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Refurbishing used GPS transmitters improves performance for subsequent deployments on greater sage-grouse

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Abstract

Global Positioning Systems (GPS) radio transmitters are increasingly used across taxa to monitor animal populations. However, GPS transmitters can be susceptible to malfunctions that may result in location errors or data loss causing potential inferential bias that can have important implications for monitored species. Research using GPS transmitters on greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) has increased, but few sage-grouse studies have evaluated GPS performance. Because sage-grouse management has been subject to intense legal and political scrutiny with consequential economic implications, reliable data acquisition is central to informed decision-making for the species. We evaluated differences in the performance of 2 commonly used solar-powered GPS transmitters (Microwave Telemetry, Inc. [MTI], Columbia, MD, USA and GeoTrak, Inc., Apex, NC, USA) deployed on sage-grouse throughout Wyoming from 2011 to 2017 and Utah from 2013 to 2019. Our investigation of GPS performance included

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daily fix inefficiency, the number of 1-day fix gaps, and transmitter loss rate. We also evaluated transmitter functionality during the nesting period including daily nesting fix inefficiency, fix error distance mean and standard deviation (i.e., accuracy and precision), and mean fix error direction. New and refurbished MTI transmitters outperformed GeoTrak transmitters in daily fix inefficiency and day gaps during most seasons. Cumulatively redeployed MTI transmitters did not perform differently than GeoTrak transmitters. Transmitter loss, daily nesting fix inefficiency, and nest fix precision did not vary significantly between the 2 transmitters. GeoTrak performed better than MTI for nest fix accuracy across all latitudes (40–45° N). The mean error direction to the nest location ranged between 105° and 135° for GeoTrak and between 135° and 155° for MTI. We recommend refurbishing transmitters following deployment to retain higher fix efficiency than cumulatively redeploying transmitters.

KEYWORDS

Centrocercus urophasianus, fix success, GPS location error, GPS performance, greater sage-grouse, solar-powered GPS transmitters, Utah, Wyoming

Fish and wildlife population monitoring has been greatly influenced by the advent of global positioning systems (GPS) technology, especially since the early 2000s. Increased GPS use has primarily been driven by the desire to acquire better knowledge to inform managers and researchers about target species (Frair et al. 2010, Latham et al. 2015). Data acquired from GPS transmitters can reveal fine-scale patterns of space use, behavior, population dynamics, and predator-prey interactions (Kays et al. 2015), while at the same time reducing telemetry bias and improving accuracy and precision beyond that available from unmarked individuals or those marked with very-high frequency (VHF) transmitters. Technological advances have allowed researchers to address new and important questions related to animal behavior that are contributing to changes in management directives and policies (e.g., Wyoming Migration Initiative https://migrationinitiative.org/, Utah Migration Initiative https://wildlifemigration.utah.gov/, Audubon Society's Bird Migration Explorer https://explorer/audubon.org). The decade from 2010 to 2020 witnessed an increase in the use of GPS transmitters and has thus been deemed the beginning of the golden age of fine-scale data acquisition for fish and wildlife populations (Kays et al. 2015, Hofman et al. 2019).

Growth in GPS transmitter market demand has sparked an array of transmitter production companies, with >40 globally producing GPS transmitters for animal research (Table S1, available in Supporting Information). Costs per transmitter vary, with smaller units costing more due to the increased cost of smaller hardware. Other costs can include monthly data fees for data acquisition. However, cost, when weighed against the value of the resulting data, makes it essential to evaluate variation in GPS data reliability (Hebblewhite and Haydon 2010). Reliability and consistency of GPS data dictate the accuracy of movement, habitat selection, and vital rate estimates (Cagnacci et al. 2010, Christin et al. 2015, Kays et al. 2015). Reliability and consistency are quantified through functionality; i.e., the transmitter's ability to record and transfer data as expected (Frair et al. 2010, Camp et al. 2016, Jung et al. 2018). Measures of GPS functionality include unit longevity and 2 primary sources of error:

spatial error and fix error (Frair et al. 2010, Camp et al. 2016). Longevity among GPS units with nonrechargeable batteries is a function of the frequency of scheduled fixes, battery charge capacity, and ambient temperatures. For solar rechargeable units, longevity is determined by the battery capacity and frequency of scheduled fixes, balanced against access to solar radiation. Spatial error, termed (in)accuracy or (im)precision, describes a registered fix that is not representative of an animal's estimated actual or approximate location (Frair et al. 2004, Cagnacci et al. 2010, Williams et al. 2012). Spatial errors can be categorized as minor (10–30 m) or large (several km or less) and must be removed or corrected before analysis (Frair et al. 2010, Morris and Conner 2017). Fix errors can describe failed location attempts, such as when the GPS transmitter attempted to register a fix and failed (Frair et al. 2010), or spurious fixes produced outside of scheduled fix acquisition times (Thomas et al. 2011).

Internal and external variables can affect GPS transmitter functionality, including longevity and spatial and fix errors. Internal variables include hardware- or software-based issues such as battery charge (Silva et al. 2017), insufficient communication with available satellites (Ranacher et al. 2016), transmitter age (García-Jiménez et al. 2020), and the fix schedule (e.g., Acácio et al. 2022). External variables can include latitude (Jung et al. 2018), vegetation characteristics (Liu et al. 2018), topography (Ironside et al. 2017), animal species and behavior (Hofman et al. 2019), climate (Schlippe Justicia et al. 2018), season (Silva et al. 2017), and solar time (Byrne et al. 2017). Many studies recommend data screening to account for errors associated with these variables (Lewis et al. 2007, Villepique et al. 2008). However, researchers must evaluate their transmitters' performance to inform their data screening process and account for errors.

