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Factors Affecting the Accuracy and Precision of Triangulated Radio Telemetry Locations of Eastern Indigo Snakes *(Drymarchon couperi)*

Radio telemetry (i.e., very high frequency or VHF telemetry) has proven an invaluable tool in understanding snake ecology because researchers can locate a telemetered snake virtually at will, thereby obtaining a relatively unbiased view of its behavior and movements (Reinert 1992; Beaupre and Duvall 1998). Researchers generally use homing techniques (Mech 1983) to obtain a visual location of a telemetered snake or its retreat site. As a result, a researcher can obtain very accurate geographic coordinates of the snake's location where accuracy is limited by the resolution and detail of field maps or aerial photos or the accuracy of a GPS unit. In contrast, many studies of mammals or birds use triangulation to estimate the locations of telemetered animals. Triangulation consists of taking directional bearings at two or more locations and then using the intersections of those bearings to estimate the animal's location (White and Garrott 1990). Triangulation introduces additional error to location estimates and the degree of error depends on many factors including the distance between the transmitter and receiver, the orientation or height of the transmitter, topography, vegetation structure, animal behavior, signal interference, or inter-observer variability (Lee et al. 1985; Garrott et al. 1986; Schmutz and White 1990; White and Garrott 1990; Townsend et al. 2007; Bartolommei et al. 2012). These errors may have significant implications for subsequent analyses of space use and resource selection.

Situations may arise where triangulation is necessary to obtain location estimates for telemetered snakes. For example, an individual may move onto property a researcher cannot access, into a large extent of flooded habitat, or into impenetrably thick vegetation. While triangulation may prove useful in these situations, triangulating telemetered snakes features several challenges. Snakes spend large amounts of time underground or in thick vegetation which may interfere with signal strength or direction. They often use the same retreat site for multiple days at a time as well as small-scale or linear habitat features (e.g., forest or wetland edges, Blouin-Demers and Weatherhead 2001; Pattishall and Cundall 2008) and this use may be difficult to detect using triangulated locations. Finally, many snake species spend the majority of their time close to the ground and the low vertical height of their transmitters can reduce triangulation accuracy (Townsend et al. 2007). All of these factors could potentially reduce triangulation accuracy below the level required to adequately address a study's objectives (Samuel and Kenow 1992; Rettie and McLoughlin 1999; Montgomery et al. 2010, 2011). While triangulation is apparently rare in telemetry studies of snakes and other herpetofauna (but see Whiting and Miller 1998), when applied, it may be particularly critical to determine the accuracy of triangulated locations given the aforementioned challenges. However, we are unaware of any studies reporting on the accuracy of triangulated locations for snakes or the factors influencing their accuracy.

JAVAN M. BAUDER*
Department of Environmental Conservation, University of Massachusetts
160 Holdsworth Way, Amherst, Massachusetts 01003, USA
PATRICK BARNHART
The Orianne Society, 579 Highway 441 South
Clayton, Georgia 30525, USA

**Corresponding author; e-mail: javanvonherp@gmail.com*

Multiple metrics are used to evaluate triangulation accuracy. Many studies report error polygons around estimated locations, such as a 95% confidence ellipse (e.g., Lenth 1981), as a measure of accuracy (Saltz 1994; Withey et al. 2001). However, these polygons provide a measure of precision, not accuracy per se, and field tests have shown that error polygons may not include the true transmitter location (Garrott et al. 1986; Nams and Boutin 1991; Withey et al. 2001). Determining accuracy requires beacon tests in the field using transmitters at known locations either attached to the study organism or placed at similar heights and orientations (Lee et al. 1985; Garrott et al. 1986). This allows a direct measurement of accuracy as either the distance between the estimated and true location (linear error), difference between bearings to the estimated and true location (angular error), or the proportion of true locations contained within an error polygon (coverage, Garrott et al. 1986; White and Garrott 1990). Because the factors influencing accuracy might differ among studies due to study-specific factors, such as study site characteristics, transmitter size, or inter-observer variability, it is necessary that researchers conduct beacon tests prior to each study under the conditions present at their study site (Withey et al. 2001).

