

EVALUATION OF AUTOMATED RADIO TELEMTRY TECHNOLOGIES FOR GROUND-
DWELLING SPECIES

by

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ABSTRACT

The Motus Wildlife Tracking System employs automated radio telemetry towers to remotely record transmitter detections. While Motus technologies have successfully been used to study large-scale space use of migrating birds, they have not been assessed for use in evaluating fine-scale space use of ground-dwelling birds. We used GLMs to estimate the accuracy, precision, and detection probability of Motus transmitters relative to standard VHF transmitters, with a focus on assessing the technology for evaluating fine-scale space use of ground-dwelling birds. Our results supported strong effects of transmitter type on transmitter performance metrics. Triangulated estimates of Motus transmitter locations were more precise and accurate than those of VHF, particularly at short distances. However, the mean observable distance of VHF transmitters ($597 \pm 69\text{m}$) was nearly twice that of the Motus transmitters ($264 \pm 30\text{m}$). In 2023, we equipped 56 sharp-tailed grouse with Motus transmitters in areas with stationary Motus towers, but only a small fraction of grouse were detected simultaneously by enough towers to estimate their locations accurately. Only 26 grouse were detected simultaneously by at least 2 towers on fewer than 30 unique occasions, none of which occurred during the critical nesting period. Although triangulation accuracy and precision were higher for handheld Motus technology than traditional VHF, reduced detection distances and inconsistent automated detection limited the utility of Motus technology for fine-scale assessments of space use for ground-dwelling birds in western Montana.

CHAPTER ONE

INTRODUCTION

In recent years, advancements in automated radio telemetry technologies, such as the introduction of the Motus Wildlife Tracking System, have changed the way researchers track wildlife. Since the 1960s, researchers have relied on radio telemetry to track many species of wildlife, although telemetry is often time- and labor-intensive (Adams 1965, Cochran et al. 1965). Automated telemetry systems have created opportunities to save time and money by reducing technician hours spent in the field locating and triangulating animals using handheld radio telemetry equipment. These systems also provide continuous detection data, whereas conventional radio telemetry methods typically involve locating an animal a couple of times weekly due to constraints in time and personnel. Research on migratory species has benefited from the use of automated telemetry, but the ability to use automated telemetry systems to study the fine-scale space use of non-migratory, ground-dwelling species has not been widely assessed (Taylor et al. 2017, Griffin et al. 2020). Initial research suggests that the detection range and location accuracy of automated telemetry is much lower for ground-dwelling animals than animals in flight (Kays et al. 2011, Ward et al. 2013, DeGregorio et al. 2015, Crewe et al. 2019). Further rigorous studies are needed to evaluate spatial resolution capabilities and limits of automated radio telemetry systems for estimating fine-scale space use of ground-dwelling species.

Traditionally, researchers have monitored ground-dwelling birds using conventional ground-based radio telemetry consisting of short-range very high frequency (VHF) transmitters and antennas mounted on towers, vehicles, or researchers to obtain animal location estimates

(Bridge et al. 2011). Early applications of VHF radio telemetry in wildlife research ranged from using radio waves to measure temperatures of penguin eggs to the development of the first radio-collars by the Craighead brothers to study grizzly bear ecology in Yellowstone National Park by locating the instrumented animals (Adams 1965, Craighead et al. 1995, Hebblewhite and Haydon 2010). Conventional VHF radio telemetry allows researchers to track wildlife movements and examine questions regarding wildlife movement, home range, and habitat use, but requires a high level of time and effort to manually detect tagged wildlife (Miller et al. 2010). These time and effort requirements limit how many individuals are tracked, the number of detections, and the temporal and spatial scale that can be sampled (Taylor et al. 2017).

In the 1980s, satellite-based communication systems such as Global Positioning Systems (GPS), Iridium, and Argos were developed creating opportunities for wildlife to be tracked remotely, but early satellite compatible transmitters were heavy and only suitable for large species, such as moose or bears (Rodgers et al. 1996, Schwartz and Arthur 1999). Advancements in recent years include reduced battery sizes, allowing smaller transmitters to be deployed on smaller species; development of miniscule solar panels, enabling transmitter batteries to sustain themselves for long periods of time; and remote data retrieval systems that upload satellite-borne data through satellite platforms and cellular networks (Miller et al. 2010). For example, satellite compatible transmitters such as Platform Transmitter Terminals (PTTs; GeoTrak Inc., Apex, NC, USA) weigh as low as 5 grams, are powered by small solar panels, and transmit data regularly using remote communication with Argos satellites (McKinnon and Love 2018). Although satellite technology reduces the need for on the ground manual tracking of wildlife using VHF transmitters, it remains a costly option with the average individual transmitter costing \$2,000 -

\$8,000 which in turn reduces sample sizes of studies due to the prohibitive costs of purchasing transmitters (Hebblewhite and Haydon 2010).

Automated radio telemetry systems (ARTS) are a rapidly developing tool in wildlife monitoring that employ VHF technology and remotely operated receivers to facilitate continuous monitoring data without the limitations of GPS technology (e.g., cost and size). Today, one of the most widely used automated telemetry systems is the Canada-based Motus Wildlife Tracking System (hereafter “Motus” or “Motus Network”). Invented in 2012, Motus is a global network of automated radio tower arrays managed by a collaboration of researchers and organizations and currently has over 1,800 receiver stations across 34 countries (Taylor et al. 2017). Animals are fitted with a single-frequency transmitter (166.380 MHz in the western Hemisphere), which can be detected either by a network of remote radio receivers on the landscape (e.g., towers or nodes) equipped with direction or omni antenna, or by handheld receivers and Yagi antennas. Each transmitter is digitally encoded with a unique identifier that is emitted through a pattern of digital pulses and used to differentiate individual detections. Transmitters are readily available and are manufactured by one of two collaborating companies – Lotek (Newmarket, ON, CA) or Cellular Tracking Technologies (CTT; Rio Grande, NJ, USA). Motus towers consist of 2 to 6 antennas mounted on a pole, which can be either 3–5-element directional Yagi antennas, 9-element directional Yagi antennas, or small omni-directional antennas. Detections of transmitters are monitored by a solar powered receiver at the base of the tower that relays detection data to the Motus database using cellular data or internet connection (Taylor et al. 2017). Towers are deployed by organizations or individual landowners and arranged on the landscape according to the interested party’s research goals. For example, many migratory studies use lines of towers

arranged in such a way to detect birds as they pass geographic landmarks (Marchand Camille et al. 2020), point-to-point arrays for detecting migratory movements and stopovers between key geographic locations (Mills et al. 2011), or strategic grid arrays to detect presence/absence in a management area (Taylor et al. 2017, DeSimone et al. 2023).

The Motus Network has primarily been used to understand large-scale, migratory movements of airborne species (Mills et al. 2011, Taylor et al. 2017, Lenske and Nocera 2018, Herbert et al. 2022). Although Motus has successfully been used to study large-scale movement ecology and phenology of migrating species, uncertainties remain in our understanding of environmental and technical factors influencing the suitability of this technology to detect wildlife and evaluate fine-scale space use, particularly of ground-dwelling species (Ward et al. 2013, Crewe et al. 2019, Paxton et al. 2022). Nine-element directional Yagi antennas used on Motus towers have an estimated detection distance of up to 15 km for unobstructed transmitters (e.g., animals in flight; Taylor et al. 2017). However, maximum detection distances have not been rigorously tested for species that primarily dwell on the ground where radio signal propagation can be impacted by vegetation and topography. Preliminary studies evaluating automated telemetry suggest a lower detection range for ground-level wildlife compared to animals at canopy-level or airborne (Kays et al. 2011, Crewe et al. 2019). Reported signal range, detection rates, and location estimates when transmitters are at or near ground-level vary considerably (Kays et al. 2011, Ward et al. 2013, DeGregorio et al. 2018, Crewe et al. 2019) and research is needed to understand how location metrics vary with topography and other environmental variables, especially when fine-scale resolution is crucial to understanding the ecology of the species. Furthermore, initial research suggests automated tower spacing, location

of the transmitter within the tower array, edge effects, and network density impact location estimate accuracy and precision (Ward et al. 2013, Taylor et al. 2017, Paxton et al. 2022). Improved understanding of automated radio telemetry technology performance will aid in designing systems for unbiased and precise estimates of fine-scale space use of ground-dwelling animals. Therefore, rigorous studies comparing automated and conventional technology methods for estimating fine-scale space use of ground-dwelling species is needed. Such comparisons of methodology will enhance understanding of technology performance across varying topography and environmental variables, leading to more accurate space-use inferences with automated telemetry data.

The reintroduction of sharp-tailed grouse (*Tympanuchus phasianellus*) into western Montana presents a unique opportunity to evaluate the suitability of the Motus automated radio telemetry technology to monitor a ground-dwelling avian species. The sharp-tailed grouse is a ground-dwelling bird that historically occurred in 21 states and 8 Canadian provinces, consequently being the most widely distributed of all prairie grouse (*Tympanuchus* spp.; (McNew et al. 2023). While sharp-tailed grouse once occupied all grass-dominated areas of Montana, populations west of the Continental Divide are thought to be extirpated, leading to a reintroduction effort by Montana Fish, Wildlife and Parks in collaboration with MPG Ranch and Montana State University (Young and Wood 2012). Sharp-tailed grouse are a model species for the evaluation of automated radio telemetry technologies to assess space use of ground-dwelling birds because they 1) spend most of their lives on the ground, and 2) use a variety of different vegetation structures and topographical features during their life-histories (McNew et al. 2023). Differing requirements for nesting and winter habitat, for example, require sharp-tailed grouse to

use a large range of habitat types across topographical ranges, allowing evaluations of technologies in varying habitat types, elevational gradients, and topographical structures such as within draws and across rolling hills.

The goal of my research was to address knowledge gaps regarding effective detection distances and the precision and accuracy of estimated locations obtained using the Motus automated radio telemetry system and associated handheld technology compared to conventional VHF technology when transmitters are at ground-level. Specifically, my objectives were to 1) evaluate and compare the effective detection distances, triangulation accuracy and precision, and monitoring effort required for Motus and VHF technologies when transmitters are at ground-level, for application in studies of ground-dwelling birds and 2) evaluate the effective detection rates, detection distances, and triangulation accuracy and precision of automated Motus towers when transmitters are at ground-level, for application in space-use studies of ground-dwelling birds.

CHAPTER TWO

METHODS

Study Area

My study area consisted of four field sites in west-central Montana: Blackfoot-Clearwater Wildlife Management Area, MPG Ranch, Red Bluff Research Ranch, and a private working ranch in the Blackfoot Valley south of Helmville, Montana (Fig. 1). These study areas are representative of intermountain valley grassland in western Montana and are either established sharp-tailed grouse reintroduction sites or have similar site characteristics to reintroduction sites in the Blackfoot and Bitterroot Valleys.

Two of my field sites are located in the Blackfoot Valley where vegetation is dominated by shrub-steppe plant communities (McNew et al. 2017). The Blackfoot-Clearwater WMA is managed by Montana Fish, Wildlife and Parks (MFWP) and situated approximately 60-km northeast of Missoula, Montana where it encompasses nearly 17,800 hectares of big game winter habitat on the north side of Highway 200 and the Blackfoot River. My study area south of Helmville, MT is centered around an approximately 5,870-hectare private ranch where the last documented sharp-tailed grouse lek persisted in western Montana (McNew et al. 2017). This site is predominantly made up of private land used for grazing livestock production. Vegetation consists of mountain big sagebrush (*Artemisia tridentata*), Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca campestris*), bluebunch wheatgrass, arrowleaf balsamroot, western yarrow (*Achillea millefolium*) and yellow salsify (*Trapopogon dubius*) with areas of Rocky Mountain

juniper (*Juniperus scopulorum*), Douglas fir (*Pseudotsuga mensezii*), and ponderosa pine (*Pinus ponderosa*) encroachment (McNew et al. 2017).

MPG Ranch is a 6,500-hectare privately owned property in the Bitterroot Valley of Montana, located approximately 40-km south of Missoula, Montana, which focuses on promoting conservation and supporting restoration and ecology research. In the Bitterroot Valley, vegetation consists of introduced forage grass species with remnants of native grass and shrub communities (McNew et al. 2017). Rangeland vegetation on MPG Ranch includes bitterbrush (*Purshia tridentata*), sagebrush (*Artemisia spp.*), rough fescue (*Festuca campestris*), bluebunch wheatgrass (*Pseudoroegneria spicata*), arrowleaf balsamroot (*Balsamorhiza sagittate*), lupine (*Lupinus spp.*), common yarrow (*Achillea millefolium*), hairy goldenaster (*Heterotheca villosa*), crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*Thinopyrum intermedium*), cheatgrass (*Bromus tectorum*), leafy spurge (*Euphorbia virgata*), western salsify (*Tragopogon dubius*), and spotted knapweed (*Centaurea stoebe*) (McNew et al. 2017; B. Larkin, MPG Ranch, personal communication). Seasonally dry draws on MPG Ranch are composed of deciduous shrub communities and aspen stands (B. Larkin, MPG Ranch, personal communication).

Red Bluff Research Ranch is a 5,500-hectare ranch located adjacent to the town of Norris, Montana and approximately 50-km west of Bozeman, Montana. The ranch is operated by Montana State University (MSU) as an agricultural research facility and maintains several hundred cattle and sheep on the ranch year-round. Perennial vegetation on Red Bluff Research Ranch includes Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), Sandberg bluegrass (*Poa secunda*), spikemoss (*Selaginella spp.*), big sagebrush (*Artemisia tridentata*), and fringed sage (*Artemisa frigida*) (Ozeran 2016).

Capture and Tagging

During April – May 2023, I captured sharp-tailed grouse in collaboration with MSU and MFWP using walk-in funnel traps at leks with ≥ 15 male grouse present. Fifty-four sharp-tailed grouse (24 females and 30 males) were fitted with digitally coded radio transmitters (Lotek Avian NanoTag NTQB2-9-2; Newmarket, ON, CA) that are compatible with automated Motus technology. Burst interval was 3 seconds, transmitters weighed approximately 12.4 g, and antenna were 7.5-inches in length. Grouse fitted with transmitters were released in the Blackfoot Valley or the Bitterroot Valley within 24 hours of capture.

Automated Motus Evaluations

Automated Motus towers in my study area were deployed prior to implementation of my study by various agencies and private landowners. I collaborated with MFWP to construct 2 towers at the Helmville, MT field site, which were added to increase coverage of the single existing tower. Tower locations were selected to maximize antenna range, accessibility for tower maintenance, cellular coverage, and to reduce signal interference. I anticipated that adding towers to the local Motus network would increase the quantity of transmitter detections and allow for multiple detections of one transmitter from differing antenna bearings. I did not place additional towers in the Bitterroot Valley study area because 9 Motus towers were already deployed on or adjacent to MPG Ranch and were estimated by Motus to provide coverage of the area based on the estimated range of 15 km when an animal is airborne and has a clear line of sight to the tower (Taylor et al. 2017). In total, the Bitterroot and Blackfoot Valleys contained 18 active Motus towers during my field season. The towers in my study area were equipped with a

combination of 6-element and 9-element Yagi antenna oriented horizontally at various angles to maximize coverage. Motus towers continuously monitored a frequency of 168.00 MHz throughout the study period.

I retrieved and filtered Motus tower detection data from the Motus database using the ‘motus’ package in R Statistical Software and associated handbook for data analysis (Birds Canada 2024). Motus detections are composed of “runs” which are sequences of hits, or detections. A run length ≥ 3 hits provides higher confidence of a true detection rather than a false detection which can be caused by random radio noise, duplicate transmitters, or aliased transmitters which occurs when two transmitters near each other produce a signal that looks like a third transmitter which is not actually present (Birds Canada 2024). I filtered Motus data by eliminating detections with short runs (≤ 3 hits) which have a high probability of being false detections and should be omitted from further analyses (Birds Canada 2024). Next, I examined the locations of the Motus towers that detected our transmitters and eliminated detections by towers that did not make biological sense – (e.g., 275 detections by the McGill Bird Observatory in Quebec). To evaluate whether I obtained a sufficient number of simultaneous detections for each individual in our data to estimate locations and home ranges, I compiled occurrences of simultaneous detections by at least two Motus towers. I defined a simultaneous detection as detections of a single transmitter occurring by two towers within a 15-minute timeframe.

Manual Radio Telemetry

Because sharp-tailed grouse are a rangeland-dependent species (Leipold et al. In review), I used Maxar aerial imagery basemap with GIS to restrict my study areas to grassland/shrubland dominated valleys farther than 200 m from conifer dominated vegetation. I used a USGS 30-m

resolution digital elevation model (DEM) to separate my study areas into 4 topographic strata based on elevation. Stratification and random sampling within strata increases precision for comparison across strata (Ramsey and Schafer 2013). Stratifying my field sites allowed me to evaluate topographical effects on technology performance across varying elevational groupings that were designed to represent sharp-tailed grouse habitat preferences throughout their life cycle. The bottom 20% of elevation at a study site was categorized as ‘Lower’ and is representative of low, herbaceous areas where sharp-tailed grouse may find brood-rearing habitat (McNew et al. 2017, McNew et al. 2023). The top 20% of elevation at a study site was designated as ‘Upper’ and is representative of bare hilltops where leks may occur, while the elevations between these two categories was designated as ‘Middle’ and represents potential nesting habitats on hillsides (McNew et al. 2017). Lastly, topographical draws on the landscape were categorized as ‘Draws’ and are representative of potential winter habitat for sharp-tailed grouse (McNew et al. 2023).

I generated random points within each topographical stratum (lower, middle, upper, and draws) using R Statistical Software v4.2.1 (R Core Team 2022) for a total of 276 locations which were distributed across my field sites. I generated 20 additional sites within each topographic stratum at each field site to be available as alternate points if the initial point was inaccessible due to property boundaries or topographical features such as rivers or cliffs. Next, I divided these points between triangulation and detection probability evaluations, such that I evaluated triangulation metrics at 127 sites and detection probability at 149 sites.

To evaluate detection probability, I constrained detection evaluations to a 1-km distance from the randomized location due to 1) spatial limits in my study area posed by vegetation type

and private property boundaries, and 2) initial observations that most Motus observations were < 1 km. I used R Statistical Software to generate detection evaluation locations along randomized bearings at 1-km distances from the initial evaluation locations and constrained plotting of these randomly selected locations within a shapefile of the study area to prevent points plotting on private property or outside of intermountain valley grasslands.

To evaluate triangulation accuracy and precision metrics in the field, I placed one Motus transmitter and one VHF transmitter, marked with flagging, at each of the randomized locations with a 1-m space between the two transmitters to reduce potential interference. Each transmitter received one triangulation evaluation. Field technicians who were blinded to transmitter placement used handheld receivers and antennae to triangulate transmitters using standard protocols (Kenward 2001). A triangulation began when the technician detected the transmitter signal and began taking bearings toward the signal source. Motus transmitters were triangulated using a Lotek SRX1200 receiver and Lotek 3-element folding Yagi antenna; VHF transmitters were triangulated using a R-1000 telemetry receiver manufactured by Communications Specialist Inc. (Orange, CA) and a 3-element folding Yagi antenna manufactured by Advanced Telemetry Systems (ATS; Insanti, MN, USA). Observers recorded conditions that may affect transmitter detection at the start of each triangulation, including distance to overhead powerlines, technician name (observer), temperature, precipitation, wind speed, and relative humidity. Additionally, observers recorded triangulation start time, end time, and the time each of the 3 bearings to evaluate effort. Start time was defined as the time when a technician began the process of obtaining bearings and end time was the time the third bearing was completed.

