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Evaluation of Automated Radio Telemetry for Quantifying Movements and Home Ranges of Snakes

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ABSTRACT.—We evaluated an automated telemetry system that can dramatically increase the amount of activity and spatial data collected for snakes. We developed methods for analyzing data from single automated receiving units (ARUs) and ARU arrays, compared results from ARUs with conventional hand tracking, and assessed previously untested assumptions used in conventional telemetry, using data from ratsnakes (*Pantherophis* spp.) in Texas and Illinois. ARU data indicated that ratsnakes spent most of their time in small home ranges (mean = 25 ha) but engaged in forays of up to 1.5 km from their core-use areas, suggesting this species may engage in central place foraging. Forays inflated home-range sizes greatly if areas were estimated using minimum convex polygons rather than 95% kernels. Large numbers of locations generated by ARUs produce more reliable home-range estimates than those from hand tracking. ARU data indicated that snakes moved in response to observers during hand tracking. Daily hand tracking produced reliable estimates of distances moved but underestimated distances by a factor of 4 when snakes were tracked every 5 days. Drawbacks of ARUs are that the error associated with individual locations exceeds that for hand-tracked locations and that the costs exceed those for hand tracking. Automated receivers can increase data greatly from radio-tracked snakes, providing novel insights unavailable from conventional hand tracking. There are drawbacks to this technology, some of which will vary among study species; therefore, researchers should evaluate the appropriateness of the technology for both the study species and the questions being asked.

Since wildlife telemetry was introduced more than 50 years ago (Adams, 1965; Cochran et al., 1965), it has proven valuable for studying animals such as snakes that are often difficult to observe in the wild (Fitch, 1987; Dorcas and Wilson, 2009). Although automation has allowed data collection to increase by orders of magnitude when telemetry is used to quantify body temperatures of snakes (e.g., Brown and Weatherhead, 2000), the methods associated with the core application of using telemetry to document the locations and movements of snakes in the wild have changed little over 50 years. Here, we present results of field tests of an automated telemetry system that has the potential to change that status quo.

Whether the goal is to determine a snake's habitat preference, frequency of movement, distance moved, or home range, the key requirement, and principle application of radiotelemetry, is to determine the snake's location. The conventional approach for doing so is to use a hand-held receiver to follow the gradient in signal strength to the snake. The logistics of tracking multiple snakes means that individual snakes are often located over intervals ranging from daily to weekly. Interpretation of the resulting data then requires incorporating several untested assumptions: for example, a snake in the same place on successive tracking episodes has not moved; a snake in a new location moved there in a straight line from its previously documented location. In addition to automated telemetry's potential for greatly increasing the number of snakes that can be tracked simultaneously and the detail of the data collected on each, the method also allows us to test these assumptions and determine the reliability of results obtained using conventional tracking methods.

Incorporation of global positioning systems into radio transmitters has allowed automated tracking of a variety of animals (Rodgers, 2001; Cagnacci et al., 2010), but the majority of snakes are too small to carry this type of transmitter (Dorcas and Wilson, 2009). The automated system tested here uses

conventional transmitters and, thus, should be suitable for any snakes large enough to be tracked using conventional methods. This system uses multiple directional antennas for each receiver and relies on differences in signal strength to detect movement and to estimate an animal's location. Although the basic principles on which the system works were established early in the history of radiotelemetry (Cochran et al., 1965), the first applications of this method have only recently emerged (Kays et al., 2011; Ward and Raim, 2011). It is unclear why it has taken so long to implement this technology, although the lack of low-cost methods for storing and analyzing the extensive data generated by an automated telemetry system no doubt contributed.

Our general goal is to assess the efficacy of automated telemetry for tracking snakes, which includes providing the first detailed explanation of the methods required for processing and analyzing the data generated by automated receivers. Although we developed and present these methods in the context of studying snakes, the general principles and approaches are applicable to data collected from any animal tracked using automated telemetry. We also address several specific questions. First, how do estimates of home-range size and distance moved compare between automated and conventional telemetry, and how much are those differences affected by the frequency with which a snake is tracked using conventional methods? Second, how frequently do snakes leave their core-use areas, and how often would hand tracking need to be conducted to detect these forays? Third, there is evidence from radiotelemetry that human activity affects snake behavior (Parent and Weatherhead, 2000), but to what extent does the activity associated with tracking snakes affect snakes (Weatherhead and Madsen, 2009)? Therefore, using automated telemetry, we investigated whether conventional tracking causes snakes to alter their behavior in response to an observer (i.e., the person hand tracking).

MATERIALS AND METHODS

Study Areas, Species, and Transmitters.—Research was conducted on ratsnakes (formerly *Elaphe obsoleta*, currently *Pantherophis*

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spp.) at Fort Hood, a military installation in central Texas, and at Kennekuk County Park in central Illinois. At both sites, ratsnakes were initially captured opportunistically. Some snakes in Illinois were subsequently captured during emergence from communal hibernacula that we located by tracking the snakes captured initially. Radio transmitters (Model SI-2T, Holohil Systems, Inc., Ontario, Canada) were surgically implanted in snakes (Weatherhead and Blouin-Demers, 2004) by veterinarians, in compliance with the University of Illinois' Animal Care and Use Committee. Transmitters were implanted only in snakes for which transmitters weighed less than 3% of snake body mass. In addition to automated telemetry, we used conventional methods to track snake movements, employing hand-held receivers (Model R-1000, Communication Specialists, Inc., Orange, CA) to locate individual snakes every 48 h. In Texas, the person hand tracking the snakes attempted to confirm the snake's location visually. In Illinois, observers often estimated a snake's location without visual detection. Snakes in Illinois were hand tracked every 48 h in 2010 and every 5–7 days in 2011.

