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Original article

Effects of plant phenology and vertical height on accuracy of radio-telemetry locations

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The use of very high frequency (VHF) radio-telemetry remains wide-spread in studies of wildlife ecology and management. However, few studies have evaluated the influence of vegetative obstruction on accuracy in differing habitats with varying transmitter types and heights. Using adult and fawn collars at varying heights above the ground (0, 33, 66 and 100 cm) to simulate activities (bedded, feeding and standing) and ages (neonate, juvenile and adult) of deer *Odocoileus* spp., we collected 5,767 bearings and estimated 1,424 locations (28-30 for each of 48 subsamples) in three habitat types (pasture, grassland and forest), during two stages of vegetative growth (spring and late summer). Bearing error was approximately twice as large at a distance of 900 m for fawn (9.9°) than for adult deer collars (4.9°). Of 12 models developed to explain the variation in location error, the analysis of covariance model (HT*D + C*D + HT*TBA + C*TBA) containing interactions of height of collar above ground (HT), collar type (C), vertical height of understory vegetation (D) and tree basal area (TBA) was the best model ($w_i = 0.92$) and explained ~ 71% of the variation in location error. Location error was greater for both collar types at 0 and 33 cm above the ground compared to 66 and 100 cm above the ground; however, location error was less for adult than fawn collars. Vegetation metrics influenced location error, which increased with greater vertical height of understory vegetation and tree basal area. Further, interaction of vegetation metrics and categorical variables indicated significant effects on location error. Our results indicate that researchers need to consider study objectives, life history of the study animal, signal strength of collar (collar type), distance from transmitter to receiver, topographical changes in elevation, habitat composition and season when designing telemetry protocols. Bearing distances in forested habitat should be decreased (approximately 23% in our study) compared to bearing distances in open habitat to maintain a consistent bearing error across habitats. Additionally, we believe that field biologists monitoring neonate ungulates for habitat selection should rely on visual locations rather than using VHF-collars and triangulation.

Key words: accuracy, error angle, height, location error, precision, radio-telemetry, vegetation

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Radio-telemetry has been used to study animal behaviour (Ozoga et al. 1982, Nelson & Mech 1999), range use and movement (Brinkman et al. 2005, Grovenburg et al. 2009, Jacques et al. 2009), habitat use and resource selection (DePerno et al. 2003, Grovenburg et al. 2010a,b) and survival (DePerno et al. 2000, Brinkman et al. 2004, Jacques et al. 2007). Triangulation is the most common technique used to estimate animal locations (Mech 1983, Springer 1979, Samuel & Kenow 1992) and very high frequency (VHF) telemetry continues to be a practical, reliable and cost effective method to study relationships between wildlife and their environment (Gilsdorf et al. 2008).

The quality of telemetry locations varies between operators and is dependent upon terrain, weather conditions, movements of the animal and distance between transmitter and receiver (White & Garrott 1986, Schmutz & White 1990, Kauhala & Tiilikainen 2002). Location error and bearing error of VHF-telemetry systems are critical for minimizing bias and generating the best data possible on free-ranging wildlife (Gilsdorf et al. 2008). Bearing error is the consistency of the system based on the standard deviation of estimated and true compass bearings (Withey et al. 2001, Gilsdorf et al. 2008), whereas location error is the average linear distance between estimated and actual locations (Zimmerman & Powell 1995, Gilsdorf et al. 2008). The power of statistical tests in habitat selection is greatly influenced by precision of bearings (White & Garrott 1986). Further, the magnitude of error associated with locations (error polygon) can bias measurements of habitat selection (Nams 1989) and failure to account for movement error can result in routes 1.5 times longer than the true route (Kauhala & Tiilikainen 2002). Researchers should strive to minimize and subsequently evaluate and report location error and bearing error of their telemetry systems (Withey et al. 2001, Gilsdorf et al. 2008).