We conducted a radio telemetry study of Eastern Indigo Snakes (*Drymarchon couperi*) as part of a movement and resource selection study. During our study, multiple telemetered snakes moved onto private lands where we were unable to obtain access from the landowner. During these instances, we used standard triangulation techniques to estimate the locations of our telemetered snakes. To determine the accuracy and precision of the triangulated locations, we conducted a series of beacon tests using known locations of telemetered snakes. In this paper, we report the accuracy and precision of our beacon tests and the effects of different factors on triangulation accuracy (i.e., linear error). We also compared two different statistical estimators commonly used to estimate triangulated locations, Andrew's estimator (AE) and Lenth's maximum likelihood estimator (MLE, Lenth 1981). Finally, we developed a multiple regression model based on our beacon tests to predict linear error for locations estimated by triangulation and identify locations which met predefined criteria for accuracy based on the spatial resolution of our environmental data.

Materials and Methods

Study area and species.—We conducted on our study on the southern 40 km of the Lake Wales Ridge in Highlands County, Florida, USA (27.21°N, 81.33°W). Our study area was a mix of natural habitats (scrub, scrubby flatwoods, mesic flatwoods,

TABLE 1. Summary statistics from beacon tests and triangulated locations for Eastern Indigo Snakes (*Drymarchon couperi*). Results are presented for Lenth's maximum likelihood (MLE) and Andrew's estimators (AE, Lenth 1981). Estimated distance is the distance from the observer to the estimated location averaged across all bearings for a given location, ellipse area is the size of the 95% confidence ellipse, predicted linear error is the distance between the true and estimated location predicted by the model-averaged parameter estimates from the multiple regression analysis of the beacon test data, and true linear error is the actual distance between the true and estimated location.

	Estimated distance (m)		Ellipse area (m^2)		Predicted linear error (m)		True linear error (m)	
	MLE	AE	MLE	AE	MLE	AE	MLE	AE
Beacon tests								
Median	134	134	627	656	35	35	41	41
IQR[1]	99–223	99–223	92–2,901	84–2,938	24–64	24–64	18–81	18–82
Range	22–617	22–613	0.2–41,038	0.2–38,393	4–212	4–212	2–265	2–264
Triangulated locations								
Median	155	165	768	795	43	43	NA	
IQR[1]	77–263	78–264	109–5,392	115–5,598	18–85	18–83	NA	
Range	20–743	20–737	1–383,484	1–373,809	4–293	4–282	NA	

[1] IQR = Inter-quartile range (25th and 75th percentiles)

forested and non-forested wetlands), cattle ranches, citrus groves, and rural and urban development. We searched for Eastern Indigo Snakes using road-cruising and visual encounter surveys around Gopher Tortoise (*Gopherus polyphemus*) burrows, although 90% of captures were made opportunistically while tracking other snakes or travelling among field sites. We selected snakes to receive radio transmitters depending on their capture location in order to distribute snakes as evenly as possible throughout our study area. We transported these snakes in large plastic boxes (30.3 L, 50.5 × 35.8 × 30.7 cm) to the Small Animal Hospital at the University of Florida, Gainesville, Florida, for transmitter implantation. We used 9 and 13.5 g SI-2T temperature sensitive transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) with smaller snakes generally receiving the smaller transmitters. Transmitters did not exceed 2% of a snake's body mass. Anesthesia and surgical procedures followed those of Reinert and Cundall (1982) and Hyslop et al. (2009). Once snakes were fully alert and recovered from anesthesia we transported them back to Highlands County and held them in large (121.9 × 147.3 × 45.7 cm), well ventilated terrariums. Snakes were held for 48–72 h after surgery except during cold periods (highs < 25°C and lows < 14°C) in Nov.–Feb. when we held each snake for 7–14 days after surgery (Hyslop et al. 2009) to facilitate healing of the incision. In these instances, snakes were released once the forecasted highs and lows for the next five days were > 25° and > 14°C, respectively. Each telemetered Eastern Indigo Snake was released into the closest burrow or brush pile to its capture location.

Field data collection.—We located each telemetered Eastern Indigo Snake a median of every two days (range 1–60) using a three element Yagi antenna and a R-1000 receiver (Communications Specialists, Inc., Orange, California). We conducted beacon tests in a haphazard manner throughout our study on telemetered snakes whose location we were able to access and which did not appear to be moving on the surface based on their transmitter signal. To conduct the beacon tests, an observer would take a set (3–5) of bearings from known locations towards the telemetered snake's location (recorded with a GPSmap 76CSx, Garmin International Inc., Olathe, Kansas, mean accuracy = 7 m) and then immediately use homing techniques to locate the snake and record its actual location. The observers deliberately varied their distance to the snake, the number of bearings used, the angle between bearings (keeping the angle between the two most extreme bearings < 160°), and the surrounding vegetation conditions in a haphazard manner. This allowed us to understand how triangulation accuracy varied under a range of conditions. When a telemetered snake was on property we could not access at the time, the observer would also take 3–5 bearings towards the snake's location. Our goal in these cases was to maximize the accuracy of the estimated location so the observer tried to get as close to the snake as possible, generally used three or four bearings (depending on the configuration of the property), and maintain an angle of 60–120° between the outermost bearings.