To evaluate detection probability in the field, observers hiked to one of the 100 randomized locations, placed one Motus transmitter and one VHF transmitter, marked with flagging, on the ground to simulate the behavior of a transmitter on a ground-dwelling bird and 1-m apart to reduce interference. Next, the observer hiked to the 1-km detection distance site associated with that site where they attempted to detect transmitters with handheld receivers and directional antennae; technicians recorded whether each transmitter was or was not heard at a 1-km distance. Factors that may affect signal transmission that were recorded in the field at the 1-km location included temperature, wind speed, relative humidity, and distance to transmission lines.

Statistical Models

I identified 10 covariates *a priori* that may affect triangulation accuracy, precision, and effective detection distances using handheld radio telemetry technologies: technology type (i.e., VHF or Motus), Terrain Ruggedness Index (TRI), topographical strata, observer distance, distance to nearest transmission line, vegetation density, air temperature, % relative humidity, wind speed, and precipitation. I considered technology type (VHF or Motus) as a covariate to evaluate whether triangulation accuracy, precision, and effective detection distances differed between the two technologies. I selected two landscape variables to evaluate the influence of topography: terrain ruggedness and topographical strata. I predicted that topography would be an important landscape feature that may affect signal transmission and thus triangulation metrics and detection probability due to signal attenuation from the physical environment (Whitehouse et al. 2007). I derived a terrain ruggedness index (TRI), which quantifies topography in terms of elevation change (Riley et al. 1999), for my study area using a 30-m resolution USGS digital

elevation model (DEM) and a Geographic Information System (ArcGIS Pro 3.1.3, Esri Inc., Redlands, CA, USA). I used an Esri tutorial for guidance in creating a geoprocessing model to build my ruggedness layer and calculated the standard deviation of elevation changes to capture variability within a neighborhood size of 3 x 3 raster cells (Sappington et al. 2007). To evaluate ruggedness of the terrain between the observer and the transmitter I took the average TRI along the linear distance between those two points with a 10-m buffer and included this as a covariate in my models. I included topographical strata (lower, middle, upper, and draw) to evaluate the influence of transmitter position on the landscape on triangulation and detection metrics. I considered the effect of proximity to transmission lines by calculating the distance between transmitter and nearest transmission line for triangulation evaluations and the distance between the observer and nearest transmission line for detection probability evaluations using GIS software. For triangulation analyses, I suspected the distance between the observer and the transmitter would affect triangulation accuracy and precision estimates (Whitehouse et al. 2007, Bannister et al. 2008, Rutz et al. 2015). Because each triangulation evaluation consisted of 3 observer distances (1 from each bearing), I calculated the average observer distance (m) for each triangulation to be included as a covariate in my models. For probability of detection analyses I measured vegetation density using visual obstruction readings (VOR) in 4 cardinal directions at each transmitter site, averaged these readings, and included them as a covariate. Lastly, I included 4 environmental variables related to weather that I thought may impact signal transmission: air temperature, wind speed, % relative humidity, and precipitation (none, drizzle, showers, rain, or snow; Thelen et al. 2005, Bannister et al. 2008, Marfievici et al. 2013).

I used Location of a Signal software (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate transmitter locations and error ellipse areas (m^2) using the Maximum Likelihood Estimator (MLE) with the χ^2 confidence distribution method (Lenth 1981, Gilsdorf et al. 2008, Berg 2015, Paxton et al. 2023). I calculated triangulation accuracy, or estimated error distance, as the Euclidian distance (m) between the known transmitter location and the estimated location from triangulation. I compared mean and dispersion of the areas (m^2) of error ellipses to evaluate the relative precision of location estimates. I removed 26 unsuccessful triangulations from further analyses because they did not have 3 intersecting bearings and therefore could not measure accuracy with an error ellipse area. I evaluated the impact of omitting these data on inferences by evaluating linear models of transmitter accuracy with and without them included. Only 8 triangulations were completed during ‘drizzle’ or ‘showers’ out of 180 and only 5 detection probability evaluations were completed during ‘drizzle’ or ‘rain’ out of 284, so I did not include precipitation in my models because we would not be able to make inferences regarding the effects of precipitation with the sample size.

Prior to developing my generalized linear models (GLMs), I examined correlations among explanatory variables using Pearson correlation coefficients for continuous variables and Kruskal-Wallis for categorical variables. I did not include temperature and % relative humidity within the same models evaluating triangulation accuracy and precision as they were correlated ($r > |0.6|$). However, in my detection probability dataset I found no correlations among continuous variables ($r > |0.6|$), thus I included temperature and % relative humidity within the same models. Topographical strata were associated with TRI in both my triangulation dataset (Kruskal-Wallis $\chi^2 = 42.972$, p-value = < 0.001) and my detection probability dataset (Kruskal-

Wallis $\chi^2 = 116.13$, p-value = <0.001) and therefore not used as covariates within the same model for either analysis. I transformed estimated error ellipse area and error distance using the natural log to normalize their residual distributions prior to fitting models and visually evaluated the log transformed data for normality.

I used 86 transmitters to complete my triangulation evaluations but reused each transmitter more than twice for only 30% of my triangulations, thus I did not consider it necessary to include a random effect on individual transmitter in my models evaluating triangulation metrics. I used 52 transmitters more than two times to complete 50% of our detection probability assessments, thus I calculated marginal and conditional R^2 estimates of variance for a mixed-effects iteration of my global model to evaluate whether a random effect on individual transmitters explained any variance in probability of transmitter detection (Nakagawa et al. 2013). I found very little difference between the marginal (marginal $R^2 = 0.601$) and conditional R^2 (conditional $R^2 = 0.607$) values for my global model, indicating that very little variation was explained by the random effect on transmitter. Therefore, I proceeded with using GLMs to evaluate detection probabilities.

To evaluate triangulation accuracy and precision, I first developed a set of candidate models representing hypotheses that technology type and observer distance would interact to influence triangulation metrics. I suspected an interaction between transmitter type and observer distance and sought to first evaluate support for effects of transmitter type and observer distance to create a base model from which to evaluate the effects of environmental and topographical covariates. To select my base model I evaluated support for both additive and interaction effects of transmitter type and observer distance. I fit GLMs with Gaussian error distributions and

compared models using Akaike's Information Criterion adjusted for finite sample size (AIC_c) using the 'AICcmodavg' package in R Statistical Software (Mazerolle 2023). Model weights (w_i) and delta AIC_c values were used to evaluate the relative support of candidate models (Burnham et al. 2002). After evaluating this first set of candidate models, I selected the best model and built a second set of candidate models that added the remaining environmental and topographical variables all at once. Parameters with 85% confidence intervals overlapping zero were considered uninformative and eliminated (Arnold 2010). I chose to use an 85% confidence interval because variables in best-approximating models supported by lower AIC values may be discarded when using a 95% confidence interval and model selection using AIC supports additional variables whose 85% confidence intervals exclude zero; thus, an 85% confidence interval is AIC compatible (Arnold 2010).

To evaluate the probability of detecting transmitters at 1 km, I first developed a candidate set of models to evaluate my hypothesis that technology type and topography would interact to influence whether a transmitter was detected at 1 km. I hypothesized that higher ruggedness would negatively impact detection probability of transmitters, particularly Motus, at a 1-km distance. I fit GLMs with binomial distributions and evaluated the relative support of candidate models by comparing models using model weights (w_i) and ΔAIC_c (Burnham et al. 2002). I evaluated model support for this first candidate set and used the most parsimonious model ($\Delta AIC_c < 2$) as the basis for formulating a second candidate set of models examining the effects of environmental and site characteristic variables on detection probability (VOR, distance to transmission line, temperature, % relative humidity, and wind). My interaction models to evaluate the effects of topographic strata and technology type on detection probabilities of

transmitters could not converge due to a lack of Motus transmitter detections at 1 km, particularly in draws. Therefore, I only included additive models containing these two covariates to evaluate the effects of topographic strata and technology type on the probability of transmitter detection.



Figure 1. Study area in west-central Montana, including the Blackfoot-Clearwater Wildlife Management Area, Helmville, MT, MPG Ranch, and Red Bluff Research Ranch field sites.

CHAPTER THREE

RESULTS

Manual Radio Telemetry

I completed 222 total triangulations of Motus ($n = 113$) and VHF transmitters ($n = 109$) placed at random but known locations using Motus and VHF handheld technologies during June – September 2022 and 2023. After excluding problematic triangulations where bearings did not intersect to allow for triangulation, 180 successful triangulations of Motus ($n = 94$) and VHF ($n = 86$) transmitters remained for analyses. Error ellipse areas ranged from $2.07 \text{ m}^2 - 322,945 \text{ m}^2$ (median = $1,273 \pm 3,659 \text{ m}^2$) and from $23.4 \text{ m}^2 - 328,006 \text{ m}^2$ (median = $4,676 \pm 6,610 \text{ m}^2$) for Motus transmitters and VHF transmitters using handheld receivers, respectively (Fig. 2). Estimated error distances (location accuracy) ranged from $1.5 \text{ m} - 461 \text{ m}$ (median = 34.9 ± 8.5) and from $4.4 \text{ m} - 2,527 \text{ m}$ (median = 97.4 ± 60.8) for Motus transmitters and VHF transmitters, respectively.

Observer distances averaged between triangulation bearings ranged from $33.4 \text{ m} - 1,936 \text{ m}$ and $18.6 \text{ m} - 2,728 \text{ m}$ for Motus and VHF transmitters, respectively. Median and mean observer distances of Motus transmitters ($140 \pm 26 \text{ m}$ and $209 \pm 26 \text{ m}$, respectively) were less than those of VHF transmitters (253 ± 65.8 and $510 \pm 65.8 \text{ m}$, respectively) indicating that Motus technology typically required technicians to be nearer the transmitter for triangulations compared to VHF transmitters (Fig. 3). Within topographical strata, the average Terrain Ruggedness Index (TRI) was slightly higher within draws (mean = 3.1 ± 0.1) and upper strata (mean = 3.2 ± 0.1) than in the middle (mean = 2.4 ± 0.1) or lower (mean = 2.2 ± 0.2) strata,

although the range was smallest for upper strata ($2.4 - 4.85 \pm 0.1$; Fig. 4). Temperatures ($^{\circ}\text{C}$) ranged from $11^{\circ}\text{C} - 40^{\circ}\text{C}$; wind speeds ranged from $0 - 27.4$ kph; and % relative humidity ranged from $14\% - 80\%$. Distance to transmission lines from transmitter locations were distributed similarly for both technologies with means of $1,429$ m and $1,234$ m and medians of $1,072$ m and 968 m during Motus and VHF triangulations, respectively (Fig. 5). The mean amount of time spent triangulating transmitters was 34 minutes for Motus and 37 minutes for VHF technologies. The amount of time spent triangulating transmitters ranged from 9 minutes – 252 minutes for Motus and 9 minutes – 136 minutes for VHF triangulations (Fig. 6). The longer triangulation times were relatively rare, with 0.02% of triangulation evaluations requiring more than 120 minutes of effort and 0.08% of triangulation evaluations requiring more than 60 minutes of effort to locate and triangulate the transmitter.

My top base model evaluating effects of technology type and observer distance on triangulation precision indicated strong support for an interaction between transmitter type and observer distance ($\Delta\text{AIC}_c = 0$, $w_i = 0.99$; Table 1). Motus transmitters had a higher location precision (smaller estimated ellipse area) at observer distances under approximately 600 m which deteriorated as the observer distance increased while precision of the VHF transmitters was generally unaffected by observer distance from the transmitter (Fig. 7). Error ellipse area increased as the distance between the transmitter and observer increased for both transmitter types ($\beta_{\text{obsdist}} = 0.0005 \pm 0.0003$ SE). I found strong support for an interaction between transmitter type and distance from observer ($\beta_{\text{motus:obsdist}} = 0.003 \pm 0.0008$ SE) which indicated a stronger rate of decline in precision for Motus transmitters as observer distance increased (Fig.

7). Across a 1 to 1000 m observation distance, mean triangulation error ellipse areas increased 19,250 m² and 2,576 m² for Motus and traditional VHF transmitters, respectively.

I used the top base model of technology type and observer distance effects as the template for formulating a candidate set of models examining effects of topography and environmental variables on triangulation precision. There was some model uncertainty between two nested models in this second candidate set. Distance to transmission lines, relative humidity, and an interaction between technology type and TRI each received some support in addition to the interaction between technology type and observer distance ($\Delta AIC_c = 0 - 0.43$, $\Sigma w_i = 0.29 - 0.52$; Table 1). However, 85% confidence intervals for the beta coefficients of the more complex model indicated distance to transmission lines to be uninformative ($\beta_{\text{distlines}} = 0.0001 \pm 0.0001$ SE; 85% CI = -0.00006 – 0.0003; Fig. 8). The additive effect of TRI was also uninformative ($\beta_{\text{TRI}} = -0.19 \pm 0.18$ SE; 85% CI = -0.48 – 0.05), however the interaction between Motus technology and TRI was supported ($\beta_{\text{motus:TRI}} = 0.602 \pm 0.24$ SE; 85% CI = 0.24 – 0.93; Fig. 8).

The top ranked model evaluating topographical and environmental effects on triangulation precision supported an interaction between technology type and average observer distance ($\beta_{\text{motus:obsdist}} = 0.002 \pm 0.0008$ SE), an interaction between transmitter type and TRI ($\beta_{\text{motus:TRI}} = 0.602 \pm 0.24$ SE), and a positive effect of % relative humidity on error ellipse size ($\beta_{\text{humid}} = 0.028 \pm 0.015$ SE). Predicted triangulation precision was higher for Motus technology than VHF when observers were within approximately 600 m of the transmitter, but precision of Motus technology rapidly deteriorated as observer distance increased above 600 m while the precision of VHF technology remained relatively unaffected by observer distance (Fig. 9). Increasing % relative humidity negatively affected triangulation precision estimates with

predicted error ellipse area sizes increasing for both technology types as % relative humidity increased (Fig. 10). As expected, there was a strong interaction between technology type and TRI suggesting that precision of Motus technology declined as TRI increased at a higher rate than for VHF which remained relatively stable across TRI with a slight increase in precision as TRI increased (Fig. 11).

The top base model of technology type and observer distance effects on triangulation accuracy (estimated error distances) supported additive effects of observer distance and transmitter type. Models that included additive and interaction effects between transmitter type and observer distance had support ($\Delta AIC_c < 2$; Table 2), however, the 85% confidence interval of the interaction effect overlapped zero and thus was uninformative ($\beta_{\text{motus:dist}} = 0.0004 \pm 0.0003$ SE; 85% CI = -0.00007 – 0.001). Triangulation accuracy decreased as average distance from the observer increased for both transmitter types ($\beta_{\text{obsdist}} = 0.002 \pm 0.0001$ SE). When observer distance increased from 1 m to 1000 m, the predicted error distance for Motus transmitters increased by 171 m, while the predicted error distance for VHF transmitters increased by 275 m (Fig. 12).

I used the top base model of technology type and observer distance effects on triangulation accuracy as the basis for formulating the next candidate set of models to examine effects of topography and environmental variables on triangulation accuracy. Distance to transmission lines, temperature, relative humidity, and an interaction between technology type and average TRI each received some support in combination with the additive effect between technology type and observer distance ($\Delta AIC_c = 0 - 1.95$, $\Sigma w_i = 0.38 - 0.85$; Table 2). The 85% confidence intervals overlapped zero for temperature ($\beta_{\text{temp}} = -0.006 \pm 0.01$ SE; 85% CI = -0.02 –

0.008) and relative humidity ($\beta_{\text{humid}} = 0.004 \pm 0.006$ SE; 85% CI = -0.004 – 0.01) and were considered uninformative (Fig. 13).

The top ranked model evaluating environmental and topographical effects on triangulation accuracy supported an interaction between technology type and TRI ($\beta_{\text{motus:TRI}} = 0.3 \pm 0.09$ SE), a main effect of TRI ($\beta_{\text{TRI}} = -0.2 \pm 0.07$ SE) and distance to transmission lines ($\beta_{\text{DistLines}} = 0.0001 \pm 0.00006$ SE). Predicted triangulation accuracy remained higher for Motus technology than VHF across all observer distances in our top ranked model evaluating estimated error distances (Fig. 14). Predicted triangulation accuracy was lower for VHF technology at lower TRI values and improved dramatically as TRI increased, while Motus triangulation accuracy held relatively stable across increasing TRI with a slight decrease in accuracy as ruggedness increased (Fig. 15). Additionally, there was only 1 VHF triangulation above a TRI value of 5 which was at an average observer distance of only 18 m, thus triangulation accuracy would be high for this triangulation obtained in rugged terrain (Fig. 16). Both technology types declined in predicted triangulation accuracy as the distance between the observer and the nearest transmission lines increased, with Motus remaining more accurate than VHF technology across all measured distances (Fig. 17).

Probability of Detecting Transmitters at 1 km

During the 2023 field season, I completed detection probability evaluations for 282 transmitter locations (133 VHF, 149 Motus) at a 1-km distance. Within topographical strata, the average TRI along the 1-km linear distance between transmitter and observer was largest within draws (mean = 3.6 ± 0.2) and upper strata (mean = 2.6 ± 0.05) than in middle (mean = 1.7 ± 0.09) or lower (mean = 1.8 ± 0.1) strata (Fig. 18). Temperatures ($^{\circ}\text{C}$) during trials ranged from

11–32°C, wind speed ranged from 0–15 kph, and relative humidity ranged from 22–65%.

Distribution of distances to transmission lines from observer locations were distributed similarly for both technologies with ranges from 4.6–3,948 m and 0.5–3,948 m with means of 808 m and 772 m for VHF and Motus evaluations, respectively (Fig. 19).

At a 1-km distance, Motus and VHF transmitters were detected on 7% (11/149 attempts) and 71% (95/133 attempts) of attempts, respectively. Motus transmitters were never detected when located within draws and were detected in lower, middle, and upper strata at a rate of 10% (Fig. 20). Detections of VHF transmitters were more evenly distributed across topographic strata, with particularly high detection rates in the middle stratum (91% success; Fig. 20).

The best model within my first candidate set evaluating the effects of topography and technology type on the probability of detection at a 1-km distance suggested strong support for the main effects of technology type and elevational strata ($\Delta AIC_c = 0$, $w_i = 0.96$; Table 3). I used this best model as the template for formulating a candidate set of models examining the effects of environmental covariates, average VOR, and distance to transmission lines on probability of detection of transmitters at 1-km distances. Model rankings indicated model uncertainty (Table 3), however the main effects of wind overlapped the 85% confidence interval ($\beta_{\text{wind}} = -0.03 \pm 0.06$ SE; 85% CI = -0.12 – 0.05) and furthermore, I did not consider the competing model to be informative because the top model was a subset of the competing model (Burnham et al. 2002, Arnold 2010).

The probability of detecting a Motus transmitter at a 1-km distance was lower than VHF ($\beta_{\text{motus}} = -4.001 \pm 0.44$ SE) and was negatively impacted by temperature ($\beta_{\text{temp}} = -0.11 \pm 0.04$ SE) and distance to the nearest transmission line ($\beta_{\text{distTlines}} = -0.0005 \pm 0.0008$ SE). The probability of

detection was higher for both technologies across the lower and middle elevational strata ($\beta_{\text{lower}} = 1.09 \pm 0.56$ SE, $\beta_{\text{middle}} = 1.52 \pm 0.61$) than upper elevation ($\beta_{\text{upper}} = 0.53 \pm 0.59$; Fig. 21).