Between 2007 and 2010, researchers began using GPS transmitters on greater sage-grouse (*Centrocercus urophasianus* hereafter sage-grouse) throughout the western United States and Canada (Stringham 2010, Dzialak et al. 2011, Fedy et al. 2012). Sage-grouse are a sagebrush (*Artemisia* spp.)-obligate galliform regarded as an indicator species of sagebrush ecosystem health (Rowland et al. 2006, Carlisle et al. 2018, Smith et al. 2021). Continuous range-wide declines (i.e., 80%; Coates et al. 2021) have resulted in multiple Endangered Species Act (ESA) petitions for listing since 2002, ultimately leading to large-scale research and collaboration efforts aimed at better understanding sage-grouse ecology and highlighting possible avenues for conservation (Connelly et al. 2011a, Duvall et al. 2017).

Research efforts have fitted sage-grouse with GPS transmitters to address critical conservation and management questions (Wann et al. 2019, Kirol et al. 2020). Despite studies using GPS transmitters to monitor sage-grouse populations, researchers have yet to evaluate transmitter performance. Research focused on other upland gamebirds has evaluated GPS transmitter performance on species such as northern bobwhite (*Colinus virginianus*; Marquardt et al. 2017) and wild turkey (*Meleagris gallapavo*; Guthrie et al. 2011). Here, we utilize a dataset compiled from 15 study areas in Utah and Wyoming to assess the functionality of the 2 most commonly-used, 22-g solar-powered, GPS-Argos Doppler transmitters (hereafter, GPS transmitters), one from GeoTrak, Inc. (Model No: GT-22GS-GPS https://www.geotrakinc.com/, Apex, NC, USA) and the other from Microwave Telemetry, Inc (MTI; Model No: PTT-100-22 Argos-GPS https://www.microwavetelemetry.com/, Columbia, MD, USA). Specifically, we compared transmitters regarding daily fix inefficiency, day gaps, and loss rate. We also assessed inefficiency during the nesting period through fix precision and accuracy with known nesting locations.

STUDY AREA

We used data from sage-grouse transmitter studies at 15 study areas (Utah = 13; Wyoming = 2; Table 1). Sage-grouse studied in the Bighorn Basin (Table 1) were located in Wyoming and a southern portion of Montana, but we refer to these sage-grouse as Wyoming for simplicity. We provide detailed information regarding prevailing climate regimes, elevational bands, and species of sagebrush that dominate these sites (Table 1).

TABLE 1 The names and locations of study areas in Utah and Wyoming, USA, where we collected data from 2 solar-powered GPS-Argos transmitters manufactured by differing companies (GeoTrak Inc. and Microwave Telemetry Inc.) and used for research on greater sage-grouse (*Centrocercus urophasianus*) between 2011 and 2019.

State	Study area	Location (lat, long)	For detailed climate/topographical information, see
Utah	West Box Elder SGMA*	41.75275° N, −113.663125° W	Sandford et al. (2017)
	East Box Elder SGMA	41.98975° N, −112.5617° W	Sandford et al. (2017)
	Rich SGMA	41.7412° N, −111.23268° W	Stringham (2010)
	Crawford Mountains	41.574225° N, −111.051675° W	Stringham (2010)
	Morgan-Summit SGMA	40.95386167° N, −111.5320567° W	Flack (2017)
	Sheeprock Mountains SGMA	39.9865° N, −112.44903° W	Robinson and Messmer (2013)
	Hamlin Valley SGMA	38.1403° N, −113.9687 °W	Beers and Frey (2022)
	Bald Hills SGMA	38.07783° N, −113.0305° W	Beers and Frey (2022)
	Panguitch SGMA	37.7325° N, −112.4823° W	Beers and Frey (2022)
	Parker Mountain-Emery SGMA	38.346267° N, −111.78883° W	Baxter et al. (2013), Duvuvuei et al. (2017)
	Anthro Mountain	39.90212° N, −110.41266° W	Duvuvuei et al. (2017)
	Strawberry SGMA	40.15624° N, −111.085° W	Baxter et al. (2013)
	Uintah SGMA	40.65332° N, −109.47004° W	Baxter et al. (2013)
Wyoming	Jeffrey City	42.585625° N, −108.1088325° W	Smith et al. (2016), Kirol et al. (2020)
	Bighorn Basin	44.46825° N, −107.80142° W	Pratt et al. (2017), Pratt and Beck (2019)

*SGMA: Sage-grouse Management Area.

METHODS

Sage-grouse in our study were marked with solar-powered GPS-Argos satellite transmitters mounted on the rump to monitor their space use and vital rates (Bedrosian and Craighead 2007; Figure 1). In Utah, researchers from Utah State University (USU) and Brigham Young University (BYU) mounted 285 GPS transmitters on 469 sage-grouse from 2013 to 2019. In Wyoming, University of Wyoming (UWyo) researchers mounted 52 GPS transmitters on 113 sage-grouse from 2011 to 2017. Our dataset comprised 582 marked sage-grouse and 337 GPS transmitters. Male and female sage-grouse were captured at night near active leks (2100 hr to 0500 hr; Connelly et al. 2003) using all-terrain vehicles, spotlights, and long-handled nets. Sage-grouse were either processed at the capture site and released or brought to nearby processing areas. Processing included aging, sexing, weighing, leg banding, recording capture locations (UTM, 12 N, NAD 83), and attaching transmitters. The MTI GPS transmitters (n = 167) included ultra-high frequency (UHF) capabilities to allow for relocating marked birds in the field. The GeoTrak GPS transmitters (n = 170) included a 3-g VHF transmitter epoxied to the side of the GPS transmitter serving the same purpose as the internal UHF signal on the MTI transmitters. Each GPS transmitter weighed 22 g without harness straps and approximately 33 g with straps included.