Triangulation.—We used LOAS 4.0 (Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate triangulated locations and 95% confidence ellipses with both AE and MLE. We found that some sets of bearings (i.e., the 3–5 bearings taken for each location) contained apparent outliers which did not intersect the rest of the bearings in the set or were markedly divergent from the other bearings. Because factors such as signal reflectance, polarization, background noise, or observer error may lead to erroneous bearings, even those taken from identical locations (Lee et al. 1985), one must decide at what level this error becomes detrimental to the ultimate goal of obtaining accurate location estimates. Other studies have excluded bearings or triangulated locations based on the angle of the bearing or the size of the error ellipse (Lee et al. 1985; Marzluff et al. 1997; Van Etten et al. 2007). After examining our data, we found that an angular difference between the bearing taken in the field and the bearing to the estimated location (estimated using either AE or MLE) > 20° represented what we felt were outlying bearings. Subsequent examination confirmed that such bearings did not intersect the other bearings in the set or were strongly divergent. We removed outlying bearings from both beacon tests and triangulated locations using the same criterion to maximize the applicability of our predictive model.

Accuracy and precision.—Our primary measure of accuracy for the beacon tests was linear error which was determined by

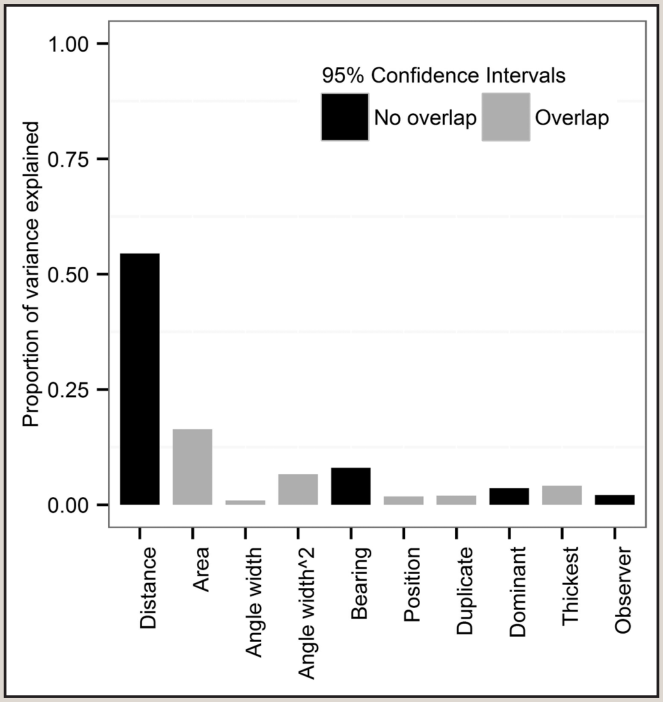

Fig. 1. Proportion of independently explained variance in linear error between true locations and estimated locations estimated using Lenth's maximum likelihood estimator (MLE) from Eastern Indigo Snake *(Drymarchon couperi)* beacon tests (N = 60). Predictor variables are distance to estimated location (Distance), size of error ellipse (Area), angle between the two outermost bearings (Angle width and Angle width^2), number of bearings (Bearing), position of the snake (Position), whether or not the snake was at a previously used location (Duplicate), dominant (Dominant) and thickest (Thickest) vegetation class traversed by the bearings for a given location, and observer (Observer). Dark shaded bars represent variables or levels (categorical variables) whose model-averaged 95% confidence intervals did not overlap zero.