Predicted probability of detection for Motus technology across elevational strata was 0.02 ± 0.58 SE, 0.06 ± 0.46 SE, 0.09 ± 0.42 SE, and 0.03 ± 0.46 SE in draws, lower, middle, and upper strata, respectively (Fig. 21). Predicted probability of detection for VHF technology was significantly higher than for Motus across all elevational strata with probabilities of 0.56 ± 0.44 SE, 0.79 ± 0.39 SE, 0.85 ± 0.42 SE, and 0.68 ± 0.35 SE in draws, lower, middle, and upper elevational strata, respectively (Fig. 21). The probability of detecting both transmitter types decreased with temperature ($\beta_{\text{temp}} = -0.12 \pm 0.04$ SE; Fig. 22) and as distance to transmission lines increased ($\beta_{\text{distlines}} = -0.0006 \pm 0.0003$ SE; Fig. 23).

Automated Motus Evaluations

I downloaded 8,608,463 detections of sharp-tailed grouse fitted with Motus transmitters (Lotek Nanotags) from the Motus network using the ‘motus’ R package (Birds Canada 2024). After filtering, 8,196,289 detections remained. I first evaluated detection of grouse by at least one Motus tower. All 54 sharp-tailed grouse fitted with Motus transmitters and released in my study areas were detected at least once by at least one Motus automated tower. The number of detections per individual by one Motus tower ranged from 60 – 4,517,274 detections (median = 11,310 detections). Total days per bird detected by one Motus tower throughout the field season ranged from 2–18 days. Each individual grouse was detected by a range of 1–13 (median = 4) towers throughout the course of the field season (non-simultaneously). Lastly, the lengths of runs per individual at a single tower ranged from 4–29,490 hits (median = 2,865 hits).

Of the 54 sharp-tailed grouse detected by at least one Motus tower, only 26 were detected by at least 2 towers simultaneously at least one time. In the Bitterroot Valley, 22 grouse out of the 26 (84%) released with Motus transmitters were detected by two towers simultaneously on an average of 4 occasions occurring on unique days (min = 1; max = 16). In the Blackfoot Valley, 4 birds out of the 28 released with Motus transmitters were detected simultaneously by two towers on an average of 21 occasions occurring on unique days (min = 14; max = 32). Thus, while detection by two Motus towers simultaneously was more likely in the Bitterroot Valley, most birds had only 4 locations on unique days whereas detection by two Motus towers simultaneously was rarer in the Blackfoot Valley (14%), but the average number of simultaneous detections on unique days for the 4 Blackfoot Valley birds (average = 21) was higher than in the Bitterroot Valley (average = 4).

Visualization of detections for female grouse with confirmed nesting dates indicate lower detections by towers during the nesting period (Fig. 24). Less than 0.01% of automated detections occurred during confirmed nesting dates of female sharp-tailed grouse in my study areas. Of the 24 female sharp-tailed grouse fitted with Motus transmitters and released in my study areas, we documented just 3 nesting attempts using handheld telemetry to locate the birds. Of the 3 females confirmed to have nests, only 2 were detected by at least two Motus towers simultaneously during the field season and none were simultaneously detected during their estimated nesting dates. During confirmed nesting periods 1 female grouse was detected by a single Motus tower on 4 unique days which occurred during the laying period. During the incubation period there were no automated detections of female grouse. The 3 nest locations of

the females fitted with Motus transmitters were located 3,858 m, 4,842 m, and 7,625 m from the nearest Motus towers (Fig. 25).

Table 1. Support for candidate models evaluating effects of covariates on error ellipse area (m^2) estimation. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	$AIC_c w_i$	Cum. w_i	LogLik
<i>Candidate models evaluating relationship between technology type and observer distance</i>						
Technology * observer dist.	5	767.05	0.00	0.99	0.99	-378.35
Technology + observer dist.	4	776.44	9.39	0.01	1.00	-384.10
Technology	3	784.45	17.40	<0.01	1.00	-389.16
Observer dist.	3	784.53	17.48	<0.01	1.00	-389.20
Null	2	800.36	33.31	<0.01	1.00	-398.14
<i>Candidate models including environmental and topographical variables</i>						
Technology*observer dist. + technology*TRI + dist. transmission tines + % humid	9	762.25	0.00	0.29	0.29	-371.59
Technology*observer dist. + technology*TRI	7	762.68	0.43	0.23	0.52	-374.01
Technology*observer dist. + technology*TRI + dist. transmission tines + % humid + wind	10	764.49	2.24	0.09	0.61	-371.59
Technology*observer dist. + technology*TRI + dist. transmission tines	8	764.62	2.37	0.09	0.70	-373.89
Technology*observer dist. + technology*TRI + dist. transmission tines + temp	9	765.16	2.92	0.07	0.76	-373.05
Technology*observer dist. + topo. strata + dist. transmission tines + % humid	10	766.26	4.01	0.04	0.80	-372.48
Technology*observer dist. + dist. transmission tines + % humid	8	766.50	4.25	0.03	0.84	-374.83
Technology*observer dist.	5	767.05	4.80	0.03	0.86	-378.35
Technology*observer dist. + technology*TRI + dist. transmission tines + temp + wind	10	767.24	5.00	0.02	0.89	-372.97
Technology*observer dist. + topo. strata	8	767.90	5.65	0.02	0.90	-375.53
Technology*observer dist. + topo. strata + dist. transmission tines + % humid + wind	11	768.15	5.91	0.01	0.92	-372.29
Technology*observer dist. + TRI	6	768.17	5.93	0.01	0.93	-377.84

Table 1. Continued.

Technology*observer dist. + technology*topo. strata + dist. transmission tines + % humid	13	768.63	6.39	0.01	0.94	-370.22
Technology*observer dist. + TRI + dist. transmission tines + % humid	9	768.71	6.47	0.01	0.96	-374.83
Technology*observer dist. + TRI + dist. transmission tines + temp	8	769.68	7.44	0.01	0.96	-376.42
Technology*observer dist. + technology*topo.	11	769.75	7.50	0.01	0.97	-373.09
Technology*observer dist. + topo. strata + dist. transmission tines + temp	10	769.86	7.61	0.01	0.98	-374.28
Technology*observer dist. + topo. strata + dist. transmission tines	9	770.07	7.82	0.01	0.98	-375.50
Technology*observer dist. + TRI + dist. transmission tines	7	770.27	8.02	0.01	0.99	-377.81
Technology*observer dist. + technology*topo. strata + dist. transmission tines + % humid + wind	14	770.79	8.55	<0.01	0.99	-370.12
Technology*observer dist. + TRI + dist. transmission tines + temp + wind	9	771.69	9.44	<0.01	0.99	-376.31
Technology*observer dist. + technology*topo. strata + dist. transmission tines	12	771.83	9.59	<0.01	1.00	-372.98
Technology*observer dist. + topo. strata + dist. transmission tines + temp + wind	11	772.12	9.87	<0.01	1.00	-374.27
Technology*observer dist. + technology*topo. strata + dist. transmission tines + temp	13	772.16	9.91	<0.01	1.00	-371.98
Technology*observer dist. + technology*topo. strata + dist. transmission tines + temp + wind	14	774.51	12.26	<0.01	1.00	-371.98

Table 1. Continued.

Null	2	800.36	38.11	<0.01	1.00	-398.14
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Table 2. Support for candidate models evaluating effects of covariates on estimated error distances (m). The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LogLik
<i>Candidate models evaluating relationship between technology type and observer distance</i>						
Technology + observer dist.	4	453.05	0.00	0.57	0.57	-222.41
Technology * observer dist.	5	453.62	0.57	0.43	1.00	-221.64
Observer dist.	3	463.37	10.31	<0.01	1.00	-228.61
Technology	3	602.91	149.86	<0.01	1.00	-298.39
Null	2	631.83	178.78	<0.01	1.00	-313.88
<i>Candidate models including environmental and topographical variables</i>						
Technology + obs. dist + technology * TRI + dist. transmission lines	7	444.66	0.00	0.38	0.38	-215.00
Technology + obs. dist + technology * TRI + dist. transmission lines + humid	8	446.28	1.62	0.17	0.55	-214.72
Technology + obs. dist + technology * TRI + dist. transmission lines + temp	8	446.45	1.79	0.16	0.71	-214.80
Technology + obs. dist + technology * TRI	6	446.61	1.95	0.14	0.85	-217.06
Technology + obs. dist + technology * TRI + dist. transmission lines + humid + wind	9	448.46	3.80	0.06	0.91	-214.70
Technology + obs. dist + technology * TRI + dist. Transmission lines + temp + wind	9	448.66	4.00	0.05	0.96	-214.80
Technology + obs. dist + TRI + dist. transmission lines	6	451.93	7.27	0.01	0.97	-219.72
Technology + obs. dist + TRI + dist. transmission lines + humid	7	452.83	8.17	0.01	0.97	-219.09
Technology + obs. dist + TRI	5	452.84	8.18	0.01	0.98	-221.25
Technology + obs. dist + TRI + dist. transmission lines + temp	7	452.95	8.29	0.01	0.99	-219.15
Technology + obs. Dist	4	453.05	8.39	0.01	0.99	-222.41
Technology + obs. dist + TRI + dist. transmission lines + humid + wind	8	454.99	10.33	<0.01	0.99	-219.08

Table 2. Continued.

Technology + obs. dist + TRI + dist. transmission lines + temp + wind	8	455.14	10.48	<0.01	1.00	-219.15
Technology + obs. dist + topo. strata + dist. transmission lines	8	455.78	11.12	<0.01	1.00	-219.47
Technology + obs. dist + topo. Strata	7	457.21	12.55	<0.01	1.00	-221.28
Technology + obs. dist + topo. strata + dist. transmission lines + humid	9	457.25	12.59	<0.01	1.00	-219.10
Technology + obs. dist + topo. strata + dist. transmission lines + temp	9	457.36	12.70	<0.01	1.00	-219.15
Technology + obs. dist + topo. strata + dist. transmission lines + humid + wind	10	459.48	14.82	<0.01	1.00	-219.09
Technology + obs. dist + topo. strata + dist. transmission lines + temp + wind	10	459.60	14.94	<0.01	1.00	-219.15
Technology + obs. dist + technology * topo. strata + dist. transmission lines	11	460.38	15.72	<0.01	1.00	-218.40
Technology + obs. dist + technology * topo. strata + dist. transmission lines + humid	12	461.96	17.30	<0.01	1.00	-218.05
Technology + obs. dist + technology * topo. strata + dist. transmission lines + humid	12	462.14	17.48	<0.01	1.00	-218.14
Technology + obs. dist + technology * topo. Strata	10	462.26	17.60	<0.01	1.00	-220.48
Technology + obs. dist + technology * topo. strata + dist. transmission lines + humid + wind	13	464.27	19.61	<0.01	1.00	-218.04
Technology + obs. dist + technology * topo. strata + dist. transmission lines + temp + wind	13	464.38	19.73	<0.01	1.00	-218.10
Null	2	631.83	187.17	<0.01	1.00	-313.88

Table 3. Support for candidate models evaluating effects of covariates on detection of transmitters at 1-km. The number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i) and log-likelihoods are reported.

Model	K	AIC_c	ΔAIC_c	AIC_c w_i	Cum. w_i	LogLik
<i>Candidate models evaluating relationship between technology type and topography</i>						
Technology + topo. strata	5	231.66	0.00	0.96	0.96	-110.72
Technology + TRI	3	239.07	7.42	0.02	0.99	-116.49
Technology * TRI	4	241.13	9.47	0.01	0.99	-116.49
Technology	2	241.68	10.03	0.01	1.00	-118.82
Topo. strata	4	373.37	141.71	<0.01	1.00	-182.61
TRI	2	373.97	142.31	<0.01	1.00	-184.96
Null	1	375.39	143.73	<0.01	1.00	-186.69
<i>Candidate models including environmental site characteristic variables</i>						
Technology + topo. strata + dist. transmission lines + temp	7	222.06	0.00	0.51	0.51	-103.83
Technology + topo. strata + dist. transmission lines + temp + wind	8	223.85	1.79	0.21	0.72	-103.66
Technology + topo. strata + temp	6	224.43	2.37	0.16	0.88	-106.06
Technology + topo. strata + dist. transmission lines + temp + humid + wind	9	225.68	3.62	0.08	0.96	-103.51
Technology + topo. strata + VOR + dist. transmission lines + temp + humid + wind	10	227.47	5.42	0.03	1.00	-103.33
Technology + topo. strata	5	231.66	9.60	<0.01	1.00	-110.72
Null	1	375.39	153.33	<0.01	1.00	-110.72

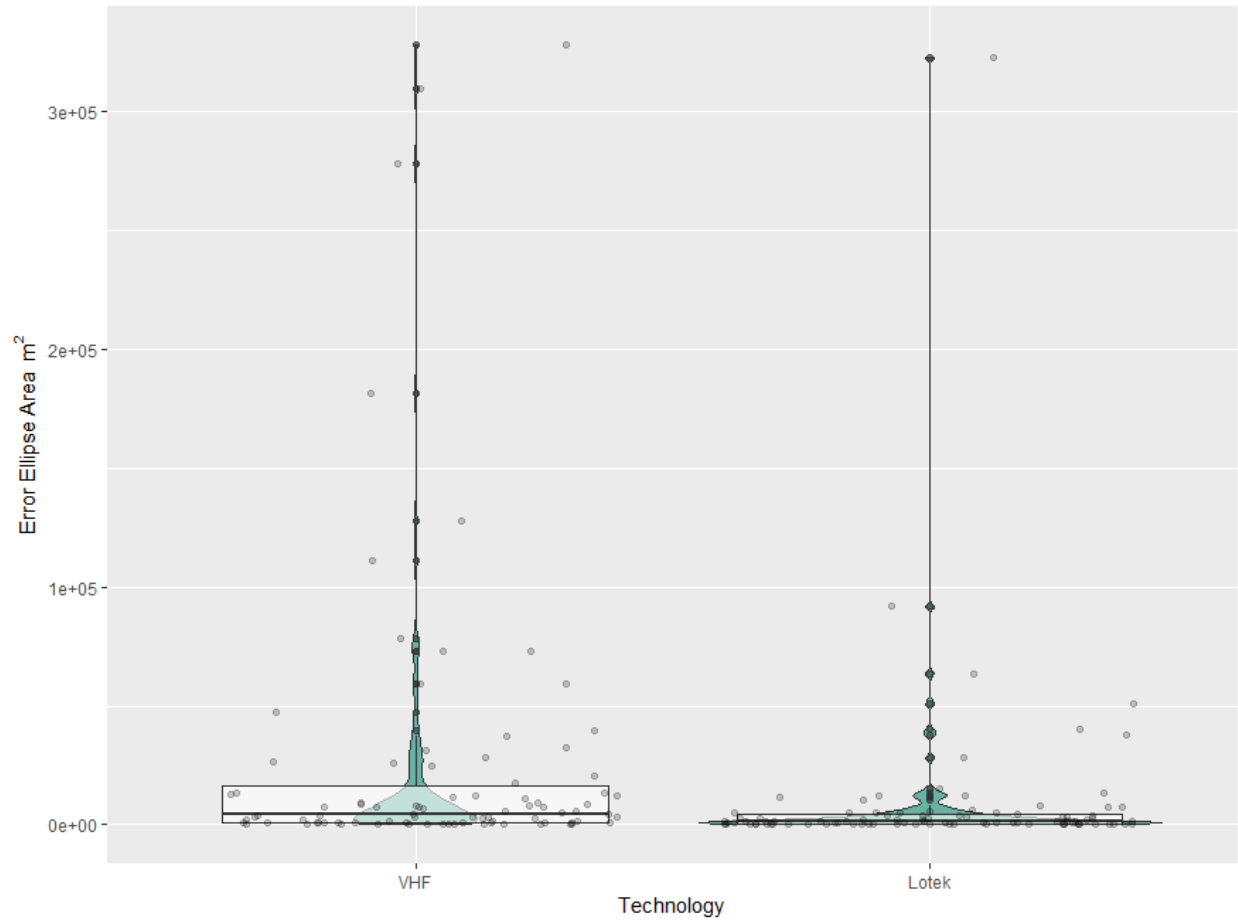


Figure 2. Violin plot illustrating the distribution of error ellipse areas (m^2), average error ellipse areas (horizontal lines), and standard errors (boxes) during triangulations for Motus and VHF handheld telemetry technologies during 2022 – 2023.

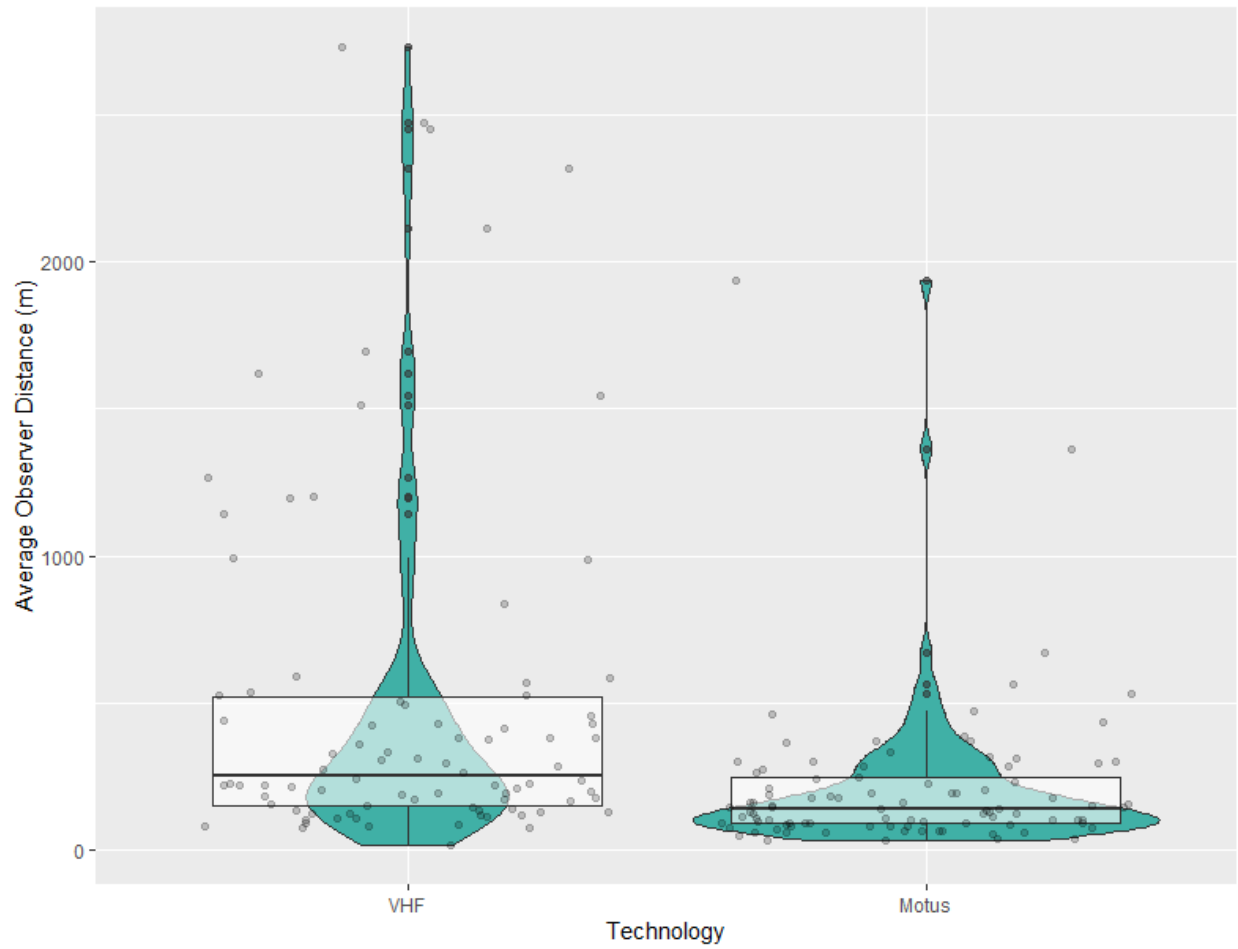


Figure 3. Violin plot illustrating the distribution of observer distances to transmitters, average observer distances (horizontal lines), and standard errors (boxes) during triangulations for Motus and VHF handheld telemetry technologies during 2022 – 2023.