Scheduled fixes occurred at the top of the minute when seconds are at 0 for all fix schedules. The manufacturer programmed fix schedules between 4 and 10 daily fixes according to specific project objectives and

FIGURE 1 Two commonly used solar powered GPS-Argos satellite transmitters made by Microwave Telemetry, Inc. (A) and GeoTrak Inc. (B) with each company's individual transmitter in the photos located above photos of their deployment on greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming between 2011 and 2019 (photo credit: C. Backen).

seasons. Global Positioning Systems units from both manufacturers transmitted fixes to the Argos satellite system according to a predetermined duty cycle that ranged from 3 to 8 days (Table S2, available in Supporting Information). Before deployment, GeoTrak and MTI manufacturers required that users charge transmitters for 2 and 5 days, respectively, at a 45-degree angle facing south to ensure the most direct sun exposure for battery charging.

Researchers monitored all instrumented females 2 to 3 times weekly during the nesting season to determine the nest initiation date. Once observers confirmed a female was nesting, they monitored the nest until failure or hatch, after which they registered a GPS coordinate of the known nest location on the ground using a handheld GPS unit at the site of the nest. Handheld GPS unit models varied, but we assumed all types had a GPS error <5 m. Due to differing vegetation measuring methods between the 3 universities, we only included USU and UWyo vegetation data. Researchers measured nest shrub height (cm) and diameter (cm) for each nest site. Using line intercept (Canfield 1941, Connelly et al. 2003) to determine average shrub cover and height (cm) across a 15-m radius from the nest site.

From remotely sensed satellite data, we calculated the average slope, aspect, and terrain roughness (see Roughness as defined in Wilson et al. 2007) using terrain in R's terra 1.6-41 package (R Core Team 2022, Hijmans 2022b). The resolution of the associated raster layers was approximately 6 m^2 (highest zoom level 14 in the function get_elev_raster in R's raster 3.6-3 package [Hijmans 2022a, R Core Team 2022], which accesses products from the U.S. Geological Survey's 3D Elevation Program). We assessed slope, aspect, and terrain roughness around each nest within an approximate 18-m radius, determined to best incorporate the 15-m radius for vegetation measurements.

We assembled and cleaned raw GPS data according to each fix schedule. We first subset the GPS dataset to eliminate fixes collected in the first 2 or 7 days for resident or translocated birds (i.e., Sheeprock Sage-grouse Management Area translocations), respectively, after the last-known alive location (LAL) or after our analysis cutoff date (0559 UTC on 1 March 2019). We censored locations following capture to allow individuals to acclimate to the transmitters and prevent potential bias associated with this period. We visually inspected the data to identify clusters of locations indicating mortalities to assign the LAL. If transmitters went offline with no apparent mortality upon inspection in the field, we assigned the last recorded location as LAL.

We then used a sequence of data cleaning steps to remove unscheduled or outlier data, which we termed 1) non-hour, 2) duplicate time, 3) incorrect schedule, and 4) spatial outlier locations (Data Screening Steps, online in Supporting Information). We also removed data containing not applicable (NAs) information present in differing categories or misaligned years of GPS company data. The data cleaning steps resulted in 167 GeoTrak transmitters and 170 MTI transmitters (Table 2). We separated nonnesting (e.g., when an individual was not nesting or initiating a nest) and nesting (e.g., a confirmed nest with nest initiation start and end date included) GPS data to avoid underestimating overall functionality simply because functionality among nesting individuals was hypothesized to be lower from nesting in high vegetation cover. The cleaned nesting dataset resulted in 35 GeoTrak transmitters and 116 MTI transmitters (Table 2). Any further data cleaning involved removing NAs to maximize data completeness per respective covariate group per analysis.

We modeled all response variables of interest (e.g., daily fix inefficiency, day gaps, etc.) using a top-down approach guided by hypothesized effects to assess model fit (Burnham and Anderson 2002). We selected model combinations from a global model, including additive effects of all covariates. We assessed correlations among all pairs of covariates using Pearson's correlation coefficients and included covariates with correlations whose absolute values were <0.6. Highly skewed continuous variables were log-transformed to improve symmetry. All generalized linear mixed-effects models were fit using the glmmTMB 1.1.5 package (Brooks et al. 2017) in R (v. 4.2.1; R core team 2022). We ran linear mixed-effect models in the lme4 1.1-30 package (Bates et al. 2015) in R (v. 4.2.1; R Core Team 2022). For our mixed effects models (all excluding transmitter loss, see below), we considered all candidate models that fell within 4 Akaike's information criterion adjusted for small sample sizes (ΔAIC_c) of the best model to be competitive for further exploration of model fit (Burnham and Anderson 2002). We report covariate results in terms of beta estimates and 95% CIs. Additionally, we report model test statistics (number of parameters [K] and ΔAIC_c) of the best-fit models

TABLE 2 Number of deployed transmitters (n = 573) per year used in analyzing the performance of solar-powered GPS transmitters manufactured by differing companies (GeoTrak Inc. [n = 291] and Microwave Telemetry Inc. [n = 282]) and used for research on greater sage-grouse (*Centrocercus urophasianus*) between 2011 and 2019 in Utah and Wyoming, USA. The analysis end date was 01 March 2019, so no new transmitters were deployed that year. Sample sizes for the nesting analyses are in parentheses.

