equipment to assess local space use by aerial insectivores.

METHODS

Automated radio-telemetry system. We established automated radio-telemetry systems at three sites near the city of Peterborough (44.3091°N, 78.3197°W) in eastern Ontario, Canada, as part of a field study of habitat use by aerial insectivores (May–August 2015). The dominant land cover at all three sites was agricultural with variable amounts of woodlots and wetlands. The terrain was hilly with elevation varying by up to 65 m across a site. Each automated telemetry system consisted of two receiving stations ~1 km apart (range = 800–1600 m). This range of distances was chosen because, although detections up to 15 km have been reported for systems similar to ours when used to detect high flying migrants (Taylor et al. 2011, Mitchell et al. 2015), the range is often much less for birds flying lower due to local topography blocking line-of-sight and high local noise levels (Wheeler 2012, pers. observ.). Based on initial tests in our study area, the range of the receiving stations was < 5 km at our study sites. In addition, because we wanted to have transmitters detected on multiple antennas during a restricted time-period for calculating bearings, the distance between receiving stations was limited. Each receiving station consisted of four 9-element Yagi antennas positioned at 90° intervals. The antennas at each station were connected to an SRX-600 datalogging receiver through an ASP-8 multiple-antenna switching unit (Lotek Wireless, Newmarket, ON, Canada). We mounted the antennas ~6 m above ground on a galvanized steel extendable mast (Delhi 9.1-m popup mast 30A, Wade Antenna, Brantford, ON, Canada) stabilized by a tripod (TRM-10L 3-m tripod, Wade Antenna). All transmitters were digitally coded Nano Tags (model NTOQB-3-2, 0.64 g, burst rates of 4.9–15.1 s, frequency = 166.300 MHz, Lotek Wireless). We therefore programmed receivers to switch between antennas every 15.5 s, completing a full detection cycle every 62 s. Each time a transmitter was detected, the antenna number, signal strength, transmitter identity, and time were recorded.

The same two receiving stations were rotated between the three study sites every 2–3 d resulting in approximately one full day of monitoring (~10 h) at each site per week. Because each detection cycle took 62 s, we grouped observations into detection cycles by rounding timestamps to the nearest minute. Because some transmitters had burst rates resulting in multiple detections per antenna during a single detection cycle, we calculated the average received signal strength of each transmitter per antenna per minute. For each study site, we set up receiver stations in the same location and orientation during each sampling period.

We estimated transmitter locations using a method based on those described previously (Larkin et al. 1996, Kays et al. 2011, Ward et al. 2013) to estimate the locations of animals using data from static automated radio-telemetry receiver stations. Following these studies, we estimated bearings using the relative signal strength received by multiple antennas at a single receiving station that have overlapping directionality patterns. Bearings from multiple receivers were then used to triangulate an animal's location.

To estimate bearings, we developed a training data set. This was accomplished using two transmitters attached to the top of a wooden stake (1.85 m). Two transmitters were used, so we could determine if our method was robust to changes in transmitter antenna angle because it affects the signal strength recorded by a receiver (Mennill et al. 2012, Ward et al. 2013). One transmitter was aligned with its antenna pointing directly toward the receiver station and the other with its antenna parallel. To determine if the bearing calculation was affected by the distance between a transmitter and receiver, we placed the calibration transmitters at ~10–20 m intervals around the receiver station at two distance radii (50 and 100 m) from the receiver station. We were constrained to testing the effect of this small difference in distance because of restricted property access and suggest that investigators in future studies test a larger distance range. At each point, we left the calibration transmitters in position for 2 min to ensure an entire detection cycle was recorded by the receiver. We collected calibration data twice at each of the six receiving station locations. Sets of calibration points at some locations were not complete due to restricted access to private property, obstacles such as buildings, and areas that were inaccessible because of thick vegetation or swamps. To deal with gaps in coverage and obtain a more general relationship, we combined all calibration data after standardizing bearings, so that antenna 1 of each receiver station pointed north (bearing of 0°), antenna 2 west (270°), antenna 3 south (180°), and antenna 4 east (90°). Because the gain settings of receiver stations differed between locations due to differences in local noise levels, we converted relative signal strength (scale = ~10–255) recorded by the receivers to approximate received signal strength in dBm adjusted for gain using the lotekPowerTodBm function in the sensorgnome R package (sensorgnome.org). We excluded relative power readings of 255 from this conversion because the SRX600 receivers "max out" at a relative signal strength of 255, i.e., the actual signal strength of these observations is unknown, but is at or above the maximum received signal strength threshold of the receiver. Training data showed the expected power pattern, with received signal strength recorded by each antenna peaking when transmitters were located directly in line with that antenna and decreasing as transmitters were moved toward neighboring antennas (Fig. 1).