In Texas we used a single automated receiving unit (ARU; JDJC Corp., Fisher, IL). The ARU was designed to be portable so that we could relocate it as necessary to have several snakes within range. In Illinois, we used an array of six ARUs. Each of these ARUs remained in the same location throughout the study, and we relied on snakes spending time within range of at least some of the ARUs in the array to document their movements.

Automated Receiving Units (ARUs).—Each ARU was connected to an array of six, three-element Yagi antennas attached to the top of a tower. We used guyed television antenna towers that ranged in height from 3 m in Texas to 15–20 m in Illinois. The azimuths of the six antennas were spaced by 60° to give 360° coverage. Each ARU was programmed to tune at intervals of 3–5 min to the radio frequency of each transmitter implanted in a snake and record the signal strengths (in dBm) from the six antennas. The search interval is programmed using custom software (provided by the manufacturer) as a text file on a standard secure digital (SD) card. An ARU can store two gigabytes of data on its SD card. We collected data from an ARU on average every seven days by replacing the SD card and downloading data onto desktop computers. Power for each ARU was provided by a 12-volt deep cycle marine battery. A newly charged battery allowed up to 70 days of operation.

Determining Activity Using a Single ARU.—In principle, detecting a snake's activity using a single ARU involves detecting changes in the bearing from the ARU to the radio-tagged snake and the amount of energy received by the ARU from the radio transmitter (signal strength). Most movements result in simultaneous changes in both signal strength and bearing. In practice, however, several other factors must be considered. First, ARUs can sometimes detect signals from other transmissions in the area, resulting in spurious records. This requires establishing criteria for identifying a spurious record and filters to eliminate those records. The approaches used to implement these filters and estimate the bearing from the ARU are provided in Appendix 1.

"Postural" changes by a snake (e.g., coiling or uncoiling) that alter the orientation of the transmitter antenna relative to the ARU antennas can also change signal strength without the snake having changed location. Resolving this problem requires determining thresholds for changes in signal strength associated with postural changes. To determine these thresholds we conducted field tests using both a simulated and a live snake

with transmitters. The simulated snake was a plastic tube, similar in diameter to a ratsnake, filled with water and containing a transmitter. The real snake was one of the subjects used in our field study that we tested prior to releasing it after its transmitter was implanted. We placed the simulated snake at five different locations and used an ARU to record 15–32 signals at each location, during which time we coiled and uncoiled the model and modified its orientation (parallel vs. perpendicular) to the ARU antenna. We put the live snake in a plastic container that we placed in three locations and used an ARU to record 5068 signals from each location. We allowed the live snake to alter its posture on its own. Although the direction of both the simulated and real snake from the ARU remained constant at each of their respective locations, there was a small amount of variation in the estimated directions (simulated snake: SD = 1.79°; live snake: SD = 1.09°). In contrast, there was substantially more variation in signal strength (simulated snake: SD = 7.08dBm; live snake: SD = 3.66dBm). The greater variation in signal strength for the simulated snake is attributable to us actively modifying its posture and orientation, unlike the live snake, which appeared to alter its posture very little. Given these results, we assumed that a change in bearing of less than 2° and a change in signal strength of less than 8dBm did not constitute a movement.

After applying the filters (Appendix 1) and thresholds described above, we added a final constraint on the data for determining movements. We considered a snake to have moved only if both the bearing and signal strength changed simultaneously. Although this restriction would fail to detect movements where the snake moved directly toward or away from the ARU, or followed a circular path around the ARU maintaining a constant distance, we considered these types of movements to be rare and probably covering only short distances. When changes in bearing and signal strength changed over the course of successive recording periods, we considered them to be a single movement. Thus, not all movements were of the same duration.

Tracking Movements and Determining Home Ranges with an ARU Array.—The general principle for locating a snake using an ARU array is to determine a bearing from each of the ARUs and estimate the location based on the intersection of those bearings. The term Automated Radio Telemetry Systems (ARTS) has been used to describe the use of multiple ARUs to estimate the location of a radio-tagged animal (Crofoot et al., 2010; Kays et al., 2011). Bearings were estimated independently for each ARU using the same equation used for monitoring activity with a single ARU, incorporating the same data filters and constraints (Appendix 1). We then determined the X- and Y-coordinates for the intersection of the bearings from all pairwise combinations of ARUs that had produced a bearing for a given signal. Finally, we used the median X- and Y-values from all the pairwise coordinates to estimate the snake's location. There are several alternatives for how the final coordinates could be estimated from the pairwise values (e.g., mean X and Y, centroid of an error ellipse). We adopted the median X- and Y-values based on field trials with a test transmitter that indicated this was the most accurate estimator.