Year	GeoTrak Inc.	Microwave Telemetry Inc.
2011		12 (10)
2012		39 (14)
2013		35 (18)
2014		44 (23)
2015	26 (0)	30 (9)
2016	67 (4)	46 (18)
2017	103 (13)	46 (15)
2018	95 (18)	30 (9)
Total	291 (35)	282 (51)

with each associated null model with and without zero-inflation, where applicable (Table 3). We evaluated model fit and assumption violations (including zero-inflation and overdispersion) using randomized quantile residuals generated through the DHARMa package (Hartig 2022) in R. If several models yielded similar ΔAIC_c values and similar DHARMa residual plots, we favored the most parsimonious predictor variable combination. For nested mixed effects models within 4 ΔAIC_c of the null model, we assessed chi-square (χ^2) goodness-of-fit using the analysis of variance (ANOVA) function in the stats package (R Core Team 2023) and report the *P*-value (Table 3). If any coefficients were found to have nonsignificant *P*-values with 95% confidence intervals (CI) that included zero, we assessed model versions with and without them, comparing their respective ΔAIC_c values and DHARMa plots to determine our best-fit model. Models with zero-inflation were refit using a zero-inflated structure capturing 2 processes: a process describing whether the device could take any fixes in a given day and a second process describing the number of scheduled fixes that occurred, given that any fixes were possible.

TABLE 3 Top models for each response variable assessed in evaluating the performance of 2 GPS company transmitters (GeoTrak Inc. and Microwave Telemetry Inc. [MTI]) deployed on greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2015 and 2019. Zero-inflation (ZI) formulas, if applicable, are included. We have included number of parameters (*K*) and the difference in Akaike's information criterion score adjusted for small sample size (ΔAIC_c) for each top model and its associated null and null with ZI formula, respectively. Random effects variables are included within parentheses, with nested random effects delineated with forward slash (/).

Model	Top model equation per response variable[a]	*K*	ΔAIC_c
Daily fix inefficiency	Daily fix inefficiency ~ 1 + (bird/sa)	3	106290.5
	Daily fix inefficiency ~ 1 + (bird/sa), ZI formula ~ 1	4	11877.8
	Daily fix inefficiency ~ gps × season + log(cdl) + (bird/sa), ZI formula ~ gps × ncr + season	20	0
Day gaps	Day gaps ~ 1 + (Bird) + offset(log(DD))	2	97.19
	Day gaps ~ gps + plp + ncr + log(cdl) + (bird) + offset(log(dl))	8	0
Daily nest fix inefficiency	Daily nest fix inefficiency ~ 1 + (transm)	2	2922.57
	Daily nest fix inefficiency ~ 1 + (transm), ZI formula ~ 1	3	715.19
	Daily nest fix inefficiency ~ ncr × dl + mr + (transm), ZI formula ~ gps + dn + sh	12	0
Mean fix error	log(Mean fix error) ~ 1 + (bird/sa)	4	6.46
	log(Mean fix error) ~ gps + nl + (bird/sa)	6	0
Fix error standard deviation	sqrt(Fix error standard deviation) ~ 1 + (bird/sa)	4	0.31[b]
	sqrt(Fix error standard deviation) ~ gps + dn + nl + (bird/sa)	7	0
Transmitter loss	Transmitter loss ~ 1	0	0

[a]bird = bird ID; cdl = cumulative deployment length (total time deployed across multiple deployments); dl = deployment length (single deployment); dn = days nesting; gps = GPS company type (MTI or GeoTrak); mr = mean terrain roughness around the nest location; ncr = new, cumulative, or refurbished deployment status; nl = nesting location latitude; plp = proportion of time the transmitter was deployed during low photoperiods; sa = study area; transm = transmitter ID; sh = average shrub height around the nest.

[b]Chi square (χ^2) goodness-of-fit test using the analysis of variance (ANOVA) function in R's stats package (R core Team 2023) for comparing the fix error standard deviation null model and the best-fit model was $\chi^2_3 = 13.101$ and $P = 0.004$, supporting rejection of the null hypothesis and differentiating goodness-of-fit between the null and best-fit model. Further model fit was then assessed through residual plots in R's DHARMa package (Hartig 2022).

We calculated daily fix inefficiency as the proportion of the unsuccessful fixes registered out of the number of scheduled fixes across the window of dates over which the transmitter was deployed and included multiple deployments, if applicable. The device registered all scheduled fixes successfully when there was zero daily fix inefficiency (hereafter, zero miss days). We modeled inefficiency on the daily scale rather than the single fix scale because we deemed daily fixes the most broadly relevant for modeling sage-grouse location data (e.g., daily survival monitoring).

Daily fix inefficiency was modeled as a zero-inflated binomial generalized linear mixed effects model (GLMER). For the zero-inflation model, we relied on hypothesis-driven notions about what might drive the tendency to exhibit more zeros. We evaluated GPS Company, transmitter deployment status at the beginning of the deployment (new, cumulative [e.g., redeployed], or refurbished), calendar-based meteorological season (Spring = 1 March–31 May, Summer = 1 June–31 August, Fall = 1 September–31 November, Winter = 1 December–Feb 28/29). For the conditional model, we considered GPS company (MTI or GT), transmitter status at the beginning of the deployment (new, cumulative [e.g., redeployed], or refurbished), calendar-based meteorological season (Spring = 1 March–31 May, Summer = 1 June–31 August, Fall = 1 September–31 November, Winter = 1 December–28/29 Feb), cumulative photoperiod summarized over the preceding 7 days (photoperiod), and either deployment length or cumulative deployment length as possible fixed effects in the conditional model. We included random intercepts for bird ID and study area in the conditional model.