Previous reports documenting influence of vegetation metrics (i.e. vertical height of vegetation, density of vegetation, tree canopy coverage, tree basal area and total tree density), vegetation growth, height of radio-collar above the ground or collar type (e.g. adult or fawn) on accuracy of VHF-telemetry results are limited. Researchers have placed collars in different habitats (Lee et al. 1985, Haskell 2007, Gilsdorf et al. 2008) and at heights $\leq$ 1 m above the ground to simulate activities of different species, including white-tailed deer *Odocoileus virginianus* (Haskell 2007, Townsend et al. 2007, Gilsdorf et al. 2008). However, those studies reported results pooled across habitats and height of collars above ground (Haskell 2007, Townsend et al. 2007). Studies should be conducted to determine whether seasonal change in vegetation affects location accuracy (Withey et al. 2001). Therefore, our objectives were to assess the influence of vegetation metrics in three habitat types (grassland, pasture and forested habitat) during two vegetation growth stages (pre-foliage (1-15 May) vs peak foliage (1-15 August)), at variable collar heights above the ground (0, 33, 66 and 100 cm) and for two collar types (adult vs fawn) on telemetry results. We predicted that telemetry error would be greater in forested habitat than in grasslands or pasture; thick vegetation would increase error due to signal bounce. Furthermore, we predicted that larger, stronger collars, as used for adult deer, would reduce error. Finally, we predicted that telemetry error would vary with height of the collar above the ground; collars closer to the ground would have greater error.

Material and methods

Study area

We conducted our study in Edmunds and Faulk counties, located in north-central South Dakota, USA, during spring (1-15 May) and summer (1-15 August) of 2009. Topography was characterized by flat to gently rolling terrain mixed with numerous pothole wetlands located among mounds of glacial till (Bryce et al. 1998), and the region was dominated by row crop agriculture (Smith et al. 2002). We evaluated three vegetation communities (pastureland, grassland and forest) to determine telemetry accuracy. Pastureland was a vegetation community composed of native mixed-grass vegetation dominated by smooth brome *Bromus inermis*, alfalfa *Medicago sativa*, switchgrass *Panicum virgatum*, big bluestem *Andropogon gerardii* and Indian grass *Sorghastrum nutans* that was managed by cattle grazing (Johnson & Larson 1999). Pastures were continuously grazed from spring to fall and vegetative cover (i.e. vertical height of overstory and understory vegetation) in pasture was less than in grassland (Grovenburg et al. 2012a,b). The grassland vegetation community was native mixed-grass vegetation dominated by western wheatgrass *Elymus smithii*, big bluestem, porcupine grass *Stipa spartea* and little bluestem *Schizachyrium scoparium* with no cattle disturbance. Grassland communities were

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composed primarily of Conservation Reserve Program (CRP) grasslands. The CRP is a voluntary program that pays landowners who enroll their agricultural land and convert it to permanent cover such as perennial grasslands (Fargione et al. 2009). CRP vegetation consisted primarily of CP1 (introduced grasses and legumes), CP2 (native grasses and legumes) and CP10 (existing grasses and legumes) plantings (Jones-Farrand et al. 2007). The CP1 plantings were composed primarily of intermediate wheatgrass *E. hispidus*, smooth brome, alfalfa and sweet clover *Melilotus* spp., whereas CP2 plantings consisted of Indian grass, switchgrass, big bluestem and little bluestem (Best et al. 1997, Higgins 2000). The forest vegetation community was limited across the landscape to small patches of planted trees or shelterbelts. This community was dominated by green ash *Fraxinus pennsylvanica*, American elm *Ulmus americana*, boxelder *Acer negundo*, hackberry *Celtis* spp. and eastern cottonwood *Populus deltoides* (Petersen 1984, Johnson & Larson 1999). We conducted telemetry operations only under optimal conditions with wind speed < 16.5 km/hour, no precipitation and mostly sunny skies and placed all collars in relatively flat ($< 0.5\%$ slope) habitat with limited elevation changes. To limit potential confounding effects of vegetation between receiver and transmitter, we estimated locations in grassland and pasture with clear line-of-sight (i.e. bearings for locations in grassland and pasture were never taken with forested cover between receiver and transmitter).

Data collection

To limit confounding effects of distance between transmitter type and receiver on location error and bearing error, we first tested possible threshold distances where bearing error differed between fawn and adult collar types. We randomly placed five model M4210 expandable breakaway fawn radio-collars (150-151 MHz) and five model M2410B adult deer radio-collars (150-151 MHz; Advanced Telemetry Systems, Isanti, Minnesota, USA) in flat, open pasture attached to wooden stakes 1.0 m above the ground and recorded the location of each collar using a Magellan Triton 1500 GPS accurate to 3-5 m (Magellan Navigation, Inc., Santa Clara, California, USA). The sensitivity of each collar was verified by the manufacturer at 66 dB for fawn collars and 52 dB for adult collars. We estimated bearings from fixed telemetry stations at distances ranging from 100 to 1,000 m and collected 120 bearings for each collar type.