For any given location determined using the ARUs, it is possible to estimate how accurately the estimated location matches the true location. The spatial accuracy of the system is affected by many factors, including the strength of the transmitter, orientation of the transmitter's antenna to the ARU antennas, the density of vegetation or other structures

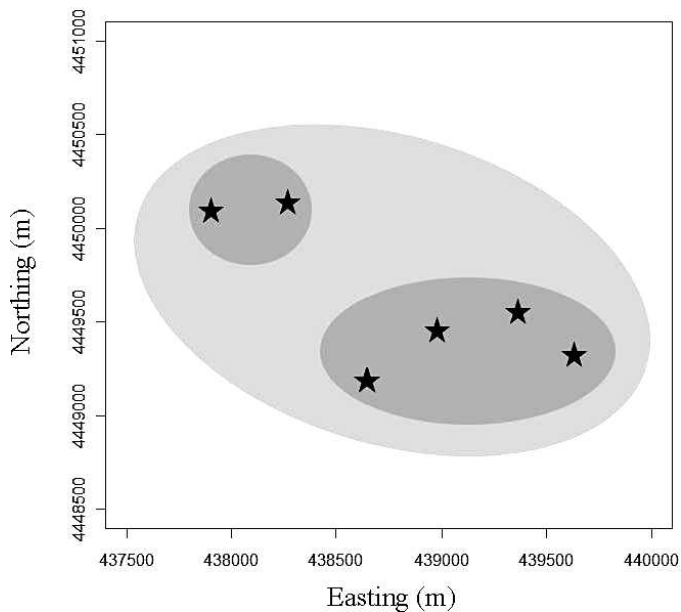


Fig. 1. The study site in east-central Illinois. Stars represent the ARU towers. The darker gray is the core area where spatial resolution averaged 28.6 m. The lighter gray is the area with an average accuracy of 77.1 m. The white portion of this 625-ha area represents the area where we can potentially detect a snake, although at the maximum distances the snake would probably have to be in the top of a tree. Spatial accuracy within the study area was highly variable with an average of 142.9 m.

between the transmitter and the ARU, and the height of the transmitter above the ground. Spatial resolution can be improved by positioning the ARUs closer to one another, but that reduces the area over which animals can be tracked. We conducted a simple field test to determine the accuracy of our estimates of a transmitter's location. We selected 20 locations randomly in the core of our study area and 10 locations in an area buffering the core area (light gray area in Fig. 1) and the area outside the core and secondary areas (white area in Fig. 1). At each location, 8–12 recordings were taken with the test transmitter's antenna being pointed in the four cardinal directions for 2–3 recordings. In the core area of the array, the average accuracy was 28.6 m $SD \pm 12.6$ m (mean difference between a GPS location and where the system estimated the locations). The GPS used in this study had an accuracy of less than 3 m. In the secondary area (the lighter gray in Fig. 1), the accuracy was 77.1 m $SD \pm 18.9$ m. Once outside the secondary area, the accuracy of locations decreased to 142.9 m $SD \pm 52.7$ m.

Statistically defining a home range can be difficult (e.g., Powell, 2000; Fieberg and Kochanny, 2005; Row and Blouin-Demers, 2006). Traditionally researchers have used minimum convex polygons (MCP), the smallest convex polygon that encompasses all the recorded locations. More recently, kernel estimators have been used to produce a distribution of how the radio-tagged animal uses its home range, in essence estimating the likelihood of finding the animal at a specific location. In the context of conventional radiotelemetry, both of these approaches have limitations. MCPs generally overestimate the size of home ranges by including space not actually used by the animal (Powell, 2000). When using kernels, the most difficult aspect is choosing a smoothing parameter (Worton, 1989). A smoothing parameter that is too low includes only areas around points where the animal was located, whereas if the smoothing value is

too high, area not used by the animal will be included. Small changes in the smoothing parameter can result in large changes in the home-range estimate (Worton, 1995).

To estimate home ranges from ARU data, we primarily used kernel estimators, although we did calculate MCP home ranges so we could compare the two approaches. We used the *adehabitat* package in R (Calenge, 2006) to produce home-range kernel estimates and MCP home-range estimates from ARU data. Least-squares cross-validation (LSCV), the most common approach for choosing a smoothing parameter, performs poorly with spatially autocorrelated data (Swihart and Slade, 1985; Worton, 1987). Because ARU data are collected so frequently relative to how often snakes move, those data will be sufficiently spatially autocorrelated that an LSCV approach is unlikely to be able to estimate a smoothing parameter. Using R, we estimated the smoothing parameter for both the X- and Y-coordinates (Fieberg and Kochanny, 2005) using the “plug-in” estimator (Sheather and Jones, 1991) and then averaged the two to produce a smoothing parameter to estimate home ranges.

We used two approaches to compare home ranges estimated using the ARU array with those estimated from conventional tracking. First, we used the ARU and hand tracking (every 48 h) data from Illinois from 2010. Second, to assess the effect of using different frequencies of hand tracking, we used ARU data to simulate tracking snakes on a 24-h, 48-h, and 5-day cycle. To simulate hand tracking, we arbitrarily assumed a snake would be located at 1000 h each day and selected the ARU-estimated location closest to 1000 h for each designated tracking date. Using simulated hand tracking is imperfect but does allow us to assess the effect of tracking frequency on home-range estimates.

To evaluate the relative accuracy of hand tracking for determining movement distances, we focused on forays outside a snake's core home range. We focused on forays for two reasons. First, the error associated with estimating snake locations using ARUs results in snakes appearing to be constantly moving small distances within their core home range (Fig. 2B), even though the snakes are probably stationary most of the time. Second, core home ranges are small enough that any true movements within the core are short and contribute little to total distances moved. We defined a snake's core home range as the 95% kernel estimated from all recorded locations for that individual. Forays were defined as movements that were at least 77.1 m outside the 95% kernel home range. We based this threshold on the average error of location estimates in the secondary area of the array (Fig. 1) because most home ranges included at least some of that area. By using this conservative definition of forays, we were certain that all movements analyzed involved substantial trips away from an individual's core home range. For each foray, we estimated the distance moved and the time elapsed between departure from and return to the core home range. We then determined the relationship between our estimates of total foray distances moved with estimates based on simulated hand tracking at various time intervals, again using the snake's location closest to 1000 h for each designated tracking date.