Transmitter status was delineated as follows: new, never deployed; cumulative, redeployed without being sent to the manufacturer; and refurbished, sent to the manufacturer for hardware and software updates prior to redeployment. We computed the daily photoperiod using the date, latitude, and longitude in WGS84 for each fix location from the package meteor 0.3-4 (Hijmans 2019) in R (v. 4.2.1; R core team 2022). We calculated the rolling summation of the previous 7-day photoperiod length because the solar-powered battery relies on approximately 3 to 5 days of quality solar exposure and may be affected by previous days' availability rather than the photoperiod length on that specific day, and we added a 2-day buffer. Deployment length was the number of days a transmitter was deployed on 1 sage-grouse from the capture date to the known/estimated end date. We obtained cumulative deployment length by calculating the total number of days that unit was deployed across multiple individuals. For refurbished units, we reset the cumulative deployment length to zero upon redeployment.

To calculate the number of full 24-hour data gaps, we counted the number of calendar dates in which no location fix was recorded (day gaps) per deployment. We modeled the number of day gaps as a GLMER with a log link, containing a random effect for bird ID and log(deployment days) as an offset. We considered GPS company, transmitter status, the proportion of days spent in low photoperiods, and either deployment length for that individual's deployment or cumulative deployment length as potential fixed effects. Because day gaps are summarized per deployment, we calculated the quantiles of the photoperiod distribution. We reported the percentage of time the transmitter had spent in photoperiods ≤25% percentile, considering this a low photoperiod.

Daily nest fix inefficiency was the proportion of unsuccessful fixes registered out of the number of scheduled fixes between the nest initiation and end dates. We used a zero-inflated binomial GLMER with a random effect for the transmitter serial ID. For the zero-inflated model, we evaluated GPS company, number of days incubating, shrub height or shrub cover, and either the slope or terrain roughness around the nest. For the conditional model, we evaluated GPS company, transmitter status, cumulative photoperiod over the previous 7 days (i.e., 7-day photoperiod), the year the transmitter was manufactured, nest shrub height and diameter (see nest sampling), deployment length or cumulative deployment length, number of days nesting, average 10- or 15-m radius shrub cover and height, and average 18-m radius slope, aspect, and terrain roughness as fixed effects.

To estimate mean nest fix error distance (i.e., accuracy) and standard deviation (i.e., precision) of transmitters, we calculated the mean and standard deviation of the distance between the known nest location on the ground and all registered locational fixes while the focal bird was nesting. We modeled both nest accuracy and nest precision as linear mixed effects models. We log-transformed the mean fix error and square-root transformed the fix error standard deviation. We considered GPS Company, transmitter status, nest location latitude, nest shrub height and diameter, deployment length or cumulative deployment length, number of days nesting, average 10- or 15-m radius shrub cover and height, and average 18-m radius slope, aspect, and terrain roughness as potential fixed effects. We considered Bird ID per study area as a random effect. We performed the same test for the university vegetation measurement method outlined above, and method again had no effect.

We assessed transmitter loss as the total number of days a transmitter was active until a loss when it no longer transmitted fixes and was not found in the field upon investigation. Transmitters still deployed on a sage-grouse at our analysis cutoff date (1 March 2019) or associated with confirmed sage-grouse mortalities were censored. Devices were not recoverable in the field if they no longer transmitted, so we could not consistently identify the cause of device loss and, therefore, did not pursue cause-specific loss analyses.

We assessed transmitter loss with a Cox proportional hazards (CoxPH) model (Andersen and Gill 1982) fit using the survival 3.4-0 package (Therneau 2022) in R (v. 4.2.1 R Core Team 2022). We considered the GPS company, the year the transmitter was new (2011–2018), and either the number of times the transmitter was refurbished or the number of times the transmitter was deployed as potential fixed effects. We considered the manufacturer year because we expected varying performance due to hardware (e.g., battery technology) and software changes between 2011 and 2018. We compared candidate models within 4 ΔAIC_c. Then we evaluated each model's beta residuals using the ggcoxdiagnostics function in the survminer 0.4.9 package (Kassambara et al. 2021), Schoenfeld individual tests using cox.zph in survival 3.4-0, analysis of deviance tables, test statistics, beta estimates, and *P*-values. If any models yielded similar AIC_c, we relied on the most parsimonious equation of predictor variables.

RESULTS

We modeled daily fix inefficiency using 139,899 daily observations across 506 sage-grouse deployments of 324 transmitters between 2011 and 2019. Average weight for males was 2,463 g ($n = 66$; min–max = 1,197–3,105 g; SD = 349.9 g) and females was 1,434 g ($n = 337$; min–max = 936–1,875 g; SD = 152.7 g). Our top model included a zero-inflation formula with an additive effect for season and an interactive effect of GPS company by transmitter status (Table 3). Compared to spring, summer had a 41% increase (95% CI = 37, 45) and fall had a 7.7% increase (95% CI = 3.6, 12) in the probability of obtaining zero miss days. Winter had 18% fewer (95% CI = −23, −14) zero miss days in comparison to spring. New and refurbished GeoTrak transmitters had a 24% (95% CI = 19, 29) and 39% (95% CI = 30, 48), respectively, higher probability of zero miss days than when cumulatively redeployed. Cumulatively redeployed MTI transmitters performed 69% worse (95% CI = −75, −62) than cumulatively redeployed GeoTrak transmitters. Relative to cumulatively redeployed GeoTrak transmitters, new and refurbished MTI transmitters exhibited a 57% (95% CI = 52, 62) and 177% (95% CI = 169, 184) higher probability of zero miss days, respectively.