Next, to evaluate factors that affect location error and to minimize bias, we used a double-blind approach and one experienced operator. Collar type, habitat type and height above ground were unknown to the telemetry operator. We randomly placed adult and fawn collars in three habitat types (forest, pasture and grassland) during two seasons to evaluate effects of changing vegetation, collar type and habitat type on telemetry error. We generated random sites by delineating equal-sized, numbered areas using ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California, USA) and randomly assigned collar type and height intervals to each site. We attached collars to wooden stakes with antennas fixed in upright positions at four intervals above the ground (0, 33, 66 and 100 cm) to simulate various activities (bedded, feeding and standing) and ages (neonate, fawn and adult) of deer and marked locations of wooden stakes with GPS (accurate to within 3-5 m). The wooden stake technique fails to account for signal absorption from the animal's body and signal attenuation or modulation due to movement of the animal (Cederlund et al. 1979, Cochran 1980, Lee et al. 1985, White & Garrott 1990). Therefore, actual precision of bearing errors with transmitters carried by animals may be poorer than indicated by our results (White & Garrot 1990). We estimated the location for a single collar type and a single height above ground at each random location.

We collected bearings using a truck-mounted null-peak antenna system equipped with a C100 electronic compass (KVH Industries, Middletown, Rhode Island, USA; Brinkman et al. 2002). We used 87 GPS-marked (accurate to within 3-5 m) telemetry stations to conduct triangulations and estimated locations using LOCATE III using the maximum likelihood estimator (Nams 2006) with a minimum of three azimuths (range 3-5) for each location; we collected 28-30 locations for each subsample (e.g. fawn collar in grassland habitat at 33 cm, pre-foliage). To collect the most precise location estimates, we used telemetry stations where at least two bearings would intersect at 90° from each location (Withey et al. 2001). To minimize potential bias, we used the same vehicle, telemetry system and operator for all bearings and calibrated the compass each day based upon manufacturer instructions. We chose telemetry stations that provided a combination of distances to transmitters with total and interior bearing angles simulating realistic telemetry condi-

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tions (Haskell 2007). Telemetry stations were located on secondary gravel roads or ranch roads > 500 m from power lines.

We used a Robel pole with 2.54-cm increments to estimate the vertical height of grassland vegetation and forest understory vegetation at collar locations and at four locations 2 m from collar locations along two perpendicular transects (Robel et al. 1970). We used a 10-factor prism to record and measure all trees > 15.24 cm in diameter (large tree) at breast height in a variable-radius plot (Sharpe et al. 1976) at collar locations. We measured all trees < 15.24 cm in diameter (small tree) at breast height in a 5.0-m fixed-radius plot at collar locations. Total tree density combined small and large trees for the basal area metric (m^2/ha). We estimated tree canopy cover using a spherical densiometer (Geographic Resource Solutions, Arcata, California, USA) at each collar location and from four points, 2 m from the collar location along each transect.

Data analysis

We used a linear mixed-effects model and Wald Z-tests to assess among-collar variability for adult and fawn collar types. We used regression analysis to determine the relationship between bearing error and distance. We used a two-way analysis of variance (ANOVA) to test for differences in distance between transmitter and receiver among collar heights above the ground and used a t-test to determine differences in distance between transmitter and receiver among collar types. We used ANOVA to test for differences in location error among habitat types at each collar height.