RESULTS

Determining Activity Using a Single ARU.—From 2006 to 2008, we obtained data from 22 snakes (6 in 2006, 15 in 2007, 1 in 2008) at Fort Hood, Texas, using a single ARU. The initial data consisted of 284,547 records, which our filters reduced to 141,145 (50%) records, primarily because of high noise or weak signals. A

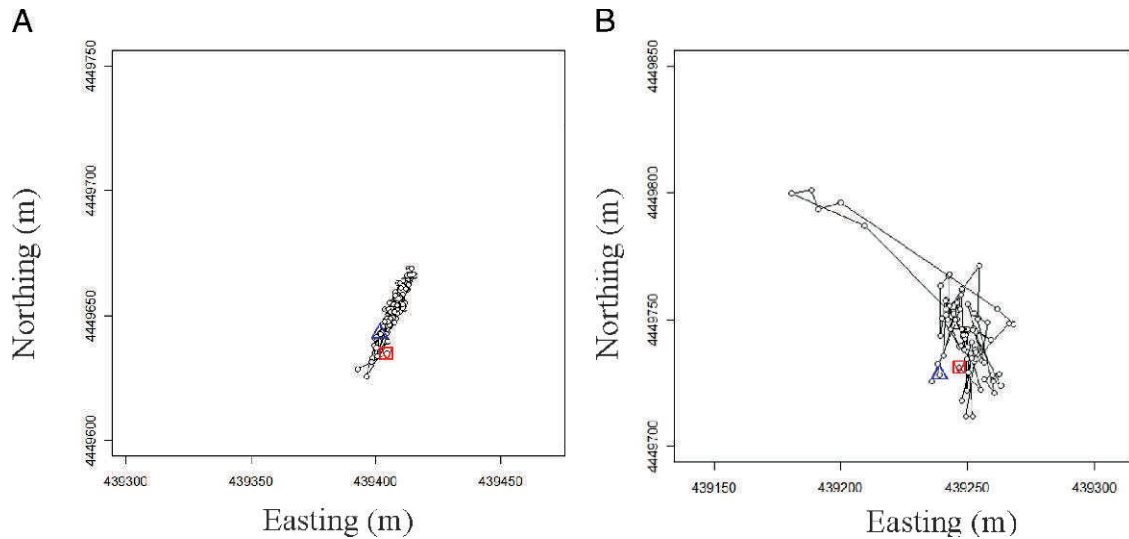


FIG. 2. (A) Locations for snake 164.305 on the afternoon/evening of 14 June 2011, illustrating variation largely resulting from error rather than from actual movements. (B) Locations for the same snake from the afternoon of 30 June 2011, illustrating some movement within the core home range and a foray away from and back to the core. Boxes represent the first location, and triangles represent the last location recorded for the snake over the given time frame. The X- and Y-axis are the Universal Transverse Mercator (UTM) coordinates (Northing, Easting).

typical 24-h record for a snake consisted primarily of long periods of low-level variation in signal strength and bearing, indicating the snake was stationary, with occasional pronounced changes in both signal strength and bearing, indicating that the snake was moving (Fig. 3). We detected a total of 3,908 movements. Hand tracking indicated that the ARU-derived index of activity was reliable. Of the 44 times the ARU data indicated that a snake had not moved in the interval between successive tracking days, hand tracking confirmed that the snake was at its previous location on every occasion. Of the 1,194 occasions that hand

tracking documented a move, the ARU data almost always indicated the snake had moved (99% agreement). The few cases of disagreement involved either short movements (6–15 m) or, in two cases, longer movements by snakes that were on the edge of the area covered by the ARU. Despite this broad agreement between the ARU and hand tracking, in 105 instances where hand tracking indicated that a snake had not moved, there were 61 cases where the ARU documented a move. These cases could indicate an error in the ARU data, or that the snakes moved, but returned to their previous location during the interval between