The conditional model contained an additive effect for the log of cumulative deployment length, interactive effects for GPS company and season, and a nested random effect for sage-grouse per study area (Table 3). We found a variance of 2.10 and a standard deviation of 1.45 for the nested random effect for individual sage-grouse per study area, indicating that daily fix inefficiencies varied among individual birds. For every magnitude-based (i.e., 1, 10, 100, etc. days) increase in the cumulative deployment length, daily fix inefficiency increased by 15% (95% CI = 14, 17). Compared to spring, GeoTrak transmitters exhibited higher inefficiency probabilities of 20% (95% CI = 16, 24) in the summer, 35% (95% CI = 31, 39) in the fall, and 46% (95% CI = 42, 50) in the winter. New and refurbished MTI transmitters exhibited a lower unsuccessful fix probability (i.e., higher fix success) than GeoTrak transmitters across all seasons except for winter (Figure 2).

The day-gap dataset included 139,407 individual transmitter days across 547 sage-grouse deployments between 2011 and 2019. Our best-fit model included additive effects for the GPS company, the proportion of days spent in low photoperiods, transmitter status, and the log-transformation of cumulative deployment length with a random effect for bird ID (Table 3). We documented a variance of 3.10 and a standard deviation of 1.76 for the

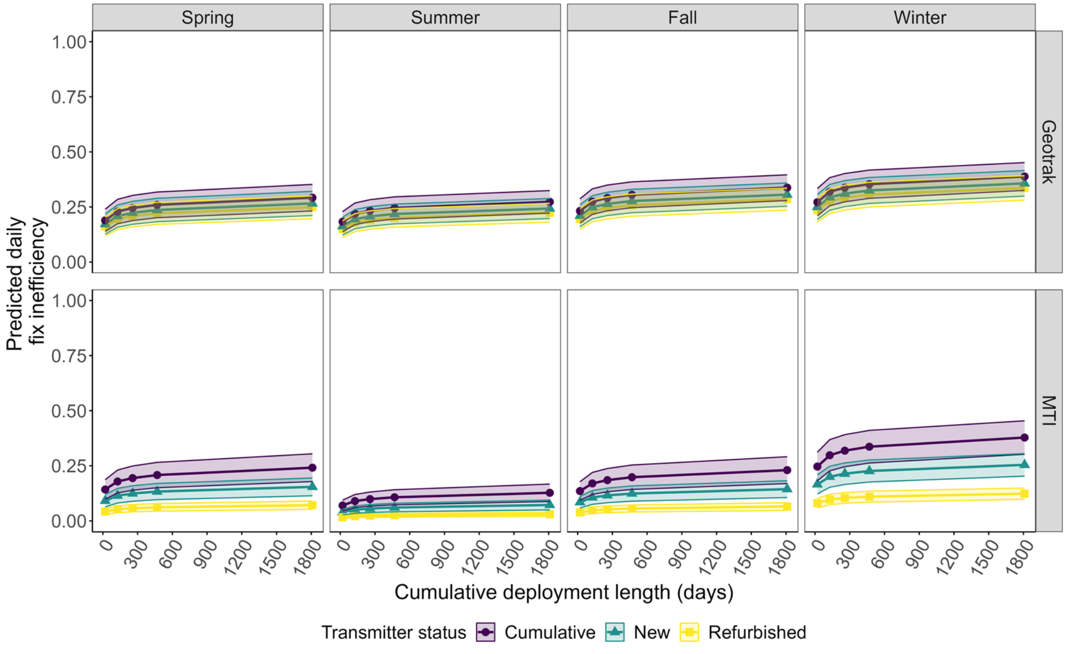

FIGURE 2 Daily fix inefficiency (unsuccessful fixes/scheduled fixes) by season per GPS Company (GeoTrak Inc. and MTI = Microwave Telemetry Inc.) and transmitter deployment status (cumulatively redeployed, new, or refurbished) across the cumulative deployment length (days) for transmitters used on greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2011 and 2019 (n = 506 sage-grouse). Transmitter deployment status was either new (never deployed after initially buying from manufacturer), cumulative (redeployed without being sent back to manufacturer), or refurbished (sent to manufacturer for hardware and software updates). For refurbished transmitters, cumulative deployment length was reset to zero.

random effect of individual sage-grouse, highlighting individual-level influences on day gaps. MTI exhibited 1.5 fewer day gaps (95% CI = −1.84, −1.12) than GeoTrak. For every magnitude-based change in the cumulative deployment length, there were 0.5 more expected full day gaps (95% CI = 0.30, 0.70) in fix locations. Increasing the proportion of time a transmitter had spent in low photoperiods increased the expected day gaps (Figure 3). New and refurbished transmitters exhibited fewer day gaps than cumulatively deployed transmitters, which is valid for both GeoTrak and MTI transmitters.

Daily nest fix inefficiency included a dataset of 2,300 nesting days across 84 individual sage-grouse and 105 nests between 2011 and 2018. Our best-fit model included a zero-inflation formula with additive effects for GPS company, days nesting, and average shrub height surrounding the nest (Table 3). Microwave Telemetry transmitters exhibited an 85% (95% CI = [47, 123]) higher probability of exhibiting zero miss days during the nesting period than GeoTrak. The probability of transmitters exhibiting zero miss days decreased by 6% (95% CI = −8, −4) per 1-day increase in the number of days nesting and decreased by 2% (95% CI = −3, −1) per 1-cm increase in the average shrub height.