We calculated error angles (bearing error) and location error (linear distance error) for all estimated locations (Zimmerman & Powell 1995, Withey et al. 2001, Gilsdorf et al. 2008). We evaluated collinearity between vegetation metrics (vertical height of overstory vegetation (VH), vertical height of understory vegetation (D), tree canopy coverage (TCC), tree basal area (TBA)) using Pearson's correlation coefficient ($|r| > 0.50$). We used analysis of covariance (ANCOVA) to determine the effects of vegetation metrics on location error and set collar type (C) and collar height above ground (HT) as categorical variables. We posited 12 *a priori* models using ANCOVA of how location error might be influenced by interactions between vegetation metrics and categorical variables based on field experience of the authors as well as previously published literature (Lee et al. 1985, Haskell 2007, Gilsdorf et al. 2008). We used Akaike's Information Criterion (AIC) to select the most parsimonious model and considered models differing by ≤ 2 ΔAIC from the selected model as potential alternatives (Burnham & Anderson 2002). We used Akaike weights (w_i) as an indication of support for each model (Burnham & Anderson 2002, Anderson 2008). We used the coefficient of determination (R^2) to determine model fit (Zar 2010). Statistical tests were conducted using SAS version 9.2 (SAS Institute 2000) with an experiment-wide error rate of $\alpha = 0.05$. We determined repeatability (i.e. index for quantifying the accuracy of measurements and consistency of variables) using the ANOVA-based approach and the rptR package in Program R version 2.14.2 (R Development Core Team 2009, Nakagawa & Schielzeth 2010); repeatability significantly > 0 was indicated by the P-value from the original model test (Donner 1986, Lessells & Boag 1987).

Results

We detected no among-collar variability for fawn ($Z = 0.34$, $P = 0.367$, $N = 120$) or adult ($Z = 0.73$, $P = 0.233$, $N = 120$) collars. We detected differences between adult and fawn collars; bearing error was approximately twice as large at 900 m for fawn (9.9°, $r^2 = 0.78$) than adult collars (4.9°, $r^2 = 0.83$; Fig. 1). To minimize bias associated with bearing error when comparing adult and fawn collars, we used maximum bearing distance for fawn (600 m) and adult collars (800 m) where bearing error was similar (approximately 4.3°). We collected 5,767 bearings and estimated 1,424 loca-

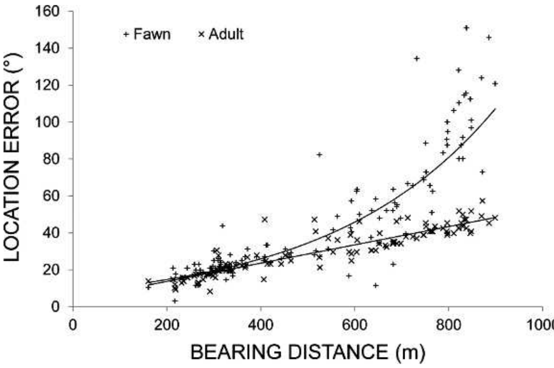

Figure 1. Bearing error as a function of bearing distance for adult ($y = 0.005x + 0.117$; $r^2 = 0.83$, $P < 0.001$, $N = 120$) and fawn ($y = 0.799e^{0.003x}$; $r^2 = 0.78$, $P < 0.001$, $N = 120$) collars in north-central South Dakota, USA, May and August of 2009.

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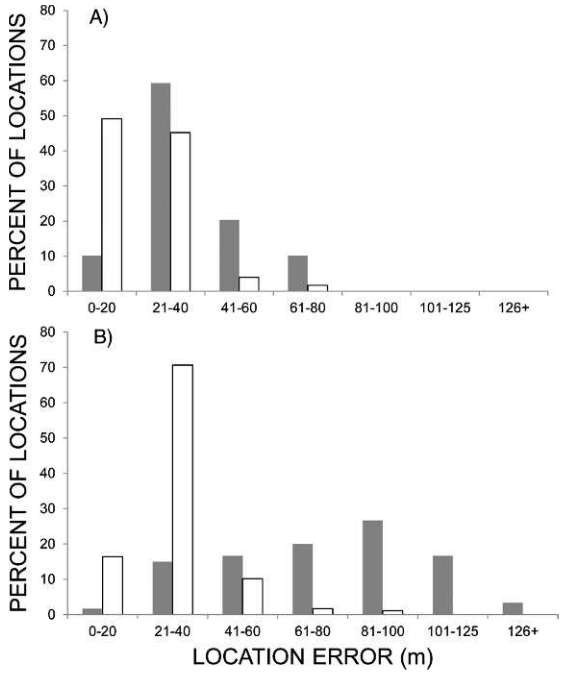

Figure 2. Frequency of estimated location error for adult (A; N = 239) and fawn (B; N = 240) collar locations on the ground (gray bars) and above ground (white bars) in pasture habitat. Location errors were pooled for 33, 66 and 100 cm above ground in north-central South Dakota, USA, May and August of 2009.