We estimated bearings based on the direction and relative signal strength of the two antennas registering the strongest signals during a detection cycle. We used the direction of the anti-clockwise antenna of the pair (hereafter, the primary antenna) as a base bearing. We then combined this with a bearing offset that estimated the degree difference between the bearing of the primary antenna and the true bearing from the receiver to the transmitter. Bearing offsets were determined using a statistical model of the relationship between bearings covering the angular range between two antennas (90°) and the corresponding standardized signal strength ratios (SSR_s). We standardized signal strength ratios, so they were centered around a value of one (theoretically corresponding to detections from a transmitter located directly between the two antennas) and changed symmetrically as a transmitter moved toward either of the two antennas (decreasing toward a value of zero near the primary antenna and increasing toward a value of two near the secondary antenna).

$SSR_s = (SS_{\text{primary antenna}}/SS_{\text{secondary antenna}})$ if $SS_{\text{primary}} \geq SS_{\text{secondary}}$, otherwise

$SSR_s = [((SS_{\text{secondary antenna}}/SS_{\text{primary antenna}}) \times -1) + 2]$,

where SS is the received signal strength registered by an antenna.

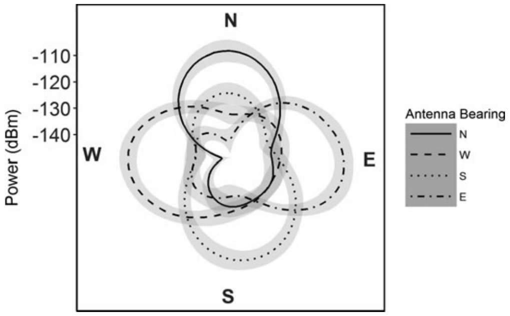

Fig. 1. Smoothed receiver power pattern: received signal strength recorded from each antenna peaked when transmitters were located directly in line with that antenna and decreased as transmitters were moved toward neighboring antennas.

Before calculating the signal strength ratio and estimating the final bearing, we had to assign an observation to a pair of antennas (quadrant of the receiver station). Identifying the correct antenna pair was complicated by missed detections, variation in received signal strength due to changes in transmitter position, signal bounce, and the power pattern typical of Yagi antennas that can result in strong signals being detected on the opposite facing antenna. To minimize incorrect assignment, we used two strategies. First, for short gaps in the data from a receiving station antenna of 3 min or less, we imputed missing data using linear approximation (implemented with na.approx from the zoo package, version 1.7-13; Zeileis and Grothendieck 2005). Second, we calculated bearings for both the primary (most likely) and secondary (next most likely) quadrant, predicting that, in many cases, only correctly assigned bearings would intersect with the bearings from the other receiver station. We restricted the dataset used in model building to include only detection cycles where we had signal strength values (either recorded or imputed) for all four antennas of the receiving station so that we were modeling the relationship under ideal conditions.

The relationship between bearings and standardized signal strength ratios showed some non-linearity, so we fit three regression models: linear, polynomial, and generalized additive with a cubic spline smoother (all implemented using the gam function from the mgcv package, version 1.8-16: Wood 2011). We used Akaike's Information Criterion (AIC; Akaike 1974) to select the best model of the set because it performs well when the objective is to determine the best model for predictive accuracy (Aho et al. 2014). Following selection of the best model, we compared a second set of models to determine if the best model was improved by the addition of distance from the receiver station and transmitter antenna angle.

The generalized additive model was the top bearing estimation model (Table 1a) and explained 74.2% of the deviance. The quadratic model also had substantial support (< 2 ΔAIC, Arnold 2010), but was not considered further because its behavior near the extremes resulted in a non-monotonic relationship that would be problematic for bearing prediction and was not upheld by visual assessment (Fig. 2). When compared to models that included terms for distance from the receiver station and transmitter antenna angle, the simplest model, with antenna bearing as the only predictor of SSR_s remained the top model (Table 1b). Using the top model, we created a table with predicted SSR_s values at intervals of 1° to use when calculating bearing offsets.

Estimating a bearing based on our model was not possible when one or more of the antennas register a maxed out reading of 255, and when only one antenna or only opposite antennas recorded a hit on a transmitter. When only one antenna was maxed out, we assigned the bearing of that antenna to that observation. If two or more antennas were

Table 1. Akaike's Information Criterion (AIC) comparison of bearing estimation models ($N = 317$ for all models).

	Model	Formula	Effective df	logLik	AIC	ΔAIC	w_i
(A)	GAM	$y \sim s(x)$	5.97	339.9	−666.9	0	0.68
	Quadratic	$y \sim x + x^2 + x^3$	5	337.7	−665.4	1.52	0.32
	Linear	$y \sim x$	3	322.4	−638.8	28.2	0
(B)	GAM	$y \sim s(x)$	5.97	339.4	−666.9	0	0.44
	GAM + angle	$y \sim s(x) + \Theta$	6.98	339.9	−665.8	1.08	0.26
	GAM + distance	$y \sim s(x) + d$	6.96	339.5	−665.1	1.83	0.18
	GAM + distance + angle	$y \sim s(x) + d + \Theta$	7.95	340.2	−664.5	2.46	0.13

(A) The generalized additive model was the top bearing estimation model and explained 74.2% of the deviance. (B) When compared to models that included terms for distance from the receiver station and transmitter antenna angle, the simplest model, with antenna bearing as the only predictor of standardized signal strength ratios (SSR_s), remained the top model.