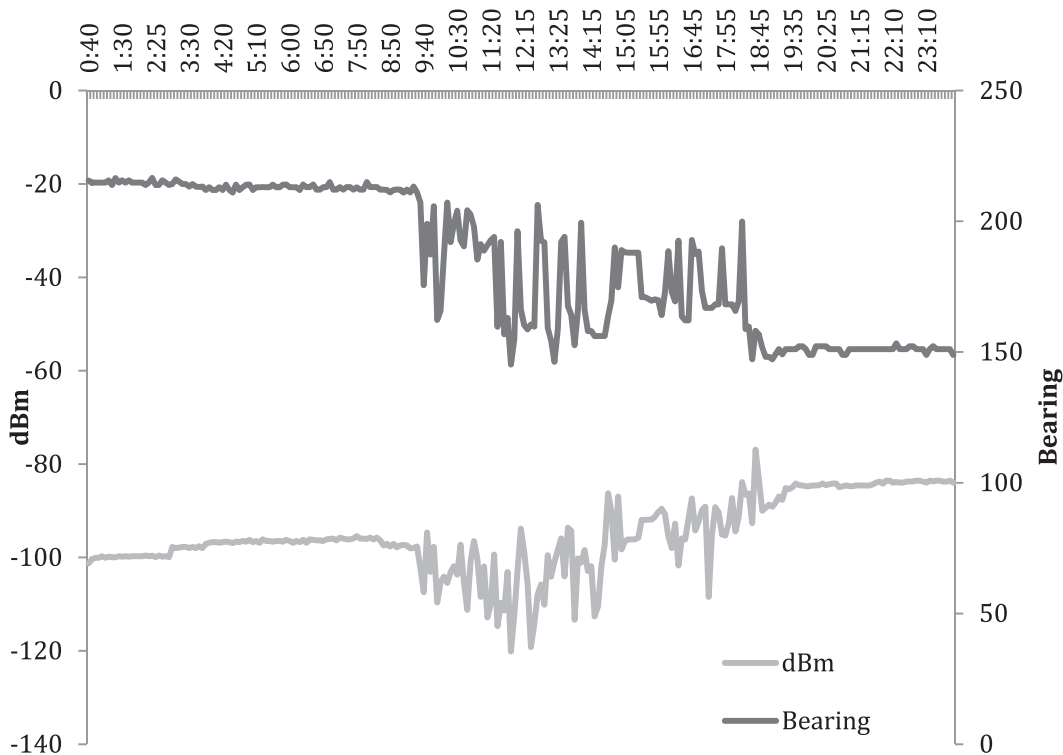


FIG. 3. Typical data associated with the activity of a snake illustrating how movement involves the simultaneous change in both signal strength and bearing. In this case, snake 172.099 moved 13 times between 0940 h and 1845 h on 29 May 2006.

TABLE 1. The 95% kernel home ranges estimated from all ARU data, conventional hand tracking, simulated hand tracking (24-h, 48-h, and 5-day), and minimum convex polygon (MCP) home ranges estimated from all ARU data. All areas are in hectares.

Snake	95% kernel ARU (n)	MCP (n)	95% Hand Track (n)	95% ARU 24hr	95% ARU 48hr	95% ARU 5 days
305 (2010)	48.3 (7,230)	435.3 (7,230)	107.2 (24)	110.5 (67)	92.3 (34)	217.4 (14)
305 (2011)	27.1 (15,036)	157.2 (15,036)	—	57.3 (63)	122.5 (22)	267.7 (14)
660 (2010)	24.3 (5,857)	145.3 (5,857)	78.5 (23)	100.1 (53)	93.8 (29)	64.9 (14)
660 (2011)	22.8 (8,285)	121.1 (8,285)	—	131.1 (40)	317.2 (20)	489.3 (13)
880 (2010)	11.3 (14,495)	63.4 (14,495)	24.0 (24)	31.4 (56)	38.5 (28)	40.6 (14)
880 (2011)	14.7 (735)	109.4 (735)	—	67.1 (64)	80.6 (32)	87.9 (18)
232 (2010)	11.9 (1,120)	203.9 (1,120)	36.9 (24)	90.9 (50)	59.2 (24)	197.9 (15)
334 (2011)	34.2 (2,800)	170.5 (2,800)	—	119.5 (33)	240.2 (17)	72.3 (10)
392 (2011)	12.1 (6,665)	113.8 (6,665)	—	92.5 (30)	268.8 (15)	418.3 (10)
632 (2011)	41.9 (3,997)	94.1 (3,997)	—	128.8 (32)	134.7 (16)	182.6 (12)

consecutive hand-tracking events. Evidence from the ARU array in Illinois (see below) indicates that ratsnakes do regularly make forays away from and back to a central location.

We had sufficient data for 15 snakes to determine whether snakes moved in response to hand tracking. Our approach for this analysis was to compare movement rates while a snake was being tracked (10 min before and after the time recorded by the tracker) with movement rates during the intervals between tracking events. We had data for 61 intervals immediately prior to a snake being located, and snakes moved on 21 (31.3%) of those occasions. We had data for 71 intervals immediately following a snake being located, and snakes moved on 9 (12.7%) of those occasions. We recorded 544 movements in the 14,659 time periods (3.7%) between hand-tracking events. Snakes were more likely to move both as the observer was approaching the snake ($G^{adj} = 48.85$, $df = 1$, $P < 0.001$) and as they departed ($G^{adj} = 7.40$, $df = 1$, $P = 0.01$). Among the 15 individual snakes, one never moved in response to an observer, six moved only during approaches, three moved only when the observer was departing, and five moved both before and after being tracked, although never both during a single tracking event.

Tracking Movements and Determining Home Ranges with an ARU Array.—In Illinois in 2010 and 2011, we tracked three ratsnakes over two summers and four ratsnakes for a single summer using the ARU array. For the snakes tracked over two years, we analyzed the years separately, giving us 10 snake-years. For addressing biological questions, this approach would not be appropriate, but our purpose here is limited to assessing the quality of the data provided by ARUs. We collected a total of 216,575 individual records using the array. This total was reduced to 66,220 (30.6%) records available for analysis as a result of applying the various filters (Appendix 1). Most excluded data resulted from either the signal received by one of the ARUs lacking sufficient strength, or the noise associated with the recording exceeded the -130dBm threshold. Data for individual snakes within years ranged from 735–15,036 records.

Based on the four snakes for which we had adequate hand-tracking data to estimate home ranges, we found that ARU and hand-tracking kernel estimates (Table 1) were positively correlated, although not statistically significantly given the small sample ($R^2 = 0.93$, $P = 0.09$, $df = 3$). Kernel estimates from hand-tracking data averaged 2.8 times larger than from ARU data. Home-range kernel estimates from simulated hand tracking every 24 h were positively correlated with those estimated using continuous ARU data ($R^2 = 0.45$, $P = 0.03$, $df = 9$), with hand-tracking values being larger on average by a factor of 3.2. The trend was positive but not significant for simulated hand tracking every 48 h ($R^2 = 0.12$, $P = 0.29$, $df = 9$), whereas there was no correlation between ARU estimates and

simulated 5-day hand-tracking estimates ($R^2 = 0.00$, $P = 0.89$, $df = 9$). Home ranges from ARU data were 7.3 times larger when estimated using MCP than using 95% kernels (Table 1).