tions (28-30 for each of 48 subsamples defined by combinations of four heights, two seasons, three habitat types and two collar types). Mean number of bearings used for locations for fawn and adult collars was 4.0 (SE = 0.1, N = 712) and 4.1 (SE = 0.1, N = 712), respectively; 84.6% of locations were estimated with $\geq$ 4 bearings. Mean bearing distance for locations was similar for heights above ground ($F_{4,\ 5761} = 0.33$, $P = 0.856$) and collar types ($t = 0.19$, df = 5,764, $P = 0.847$). We collected 704 pre-foliage locations and 720 peak-foliage locations. Because bearing error and location error were highly correlated for fawn ($r^2 = 0.93$) and adult ($r^2 = 0.74$) collars, we investigated only the relationship of location error with collar height, collar type and vegetation metrics in our models.

Frequency distribution of location errors indicated that 94.4 and 87.0% of adult and fawn location errors, respectively, were < 40 m for collars above the ground (Fig. 2A); whereas 69.5 and 16.7%, respectively, were < 40 m for collars on the ground (see Fig. 2B). During the pre-foliage period, location error differed among habitat types for adult ($F_{2,85} \geq 3.04$, $P \leq 0.044$) and fawn ($F_{2,79} \geq 7.79$, $P \leq 0.001$) collars at all four intervals above the ground (0, 33, 66 and 100 cm); location error was larger in forest than in

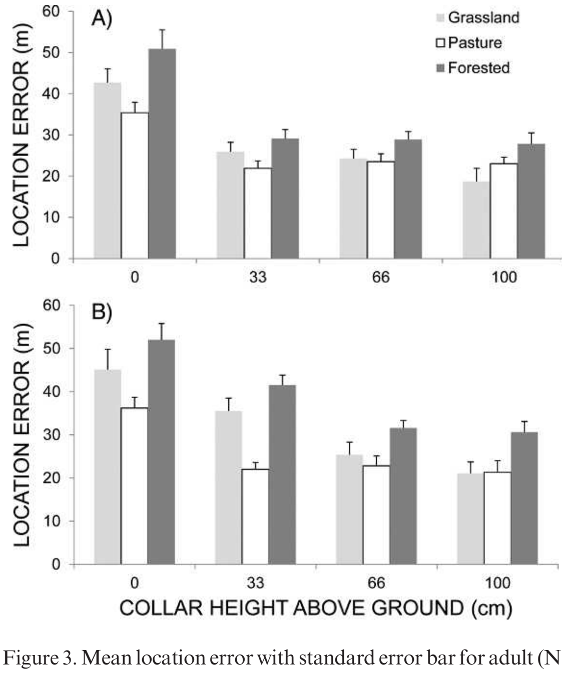

Figure 3. Mean location error with standard error bar for adult (N = 712) collar locations at 0, 33, 66 and 100 cm height above the ground in three habitat types (pasture, grasslands and forest) during A) pre-foliage (1-15 May) and B) peak foliage (1-15 August) seasons in north-central South Dakota, USA, 2009.

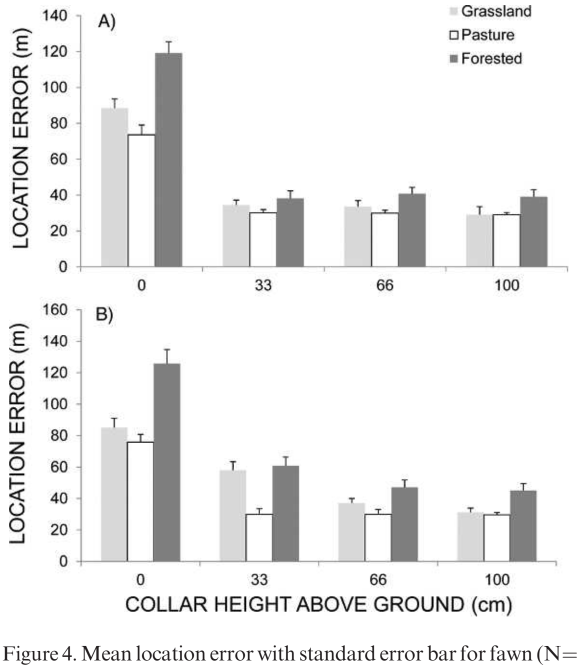

Figure 4. Mean location error with standard error bar for fawn (N = 712) collar locations at 0, 33, 66 and 100 cm height above the ground in three habitat types (pasture, grasslands and forest) during A) pre-foliage (1-15 May) and B) peak foliage (1-15 August) seasons in north-central South Dakota, USA, 2009.