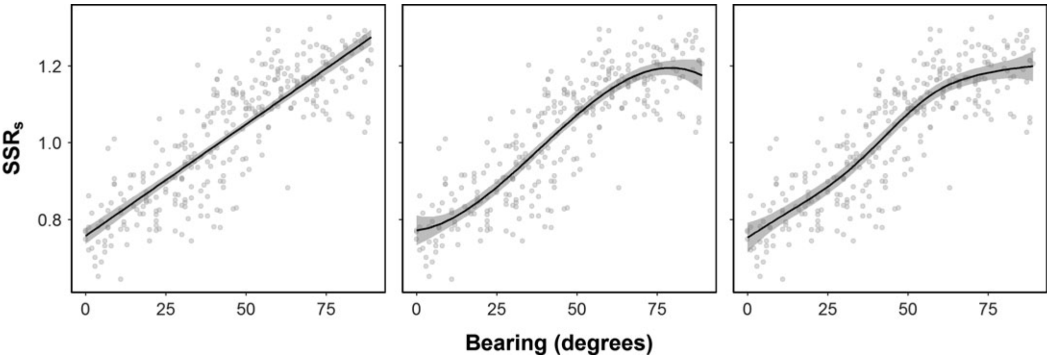

Fig. 2. Comparison of linear (left), quadratic (middle) and generalized additive (right) bearing estimation models. SSRs = standardized signal strength ratio.

maxed out, we classified the observation as "close" to that receiver station and determined the median and maximum distance radii for these observations to be 14 and 171 m, respectively, using test transmitters. Finally, if only one antenna detected the transmitter, we assigned the observation the bearing of that antenna and, if only opposite antennas detected the transmitter, we assigned the observation the bearing of the antenna with the stronger detection.

Once bearings were calculated, we estimated transmitter locations as the point of intersection between bearings from the two receiver stations during simultaneous detection cycles. Intersections were constrained to be within the maximum detection distance (15 km) reported in other studies for similar systems (Taylor et al. 2011, Mitchell et al. 2015). When a single detection cycle resulted in multiple estimated locations, we used the first location if all estimated locations were within 75 m of each other, observations with multiple intersections ≥ 75 m apart were discarded. We chose this cut-off because 75 m fell within the range of mean location error reported in other studies using automated radio-telemetry systems to triangulate (Kays et al. 2011, Ward et al. 2013).

Reference transmitters. To check for variation in the functioning of the receiver stations while collecting data, we set up four reference transmitters in the same position and orientation each time the receiver stations were active. Each transmitter was located 2–3 m above ground on a wooden stake attached to a permanent wooden structure in the landscape (e.g., fencepost or tree). Plots of mean relative signal strength for each antenna-transmitter combination against time were used to identify times when data collected by the receivers were unreliable (e.g., signal interference from weather or noisy machinery). Assessment was based on hourly averages to separate large fluctuations from short-term variations. If multiple reference transmitters showed variable patterns or deviated from the expected pattern given the transmitters location and the orientation of the antennas at the receiver station, we removed those hours of data from the dataset. If only one of the four reference transmitters showed an unusual pattern, we assumed that the antenna with the unusual pattern was being obstructed temporarily (e.g., moving vegetation, bent transmitter antenna, or interruption in line of sight by a vehicle) so we did not censor data in this situation. Based on our criteria, 5 h of data from a total of 307 h (2%) were excluded from analyses.

Known transmitter location tests. To assess the accuracy of locations estimated using the automated system, we performed two tests with transmitters in known locations. One test used stationary transmitters and the other used moving transmitters. For the stationary test, we placed transmitters 0.6–3.4 m above ground at set locations ($N = 82$) within ~2 km of receiver stations. Several locations were visited on multiple days. At each location, the transmitter was turned so that its antenna faced in each cardinal direction for 2 min, resulting in a total of 8 min of data for each location. For the moving transmitter test, we attached two transmitters (antennas oriented at 90° to each other) on wooden stakes to a vehicle. Transmitters were positioned 1.25 m above the vehicle roof. We then drove along roads to a maximum distance of 5.6 km from receiver stations. We recorded the location and speed of the vehicle every 30 s using a handheld GPS (vehicle mean speed = 19 km/h, range = 0–65 km/h). To assess the effect of transmitter antenna angle on the accuracy of location estimates, we combined the data from test transmitters positioned in the same location with different antenna positions to create a "mixed" antenna angle dataset. This was done by randomly selecting which transmitter's received signal strength was assigned to each antenna during each detection cycle. Data from known location tests were also used to estimate the detection range for each receiver station.