Every snake monitored engaged in forays from their home range (range = 3–11). The straight-line distance from the edge of the core area to the furthest point of the foray averaged 418.4 m with a maximum of 1,596.0 m. The average duration of a foray was 58.0 h, with more distant forays taking more time ($R^2 = 0.36$, $P < 0.01$, $df = 65$). Simulated hand tracking every 24 h encountered snakes on 62% of the forays we recorded. Hand tracking every 48 h detected 45% of forays, whereas tracking every 5 days encountered only 13% of forays. The straight-line distance between the furthest point of a foray and the core home range was significantly correlated with the total distance travelled on a foray ($R^2 = 0.72$, $P < 0.001$, $df = 65$), although actual distances travelled averaged 1.8 times longer than straight-line maximum distances. Even when hand tracking encountered a snake on a foray, the snake would seldom be at the furthest point on that round trip. Therefore, to get a more realistic view of how estimates of distances travelled on forays varied with tracking frequency, we again used simulated hand tracking. Tracking every 24 h provided a reliable index of distances travelled ($R^2 = 0.92$, $P < 0.001$, $df = 65$) and underestimated distances only by a factor of 1.3. At a tracking frequency of 48 h, the hand-tracking estimates were still reliable indices of distances moved ($R^2 = 0.78$, $P < 0.001$, $df = 65$) but underestimated distances by a factor of almost 2. Tracking every 5 days provided a weaker index of how far snakes moved ($R^2 = 0.54$, $P < 0.001$, $df = 65$) and underestimated those distances by a factor of 3.7 (Fig. 4).

DISCUSSION

Our study demonstrated that automated telemetry has considerable potential to contribute to field studies of snakes and improve on what can be done using conventional telemetry. Despite this potential, however, automated telemetry does have some shortcomings.

Issues with Conventional Radiotelemetry.—Automated radiotelemetry revealed potential problems with each of the issues we investigated regarding conventional radiotelemetry. First, we found that ratsnakes were more likely to move immediately before or after an observer located them by hand tracking. Hand tracking often requires that the observer move around a snake to pinpoint its exact location, increasing the chance that the snake is disturbed. Movements were of short duration, hence were likely to involve snakes seeking cover. Thus, this disturbance would be a problem if the goal of the study were to document microhabitat selection or the incidence of behaviors such as basking but should

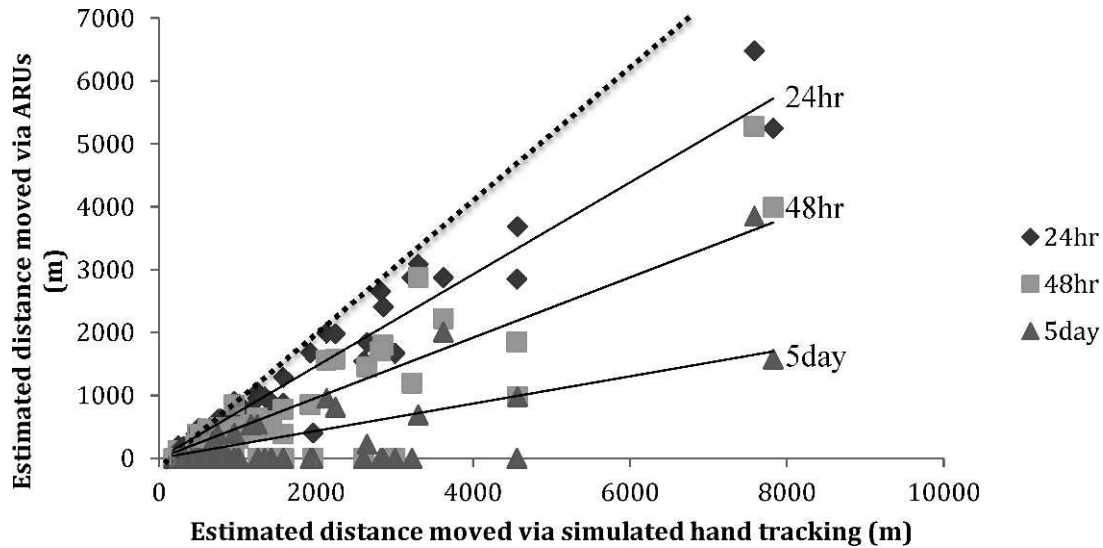


FIG. 4. The correlation between the estimated foray distance as determined via the ARUs and the 24-h, 48-h, and 5-day simulated conventional hand tracking. The dashed line represents a 1 : 1 relationship. All simulated hand tracking underestimates the distance moved when compared to the ARU.

have little or no effect on home-range analyses. The extent to which conventional tracking disturbs snakes seems likely to vary substantially among species. For species that rely on being cryptic to avoid detection (e.g., Prior and Weatherhead, 1994), the effects are likely to be small, whereas the effects could be pronounced for species that avoid predators by early detection and fast escape.

ARUs revealed that ratsnakes travelled further than was estimated using conventional tracking and that the reliability of estimates declined with the frequency of conventional tracking. Hand tracking every 24 h produced reliable estimates of distances, but locating snakes every five days underestimated distances by a factor of 4. The decline in accuracy resulted from less frequent tracking missing, in whole or in part, forays the snakes made away from and back to their core home ranges (Fig. 5). Even if hand tracking always found foraging snakes at their furthest distance from the core home range, the estimated distance travelled by snakes would still be only half the true distance travelled. These patterns we identified for ratsnakes in Illinois will almost certainly differ among species. For example, the extent to which conventional tracking underestimates travel distances should be greater for more active species because they will move more often between tracking events.