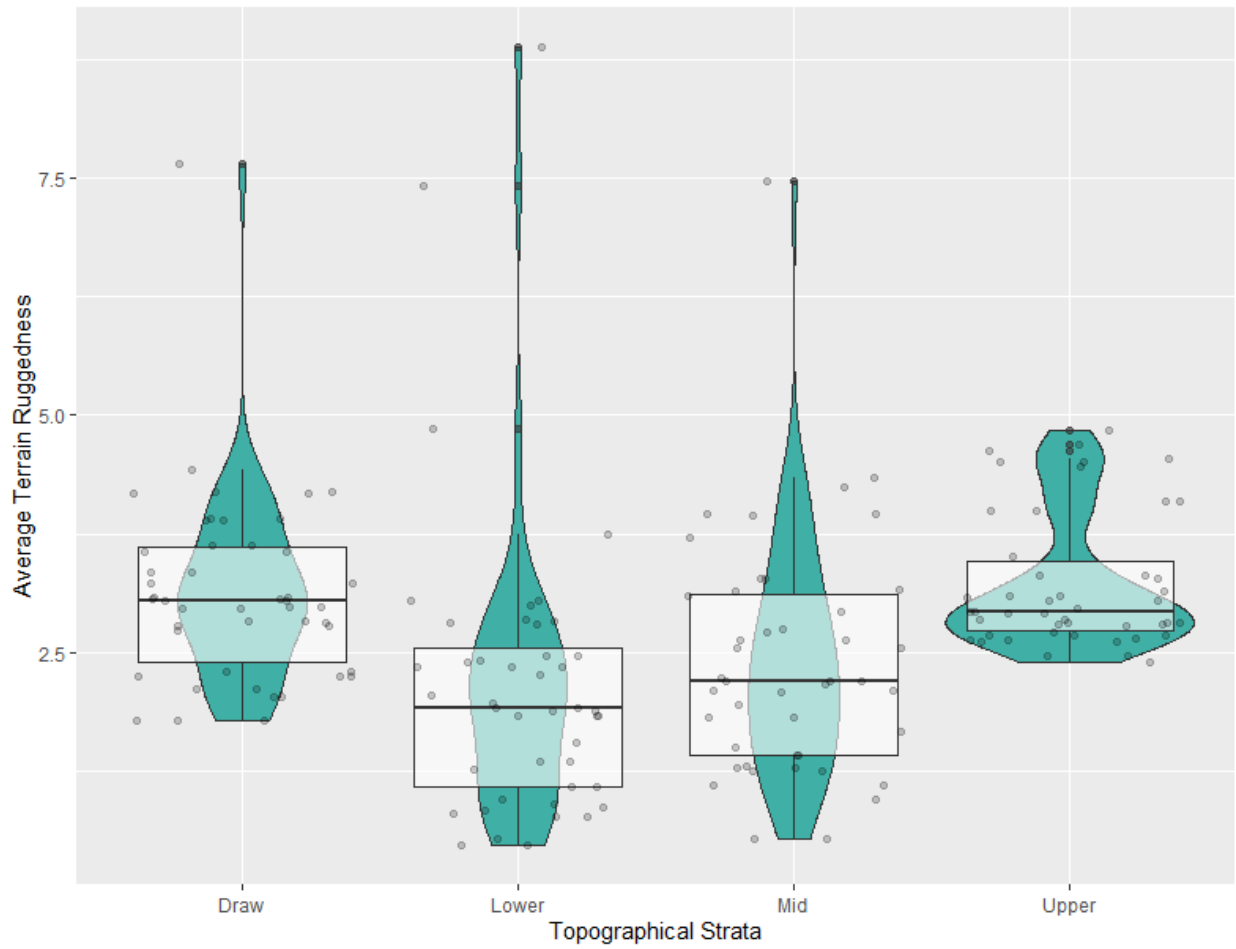


Figure 4. Violin plot illustrating the distribution of Terrain Ruggedness Index (TRI) values, average TRI (horizontal lines), and standard errors (boxes) across topographical strata during all triangulations during 2022 – 2023.

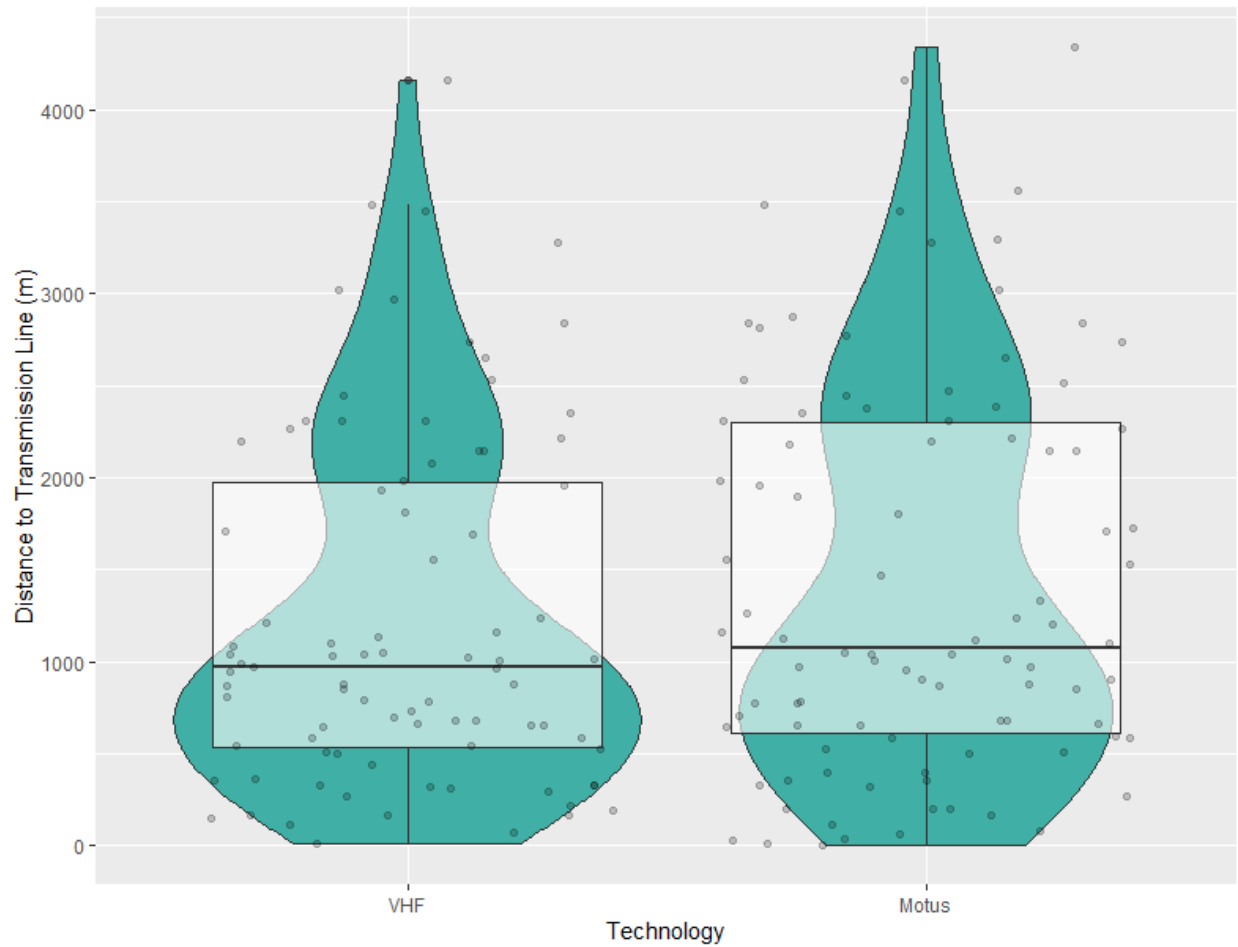


Figure 5. Violin plot illustrating the distribution of distances between transmission lines (m) and transmitters, average distances to transmission lines (horizontal lines), and standard errors (boxes) during triangulation efforts for Motus and VHF technologies during 2022 – 2023.

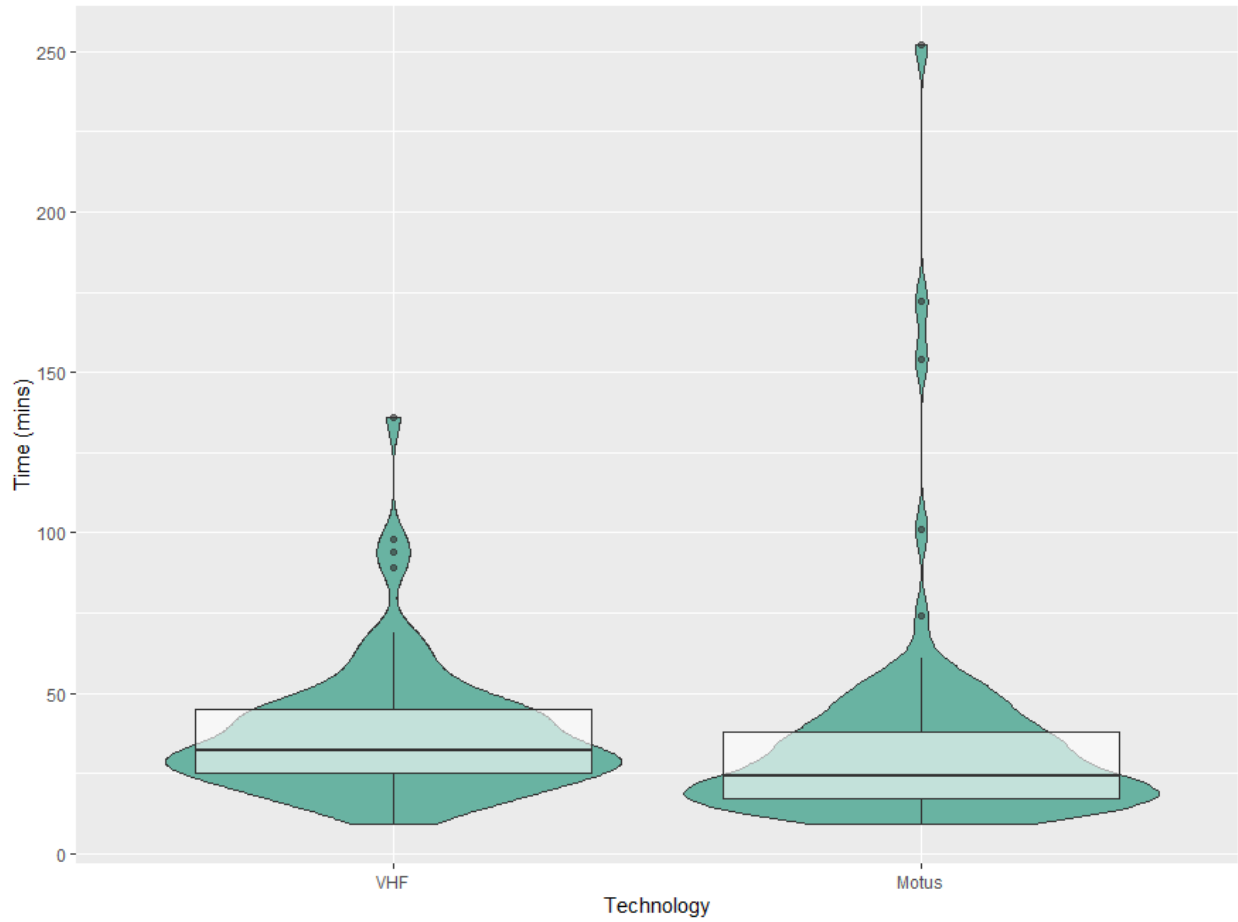


Figure 6. Violin plot illustrating the distribution of the amount of time (minutes) spent completing triangulations, average number of minutes (horizontal lines), and standard errors (boxes) during triangulation efforts for Motus and VHF technologies during 2022 – 2023.

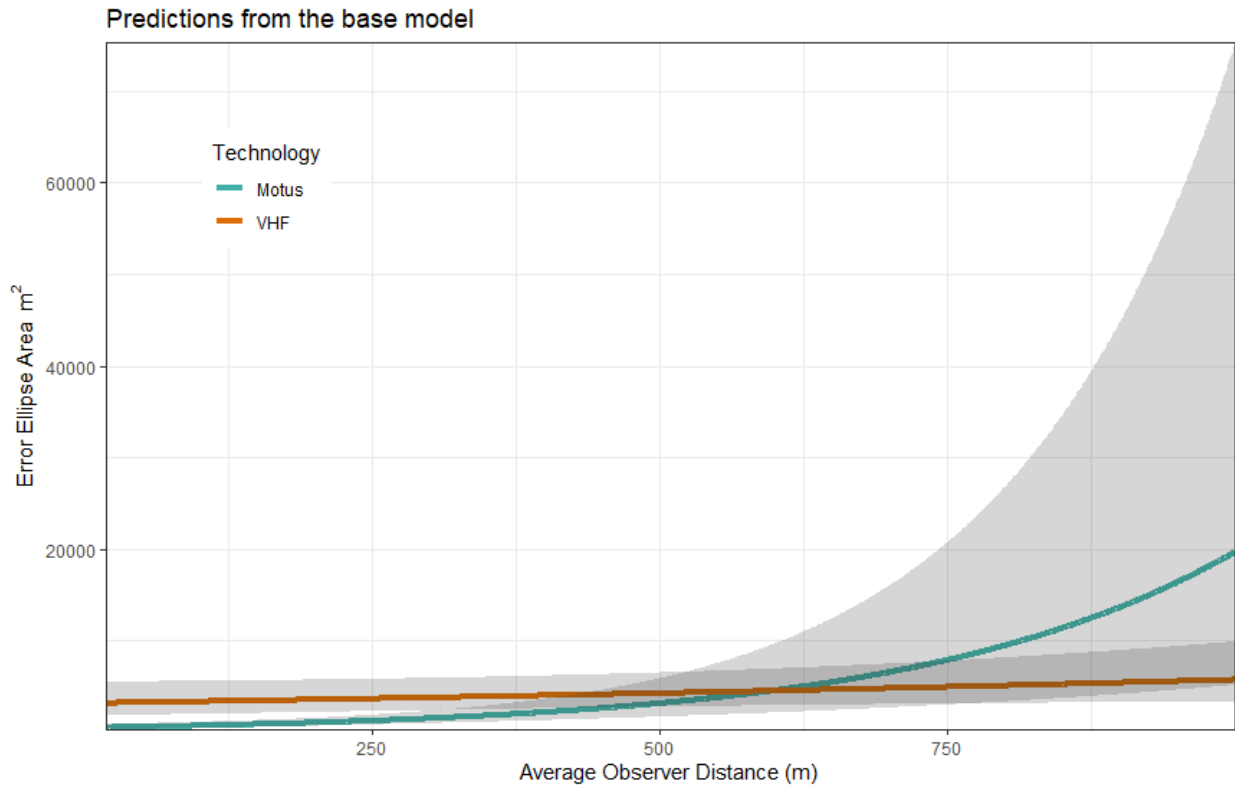


Figure 7. Predicted relationship ($\pm 95\%$ confidence intervals) from the best base model between error ellipse area (m²) and observer distances for Motus transmitters and VHF transmitters up to 1000m observer distance.

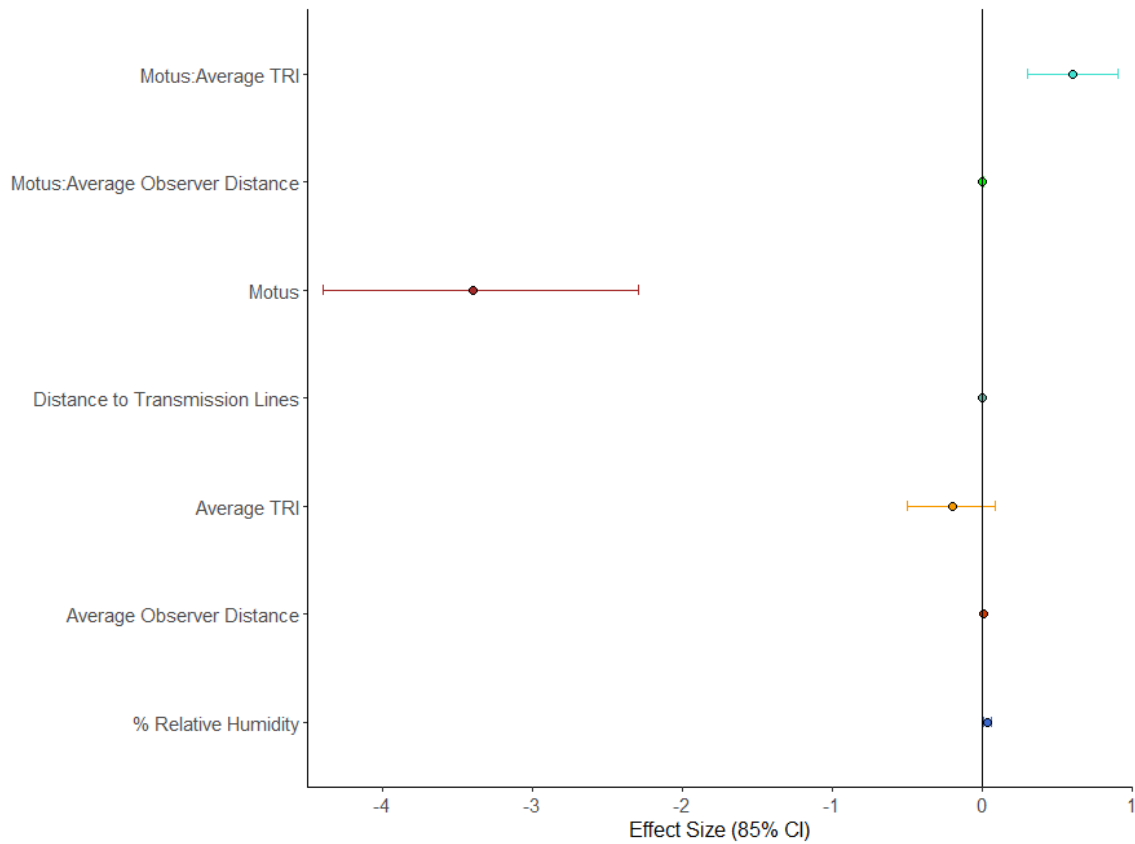


Figure 8. Effect size ($\beta \pm 85\%$ confidence intervals) for each variable considered in our model uncertainty evaluations examining estimated error ellipse areas (m^2). Coefficients are not scaled which causes some of the effect sizes to look like they overlap zero when they in fact do not. The 85% confidence intervals of distance to transmission lines and average Terrain Ruggedness Index (TRI) are the two effect sizes that truly overlap zero.