Factors affecting location error. We examined several factors expected to influence location error, including: (i) the angle of intersection between bearings, all else being equal, bearings with intersection angles that fall in the range 45–130° have higher accuracy (Springer 1979), (ii) bearings from receivers to transmitter calculated based on data from a single antenna or a pair of antennas, (iii) mean noise, calculated as the average electromagnetic noise recorded by a receiver during a single cycle through all the antennas, and (iv) bearings calculated with recorded versus imputed data. Based on the relationships between each of the factors and location error, we developed and tested a set of filters. We assessed each filter using data from known transmitter location tests to determine the effectiveness of the filter in reducing location error and the corresponding loss of data. We also compared location error between moving and stationary test transmitters, between test transmitters with constant antenna angles versus changing antenna angles, and as a factor of mean distance of the transmitter from the receiver stations.

Field test. We used telemetry data from four Barn Swallows, one Cliff Swallow, and one Eastern Phoebe captured and radio-tagged at the same study site (two different barns) as a test of the system's ability to track rapidly moving birds under field conditions. We used data from individuals of these three species because we were interested in variation in detectability between species of aerial insectivores and had limited interspecific data available. We expected the Cliff Swallow to have higher detectability than the Barn Swallows and Eastern Phoebe because Cliff Swallows have a higher typical foraging height (≥ 50 m, Brown et al. 2017) than Barn Swallows (< 10 m, Brown and Brown 1999) and Eastern Phoebes (< 10 m, Weeks 2011).

We captured birds using mist-nets set up across open barn doors and each bird was fitted with a digitally coded Nano Tag transmitter weighing 0.64 gm, or ~3–4% of body mass. Transmitters were programmed with a 12-h on/off cycle to extend battery life. We attached radio-transmitters to clipped feathers in the interscapular area using ethyl cyanoacrylate adhesive (Gorilla Glue; Gorilla Glue Co., Cincinnati, OH). Before being glued to the clipped feathers, transmitters were first glued to a small piece of black cotton fabric slightly larger than the transmitter to increase the surface area of attachment. We used this "clip and glue" method, similar to that described by Raim (1978) and Johnson et al. (1991), because, using this method, reasonable retention times (≥ 25 d) have been reported for another aerial insectivore (Chimney Swifts, *Chaetura pelagica*; Diemer et al. 2014) and other attachment methods have more often been reported to negatively affect birds (Barron et al. 2010). All birds were banded with United States Geological Survey aluminum leg bands (issued by the Canadian Wildlife Service) and released at the site of capture. We determined when transmitters fell off by examining plots of received signal strength over time that showed transmitters signals recorded by each antenna either stabilizing or disappearing. We also tracked tagged birds using a SRX400 receiver with a handheld 3-element Yagi antenna to ground truth locations estimated using data from the stationary receiver stations. Because swallows often forage in groups and move at high speeds, tracking individual birds to locations and obtaining either visual confirmation or bearings for triangulation was not possible. Instead, we used a method similar to that outlined in Saldanha (2016). An observer stood at one of 82 locations (the same as those used for stationary transmitter tests) spread across the study sites and rotated the handheld Yagi antenna by ~90° every 30 s for 8 min. Tests of detection distance, including with a direct line-of-sight between transmitter and receiver, at the same gain level used for hand-tracking (gain = 50) showed a range of ~350 m (although, in one instance, a transmitter was detected > 450 m away). Based on this, when detected, birds were assigned as present within a 350-m-radius circle centered on each handheld tracking location.

For birds with more than 30 locations after filtering (Seaman et al. 1999), we calculated 95% area corrected autocorrelated kernel density (AKDE_C) home ranges using the R package ctmm (Calabrese et al. 2016). We chose to use an autocorrelated kernel density estimator (AKDE) because relocations of individual birds were sometimes only 1 min apart. This meant that the assumption of independent and identically distributed data required for the more commonly used kernel density estimators (KDEs) (Silverman 1986) was unrealistic for our data. Instead of assuming independence between animal relocations, an AKDE incorporates information on the autocorrelation structure in an animal's movement data (Fleming et al. 2015). This is done by first fitting a movement model to the data, then using this movement model in the calculation of the autocorrelated kernel density estimate (Calabrese et al. 2016). To obtain starting values for the movement model, we used a variogram (semi-variance in position as a function of the time lag between observations). We fit three different movement models: (i) independent and identically distributed (IID), (ii) Ornstein-Uhlenbeck (OU) that incorporates autocorrelation in location, and (iii) Ornstein-Uhlenbeck-F (OUF) that incorporates autocorrelation in both location and velocity (Calabrese et al. 2016). Following Calabrese et al. (2016), we ranked the three movement models based on Akaike's Information Criterion corrected for small sample size (AIC_C; Hurvich and Tsai 1989) and then used the top model to estimate a bird's partial home range and utilization distribution (UDs).

We used a resource utilization function (RUF) to determine if use of a location was related to the proximity of a bird's nest site (i.e., the barn where a bird was captured). A bird's relative use of space across their home range was calculated using their UD (Marzluff et al. 2004, Kertson and Marzluff 2011) clipped to remove areas outside the detection zone of the automated telemetry system. We sampled 2000 random locations from the bird's clipped UD and assigned each location a value between 0 (low use) and 1 (high use) based on the height of the bird's UD at that location. We modeled relative use as a function of distance to nest using beta-regression with a logit link (Ferrari and Cribari-Neto 2004), and implemented with the betareg package in R (Cribari-Neto and Zeileis 2010). We checked for evidence of a non-linear relationship between relative use and distance to nest and included a squared term if the relationship was non-linear.