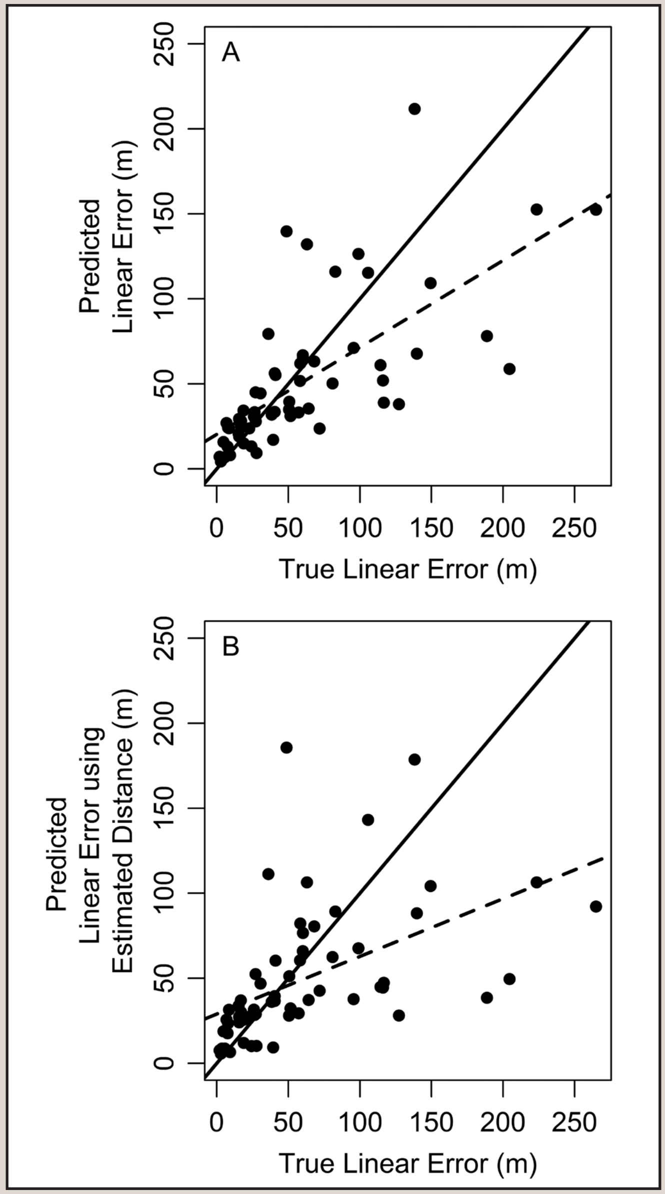

Fig. 2. Relationship between true linear error and predicted linear error using a model-averaged parameter estimates from a multiple regression analysis (2A) and a single-variable regression model containing only estimated distance (2B) from beacon tests (N = 60) of radio telemetered Eastern Indigo Snakes *(Drymarchon couperi)*. The solid line represents a one-to-one relationship between true and predicted linear error and the dashed line represents the observed relationship.

measuring the distance between the snake's actual location and the MLE or AE estimated location. We also assessed accuracy by calculating bias as the angle between the snake's actual location and each bearing (i.e., angular error) averaged across all bearings (N = 211, Withey et al. 2001). We also measured coverage as the proportion of actual snake locations that were contained by their respective MLE and AE error ellipses. To quantify precision, we used the size of the 95% confidence ellipse (ellipse area) and the standard deviation of the angles between the snake's actual location and each bearing across all bearings (angular precision).

Statistical analysis.—For each set of bearings (both beacon tests and triangulated locations), we measured the mean distance from the observer to the MLE or AE estimated location (estimated distance). We also measured the width of the angle between the two outermost bearings within each set (angle width). We characterized the dominant vegetation class (dominant vegetation) for each bearing set as forested (dominated by trees > 4 m tall and including citrus, bayheads, riparian forests, hammocks), shrub (primarily fire suppressed scrub and scrubby flatwoods with vegetation 2–4 m tall), and open (vegetation height < 2 m including scrub, scrubby flatwoods, pasture, and non-forested wetlands) using National Agriculture Imagery Program (NAIP) aerial imagery taken in Dec. 2011. We inspected the length of each bearing within a set using Google Earth and visually estimated the proportion of each vegetation class intersecting each bearing between the observer and the telemetered snake. We assigned each set of bearings to the vegetation class containing the greatest cumulative proportion across all bearings. However, the presence of dense vegetation along one bearing could potentially skew results even if other bearings are unobstructed. We therefore included a separate vegetation variable (thickest vegetation) where we assigned each set of bearings to the thickest vegetation class intersecting > 50% of any bearing in that set. We recorded the total time taken to complete each beacon test or triangulated location for the 50 (94%) beacon tests and 80 (77%) triangulated locations for which we record time at each bearing. We also recorded the time from when the bearings were taken (measured as the median time between the first and last bearing) and when the snake was located. For beacon tests, we recorded whether or not the telemetered snake was in a location where it had been previously located to evaluate the influence of potential bias in triangulation caused by the snake repeatedly using the same retreat site. We also recorded each telemetered snake's position upon location following a beacon test (underground, on the surface but stationary, or on the surface and moving).