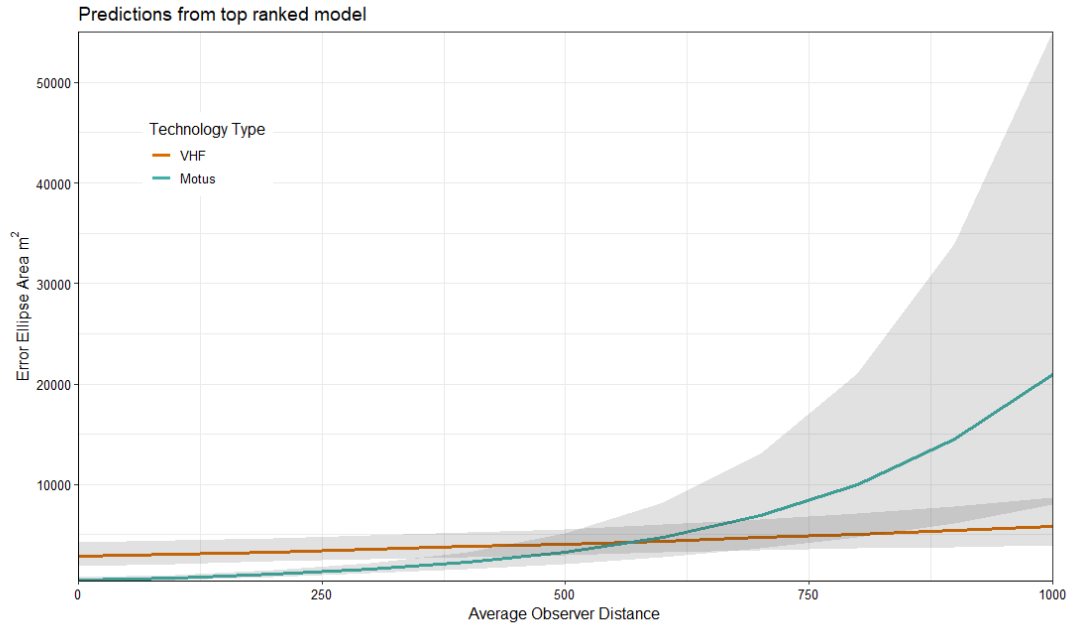


Figure 9. Top model predicted relationship ($\pm 85\%$ confidence intervals) between error ellipse area (m²) and observer distances for Motus transmitters and VHF transmitters up to 1000m observer distance.

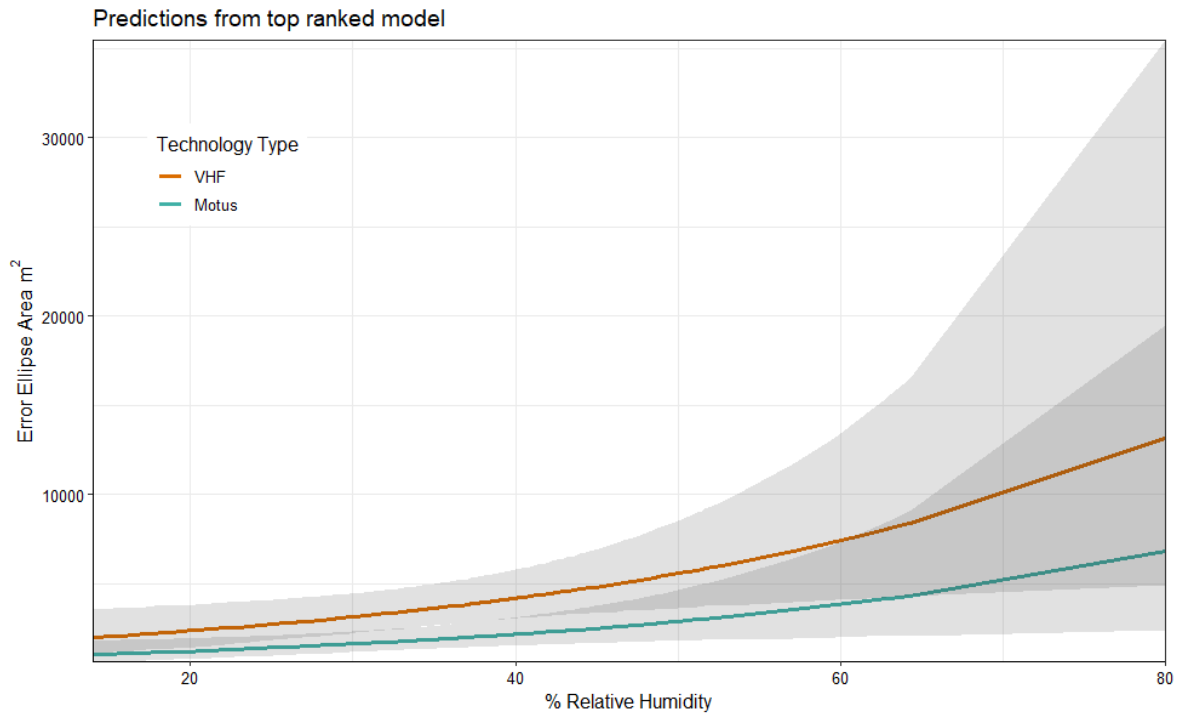


Figure 10. Top model predicted relationship (\pm 85% confidence intervals) between error ellipse area (m²) and % relative humidity for Motus transmitters and VHF transmitters up to 80% relative humidity.

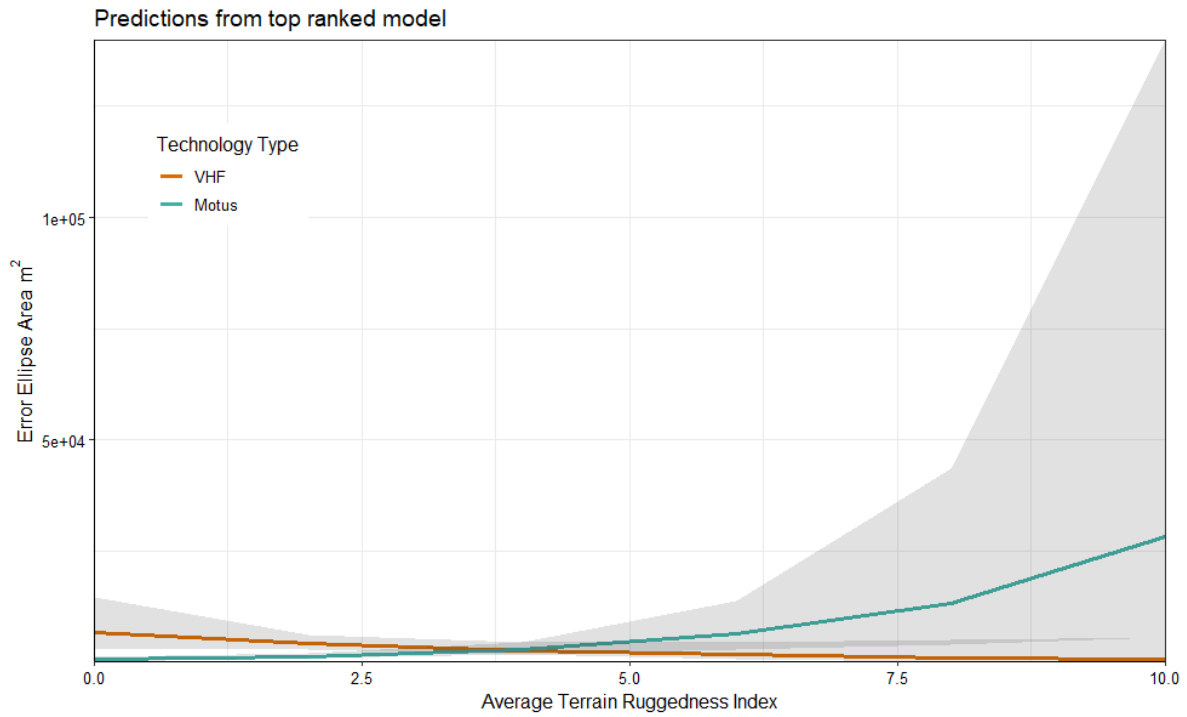


Figure 11. Top model predicted relationship ($\pm 85\%$ confidence intervals) between error ellipse area (m^2) and average Terrain Ruggedness Index (TRI) values for Motus transmitters and VHF transmitters.

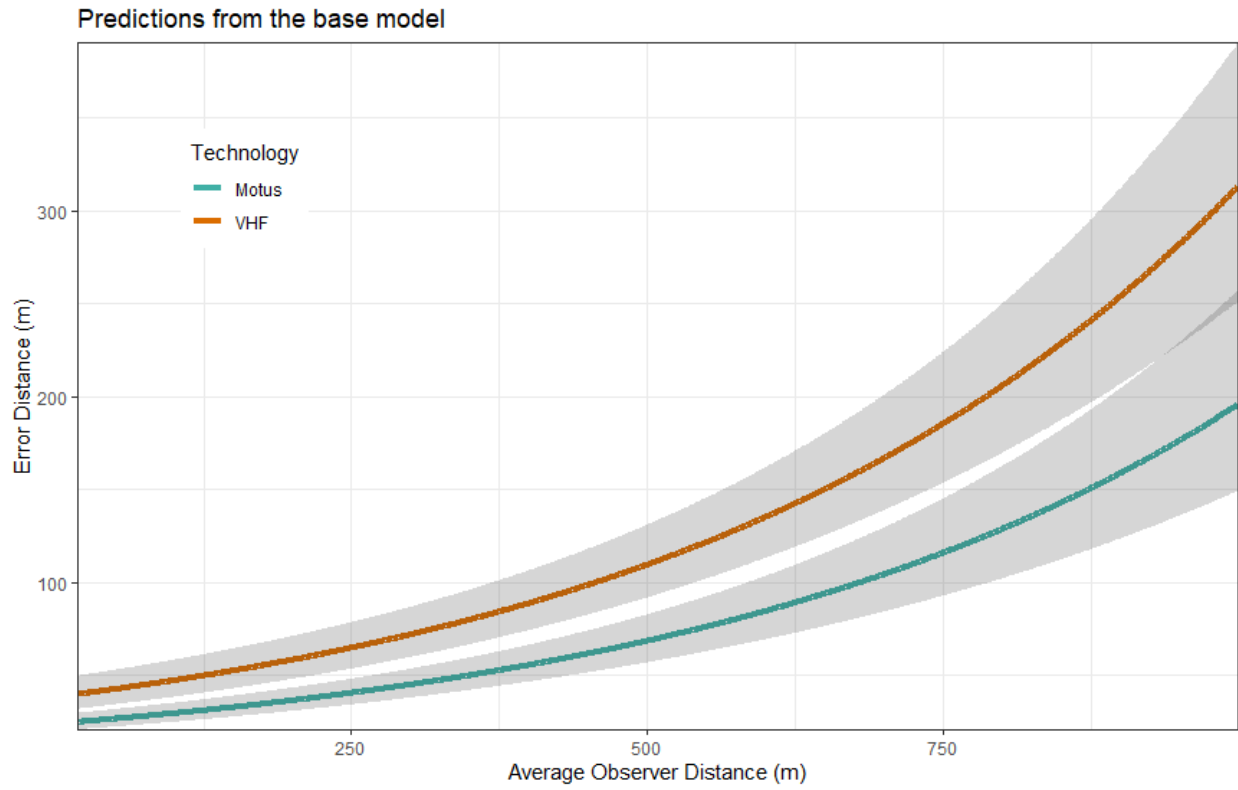


Figure 12. Best base model predicted relationship ($\pm 95\%$ confidence intervals) between estimated error distances and observer distances for Motus transmitters and VHF transmitters up to 1000m observer distance.

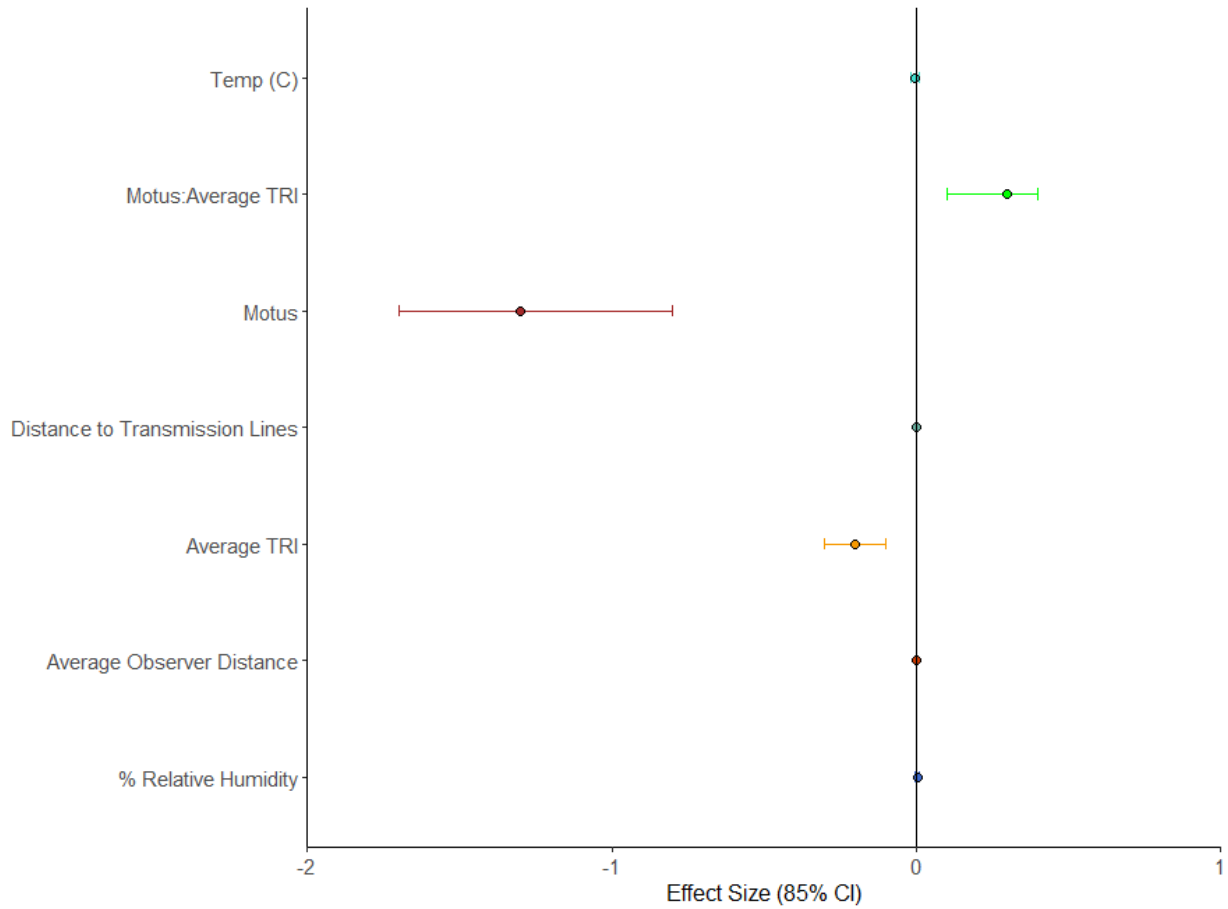


Figure 13. Effect size ($\beta \pm 85\%$ confidence intervals) for each variable considered in our model uncertainty evaluations examining estimated error ellipse distances (m). Coefficients are not scaled which causes some of the effect sizes to look like they overlap zero when they in fact do not. The 85% confidence intervals of temperature and % relative humidity are the two effect sizes that truly overlap zero.

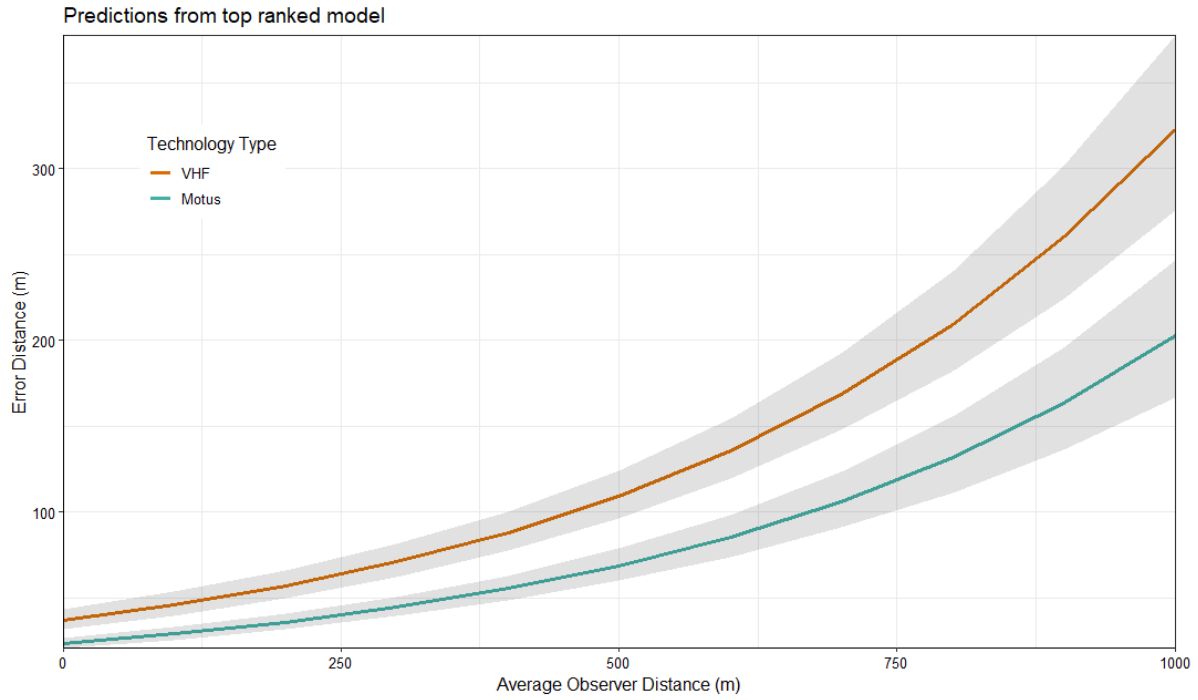


Figure 14. Top model predicted relationship (\pm 85% confidence intervals) between estimated error distance (m) and observer distance for Motus transmitters and VHF transmitters up to 1000m observer distance.

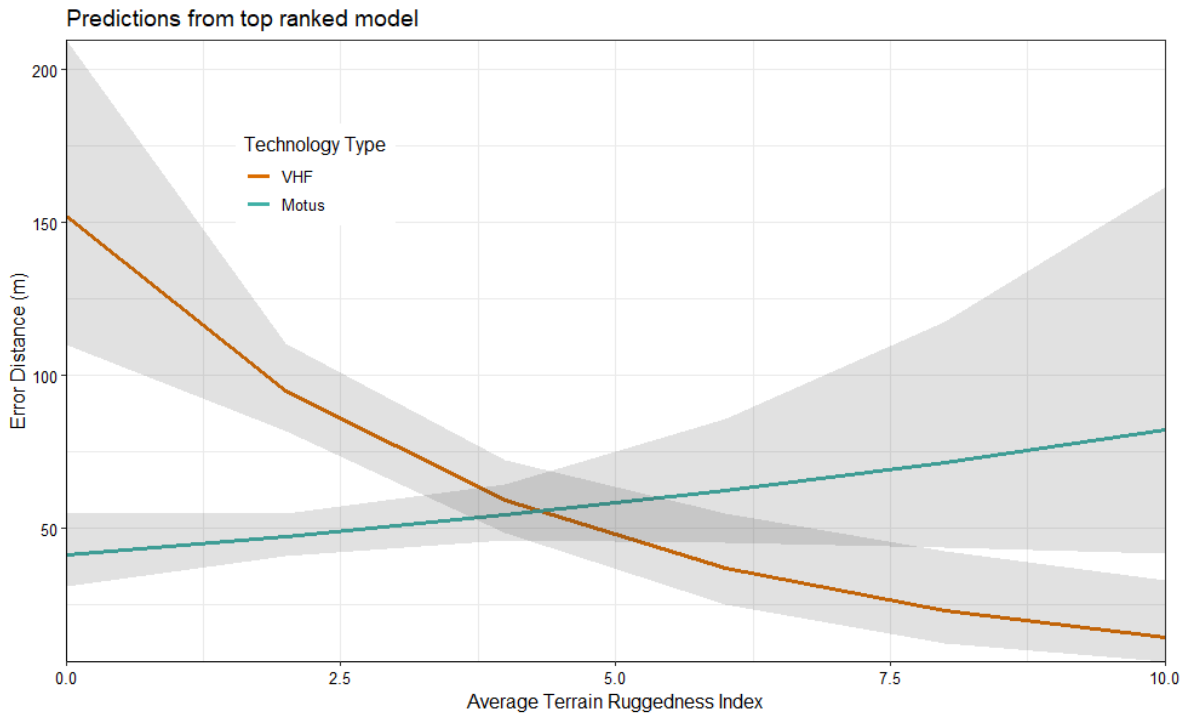


Figure 15. Top model predicted relationship ($\pm 85\%$ confidence intervals) between estimated error distance (m) and average Terrain Ruggedness Index (TRI) values for Motus transmitters and VHF transmitters.