Researchers using conventional radio tracking assume that a snake found in the same location on successive tracking days did not move. We found two types of evidence that suggest that, at least for ratsnakes, this assumption is occasionally wrong. We found that hand tracking agreed closely with data from a single ARU regarding whether or not a snake had moved, but on some occasions the ARU detected a move not documented by hand tracking. With the ARU array, we found that ratsnakes made forays away from and back to their core home ranges. Because locations from ARU data are less precise than from hand tracking, we do not know how often snakes returning from forays went back to the exact location from which they departed, although in some instances snakes departed from and returned to the same building they used as a retreat site. Thus, our data are sufficient to tell us that there are some movements that involve a snake returning to the same location and that some of these movements would not be detected by

conventional tracking. These forays suggest that ratsnakes may be engaging in central place foraging (Orians and Pearson, 1979), a behavior not typically associated with snakes (a literature search of central place foraging produced 449 records, none of which involved snakes). If this proves to be a common foraging strategy for some snake species, a conventional radiotelemetry study of those species would underestimate the amount those snakes move.

Home-range 95% kernel estimates from ARU data were substantially smaller than those based on simulated or actual hand tracking. This difference is a result of ARUs generating far more locations than simulated and conventional hand-tracking approaches. When using kernel estimators, the smaller sample sizes of the simulated and conventional hand-tracking locations result in the use of larger smoothing parameters. The over smoothing that results means that estimated home ranges include areas not used by the snake (Horne and Garton, 2006). The MCP estimates were much larger than kernel estimates when both were calculated using the same ARU data. The MCP approach is extremely sensitive to points outside the core area (Powell, 2000), which resulted in home-range estimates being based largely on the location of forays. By contrast, the 95% kernel is sensitive to where a snake spends most of its time (i.e., the core area); thus, forays are largely irrelevant to kernel estimates. If the goal is to identify the area or habitat used most by a snake, kernel estimates may be the most appropriate approach. To facilitate comparisons among studies that collect data using different methods and sample at different intensities, providing both kernel and MCP estimates may be helpful. If forays are an important aspect of a species' biology, however, plots of all locations overlaid on the kernel estimates will be most informative about a snake's movements and spatial patterns.

Pros and Cons of ARUs.—The most obvious advantage of tracking snakes using ARUs is that automation greatly increases the amount of data that can be collected per individual and potentially the number of individuals that can be tracked simultaneously, with much less human involvement, at least during the time snakes are being tracked. Because data are collected around the clock and potentially for as long as

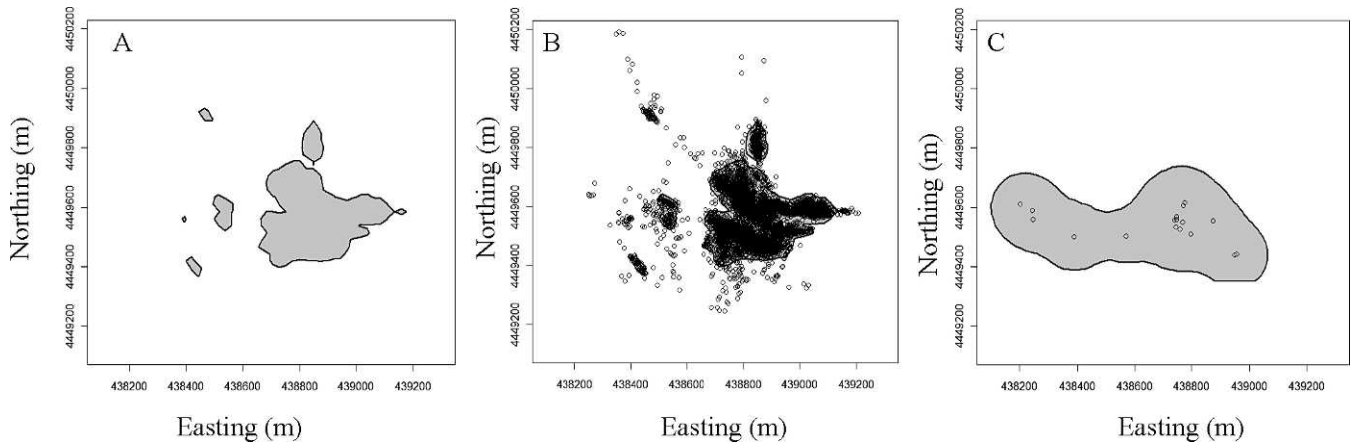


FIG. 5. Home-range kernel estimate for snake 164.880 from ARU data for 2010 (A) without individual locations, (B) with individual locations, and (C) estimated from hand-tracking locations (shown as circles). The home range determined using ARU data is smaller than that from hand tracking (11.3 vs. 24.0 ha) because the former does not include forays in the 95% kernel.

transmitters continue to operate, the activity and movement profiles generated are far more complete than would be possible with conventional tracking. For example, many snakes appear quite flexible in shifting between diurnal and nocturnal activity (Gibbons and Semlitsch, 1987), a behavior that is relevant to topics such as predator–prey interactions, sensory biology, and response of snakes to climate change (Weatherhead et al., 2012). Investigation of nocturnal behavior will be greatly enhanced using ARUs (Sperry et al., 2013).