We used the beacon test data to evaluate the effects of estimated distance, angle width, ellipse area, number of bearings (3–5), observer (N = 3), position, previous location, and dominant and thickets vegetation class on linear error for AE and MLE locations. We hypothesized that angle width would have a quadratic rather than a linear effect (Haskell and Ballard 2007) so we only considered the quadratic effect of angle width. Estimated distance, ellipse area, and linear error were log transformed to correct for non-normality. Estimated distance and ellipse area were moderately correlated (Spearman's rank correlation, $r_s = 0.63$) but all other continuous variables had comparatively low colinearity ($|r_s| \leq 0.26$). Although we hypothesized that each of our predictor variables would influence linear error, we had no *a priori* reason to use any particular combination of these variables. Additionally, we were interested in understanding the independent contribution of each variable to the variation in linear error. We therefore fit linear regression models to all possible subsets of our variables. This allowed us to use hierarchical variance partitioning to estimate the independent contribution of each variable to the variance of the global model as a means of identifying the most causal factor (Chevan and Sutherland 1991; Mac Nally 2000). We used the hier.part package (v. 1.0-4, Walsh and Mac Nally 2013) to calculate the independent contributions of each variable. Because our ultimate goal was to predict linear error using data from the beacon tests, we used model-averaging (Burnham and Anderson 2002) across all our models with Akaike's Information Criteria adjusted for small sample sizes (AIC_c) in the MuMIn package (v. 1.10.0, Barton 2014) to obtain model-averaged parameters and 95% confidence intervals. We evaluated the predictive accuracy of our model by comparing the difference between true linear error and predicted linear error for the beacon test data. We then used these model-averaged parameters to predict linear error for the triangulated locations and recorded the number of triangulated locations with predicted accuracy ≤ 15 and 30 m. We selected these cutoffs because these were the pixel sizes of available land cover maps for our study area and thus represent possible minimum accuracies for resource selection analyses. All statistical analyses were conducted in R v. 3.0.2 (R Development Core Team 2013).

Results

We surgically implanted radio transmitters into 32 Eastern Indigo Snakes. Two individuals were lost < 30 days of release, presumably because of transmitter failure. We conducted 63 beacon tests using 19 telemetered snakes. The AE failed to produce estimates for three beacon tests despite the absence of potential outlying bearings so we excluded them from subsequent analyses to facilitate comparison between AE and MLE. Median distance from the observer to the beacon was 145 m (range: 21–606 m). Median angle width was 105° (range: 39–176°). Median time between the first and last bearings for each beacon test was 14 min (range: 5–41 min). The median time between taking the bearings and locating the telemetered snake was 29 min (range: 9–133 min). Excluding the maximum value of 133 min reduced the maximum to 67 min. Forty-one snakes (68%) were underground while 17 (28%) were moving on the surface and two (3%) were stationary on the surface. We used three bearings in 34 (57%) of our beacon tests, four bearings in 21 (35%), and five bearings in five (8%). We classified 38 (63%) bearings as having a dominant vegetation class of open, 16 (27%) as shrub, and 6 (10%) as forested. We classified 19 (32%) bearings as having a thickest vegetation class of open, 29 (48%) as shrub, and 12 (20%) as forested.

The AE and MLE produced similar estimates of accuracy and precision (Table 1). The maximum difference in linear error between each estimator was 3 m although the median difference between the two estimators was marginally significant ($V = 684$, $P = 0.0897$). Mean bias was 1.41° (median = 2.53°) and angular precision was 16.50°. However, a single bearing had an extremely large angular error (102°). Excluding this value changed the mean bias to 1.97° (median = 2.54°) and angular precision to 14.92°. Coverage was low as only seven (12%) and eight (13%) (MLE and AE, respectively) confidence ellipses included the true location. Median ellipse size was greater for AE than MLE (Table 1) but this difference was not statistically significant ($V = 852$, $P = 0.6454$).

Because of the moderate correlation between estimated distance and ellipse area we repeated our beacon test analyses excluding ellipse area from our pool of predictor variables. Our results were similar so we report the results using all predictor variables. Results were also similar between MLE and AE so we report the results of the former because of its lower failure rate. Distance to estimated location was present in all the best supported models ($AIC_c < 2$; Table 2) and explained almost half of the variance in linear error (Fig. 1). Linear error increased with increasing distance from estimated location (Table 3). All other predictor variables explained comparatively little variation in linear error and only the number of bearings, dominant vegetation class, and observer had model-averaged 95% CI that did not overlap zero (Fig. 1). Linear error was greatest when three bearings were used and mean linear error decreased by 42% and 50% when four and five bearings where used, respectively (Table 3). Mean linear error varied by up to 48% among the three observers. Mean linear error decreased by 59% and 47% when the dominant vegetation class traversed by all bearings within a set was shrub and open, respectively, instead of forest.