Our response variable of relative use was spatially autocorrelated because it was derived from the bird's UD. It therefore violated the independence assumption of regression analysis causing an increase in the probability of a Type 1 error (Legendre et al. 2002). To account for this, we used Moran's I correlograms to examine the spatial autocorrelation in the residuals of each bird's model and determine the approximate distance over which the autocorrelation occurred. For this distance, we calculated an inverse distance weighted residual autocovariate (RAC; Crase et al. 2012) with the function autocov_dist from the R package spdep, using symmetric weights (Bivand et al. 2013, Bardos et al. 2015, Bivand and Piras 2015). We evaluated model fit using the pseudo R^2 measure defined by Ferrari and Cribari-Neto (2004). All data processing and analysis was done in R (version 3.3.3, R Development Core Team 2016).

RESULTS

Known location transmitter tests. Bearings calculated for known location transmitter tests had similar mean errors (−2.5 to 4.9°) across tests, but were generally higher for mixed versus fixed antenna angle tests (Table 2). For triangulated locations, median error ranged from 178 to 809 m before filtering, with greater error associated with both moving and mixed antenna angle tests (Table 2).

Location error increased with transmitter speed, but was similar up to 30 km/h with most error values in the 0–1000 m range (Fig. 3). As expected, bearing pairs with small

Table 2. Mean bearing and median location error for tests with transmitters at known locations.

Test	Multiple antennas	Bearing error ± SD (°)	Location error (m)
Stationary–fixed angle	No	0.2 ± 21.4	383
	Yes	−2.5 ± 13.3	178
Stationary–mixed angle	No	3.3 ± 22.3	518
	Yes	0.7 ± 21.5	NA
Moving–fixed angle	No	2.1 ± 21.0	809
	Yes	2.2 ± 21.6	292
Moving–mixed angle	No	−1.5 ± 21.2	702
	Yes	4.9 ± 18.3	NA

Results shown separately for stationary and moving transmitters with fixed and mixed antenna angles, and for bearings calculated using information either from multiple antennas or a single antenna. Location error only includes cases where locations were triangulated.

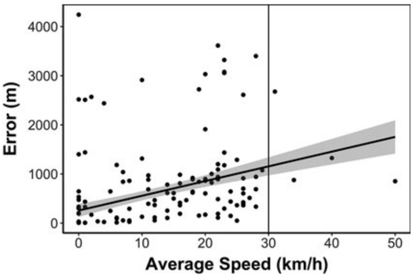

Fig. 3. Relationship between transmitter movement rate and location error based on test locations.

intersect angles (< 45°) resulted in locations with large errors, but bearing pairs with large intersect angles (> 135°) did not result in a corresponding increase in location error (Fig. 4). Locations estimated with at least one bearing calculated using data from only a single antenna had higher location error than those with bearings estimated using data from multiple antennas (Fig. 4). Location error also increased with the mean distance of test locations from receiver stations (Fig. 4). We found no clear relationship between location error and the other variables tested, i.e., mean noise and bearings calculated using recorded versus imputed values. Two filters were equal in their lowest median and maximum location error, and we chose the more conservative combination filter that removed all locations estimated with bearings calculated using data from only a single antenna and any observations with intersection angles < 45° (Table 3). The maximum distance of detection of test transmitters varied from 2.5 to 3.6 km across receiver-station locations (Table 4). However, maximum detection distance was not positively related to gain level (Table 4).

Field test. Our automated telemetry receivers recorded 17,634 detections of the six radio-tagged birds. The Cliff Swallow had the highest detection rate followed by the Eastern Phoebe and the Barn Swallows (Table 5). Due to missed detections and bearings that did not intersect, few handheld tracking detections coincided in time with locations derived from the automated telemetry system so direct

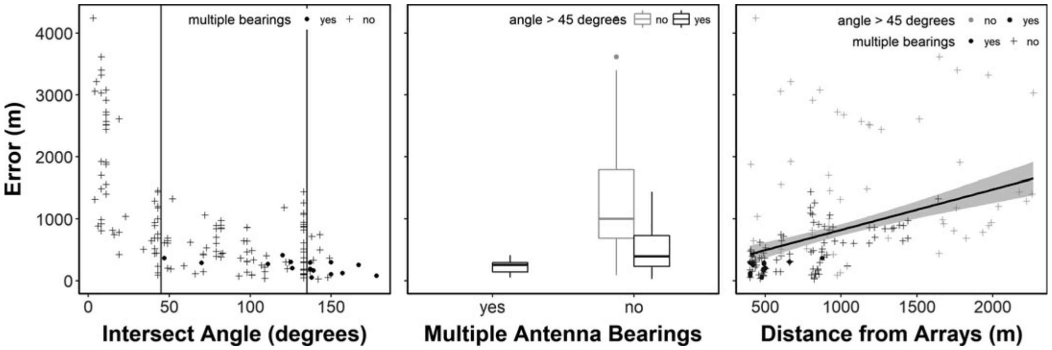

Fig. 4. Additional factors affecting location error, including angle of bearing intersect (left), single or multiple antennas used to calculate bearings (middle), and mean distance from test locations to receiver stations (right).