There are several shortcomings of using ARUs. First, offsetting some of the time savings realized through automation, researchers must invest time erecting ARU towers at the outset of a study and maintaining the system during the study (e.g., replacing batteries, downloading data, checking for malfunctions). Second, a snake has to remain within range of ARUs for data to be collected, and those data become less reliable when the snake is on the periphery rather than the center of an array. Third, unlike hand tracking, where a snake's position can be determined within a few meters (i.e., the resolution of the GPS unit), locations determined by ARUs have errors of tens of meters at best. The only other test of the accuracy of an ARU array is a recent study from Barro Colorado Island, Panama, where the estimated accuracy was 42 m (SD 34 m) within the core area of the study site (Kays et al., 2011). Thus, ARUs will be most useful for studying snakes whose movements substantially exceed this measurement error. Inaccuracy of determining locations will also limit the value of ARUs in studies of habitat selection where habitat patches are small enough that the error of ARU locations could regularly assign locations to the wrong habitat. Countering this shortcoming, however, is the detailed home-range estimates provided by ARUs. As long as habitat composition is based on analysis of home-range maps rather than individual locations, the results should be highly reliable. The quality of data provided by ARUs is affected by the filters used to eliminate spurious records. In this study, knowledge of ratsnake ecology helped us refine the filters. When working with other species, different filters may be needed.

There are significant costs associated with establishing an ARU array, including erection and maintenance costs. For the towers we used in Illinois, each tower (tower segments, guy wires, cables, antennas, battery, miscellaneous other materials) cost approximately \$2,300 (US) without the ARU. Cost per ARU

was approximately \$5,000. Larger arrays can collect more accurate data from more animals, but there is no appreciable economy of scale for purchasing the equipment. Although we did not incorporate the feature here, the ARUs we used can also be programmed to record body temperatures using transmitter pulse rates, simultaneous with tracking movements. Therefore, in a study designed to document both movements and thermal ecology, no duplication of costs would be required to automate data collection for both.

Automated telemetry has the potential to enhance enormously the study of snake activity and movement. Because this technology is not without limitations, however, to be most effective it must be coupled with both appropriate species and appropriate questions. Furthermore, given that conventional telemetry also has advantages, future research seems likely to benefit from using a combination of the two technologies.

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APPENDIX 1. Description of the filters and thresholds used to estimate the bearing of the radio-tagged snake from the ARUs, the location of radio-tagged snakes, and the methods for determining the home range of snakes using ARU data. Bearing estimation filters were provided by the developer of the ARUs. Location filters were developed based on experience with the ARUs and using our familiarity with the biology of the snakes (i.e., the distance moved between consecutive locations) from conventional radio tracking. Information about the R-code used to implement these filters is available from M. P. Ward.

Filters	The issue the filter is intended to address
<p>Bearing estimation filter The strength of the strongest noise recorded must be less than -130dBm.</p>	<p>Electromagnetic noise can result in apparent signals that appear to be from the radio transmitter. Noise is determined by measuring signal strength received between transmitter pulses. If electromagnetic noise is not an issue, then the noise will be relatively low. However, if the noise is greater than -130dBm, the data are filtered from the dataset.</p>
<p>The strength of the signal on the second strongest antenna must be greater than -130dBm.</p>	<p>In general, the stronger the signal the more accurate the bearing estimation. Therefore, if the signal strength on the second strongest antenna is weak ($\leq -130\text{dBm}$), the data are filtered from the dataset.</p>
<p>The two antennas with the strongest signal strengths must be adjacent to one another.</p>	<p>In practice, signals should be strongest for the antenna most closely directed toward the snake and become progressively weaker in the adjacent antennas that are oriented further from the snake. If the two strongest signals are received by antennas that are not adjacent to each other, it suggests that noise (e.g., lightning, two-way radios), multipath issues (i.e., signals that bounced and, therefore, are not taking a direct path from the transmitter to the receiver), or extremely poor signal strength account for the signal of at least one of the antennas; thus, these data are excluded.</p>
<p>Location filters Locations must be in the correct relative direction from the ARU.</p>	<p>Because of the approach we used to estimate locations, it is possible that, if a snake was almost directly between two ARUs, the variation inherent in the bearing estimation could result in the bearings not intersecting until one of the bearings stretched around the world, which can result in the estimated location being on the opposite side of an ARU from its true location. For example, if the antenna receiving the strongest signal was pointed north but the estimated location was south of the ARU, the location must be incorrect. Any such cases were removed from the data.</p>
<p>Locations must be within the study area.</p>	<p>Because the error associated with locations determined using ARUs increases with the distance the transmitter is from the array, we restricted locations to a 2-km^2 area centered on the array based on field tests. Any locations outside this area were excluded.</p>
<p>The distance moved by a snake must be less than 100 m between consecutive locations.</p>	<p>Although a ratsnake could potentially move 100 m within 3 min, such an event is likely to be very rare. Therefore, for a snake to move 100 m in 3 min and then 3 min later have returned to its previous location is unlikely to ever happen. Such movements were recorded occasionally, apparently as a result of multipath, a phenomenon in radio telemetry (and other forms of wireless transmissions) where the signal reaching the receiver takes more than one path. In our study, these events were commonly associated with snakes that spent time near metal sheds, where signals presumably “bounced” off sheds, creating multipath reception. We addressed this by excluding consecutive locations that were more than 100 m apart.</p>
<p>Human eye filter</p>	<p>Although the distance moved filter (#3 above) helped address the multipath issue, there were some instances where either a snake would move ~ 90 m and then return to its previous location the next reading or where a snake suddenly moved next to a garage and then immediately returned to its previous location. Based on the location and time of day, we suspect that latter situation involved the signal being received coming from a remote-control garage door opener. The best way to identify these spurious results is visual examination of plots of successive snake locations. We produced Google Earth files (kml files) and plotted the path of snakes via the plot function in R to identify potential irregularities. In total, less than 0.01% of the data were removed via this method. However, failure to remove these points would have had a strong effect on home-range estimates because the points were extreme outliers.</p>