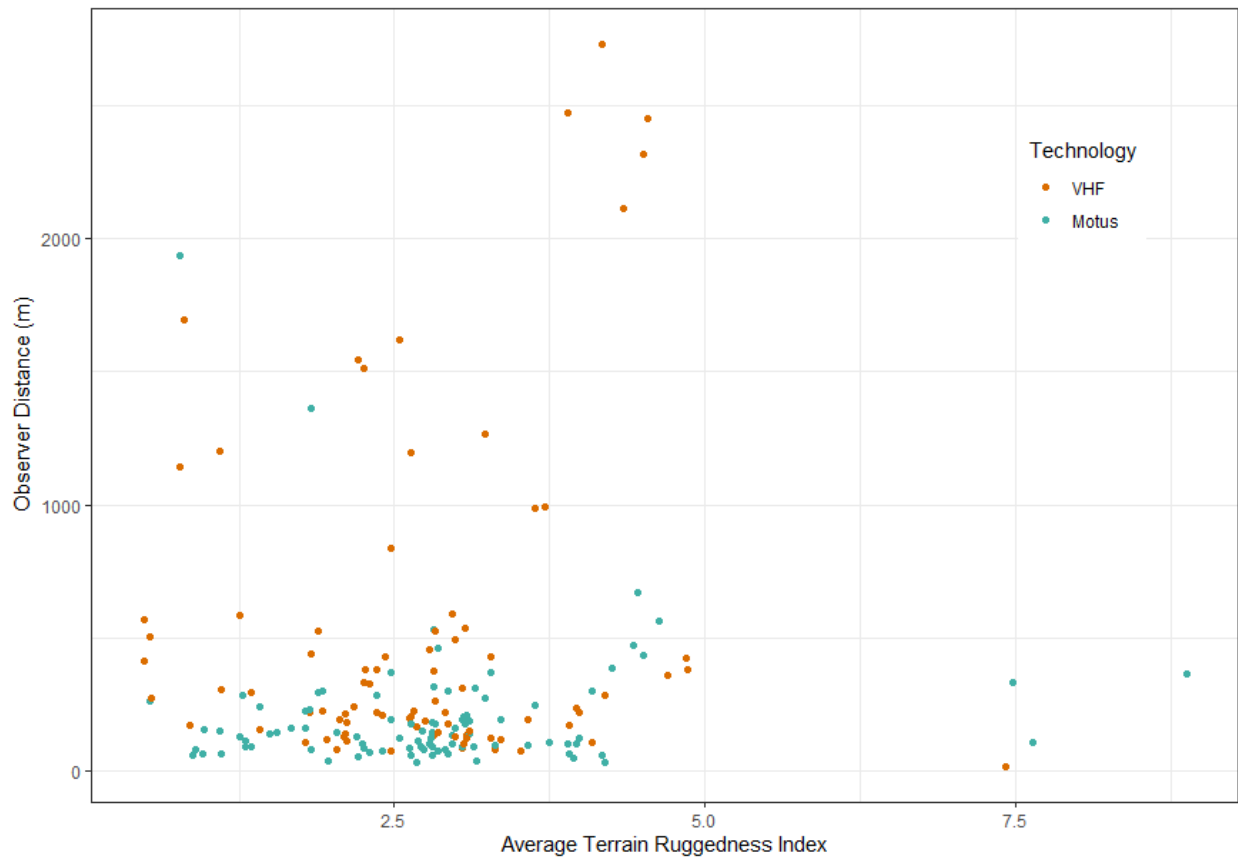


Figure 16. Observer distances (m) during triangulations of VHF and Motus technologies across average Terrain Ruggedness Index (TRI) values during handheld telemetry evaluations.

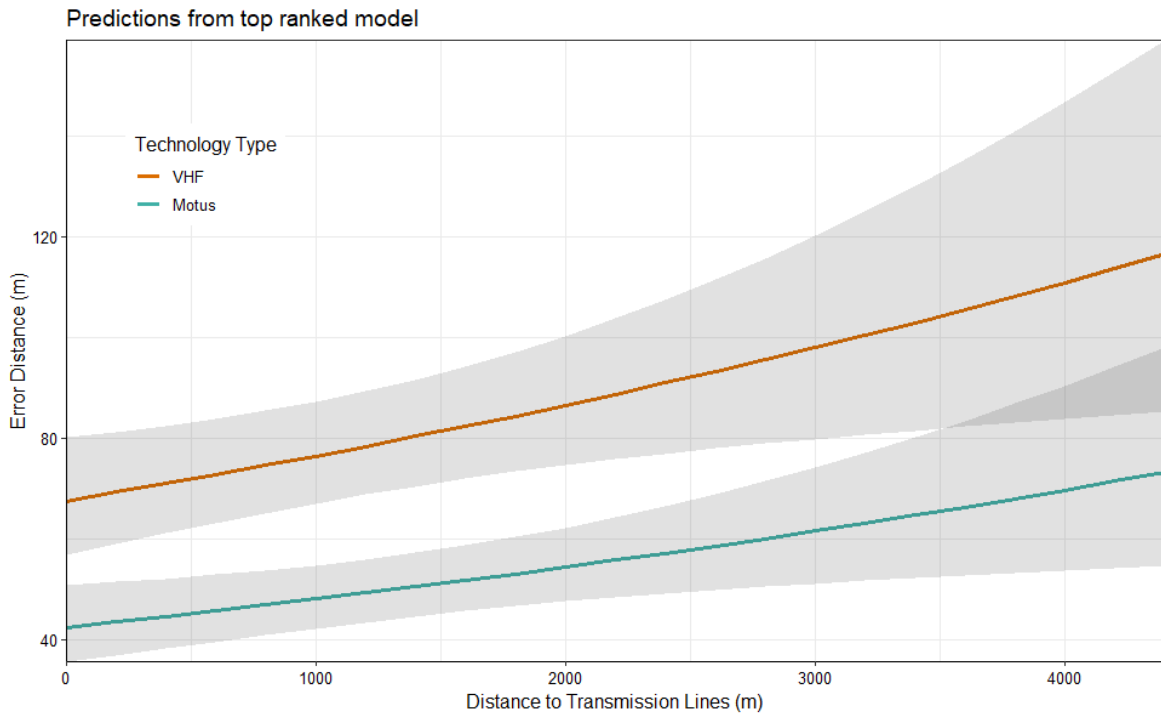


Figure 17. Top model predicted relationship ($\pm 85\%$ confidence intervals) between estimated error distance (m) and distance from observer to transmission lines (m) for Motus transmitters and VHF transmitters.

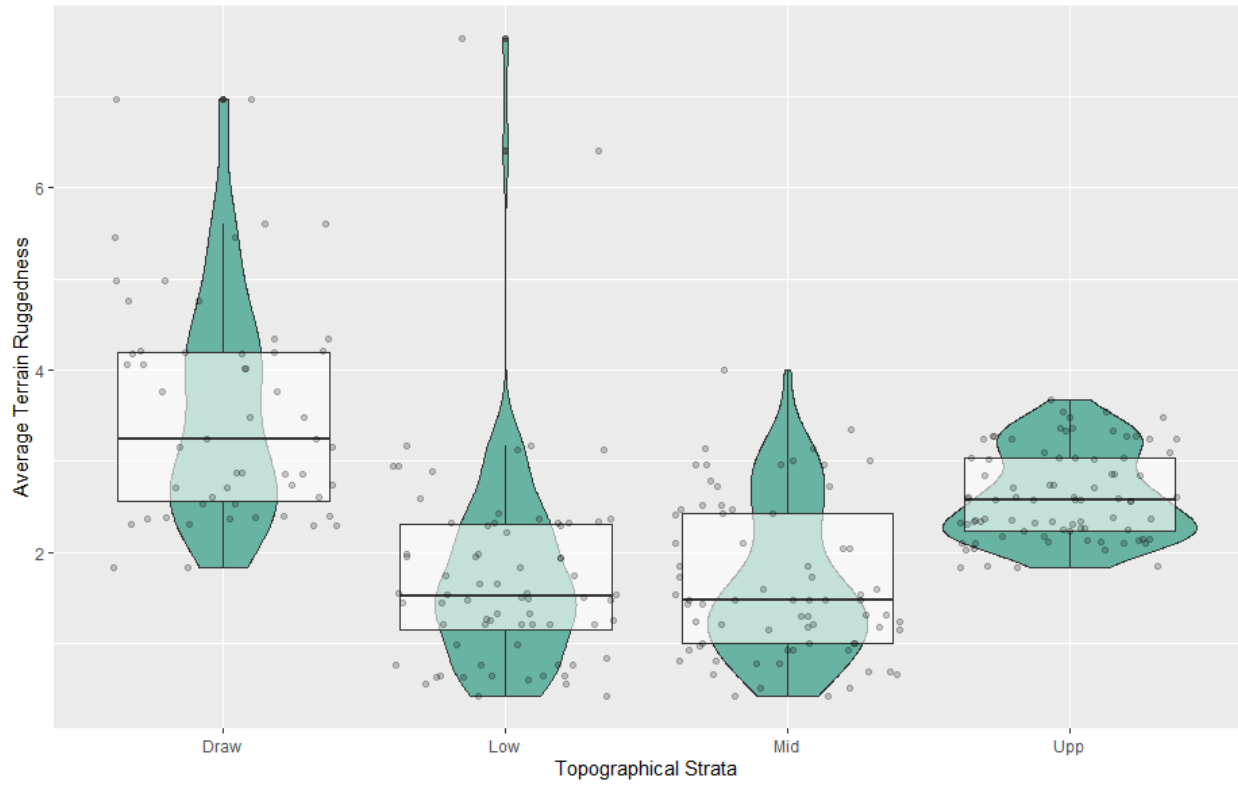


Figure 18. Violin plot illustrating the distribution of Terrain Ruggedness Index (TRI) values, average TRI (horizontal lines), and standard errors (boxes) across topographic strata during detection probability evaluations for both technology types (Motus and VHF) during 2023.

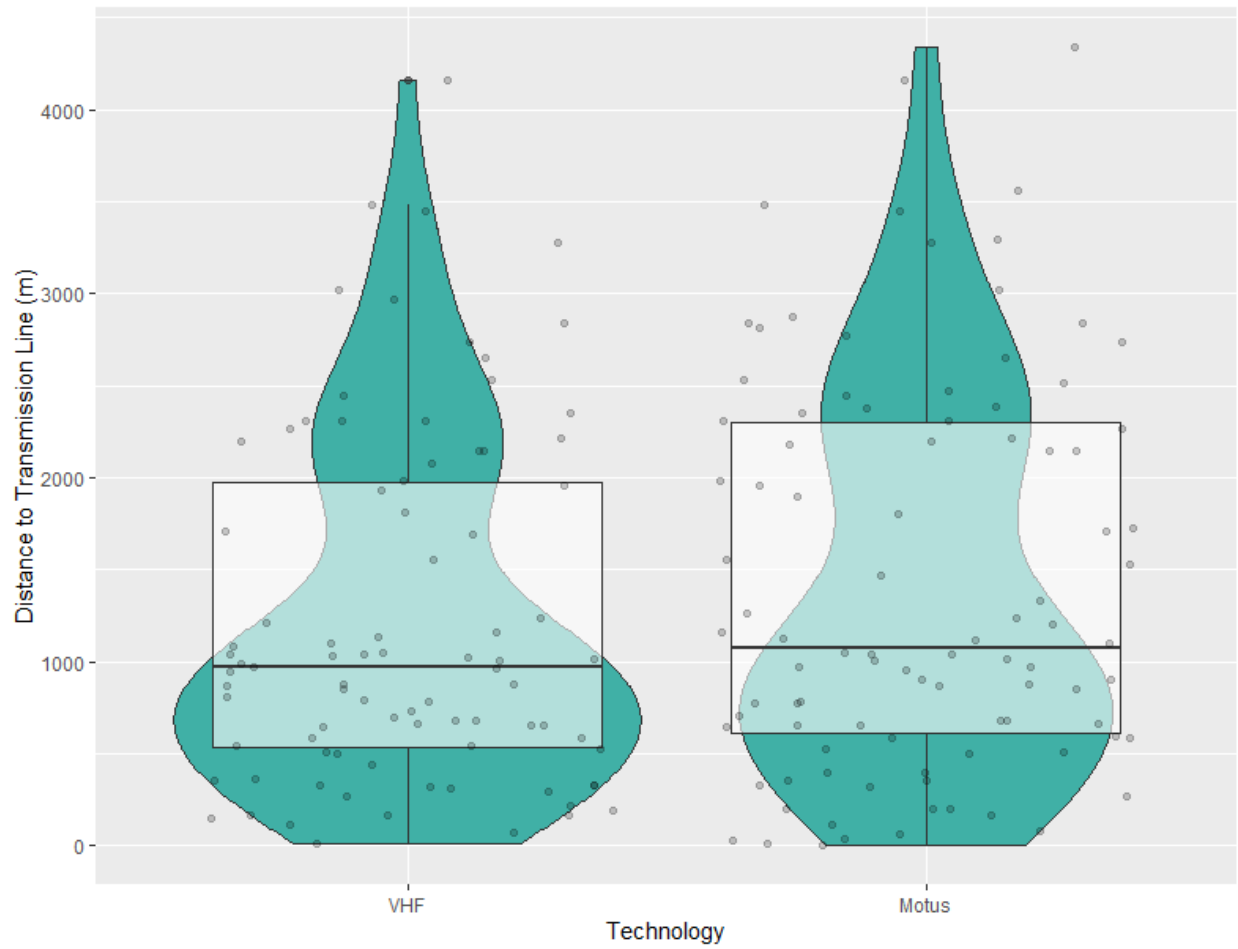


Figure 19. Violin plot illustrating the distribution of distance to transmission lines (m), average distance (horizontal lines), and standard errors (boxes) for VHF and Motus technologies during 2023 detection probability evaluations.

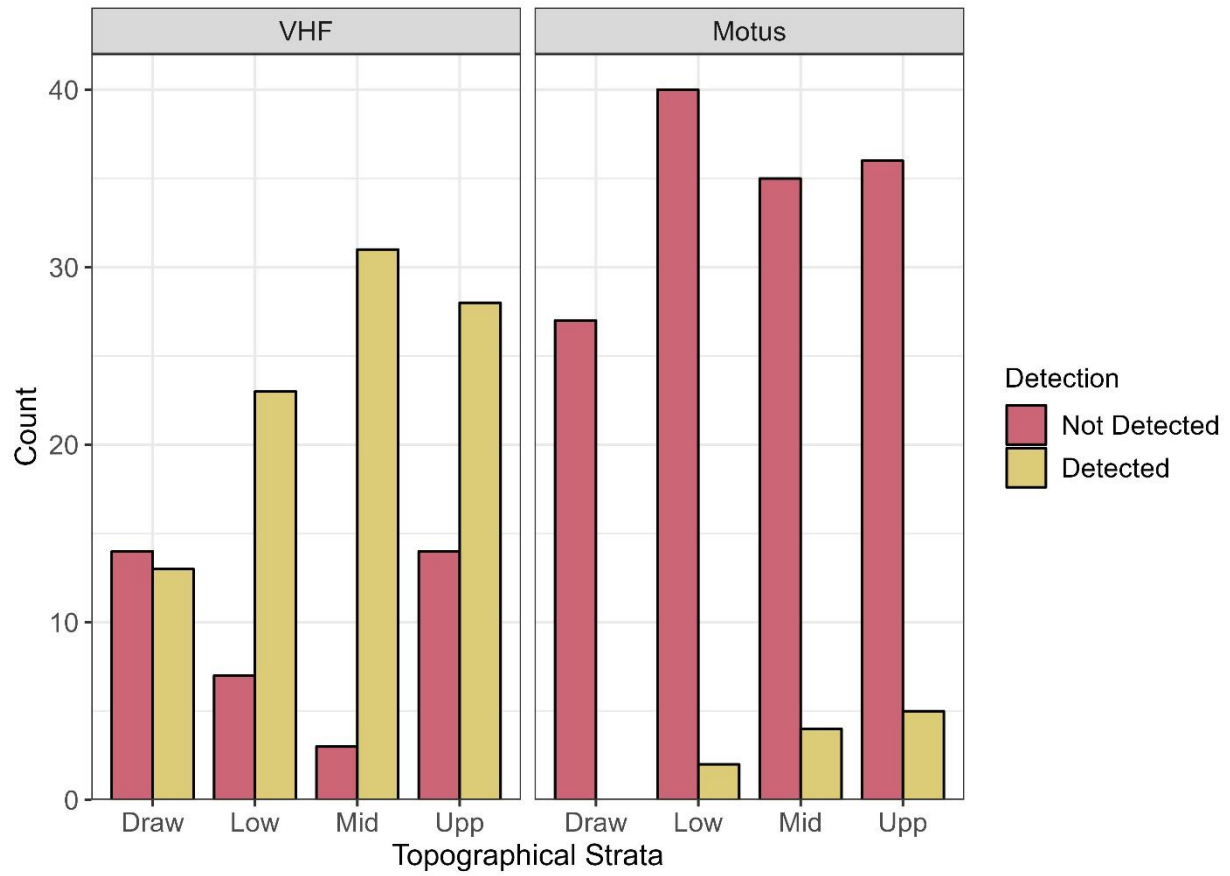


Figure 20. Counts of whether transmitters were detected or not detected for VHF and Motus transmitters at a distance of 1-km across topographical strata (draws, lower, middle, and upper).