The median difference between true and predicted linear error for the beacon tests was -1.13 m (range: -91–146 m) and was not significantly different from zero ($V = 1035$, $P = 0.3790$). The median difference between true and predicted linear error for the beacon tests predicted using only estimated distance was -2.34 m (range: -138–173) and was not significantly different from zero ($V = 1001$, $P = 0.5291$). Although the differences between true linear error and predicted linear error using the model-averaged parameter estimates and estimated distance were not significantly different ($V = 948$, $P = 0.8109$), our predictions of linear error were improved by using the model-averaged parameter estimates (Fig. 2). Eleven (18%) and twelve (20%) beacon tests had true linear error ≤ 15 m with MLE and AE, respectively. Nine (15%) and 10 (17%) beacon tests had predicted error ≤ 15 m with MLE and AE, respectively. Twenty-four (40%)

Table 2. Top multiple regression models predicting linear error between true locations and triangulated locations estimated using maximum likelihood from Eastern Indigo Snake (*Drymarchon couperi*) beacon tests (N = 60). For each model we report Akaike's Information Criteria corrected for small sample sizes (AIC_c), delta AIC_c (AIC_c), the AIC_c model weight (w_i), and the adjusted R^2. Only models with AIC_c < 2 are reported; a total of 381 models were considered. Angle width includes a quadratic effect.

Model	AIC_c	AIC_c	w_i	R^2
Distance + ellipse area + angle width + no. of bearings + observer	138.28	0.00	0.067	0.63
Distance + angle width + no. of bearings + observer	138.93	0.66	0.049	0.62
Distance + no. of bearings + observer	139.25	0.97	0.041	0.60
Distance + angle width + dominant vegetation + duplicate location	139.43	1.15	0.038	0.61
Distance + angle width + dominant vegetation	139.48	1.20	0.037	0.60
Distance + no. of bearings + duplicate location	139.54	1.26	0.036	0.59
Distance + ellipse area + no. of bearings + observer	139.55	1.28	0.036	0.60
Distance + angle width + no. of bearings + observer + duplicate location	139.62	1.35	0.034	0.62
Distance + no. of bearings + thickest vegetation + duplicate location	139.65	1.38	0.034	0.60
Distance + angle width + no. of bearings + dominant vegetation + duplicate location	139.67	1.39	0.034	0.62
Distance + ellipse area + angle width + dominant vegetation	140.08	1.80	0.027	0.60
Distance + no. of bearings + dominant vegetation + duplicate location	140.12	1.84	0.027	0.60

and 22 (37%) beacon tests had true and predicted linear error, respectively, ≤ 30 m for both estimators.

We collected 116 triangulated locations from 16 telemetered snakes. The AE failed to produce estimates for nine beacon tests so we excluded them from subsequent analyses to facilitate comparison between AE and MLE. Distance from observer to estimated location ranged from 20–737 m and 20–743 m for AE and MLE, respectively (Table 1). Median time between first and last bearing was 15 min (range: 3–85 min) and median angle width was 94° (range: 22–178°). We used three bearings for 44 (41%) triangulated locations, four bearings for 52 (49%), and five bearings for 11 (10%) of our triangulated locations. We classified 78 (73%) bearings as having a dominant vegetation class of open, 11 (10%) as shrub, and 18 (17%) as forested. We classified 40 (37%) bearings as having a thickest vegetation class of open, 27 (25%) as shrub, and 40 (37%) as forested. Median ellipse size estimated with AE was significantly greater than median ellipse size estimated using MLE ($V = 1{,}642$, $P = 0.0001$, Table 1).

We used all variables from the beacon test analysis for predicting linear error for our triangulated locations except the snake's position and whether or not it was at a previously used retreat site because these variables were unknown for triangulated locations. Median predicted linear error for the triangulated locations was very similar between AE and MLE (Table 1). Median difference in predicated linear error between the two estimators was significantly different from zero ($V = 4699$, $P < 0.0001$) but the magnitude of this difference was very small (median = 0.28, 25th percentile: 0.04, 75th percentile: 1.21). Predicted linear error was ≤ 15 m for 25 (23%) triangulated locations and ≤ 30 m for 40 (37%) triangulated locations for both estimators.