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Table 1. Mean and 95% confidence intervals for vegetation metrics during pre-foliage (1-15 May) and peak-foliage (1-15 August) periods used for analysis of covariance to estimate very high frequency (VHF) telemetry location error. D = vertical height of understory vegetation (cm), TCC = tree canopy cover (%) and TBA = tree basal area (m^2/ha).

	Pre-foliage		
Habitat type	D	TCC	TBA
Pasture	11.8 (11.6-12.0)		
Grassland	23.8 (23.2-24.4)		
Forested cover	21.4 (21.0-21.8)	36.6 (35.4-37.8)	10.7 (5.0-16.4)
	Peak-foliage		
Habitat type	D	TCC	TBA
Pasture	11.9 (11.7-12.1)		
Grassland	58.2 (56.9-59.6)		
Forested cover	55.4 (53.4-57.4)	69.6 (67.8-71.4)	11.6 (5.5-17.7)

grasslands or pasture (Figs. 3 and 4). During the peak-foliage period, location error differed among habitat types for adult ($F_{2,87} \geq 3.69$, $P \leq 0.029$) and fawn ($F_{2,87} \geq 6.19$, $P \leq 0.003$) collars at all four intervals above the ground (0, 33, 66 and 100 cm); location error was larger in forest than in grasslands or pasture (see Figs. 3 and 4).

Pearson correlation indicated that the vertical height of overstory vegetation and vertical height of understory vegetation were correlated (r = 0.79). Therefore, we used vertical height of understory vegetation, tree canopy cover and tree basal area for model analyses (Table 1). The model (HT*D + C*D + HT*TBA + C*TBA) was the best approximating model (w_i = 0.92; Table 2) of location error. This model was $\geq$ 4.9 ΔAIC units from remaining models and weight of evidence supporting this model was > 11.5 times that of remaining models. The top-ranked model indicated that HT, D, C, TBA, D*HT, TBA*HT, C*D and TBA*C explained approximately 71% ($R^2 = 0.71$) of the variation in location error. Vegetation metrics influenced location error (Table 3), which increased with greater vertical height of understory vegetation and tree basal area. Also, parameter estimates (see Table 3) differed in location error among categorical variables. Location error was larger for both collar types at 0 cm above the ground, and error for 33 and 66 cm above ground was similar to 100 cm above the ground. Additionally, location error was less for adult than fawn collars; mean location error for fawn collars was greater than adult collars at all heights above the ground (see Figs. 3 and 4). Interaction of

Table 2. Akaike's Information Criterion (AIC) model selection of *a priori* analysis of covariance models to determine the influence of vegetation metrics, height of collar above the ground and collar type on very high frequency (VHF) telemetry location error in north-central South Dakota, USA, May and August of 2009. HT = height of collar above ground (0, 33, 66 or 100 cm), D = vertical height of understory vegetation, C = collar type (adult or fawn), TBA = tree basal area, TCC = tree canopy cover, * indicates interaction between vegetation metric and categorical variable, K = number of parameters, ΔAIC = difference in AIC relative to minimum AIC and w_i = Akaike weight (Burnham & Anderson 2002).

Model	K	AIC	ΔAIC	w_i
HT*D + C*D + HT*TBA + C*TBA	21	12809.10	0.00	0.92
HT*D + HT*TBA + HT*TCC + C*D + C*TBA + C*TCC	30	12814.00	4.90	0.08
HT*D + HT*TCC + C*D + C*TCC	21	12880.60	71.50	0.00
HT + C + D + TCC + TBA	6	12946.10	137.00	0.00
HT*D + C*D	10	13000.20	191.10	0.00
HT + C + D	4	13047.30	238.20	0.00
HT	2	13360.00	550.90	0.00
C + D + TBA	4	13520.50	711.40	0.00
C	2	13639.50	830.40	0.00
TBA + TCC	3	13724.20	915.10	0.00
TBA	2	13721.50	912.40	0.00
D	2	13758.20	949.10	0.00

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Table 3. Parameter estimates and 95% confidence intervals from top-ranked analysis of the covariance model to determine the influence of vegetation metrics, height of collar above the ground and collar type on very high frequency (VHF) telemetry location error. HT = height of collar above ground (0, 33, 66 or 100 cm), D = vertical height of understory vegetation, C = collar type (0 = adult and 1 = fawn), TBA = tree basal area, TCC = tree canopy cover, LCL = 95% lower confidence limit and UCL = 95% upper confidence limit.