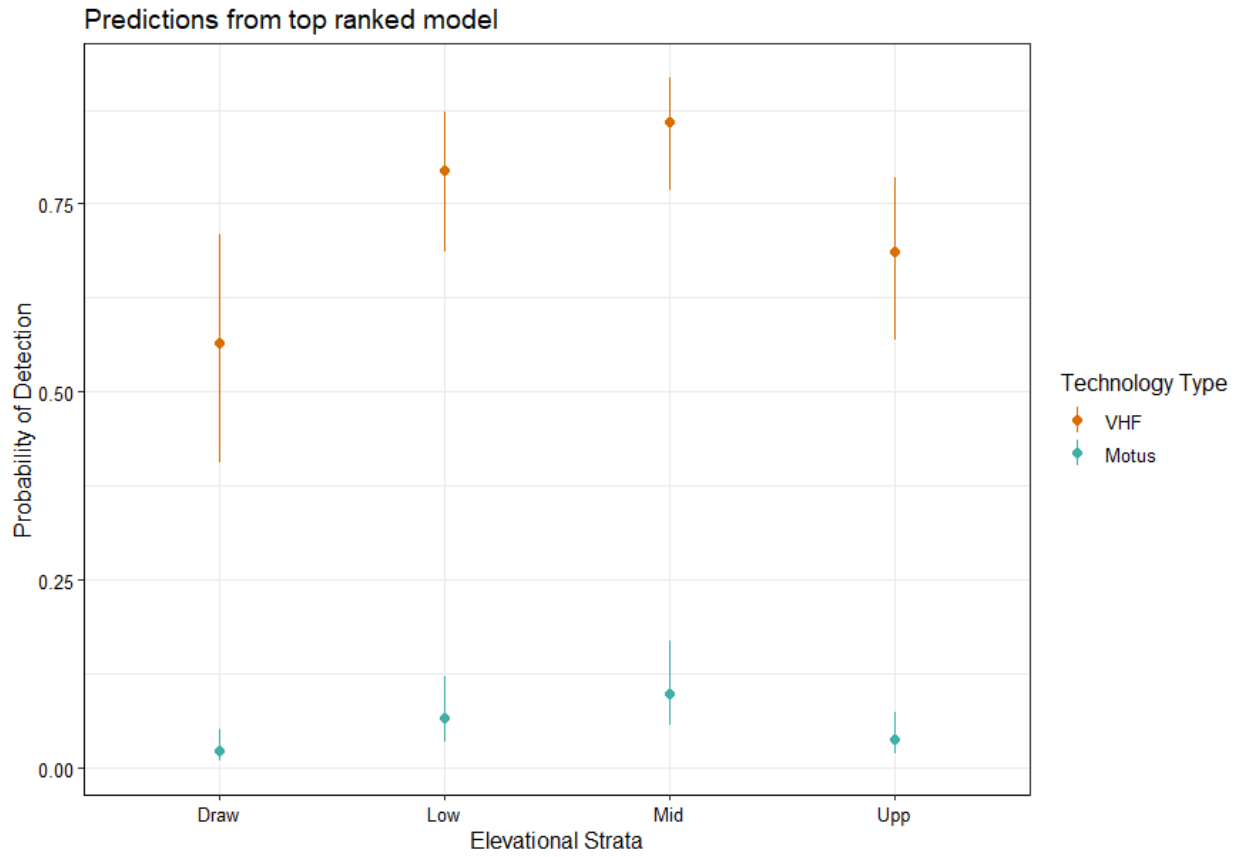


Figure 21. Top model predictions ($\pm 85\%$ confidence intervals) of the probability of detecting VHF and Motus transmitters at a distance of 1 km across elevational strata (draws, lower, middle, and upper strata) during 2023 detection probability evaluations.

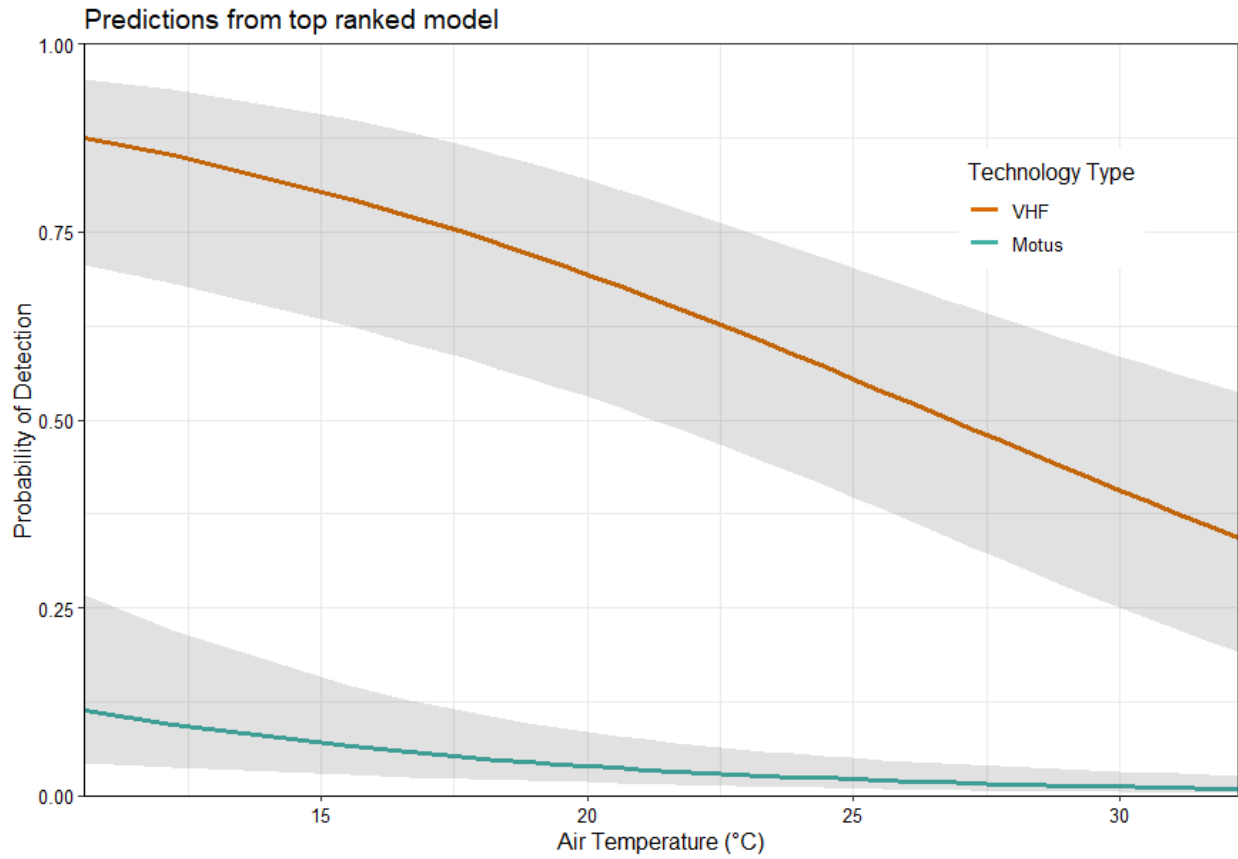


Figure 22. Top model predicted relationship ($\pm 85\%$ confidence intervals) between the probability of detection and air temperature ($^{\circ}\text{C}$) for VHF and Motus technologies during 2023 detection probability evaluations.

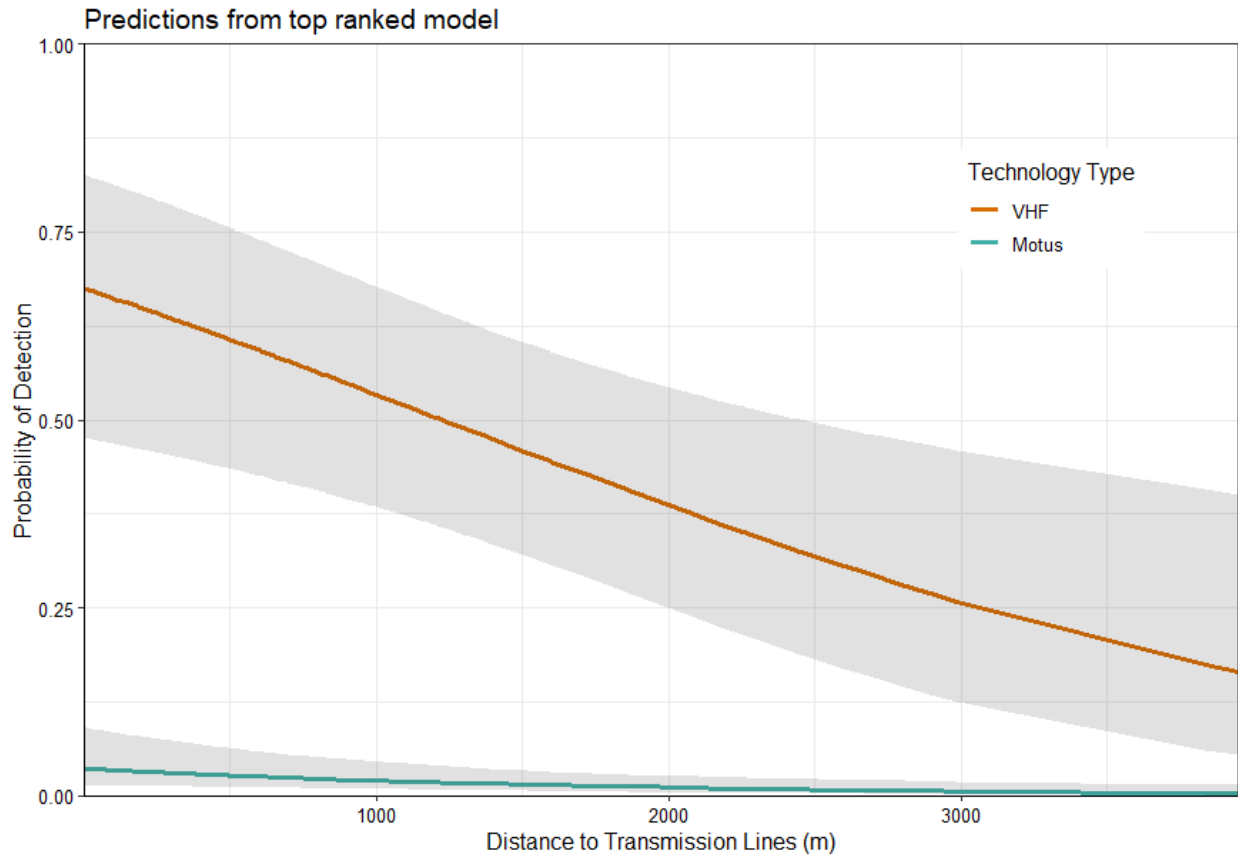


Figure 23. Top model predicted relationship (\pm 85% confidence intervals) between the probability of detection and distance between observers and nearest transmission lines (m) for VHF and Motus technologies during 2023 detection probability evaluations.

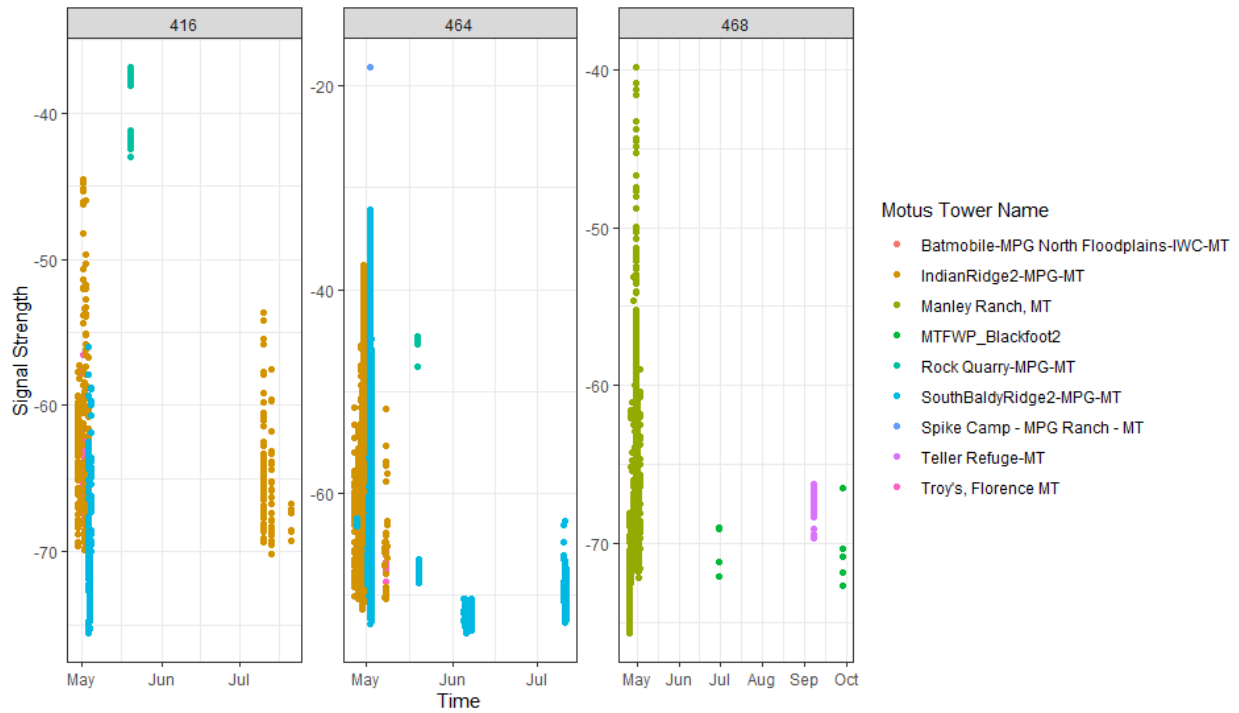


Figure 24. Automated Motus tower detections for 3 female sharp-tailed grouse (Transmitter IDs 416, 464, and 468) with confirmed nests. Female 464 was detected by a single tower during the first 5 days of the laying period; no females were detected during incubation.

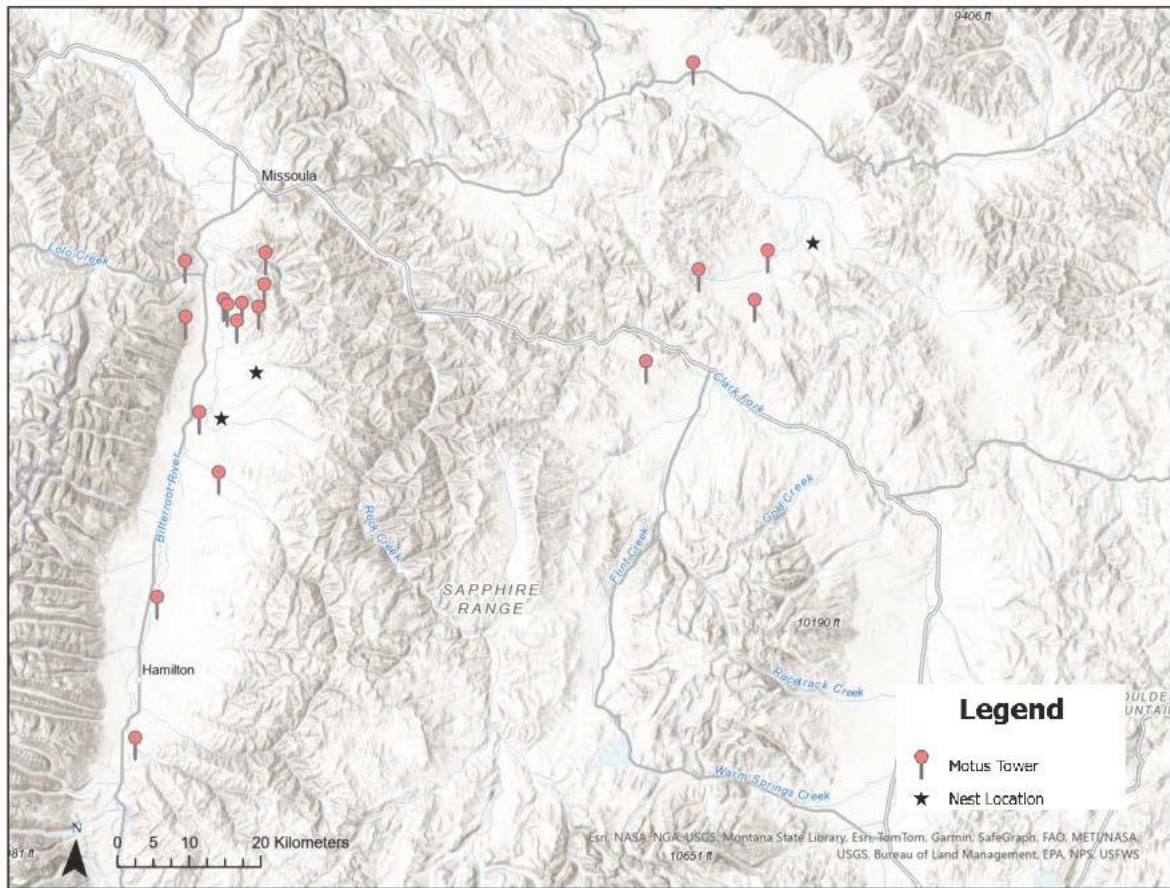


Figure 25. Map displaying the locations of Motus towers in the Bitterroot Valley and Blackfoot Valley and the 3 nest locations of the female sharp-tailed grouse fitted with Motus transmitters. Nest locations were at distances of 3,858 m, 4,842 m, and 7,625 m from the nearest Motus towers.

CHAPTER FOUR

DISCUSSION

Performance of automated radio telemetry technologies across topographical and environmental variation for monitoring ground-dwelling birds is poorly understood. My study provides insight into the performance of Motus telemetry technology compared to conventional VHF technology when transmitters are at ground level and complements the work of previous studies evaluating automated telemetry performance (Kays et al. 2011, Ward et al. 2013, Crewe et al. 2019, Paxton et al. 2022). To my knowledge, this is the first study to evaluate automated telemetry for ground-dwelling birds specifically. Although triangulation accuracy and precision in my study were higher for handheld Motus technology than traditional VHF, I found reduced detection distances and inconsistent automated detection limited the utility of Motus technology for fine-scale assessments of space use for ground-dwelling birds in western Montana.

Results from my study support strong effects of technology type on transmitter performance metrics when comparing the spatial resolution capabilities of conventional VHF versus Motus handheld technologies. Triangulated estimates of Motus transmitter locations using handheld technology were more precise and accurate than those of VHF, particularly at short distances. On average, triangulation of Motus transmitters resulted in estimated transmitter locations that were 96% more precise and 73% more accurate than those of the VHF technologies. However, the mean observable distance of VHF transmitters was nearly twice that of the Motus transmitters indicating observers had difficulty locating and triangulating Motus transmitters unless they were within approximately 250 m of the transmitter. The need for observers to be so close to transmitters to obtain precise and accurate triangulations using

handheld Motus equipment raises concerns about impacts to the behavior of wildlife due to observer proximity on the landscape which could subsequently influence inferences made about space use. While increased precision and accuracy would be beneficial when monitoring colonial breeding birds, for example, increased false detections of Motus transmitters would be problematic when Motus fitted animals are clustered together due to tag aliasing.

Relative Performance of Handheld Motus and VHF Technology

My study results suggest triangulation accuracy and precision are strongly impacted by the distance between the observer and the transmitter. Predicted triangulation precision declined rapidly for Motus technology as observer distance increased compared to VHF technology. Predicted accuracy of triangulations using Motus technology were more accurate than that for VHF technology across all observer distances. Notably, however, the mean observer distance for Motus technology was approximately half that of VHF technology, suggesting that observers were often nearer Motus transmitters during triangulations which would ultimately result in improved location estimate accuracy and precision. Radio transmitters send radio waves to receivers at varying signal strengths that degrade over distance due to background noise, temperature, reflection and attenuation of the signal due to objects in the environment, and distance between the antenna and the ground (Whitehouse et al. 2007, Bannister et al. 2008, Rutz et al. 2015). Reduced triangulation accuracy and precision as observer distance increased in my study was likely related to increased signal degradation as distance between the transmitter and observer increased. Both Motus and traditional VHF transmitters emit VHF signals, however Motus transmitters are programmed to transmit a series of 4 pulses at intervals of 3 seconds on a single frequency (166.380 MHz in the Western Hemisphere) whereas traditional VHF

transmitters each have a unique frequency on which they emit a single beep, typically at shorter intervals of 1-2 seconds. Difficulties triangulating Motus transmitters using handheld Motus equipment in my study may have been due partially to the inability to focus on one transmitter because they share a single frequency as well as the longer intervals between pulses compared to traditional VHF technology.