Table 3. Comparison of location filters based on two factors affecting error: angle of bearing intersect, and information from multiple antennas used to calculate bearings.

Filter	Median (m)	Range (m)	*N*
None	604	27–4243	229
F1[a]	368	27–1440	146
F2[b]	254	50–414	15
F3[c]	254	50–414	15

[a] F1 – all observations with bearing intersect angles < 45° removed.

[b] F2 – all observations with one or more bearings calculated based on information from only one antenna removed.

[c] F3 – both F1 and F2 applied.

Table 4. Maximum detection distance for each receiver station based on the furthest point a transmitter was detected during known location tests.

Receiver station	Distance (m)	Receiver gain
Site 1 - A	3339	60
Site 2 - A	2459	80
Site 3 - A	3609	75
Site 1 - B	3380	65
Site 2 - B	3268	80
Site 3 - B	3415	65

All test transmitters were located from 0.6 to 3.4 m above ground and within 5.6 km of receiver stations.

comparison was only possible for two location estimates. In these two cases, handheld detection zones and automated telemetry system error buffers did not overlap and were separated by 47 and 230 m (Fig. 5). All but two locations where birds were detected during hand-tracking were within the same area as automated telemetry-derived locations (Fig. 6). Filtering removed an average of 89% of bird location estimates, leaving only one bird (a Cliff Swallow) with enough locations for analysis of space use (Table 5). Consistent with our prediction, the Cliff Swallow showed decreasing relative use with increasing distance from its nest site (distance to nest: $\beta = 1.6 \times 10^{-3}$, SE = 2.6×10^{-4}, [distance to nest]^2: $\beta = -9.3 \times 10^{-6}$, SE = 3.3×10^{-7}, Pseudo $R^2 = 0.90$; Fig. 7).

DISCUSSION

We found that a minimal automated radio-telemetry system, consisting of only two receiver stations, can be used to collect data on space use by aerial insectivores with an accuracy similar to manual radio-telemetry. After removing unreliable location estimates, median location error for our system was 250 m (range = 50–414 m), within the range reported for manual telemetry when locations are triangulated (White and Garrott 1990, Marzluff et al. 1994, Zimmerman and Powell 1995, Kauhala and Tiilikainen 2002) and similar to that reported when using manual telemetry to track aerial insectivores (Saldanha 2016). Although this low level of location accuracy limits any conclusions concerning habitat use, especially when habitat patches are small and single location estimates are important (Montgomery et al. 2010, 2011), the ability of automated telemetry systems to collect hundreds of location estimates of an

Table 5. Total number of days each radio-tagged bird was detected by a receiver station at least once (tracking days), mean detection ratio (number of antenna cycles where bird was detected per day/total number of antenna cycles per day), and number of locations estimated before and after data filtering.

Tag ID	Species[a]	Tracking days	Detection ratio ± SE	Number of locations before filtering	Number of locations after filtering
134	CLSW	6	0.73 ± 0.02	1333	354
164	EAPH	3	0.62 ± 0.04	1217	11
142	BARS	3	0.47 ± 0.03	558	20
144	BARS	4	0.38 ± 0.09	159	11
158	BARS	2	0.35 ± 0.11	119	11
159	BARS	1	0.41 ± 0.12	106	18

[a] BARS, Barn Swallow; CLSW, Cliff Swallow; EAPH, Eastern Phoebe.

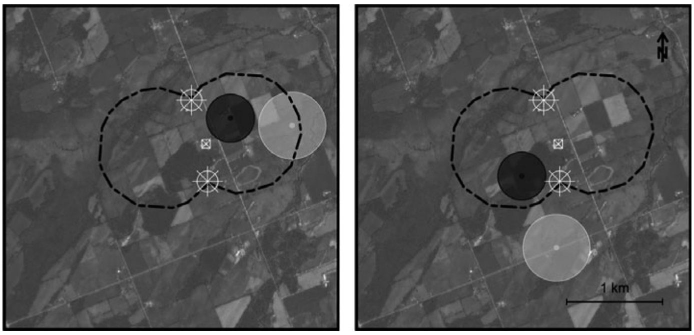

Fig. 5. Comparison between locations of a Cliff Swallow estimated during the same minute using both the automated telemetry system (black points with median error buffer) and handheld tracking (white points with detection range). Dashed black line shows effective coverage of the automated telemetry system based on telemetry filtering constraints. Locations of the barns (white squares) and receiver stations (white pinwheels) are also shown.