Discussion

Our results show that distance to estimated location had the strongest effect on linear error, consistent with other triangulation studies (Marzluff et al. 1997; Bartolommei et al. 2012). Additionally, the predictive ability of our multiple regression models was poorest at large distances as indicated by the large residual errors shown in Fig. 2. Angular error is magnified with increasing distance from the transmitter and other factors, such as poor signal quality, may have a greater effect over long distances (Hupp and Ratti 1983; Saltz and Alkon 1985). Reducing distance between the observer and telemetered animal is often used to reduce triangulation error in studies not reporting the use of beacon tests (e.g., Dickson et al. 2005). However, other studies have not reported a strong effect of distance to estimated location on accuracy (Hupp and Ratti 1983; Haskell and Ballard 2007) suggesting that, while reducing estimated distance may reduce triangulation error, it may not guarantee sufficient accuracy for a study's objectives. The size of the 95% confidence ellipse explained the second greatest amount of variation in linear error although the model-averaged 95% confidence intervals overlapped zero. However, these ellipses rarely contained the true location during beacon tests. This result is consistent with previous studies (Nams and Boutin 1991; Withey et al. 2001) and reinforces caution in using the 95% confidence ellipse to infer accuracy. We found relatively little support for angle width although Haskell and Ballard (2007) found a strong quadratic effect of angle width and recommended an angle width of 90–100° to maximize accuracy.

Features common to many radio telemetry studies on herpetofauna likely influenced our triangulation accuracy. In particular, the low vertical height of our transmitters (at or below ground level) may have reduced our accuracy. Townsend et al. (2007) found approximately a four-fold increase in angular error (6.43° to 24.37°) when reducing a transmitter's height from 92 cm to 15 cm above ground-level. Many snakes and other herpetofauna also spend large amounts of time underground or in thick vegetation which could similarly reduce triangulation accuracy (Lee et al. 1985; White and Garrott 1990). Beacon tests taken where bearings primarily passed through shrub vegetation were less accurate than those in forested vegetation. This result could be due to the dense vegetation structure of the habitats we classified as shrub. Snake position had very little influence on linear error despite the fact that most individuals located on the surface during beacon tests were moving (17 of 60 beacon tests). This suggests that any movement between when the bearings were taken and when the snake was located was small relative to the degree of error in our triangulations.

Table 3. Model-averaged parameter estimates, standard errors, and 95% confidence intervals from a multiple regression analysis of Eastern Indigo Snakes (*Drymarchon couperi*) radio telemetry beacon tests (N = 60). Log of distance between true location and triangulated location estimated using Lenth's maximum likelihood estimator (MLE) was used as the response variable. The reference levels for number of bearings, observer, dominant and thickest vegetation, and position were five bearings, observer #3, forested, and moving, respectively.

	Estimate	SE	Lower CI	Upper CI
Intercept	0.0130	1.4981	-2.9233	2.9493
Four bearings	-0.5511	0.2391	-1.0197	-0.0825
Five bearings	-0.6872	0.3935	-1.4585	0.0840
Observer 1	-0.2009	0.2447	-0.6804	0.2787
Observer 2	-0.6542	0.3210	-1.2834	-0.0250
Log (estimated distance)	1.0140	0.1473	0.7253	1.3027
Log (ellipse area)	0.0614	0.0501	-0.0368	0.1597
Angle width	-0.0402	0.0231	-0.0854	0.0049
Angle width2	0.0002	0.0001	0.0000	0.0004
Duplicate location	-0.4021	0.2676	-0.9266	0.1225
Dominant vegetation (open)	-0.6301	0.3734	-1.3620	0.1017
Dominant vegetation (shrub)	-0.8882	0.4287	-1.7285	-0.0480
Thickest vegetation (open)	-0.4953	0.3066	-1.0962	0.1055
Thickest vegetation (shrub)	-0.4618	0.2907	-1.0316	0.1079
Position (stationary on surface)	-0.1427	0.5721	-1.2640	0.9786
Position (underground)	-0.0700	0.2542	-0.5682	0.4282

Including these locations improves the applicability of our predictive model, even at the risk of under-predicting accuracy, because such small-scale movements or even whether an animal is underground or on the surface are undetectable during triangulation. Nevertheless, animal movement while bearings are taken can reduce triangulation accuracy (Schmutz and White 1990) and many studies employ multiple observers (Marzluff et al. 1997) or limit the time between bearings (Cimino and Lovari 2003; Dickson et al. 2005) to minimize this error. A post-hoc analysis showed that the median time between the first and final bearing to when the snake was located (i.e., time to location) was positively correlated with linear error ($r_s = 0.67$, $P < 0.0001$) suggesting that accuracy was improved by locating the snake soon after the bearings were taken. However, time to location was also correlated with estimated distance ($r_s = 0.63$, $P < 0.0001$) and these patterns held true when considering underground snakes as well as those moving on the surface. This suggests that the relationship between linear error and time to location may have been an artifact of the observer taking longer to locate snakes that were further away from where the bearings were taken. Additionally, there was no significant difference in time to location between snakes underground or on the surface ($W = 304$, $P = 0.3884$).