Parameter	Level	Estimate	LCL	UCL
Intercept		27.82	23.35	32.29
HT	0	31.27	25.63	36.91
HT	33	5.24	1.39	9.10
HT	66	2.87	-2.77	8.51
HT	100	0.00		
D		0.22	0.10	0.34
D*HT	0	0.32	0.20	0.44
D*HT	33	0.44	0.28	0.60
D*HT	66	-0.06	-0.27	0.10
D*HT	100	0.00		
TBA		0.41	0.27	0.55
TBA*HT	0	0.76	0.56	0.96
TBA*HT	33	-0.12	-0.30	0.06
TBA*HT	66	0.14	-0.06	0.34
TBA*HT	100	0.00		
C	0	-9.79	-13.83	-5.75
C	1	0.00		
D*C	0	-0.23	-0.35	-0.11
D*C	1	0.00		
TBA*C	0	-0.38	-0.52	-0.24
TBA*C	1	0.00		

vegetation metrics and categorical variables indicated significant effects on location error (see Table 3). Vertical height of understory vegetation increased location error at collar heights of 0 and 33 cm above the ground and tree basal area increased location error for collars 0 cm above the ground. Furthermore, collar type interacted with vertical height of understory vegetation and tree basal area; location error was less for adult collars with increasing vertical height of understory vegetation. Also, tree basal area interacted with collar type; location error was less for adult collars with increasing tree basal area (see Table 3). The estimate of repeatability for location error (R_A = 0.76, 95% CI = 0.68-0.85) was > 0 ($P < 0.001$).

Discussion

Location error varied among collar heights above the ground; accuracy was better for adult and fawn collars at varying distances above the ground than for collars on the ground. Transmitters at ground level were affected by minimal changes in slope, resulting in signal bounce. Large accuracy errors have been attributed to signal bounce from non-line-of-sight (NLOS) receiving points (Garrott et al. 1986), and signal bounce from environmental obstructions can have pronounced effects on bias estimation and measurement of precision (Lee et al. 1985). Transmitters less than half a wavelength from the ground (approximately 1 m at 150 MHz) may have noticeably affected signal propagation (Cochran 1980, Withey et al. 2001). Although signal bounce can be easily detected when testing a system, large accuracy error due to signal bounce may be impossible to detect when transmitter location is unknown; 52% of transmitter locations which were not within line-of-sight of the receiving antenna produced bearings with large mean errors (Garrott et al. 1986). Kauhala & Tiilikainen (2002), with a radio-transmitter fixed on the lower leg of a researcher, documented that location error increased the length of route of movement by a factor of 1.5. Additionally, only 33% of estimated locations were in the correct habitat patch, with accuracy better in larger habitat patches (Kauhala & Tiilikainen 2002). Importantly, during our

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study, location error of collars located on the ground (representing a bedded neonate ungulate or a small mammal) was greater than for collars located at 33 cm above the ground (distance similar to bootleg fixed radio-transmitter; Kauhala & Tiilikainen 2002) by a factor of 0.75 and 1.45 for adult and fawn collars, respectively. Minimal variation in topography can have a significant influence on bearing error (Townsend et al. 2007). We suspect the increased location error for collars on the ground would result in increasingly biased location estimates (White & Garrott 1990), potentially contributing to significant errors in estimation of movement, habitat selection (Kauhala & Tiilikainen 2002, Townsend et al. 2007) and home range. We suggest that field biologists monitoring neonate ungulates for habitat selection account for the potential of inflated location errors during study design or rely on visual locations rather than those estimated from triangulation.

Mean location error differed between pre- and peak-foliage periods; we suspect that dense vegetation may have increased error through increased signal bounce. Kauhala & Tiilikainen (2002) observed that location error varied between seasons, being larger in summer than in winter. Distance between transmitter and receiver were similar between seasons and seasonal location error differences strongly supported that increased vegetation in summer affected the radio signal (White & Garrott 1990, Kauhala & Tiilikainen 2002). Signal bounce can occur due to reflective surfaces, such as wet snow or dense vegetation (Beaty & Tomkiewicz 1990, Samuel & Fuller 1996, Withey et al. 2001). During our study, location error increased for collars that were obstructed by vegetation. Vegetation in pastures did not influence telemetry error because grazing by cattle removed much of the vegetative biomass, whereas grasslands without grazing pressure had taller, denser vegetation that obstructed collars and increased telemetry error.