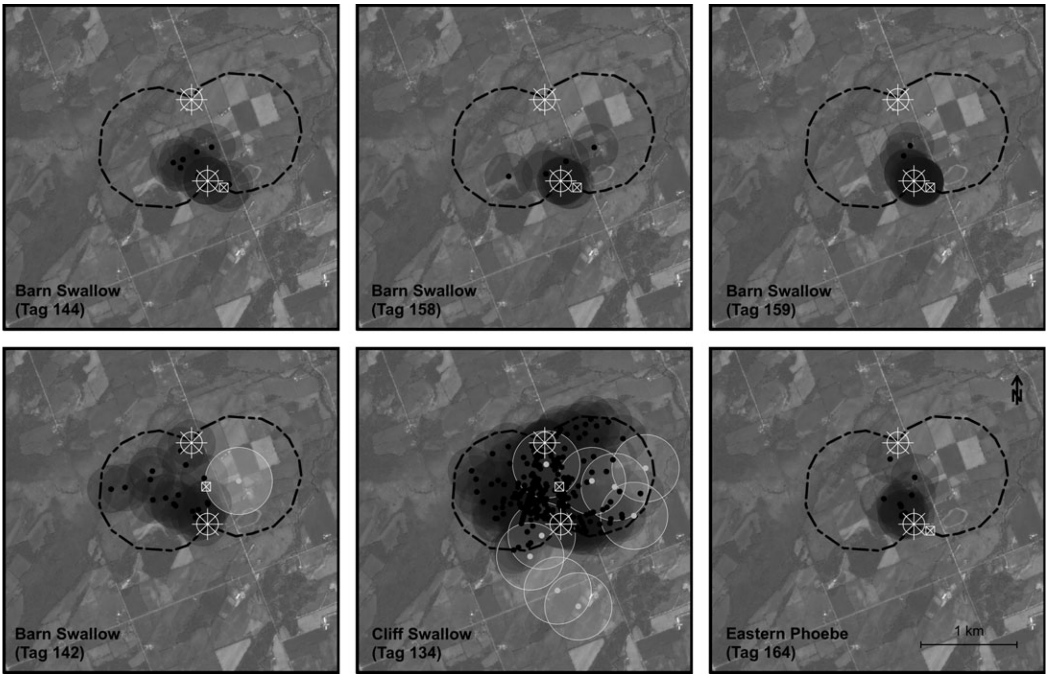

Fig. 6. Filtered bird locations estimated using the automated telemetry system (black points with median error buffers) and handheld telemetry detections (white points with detection range). Dashed black line shows effective coverage of the automated telemetry system based on telemetry filtering constraints. Locations of barns are shown as white squares and receiver stations as white pinwheels.

individual makes it possible to estimate the location of home ranges and high-use areas in the landscape even when error associated with single locations is relatively large (e.g., Fig. 7).

To improve both location accuracy and increase the percentage of usable location estimates collected, we suggest that, in future studies, investigators incorporate one or more modifications of our system. First, we

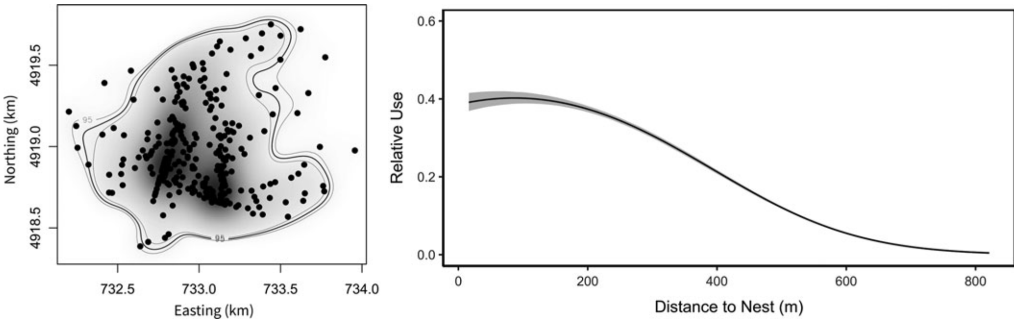

Fig. 7. Autocorrelated kernel density home range of a Cliff Swallow built using data collected by an automated radio-telemetry system consisting of two receiver stations (left). The relationship between predicted relative use and distance to nest site for the same Cliff Swallow. Gray shading indicates 95% confidence interval (right).

recommend use of receivers that simultaneously record signals detected by all antennas (e.g., Sensorgnome receivers; Taylor et al. 2017). This would eliminate error introduced by movement of birds while data for a location fix are being obtained (Schmutz and White 1990). Simultaneous detections would also reduce the error introduced when transmitter angles change during a single fix. Alternatively, increasing transmitter pulse rates would increase the probability of simultaneous detection of signals at multiple receiver stations and reduce error due to bird movement and changes in transmitter angle. However, increasing pulse rate also decreases transmitter battery life, so researchers need to consider the goals of their study and the trade-off between data resolution and total tracking time.