We observed very little difference in precision or accuracy between MLE and AE, consistent with other studies (Haskell and Ballard 2007; Withey et al. 2001). However, AE failed to converge in some instances. When reflected signals are common, AE appears to outperform MLE, although both estimators perform similarly in the absence of signal reflection (Garrott et al. 1986; White and Garrott 1990). We observed relatively little signal reflection in our study area although we occasionally had difficulty determining the signal's bearing or recorded bearings that did not intersect the other bearings in a set. This may have been caused by thick or damp vegetation or other unknown factors. These bearings would likely have been removed as outliers so this may have contributed to the similarity of our results. Previous studies comparing MLE and AE do not report the treatment of outliers or included them to test the method's sensitivity. However, outlying bearings were present in only 10 of our 60 beacon tests and 15 of our 107 triangulated locations. In four beacon tests removing the outlier allowed both estimators to converge and removing outlying bearings in another three beacon tests reduced linear error by 4, 37, and 56 m. However, removing outliers increased linear error increased in the remaining three beacon tests by 1, 9, and 91 m. While defining outliers involves subjectivity at some level, erroneous bearings may ultimately become detrimental to the goal of accurately estimating triangulated locations (Garrott et al. 1986).

Less than 40% of our triangulated locations met our criteria for suitable accuracy. The criteria for suitable accuracy will depend on the study objectives, composition of the landscape, and degree of error relative to the study organism's movement. For example, Moser and Garton (2007) found that fixed kernel home range size was relatively robust to triangulation error provided the degree of error is small relative to home range size. They used the median Circular Error Probable (CEP, Moen et al. 1997), the area of a circle with a radius that contains 50% of estimated locations, as a measure of error and found that a ratio of CEP to home range size < 0.01 had relatively little effect on fixed kernel home range estimates. Using our median observed linear error (41 m) to calculate CEP and a mean home range size of 140 ha (J. Bauder, unpubl. data), our error ratio was 0.004. Based on our median observed linear error, home range size would need to be > 53 ha to maintain an error ratio < 0.01. While Eastern Indigo Snake home range sizes regularly exceed this size (Breininger et al. 2011; Hyslop et al. 2014), many snake species maintain smaller home ranges (Bauder et al., *in press*; Row and Blouin-Demers 2006) suggesting that the degree of triangulation error observed in our study may be too great to produce reliable home range estimates for many snake species. These errors may also be compounded in linear or irregularly shaped home ranges. Resource selection analyses can also be sensitive to triangulation error. Montgomery et al. (2011) found that triangulation errors are compounded with fine-resolution (e.g., 10 m vs. 30 m pixels) categorical raster data and small patch sizes. Using their simulation results and our median observed linear error (41 m), accuracy of habitat classification at patch sizes from 0.5–50 ha would range from 52–81% and 62–84% at 10 m and 30 m pixels, respectively. Many snakes use small-scale or linear habitat features (Blouin-Demers and Weatherhead 2001; Pattishall and Cundall 2008) and triangulated locations may require a higher degree of accuracy than we obtained in order to detect use of such features.

Our results suggest that the error associated with triangulation may be insufficient for snake radio telemetry studies. We recommend that researchers avoid triangulation in snake radio telemetry studies and use beacon tests to directly measure linear error when triangulation is used. Researchers should use data from beacon tests to predict the linear error of triangulated locations to determine which locations are sufficiently accurate given the study's objectives. Our study also offers suggestions for minimizing linear error. The observer should minimize the distance between themselves and the transmitter. Bearings should be taken within the shortest amount of time or simultaneously with multiple observers to minimize the potential for animal movement. The same observers should be used throughout the study because inter-observer variability may be high. Finally, we recommend that observers plot their bearings while in the field using field maps or computers. This will allow them to identify potentially erroneous bearings and reestimate a location while still in the field instead of discarding outlying bearings.

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