The conditional model included an additive effect for the mean topographic roughness surrounding the nest and an interactive effect for transmitter deployment status and deployment length with a random effect for the transmitter ID (Table 3). We found a variance of 6.90 and standard deviation of 2.63 for the random effect of individual transmitters, indicating that individual transmitters varied substantially in their performance when birds were nesting. Our data were structured such that parsing transmitter effects from effects of the birds themselves was difficult, so this variance may actually be attributable to behaviors of individual birds as opposed to performance of individual devices. To account for potential differences between university vegetation measuring

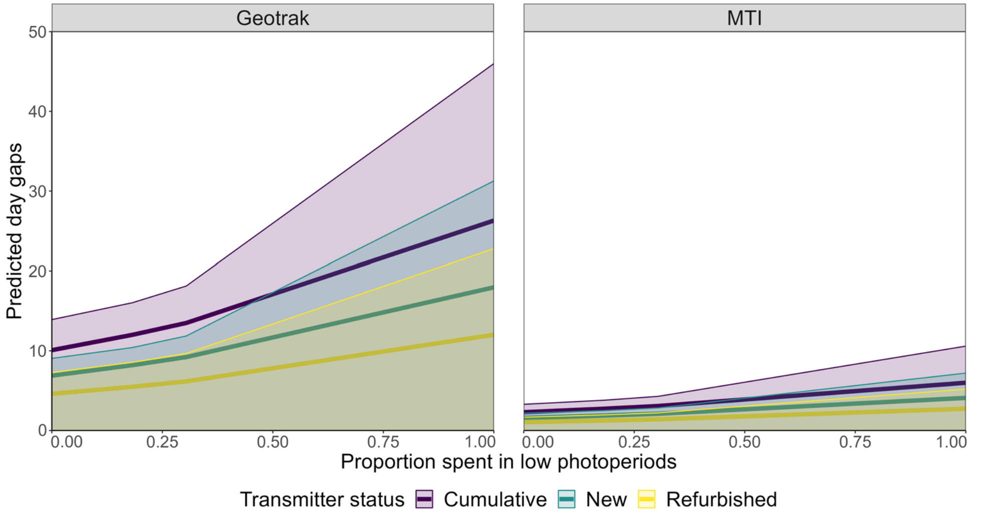

FIGURE 3 Predicted day gaps (full days when the transmitter fails to register any fixes) across the scaled proportion of days the transmitter spends in low photoperiod (≤25th percentile of photoperiod length) per GPS company (GeoTrak Inc. and MTI = Microwave Telemetry Inc.) for transmitters deployed on greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2011 and 2019 ($n = 547$ transmitter deployments on individual sage-grouse). Transmitter deployment status was either new (never deployed after initially buying from manufacturer), cumulative (redeployed without being sent back to manufacturer), or refurbished (sent to manufacturer for hardware and software updates).

methods, we considered a categorical method (e.g., USU or UWyo) fixed effect. However, it was not significant and thus we removed it. For every 1-unit increase in mean terrain roughness surrounding the nest location, the probability of daily fix inefficiency increased by 52% (95% CI = 34, 71). New transmitters exhibited a 0.80% (95% CI = −0.9, −0.6) lower probability of missing fixes than cumulatively redeployed transmitters as their respective deployment lengths increased (Figure 4). Refurbished transmitters exhibited a 42% (95% CI = 18, 66) higher probability of missing fixes than cumulatively redeployed transmitters as deployment length increased, though this may be a function of the low sample size of refurbished transmitters in this nesting dataset rather than reflecting actual performance. The DHARMa residual plots suggest other relationship(s) in the observed response that we may not be considering (Figure S1, available in Supporting Information). We plotted this response variable per individual's nesting period to explore nest fix inefficiency further. Our best-fit model could not accurately determine a relationship that fully explained this variation (Figure S2, available in Supporting Information).

The model evaluating the mean fix error distance from each fix to the nest relied on a dataset of 92 nests for 76 individuals. We were not able to differentiate between an error location and a female movement from the nest (i.e., nest recess; Coates and Delehanty 2008, Dudko et al. 2019) due to the courseness of the fix interval data, lack of access to dilution of precision per fix (Liu et al. 2018), and no empirical observations of female nest recesses. Thus, we defined both error and nest recesses as an off-nest location and found the combined proportion to account for 33% of the fix locations. Our best-fit model included fixed effects for GPS company and nest location latitude with a nested random effect for birds per study area (Table 3). The random effect of individual sage-grouse per respective study area had a variance of 0.15 and a standard deviation of 0.39, indicating limited variation in fix error distances among individual sage-grouse within specific study areas (Schielzeth and Nakagawa 2013, Harrison et al. 2018). Both GPS companies' mean fix error decreased as latitude increased (Figure 5A). Microwave Telemetry transmitters were associated with mean fix errors 0.64 m (95% CI = 0.29, 1.00) farther from the nest site than GeoTrak. For every one-unit increase in latitude, mean fix error decreased by 0.19 m (95% CI = −0.26, −0.11). The