Although observers experienced difficulties locating and triangulating Motus transmitters relative to VHF transmitters, the average amount of effort spent completing triangulations was similar across technology types. Three triangulations of Motus transmitters required over 150 minutes of effort whereas no triangulations of VHF transmitters extended past 136 minutes. Triangulations requiring more than 1 hour of effort were rare for both technology types. Observers began recording time spent triangulating when they obtained the first bearing for the triangulation and stopped recording time when they took the third bearing. I was unable to evaluate the amount of time spent locating the signal of a transmitter prior to triangulation initiation because Motus transmitters were so difficult to detect in the field and were often subject to interference from other Motus transmitters nearby. Motus transmitters are programmed to operate on one radio frequency (166.380 MHz in the western Hemisphere) which allows for continuous scanning of transmitters by Motus towers rather than scanning individual frequencies as is standard for traditional VHF monitoring. When using Motus handheld receivers this feature is not ideal because all Motus transmitters within range are detected at once and, while individual transmitter identification is still possible, we were unable to configure the receiver to filter individual transmitter detections. Thus, a major difficulty in the field when triangulating Motus transmitters was interference and disruption of triangulation efforts due to other nearby Motus

transmitters. For example, it was common to be partway through a Motus triangulation when a second Motus transmitter signal would be received at a stronger signal strength than the initial transmitter, drowning out the signal of the first transmitter. This made it difficult to quantify the amount of effort spent locating Motus transmitters because observers often began searching for one transmitter but would lose the signal due to interference from a second transmitter or would decide to triangulate the interfering transmitter first before returning to locating the first transmitter, disrupting the ability to record the amount of time truly searching for the first transmitter.

I expected increased levels of terrain ruggedness to negatively affect triangulation accuracy and precision by increasing signal interference and attenuation (Whitehouse et al. 2007, Rutz et al. 2015), particularly for Motus technology. Interestingly, VHF technology exhibited the opposite relationship with decreased predicted triangulation accuracy at lower TRI values and large improvements in accuracy as TRI increased. Predicted triangulation precision using VHF technology was less dramatically affected by TRI than triangulation accuracy, yet still exhibited a slight improvement in precision with increasing TRI. However, observer distances during triangulation were larger at lower TRI values, particularly for VHF technology suggesting the low triangulation accuracy at low TRI values may be related to the ability of observers to detect and triangulate VHF transmitters from farther distances. Conversely, both Motus triangulation accuracy and precision behaved as I expected and declined steadily across increasing TRI, indicating lower accuracy and precision estimates in more rugged terrain. While the relationship between VHF technology and TRI was unexpected, observers could detect VHF transmitters from much farther distances at low TRI values, thus reducing triangulation accuracy and

precision in flat landscapes because they were farther from VHF transmitters during triangulations. The relationship between observer distance and triangulation accuracy and precision is supported by our results suggesting decreased accuracy and precision at farther observer distances for both technology types. Similarly, the ability for observers to detect VHF transmitters from greater distances may have been reduced at higher TRI values, resulting in observers being closer to transmitters in higher TRI and obtaining more accurate and precise location estimates. When examining observer distances in our data, most triangulations occurred in low TRI with a larger spread of observer distances, while only 4 triangulations occurred above the mid-range of TRI, only one of which was VHF which was conducted at very close range of approximately 18 m, indicating that observers were triangulating from greater distances across low TRI levels, particularly while using VHF technology which may explain the observed relationship between triangulation metrics and TRI predicted by our top ranked model.

To my knowledge, my study is the first to consider the effects of transmission lines on triangulation accuracy and precision. Previous studies investigating effects on radio users from high frequency and broadband power line communication system interference suggest a portion of the signal power radiates from the network into the surrounding area, increasing the radio noise floor and interfering with existing radio services such as radio communications, shortwave and TV broadcasting, and amateur radios (Fenton and Brown 2002, Liu and Greenstein 2010). I expected proximity to transmission lines to negatively affect signal detection and location estimates due to increased noise from interference, reducing the observer's ability to obtain accurate location estimates particularly near transmission lines. Contrary to my expectations, both technology types showed the opposite relationship. Predicted triangulation accuracy

declined for both Motus and VHF technologies as the distance between the observer and the nearest transmission lines increased, with Motus remaining more accurate than VHF technology overall. Furthermore, I found probability of detection was higher when observers were near transmission lines. My results were surprising as I experienced significant interference when attempting to detect and triangulate transmitters in the field, particularly Motus transmitters, when near a transmission line. I further examined observer distances and TRI values in relation to distance from transmission lines but found no evidence either of these covariates might be correlated or muddling interpretation of the relationship. Additionally, the distributions of distances between observer and transmission line and distances between transmitter and transmission line during detection probability evaluations were nearly identical, thus I found no indication that this relationship was related to the location of the transmitter in relation to the transmission line rather than the observer location. Future research is needed to better understand the influence of transmission lines on triangulation accuracy and precision when estimating wildlife locations using VHF radio technologies in semi-urban landscapes that contain transmission lines.

My results suggest that weather may affect triangulation metrics and detection probabilities when using handheld radio telemetry technologies in the field. I did not find an effect of wind on triangulation metrics or detection probability; however increasing temperatures negatively affected probability of detection for both VHF and Motus technologies and increasing % relative humidity negatively impacted triangulation precision for both technology types. Previous research has found a reduction in both radio signal strength and in radio communication range that decreases linearly as temperature increases (Bannister et al. 2008), which may explain

my observations of reduced detection at higher temperatures. Increased humidity has been shown to improve propagation of radio waves (Thelen et al. 2005, Marfievici et al. 2013), however, I observed lower triangulation precision at higher values of % relative humidity. Identifying threshold values that minimize the impacts of both temperature and humidity may help improve location estimates and detection probabilities when using radio telemetry during monitoring efforts.

Although estimated precision and accuracy of triangulated Motus transmitters was higher than VHF transmitters, observers had to be much closer to detect Motus transmitters. My results of low detection for Motus transmitters at 1-km are consistent with previous research demonstrating the detection range of automated telemetry technology to be less than 1 km when animals are foraging on the ground, although this study was evaluating the detection range of antennas on automated towers rather than handheld antennas (Crewe et al. 2019).

Predicted detection probabilities of both VHF and Motus technologies exhibited similar relationships with topographic strata; the probability of detecting a transmitter was highest when transmitters were in lower and middle strata. However, the probability of detecting a Motus transmitter in any given strata was less than 0.12 while the probability of detecting VHF was > 0.50 regardless of strata. Varying detection probabilities across different topographic strata is likely due to the complexity of the environment blocking, reflecting, and weakening the signal strength of radio waves between the transmitter and the observer (Liberti and Rappaport 1992, Whitehouse et al. 2007). I expected detection probabilities to vary between topographic strata due to the differences in topography and elevation between strata. For example, transmitters located in draws are at the bottom of V-shaped drainages surrounded by steep hillsides that

would likely block, reflect, or weaken the signal strength of radio waves. Conversely, I expected the upper strata, which was composed of the top 20% of the elevational gradient, to have higher detection probabilities because transmitters in the upper strata would be located at higher elevations with less topography to interfere with radio wave propagation.

Performance of Automated Motus Technology for Sharp-tailed Grouse

Overall, my study found limited and inconsistent simultaneous detections by automated Motus towers to limit the applicability of this technology for monitoring sharp-tailed grouse in western Montana. While all sharp-tailed grouse fitted with Motus transmitters in our study area were detected by at least one tower over the course of the season, only 26 of 54 grouse were detected by at least 2 towers simultaneously, none of which occurred during the critical nesting period for females. Thus, I was unable to monitor nesting behavior or evaluate even seasonal space use metrics using the array of automated Motus towers in our study area. Previous studies suggest that a minimum of 30 unique locations per bird are needed to prevent biased home range estimates (Seaman et al. 1999, Milligan et al. 2020). Simultaneous detections were below this threshold for 25 of 26 grouse; only one male STGR had 32 simultaneous detections by multiple towers on unique days. Moreover, grouse in our study were not detected simultaneously by three Motus towers, precluding the estimation of space use by standard triangulation. Therefore, estimation of sharp-tailed grouse space use and habitat selection was not possible using automated collection of Motus-equipped grouse at our study areas.

The limited ability of Motus towers to detect sharp-tailed grouse in our study areas may be due to interference of signal transmission when transmitters are at ground-level. While

estimated detection range for Motus towers has been found to be as high as 15 km for airborne animals (Taylor et al. 2017), there are many factors related to complex outdoor environments and animal behavior that reduce radio signal strength (Whitehouse et al. 2007, Rutz et al. 2015) and consequently reduce the detection distance of Motus towers for ground-level transmitters. Nest locations of females fitted with Motus transmitters in my study area were located at distances ranging from 4 – 8 km from the nearest Motus towers, however these females were never detected by the Motus towers during incubation. The ground itself as well as low foliage and even short grass scatters and absorbs radio waves (Whitehouse et al. 2007, Kays et al. 2011), which may have decreased the ability of radio waves from sharp-tailed grouse in our study to transmit far enough to reach the Motus towers arranged around our study areas, particularly during the nesting period. Additionally, ground-dwelling birds may often be positioned in a manner that points transmitter antenna toward the ground, exacerbating signal attenuation and likely lowering detection probabilities (Crewe et al. 2019). A study comparing detection by automated Motus towers between ground foraging sparrows and canopy foraging songbirds found reduced detection abilities for birds foraging on the ground, with an estimated detection range of only 300 m when temporal precision to investigate changes in movements and activity levels was required (Crewe et al. 2019). Furthermore, a study of automated telemetry in the tropical rainforests of Panama found signal strength to be greatly reduced for transmitters within a few meters of the ground and researchers were unable to triangulate locations of small animals even with towers spaced 800 m apart (Kays et al. 2011). Thus, interference of radio waves and tower placement may play large roles in the ability for an automated radio telemetry array to detect and estimate locations of ground-dwelling birds.

Placement of towers and orientation of antennas atop the towers are important considerations for future research evaluating the use of automated telemetry for ground-dwelling birds. Motus towers in my study area were spaced irregularly, with the nearest spacing between towers approximately 900 m. Most of the towers in my study area were spaced between 2 – 10 km apart (yet within 5 km of sharp-tailed grouse release locations) which was not sufficient to obtain simultaneous detections of transmitters at ground level. I expected additional Motus towers deployed by other studies or private landowners in the vicinity of our study area to increase our detections, however they were too far apart to result in simultaneous detections and only served to occasionally detect sharp-tailed grouse who dispersed from the release sites. Other studies suggest towers may need to be spaced less than 800 m apart to triangulate locations of animals with smaller transmitters, particularly those at ground level due to reduced signal strengths between ground-level and canopy-level (Kays et al. 2011). Additionally, the ability to triangulate locations requires accurate bearings which can be estimated from signal strengths but requires uniform antenna configuration with spacings of 60° between each antenna (Ward et al. 2013, DeGregorio et al. 2015, Smetzer et al. 2021, Paxton et al. 2022). Antenna on our towers were oriented in such a way to maximize coverage of the study areas but were not uniformly positioned around the tower which would have limited our ability to calculate accurate bearing estimates if we had received sufficient simultaneous detections to do so.

Monitoring of ground-dwelling birds may benefit from the use of automated Motus technology if the focus of the research is related to presence/absence within a small study area or for estimating activity levels outside of the breeding season. Studies concerned with understanding grouse lek attendance may benefit from this technology due to the tendency for

leks to occur on exposed hilltops with low vegetation that would ideally result in higher detection probabilities due to less radio signal interference from complex topography and vegetation. Towers may offer hunting perches for avian predators near leks where tall perches are historically scarce (Dwyer and Doloughan 2017). Thus, researchers will need to consider a distance between the tower and lek that ensures high detection probabilities but does not increase risk of predation due to the possibility of predators using the towers as perches near a lek. The ability of Motus towers to simultaneously detect transmitters at ground-level allowing researchers to estimate locations would require a higher density of towers than I had in my study area, which would increase the monitoring costs and reduce the study area size, especially if towers need to be spaced evenly under 1-km apart. The utility of Motus automated telemetry for monitoring ground-dwelling birds may be inhibited by funding and study area size.

Management Implications

Recent advances in automated radio telemetry technologies, such as Motus, promise novel methods of monitoring wildlife that are cost-effective and require less intensive field monitoring than traditional methods. Opportunities to apply automated telemetry to wildlife monitoring programs are increasing due to reduced transmitter sizes, allowing transmitters to be deployed on species as small as butterflies (Fisher et al. 2021). Automated radio telemetry technologies have successfully been used to evaluate space-use of airborne and canopy-level species (Smetzer et al. 2021, Paxton et al. 2023) with estimated detection distances of up to 15 km for airborne species (Taylor et al. 2017). However, my results reveal limited ability of automated Motus towers to monitor the space use of sharp-tailed grouse, and likely other ground-dwelling species of wildlife. Triangulation accuracy and precision in my study were

higher for handheld Motus technology than traditional VHF, however, reduced detection distances and inconsistent automated detection limited the utility of Motus technology for fine-scale assessments of space use for ground-dwelling birds in western Montana.

Consistent with previous studies which found detection distances of automated telemetry towers to be lower for wildlife at ground-level versus canopy-level (Crewe et al. 2019), I found reduced detection distances for the handheld Motus technology when compared to conventional VHF technology. Fine-scale space use of wildlife is useful information for wildlife managers, and is particularly critical following translocations to inform future restoration efforts and management decisions (Snyder et al. 1999, Teige 2021), especially for species that require large numbers to establish sustaining populations, such as prairie grouse (Milligan et al. 2018). Reduced detection distances of automated towers (Crewe et al. 2019) and of associated handheld equipment in addition to inconsistent automated detections when estimating locations of ground-dwelling species may be problematic for effective monitoring, particularly when fine-scale habitat characteristics are desired to inform habitat management and reintroduction efforts.

Although my study found limitations posed by automated telemetry when monitoring ground-dwelling birds, I also found higher accuracy and precision of triangulations using handheld Motus technology indicating there may be applications for using Motus when precision and accuracy are more important than detection distances. However, further evaluations will need to be completed to assess whether triangulation using Motus towers provides similarly high precision and accuracy to the handheld technology. The benefits of high precision and accuracy using Motus handheld equipment may be outweighed by the reduced observer distance compared to traditional VHF because observers would need to be closer to individual animals to

triangulate, which may alter the animal's space use and any inferences that can be made from locations. Additionally, further assessments may be beneficial to inform tower configurations that may improve simultaneous detection rates of ground-dwelling species. While the limited detection distances of automated technology pose constraints when transmitters are near ground-level, there may be optimal tower placement that could increase simultaneous detections, such as reducing the distances between towers to an ideal threshold.

To improve upon and further evaluate detection capabilities of Motus towers for future monitoring efforts of sharp-tailed grouse or other small ground-dwelling species I recommend placing towers in a grid at 1-km distances from each other. Nesting sharp-tailed grouse in my study area were not detected by a Motus tower even when the nest location was within 4 km of the nearest tower. Previous studies suggest detection ranges less than 1 km for ground-foraging songbirds (Crewe et al. 2019) and small terrestrial animals (animal weight < 10 kg) such as rats (Kays et al. 2011). In a tropical rainforest setting, towers spaced 800 m apart were unable to obtain sufficient simultaneous detections by >3 towers to triangulate locations of small terrestrial animals (Kays et al. 2011). Similarly, songbirds fitted with Avian Nanotag NTQB-1 (Lotek Wireless Inc., Newmarket, Canada) weighing 0.35 g had maximum detection distances of approximately 300 m when foraging at ground-level and 600 m when foraging at mid-canopy when temporal precision was required for evaluating movements of individuals (Crewe et al. 2019). The sharp-tailed grouse in my study were fitted with Avian Nanotag NTQB-9-2 (Lotek Wireless Inc., Newmarket, Canada), which weighed ~12.4 g with a 7.5-inch antenna length. The larger battery size of the 12.4 g transmitters used in my study would presumably increase the detection range to be higher than the smaller 0.35 g transmitters used for the songbird study.

Based on these previous studies, transmitter specifications, and the differences in vegetation between my study site and those of previous studies (e.g., tropical rainforest versus grassland), I estimate Motus towers in my study area would be able to detect a ground-level sharp-tailed grouse sized transmitter at a distance of 1 km. Thus, to optimally configure a Motus tower array for monitoring sharp-tailed grouse in western Montana this would require regular spacing of 1-km distances between Motus towers. For monitoring efforts of sharp-tailed grouse at the Helmville, MT field site I recommend a total of 42 Motus towers placed in a 1-km grid across the reintroduction site. On MPG Ranch I recommend a total of 29 Motus towers placed in a 1-km grid across the rangeland portion of the ranch to maximize monitoring efforts of released sharp-tailed grouse. The approximate cost per tower for raw materials is \$5,000 with monthly data charges of approximately \$5.30 per Motus tower (J. Kuntz, Montana Fish, Wildlife, and Parks, personal communication). The cost of materials to implement this array of Motus towers would be \$210,000 at the Helmville, MT release site and \$145,000 at the MPG release site. Due to landscape topography and vegetation in the study areas it may be difficult to place towers in exact 1-km spacing because there are other considerations regarding tower placement to maximize detection distances, such as selecting placement sites on higher terrain and above tree canopies. Tower placement should be carefully assessed for each location to maximize detection probabilities, perhaps requiring a buffer of 300 m around each grid point within which the tower could be placed in the ideal topographical situation. Additionally, implementation of an array of towers this dense may be difficult to achieve not only within the established sharp-tailed grouse reintroduction sites, which are working ranches, but especially on surrounding private properties and public lands. Dependent on agreement with property managers, monitoring efforts using this

tower array would likely be limited to the property boundaries of the reintroduction sites which would therefore limit monitoring of individual grouse when they leave the site or make large exploratory movements away from the reintroduction location. A grid of Motus towers spaced at 1-km distances to obtain simultaneous detections is likely an unrealistic goal for monitoring sharp-tailed grouse in western Montana due to the sheer density of towers it would require.

Regarding Motus tower specifications, I recommend using 9-element directional Yagi antennas oriented at consistent angles and heights on each Motus tower to allow for calculation of bearings from the tower to the source of the radio signal (Paxton et al. 2023). Each Motus tower should consist of six 9-element antennas mounted on 6 – 10 m tall masts with antenna oriented 60° apart for 360° detection coverage (Paxton et al. 2023). Intentional and consistent 60° spacing is critical for estimating bearings and triangulating locations of animals when simultaneous detections are achieved (Ward et al. 2013, DeGregorio et al. 2015, Smetzer et al. 2021, Paxton et al. 2023). Managers should also note that data processing required for Motus detections is time consuming and requires large amounts of computer processing capabilities and storage space. The number of detections depends on the project scale but generally number in the millions or billions and may take multiple days to download from the Motus database depending on internet speed and computer capabilities.

Opportunities to use the Motus network for monitoring that does not require simultaneous detections remains a possibility. While simultaneous detections in my study were low, overall detections of individual grouse by at least one Motus tower was much higher and ranged from 60 detections of an individual to over 4 million detections of an individual over the course of the field season. One potential application of Motus technology for sharp-tailed grouse monitoring

may be to use Motus towers to monitor lek attendance. Placing a single Motus tower within range of known leks would provide managers with individual grouse lek attendance metrics including time and dates of individual arrival and departure from the lekking area, numbers of marked individuals attending leks, and lek fidelity of marked individuals. The distance from the lek should be such that it reduces hawk perch availability while still maximizing detection of ground-level transmitters. Managers should also consider the increased risk of higher levels of false detections when animals fitted with Motus transmitters are concentrated in an area together due to tag aliasing, which is when two transmitter signals overlap to produce a signal that looks like a third transmitter that is not actually present.

Overall, increasing the density of towers to improve coverage and simultaneous detections would require large up-front costs to establish a larger quantity of towers and receivers on the landscape and may be problematic to implement due to landowner permissions and overall feasibility of installing a dense array of towers. Additionally, it is difficult to track individuals who make large exploratory movements outside of the coverage area. Managers will need to carefully consider the costs and benefits of using automated radio telemetry networks to monitor ground-dwelling species before implementing an array in their study system. Managers monitoring ground-dwelling birds using automated Motus technology would benefit from focusing on research goals that do not require simultaneous detections of individuals but instead focus on presence/absence within a study area or activity levels outside of the nesting season, such as lek attendance.

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