Location error was influenced by tree basal area; accuracy was greater in areas with fewer trees. Similar to our results with VHF-collars, forest influenced GPS-collar performance; reduced fix rates and accuracy occurred with increasing density of forest (D'Eon et al. 2002). Testing in three forested sites resulted in error polygons too large to determine locations of test transmitters (Hupp & Ratti 1983, Withey et al. 2001). Therefore, signal strength and accuracy can decrease if antennas are close to tree limbs or under large trees (Hupp & Ratti 1983, Cottam 1988, Withey et al. 2001). Additionally, foliage in a hardwood forest area increased the proportion of bearing error (Chu et al. 1988, Withey et al. 2001). Conflicting results have been documented concerning the influence of wooded habitat types on accuracy, emphasizing the importance of a beacon study unique to each study area (Withey et al. 2001). However, if error polygons surpass the size of forested patches (i.e. shelterbelts in our study area), resource selection analysis would be biased without accounting for signal bounce (Porter & Church 1987). For example, during our study, 65.2% (313 of 480) of error polygons for locations in forest patches overlapped other habitat types. Bearing distances in forest need to be decreased (approximately 23% in our study) compared to bearing distances in open habitat to maintain a consistent bearing error across habitats.

Accuracy differed between collar types; mean location error was smaller for adult than for fawn collars. Differences in sensitivity between adult (51-53 dB) and fawn (65-66 dB) collars may partially explain accuracy differences documented during our study. The adult collars used were 3-stage transmitters, which had a 12 dB increased range compared to our 2-stage fawn transmitters (T. Garin, pers. comm., Advanced Telemetry Solutions). We suspect that greater error of fawn collars resulted from lower signal strength and increased signal bounce. Further, we speculate that behavioural differences between adults and fawns may exacerbate increased location error caused by lower signal strength of fawn collars. For instance, fawns make use of microhabitat characteristics such as tall grass and woody cover when selecting bed sites (Huegel et al. 1986, Grovenburg et al. 2010b), potentially contributing to greater accuracy error. Therefore, researchers may need to rely on visual locations if their objective is assigning habitat use.

Location error differed between habitat types and was greater in forest than in grassland or pasture. In forest and grassland, location error was influenced by dense understory vegetation and increasing tree basal area. Studies of habitat use in complex vegetative mosaics require precise locations (White & Garrott 1990); therefore, researchers need to test their telemetry system in each study area. Signal bounce contributes to inaccurate location estimates that should be identified

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prior to data collection (Garrott et al. 1986). Though accuracy and precision of telemetry location data is well-documented in the ecological literature (White & Garrott 1986, Schmutz & White 1990, Kenward 2001, Kauhala & Tiilikainen 2002), to our knowledge, our study is the first to quantify the effects of vegetation metrics on telemetry location error across variable habitat types, collar types and collar height above the ground using large numbers of VHF bearings (N = 5,767) and locations (N = 1,424). Researchers need to consider study objectives, life history characteristics of the study animal, signal strength of collar, topographical changes in elevation, habitat composition and time of year (accounting for vegetative growth changes) when designing telemetry protocols. For example, our results indicate that special attention is needed to minimize location error when animals are radio-tracked in forest with dense understory vegetation, and when the animal being radio-tracked has a physical (e.g. mesomammal) or behavioural tendency (e.g. bedded or feeding) that results in the transmitter being close to the ground. If research goals rely on obtaining accurate and precise telemetry locations (e.g. resource selection, habitat use or microhabitat analyses), researchers must understand the magnitude and direction of bias in telemetry error and incorporate this information into study designs. Our results will aid others in designing telemetry studies and optimizing interpretation of telemetry location data and should be directly applicable to any study of comparably sized animals (e.g. roe deer *Capreolus capreolus*, pronghorn antelope *Antilocapra americana* and African antelope such as impala *Aepyceros melampus* and lesser kudu *Tragelaphus imberbis*).

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