We also recommend, if possible, use of a minimum of three receiver stations, acknowledging that the addition of receiver stations is expensive and may be limited by restricted access to sites. Accuracy of triangulated locations increases with the number of azimuths used to estimate them (White and Garrott 1990), and investigators using fixed automated radio-telemetry systems have used more than two receiver stations to estimate locations (Kays et al. 2011, Ward et al. 2013, 2014, Celis-Murillo et al. 2017). This partly explains why our location error was greater (a few hundred meters) than reported in previous studies (< 100 m; Kays et al. 2011, Ward et al. 2013).

Finally, we recommend increasing the number of antennas at each receiver station. Although increasing the cost of the system, this should result in more accurate calculation of bearings because the angular distance covered by each pair would be reduced. Consistent with this, other studies where six antennas per receiver station were used instead of four have reported smaller bearing errors than in our study (Larkin et al. 1996, Kays et al. 2011, Ward et al. 2013). Another important consideration is the number of elements per antenna, antennas with fewer elements have a shorter detection distance, but wider detection pattern (Kenward 2001), therefore requiring fewer antennas to avoid gaps in coverage. Unlike previous studies, background noise did not affect the accuracy of our location estimates, likely because signals from coded transmitters used in our study are more easily distinguished from background noise than those of beeper transmitters (Lotek Wireless personnel, pers. comm.).

We found that location error increased with transmitter speed for known location tests. This is expected because, as the speed of a transmitter increases, the distance it moves during the time required to obtain a fix also increases (Schmutz and White 1990). We were unable to directly separate out error due to the distance the transmitter moved from error due to the telemetry system. However, our tests indicated that the increase in location error with speed was small for speeds up to 30 km/h. This suggests that the low resolution of the system accounted for most of the location error when transmitters were moving at speeds of < 30 km/h.

We found no increase in error for locations estimated from bearings with wide intersect angles (> 135°), a result likely explained by the location of our receiver stations. Triangulated locations with wide intersect angles are expected to be associated with large errors because, when the angle of intersection is wide, slight variation in bearing estimates results in large changes in where the bearing lines cross (Springer 1979). In our setup, this was counterbalanced by the shorter distances between receivers and transmitters in the areas were large intersect angles occurred, i.e., near the line directly between the two receiver stations.

Although handheld telemetry detections overlapped automated telemetry location estimates in most cases, some did not overlap or were in less used areas based on our automated radio-telemetry system. One possible explanation for this is that, at the time of those detections, the bird was flying low and the transmitter signal did not reach one or both of the receiver stations because of topographic barriers (Etherington and Alexander 2008). Another is that the bird was only briefly present and had moved by the time it was detected by the automated system. The two instances where we detected a bird while hand-tracking and had estimated locations from the automated system for the same time point showed close, but non-overlapping, error buffers and detection radii, consistent with movement during the minute required to obtain a fix. In at least a few cases, these discrepancies are explained by the location of the handheld detection falling outside the area covered by the automated radio-telemetry system based on filtering restrictions.

Detection ratios varied, with the Cliff Swallow having a higher detection ratio than the Barn Swallows and Eastern Phoebe. The relatively high detection ratio for the Cliff Swallow is consistent with their high foraging height (≥ 50 m, Brown et al. 2017) compared to Barn Swallows (< 10 m, Brown and Brown 1999) and Eastern Phoebes (< 10 m, Weeks 2011) which would reduce the chance of missed detections due to interference from topographic barriers (Etherington and Alexander 2008).

Automated radio-telemetry systems have several advantages over conventional radio telemetry including the need for fewer field technicians, more frequent recording of locations, and reduced risk of affecting the behavior of animals being tracked (White and Garrott 1990, Larkin et al. 1996, Kays et al. 2011, Ward et al. 2013). Use of these system is constrained by the cost associated with establishing and maintaining an automated telemetry array network (Ward et al. 2013) and obtaining permission from land owners to place receiver stations in appropriate locations. Our results suggest that a minimal automated telemetry system can be used successfully to study local space use of aerial insectivores. However, researchers planning to use such systems need to carefully consider the advantages and disadvantages of the design and components of such systems because they can have large effects on the quantity and accuracy of the data collected.

ACKNOWLEDGMENTS

We thank the many landowners that allowed us access to their properties for capturing birds, manual radio-tracking, and system calibration. An extended thanks to those landowners who let us set up automated radio-telemetry receiver stations. Research was funded by the Ontario Ministry of Natural Resources and Forestry. Support was provided by an Ontario Graduate Scholarship (OGS) to AKL, and the Natural Sciences and Engineering Research Council of Canada (NSERC) through a Canada Graduate Scholarship to AKL and a Discovery Grant to JJN. Procedures for trapping birds and attaching radio-transmitters were approved by Trent University's Animal Care Committee. We would also like to thank E. Nol, J. Schaefer, B. Pond, W. Burr, and G. Mitchell for valuable advice during project conception and data analysis, and B. McClenaghan, V. Von Zuben, R. Marrotte, A. Anderson, D. Chronowic, and S. Bossuyt for assistance in the field.

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