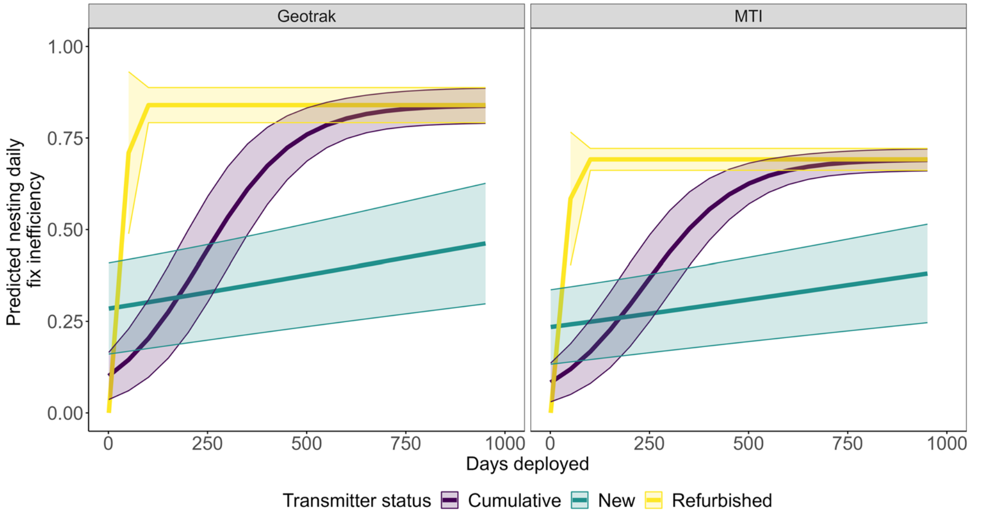

FIGURE 4 Daily nesting fix inefficiency (unsuccessful fixes/scheduled fixes) during the nesting period for nesting individuals by the number of days deployed on the individual the given nesting day (n = 2,300 combined nesting days across 84 individuals and 105 nests) per GPS company (GeoTrak Inc. and MTI = Microwave Telemetry Inc.) for nesting greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2011 and 2018. Transmitter deployment status was either new (never deployed after initially buying from manufacturer), cumulative (redeployed without being sent back to manufacturer), or refurbished (sent to manufacturer for hardware and software updates).

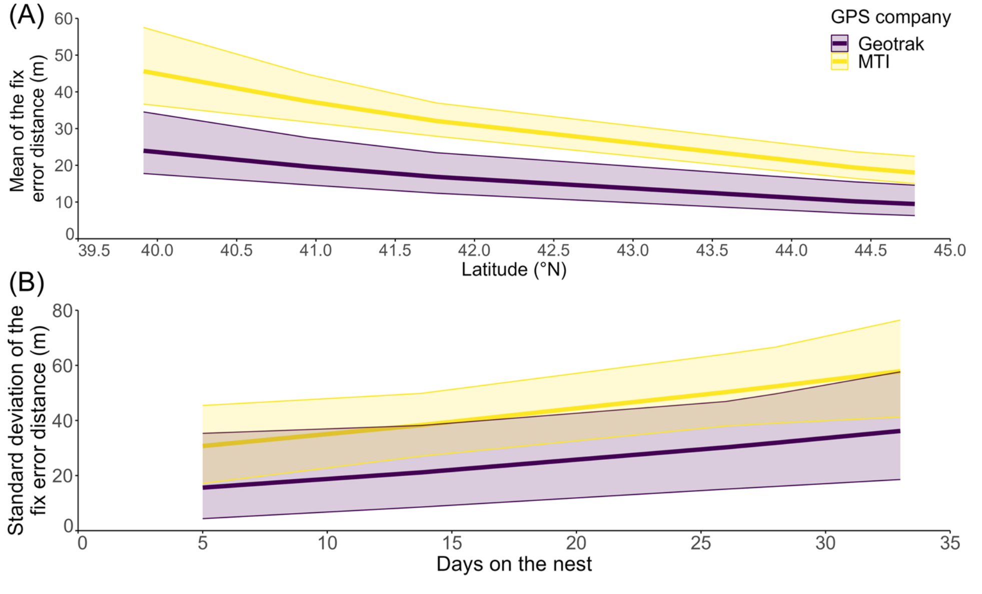

FIGURE 5 Solar-powered GPS transmitter fix error distance for nesting greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2011 and 2018. A) Distance mean: Predicted mean of the nest fix error distance (from the nesting location to the registered fix location) by latitude (°N) per GPS company (GeoTrak Inc. and MTI = Microwave Telemetry Inc.; n = 92 nests); B) Distance standard deviation: Predicted standard deviation of the nest fix error distance by days spent on the nest for each sage-grouse nesting period (n = 92 nests). Both y axes in A and B have been back-transformed (mean fix error was log-transformed, and fix error standard deviation was square-root-transformed).

model evaluating the standard deviation of the fix error distance from each fix to the nest relied on the same dataset. Our best-fit model included fixed effects of GPS company, days spent on the nest, and latitude, with a random effect for individual birds per study area (Table 3). The random effect had a residual variance of 5.05 and standard deviation of 2.25, and the nested random effect of individual sage-grouse per study area exhibited a variance of 0.68 with a standard deviation of 0.82. Standard deviation for the fix error increased by 0.07 m (95% CI = 0.007, 0.13) for each day spent nesting for both GPS transmitters (Figure 5B). For every one-unit increase in latitude, fix error standard deviation decreased by 0.40 m (95% CI = −0.77, −0.01). The mean error direction from the reported fixes to the nest location ranged between 105° and 135° for GeoTrak and between 135° and 155° for MTI (Figure 6).

The transmitter loss analysis used a dataset encompassing 266 transmitters with 40 loss events from 2011 to 2019. Our best-fit model was the intercept-only model (Table 3), suggesting no difference in loss events by transmitter type, manufacturer year, or number of times refurbished or deployed. The predicted loss rate across all transmitters' ages remains relatively high through time, with a ≤50% hazard of losing transmitters up to ~1,300 days (~3.6 years; Figure 7).

DISCUSSION

Recent improvements in GPS technologies have allowed researchers and resource managers to acquire fine-resolution spatiotemporal data remotely that ameliorate analytical frameworks and guide real-time management actions. Our study evaluated the performance of 2 GPS transmitters commonly deployed on sage-grouse. Between 2011 and 2019, new and refurbished MTI transmitters functioned better in general fix performance than new and refurbished GeoTrak transmitters, where MTI exhibited lower daily fix inefficiency and fewer day gaps during most seasons except for winter. Cumulatively redeployed MTI transmitters, however, did not perform differently than GeoTrak transmitters. Additionally, MTI outperformed GeoTrak during the nesting period for daily nest fix inefficiency zero miss days (i.e., estimated to have a higher probability of days with 100% fix efficiency). However, GeoTrak outperformed MTI in exhibiting a lower fix error distance

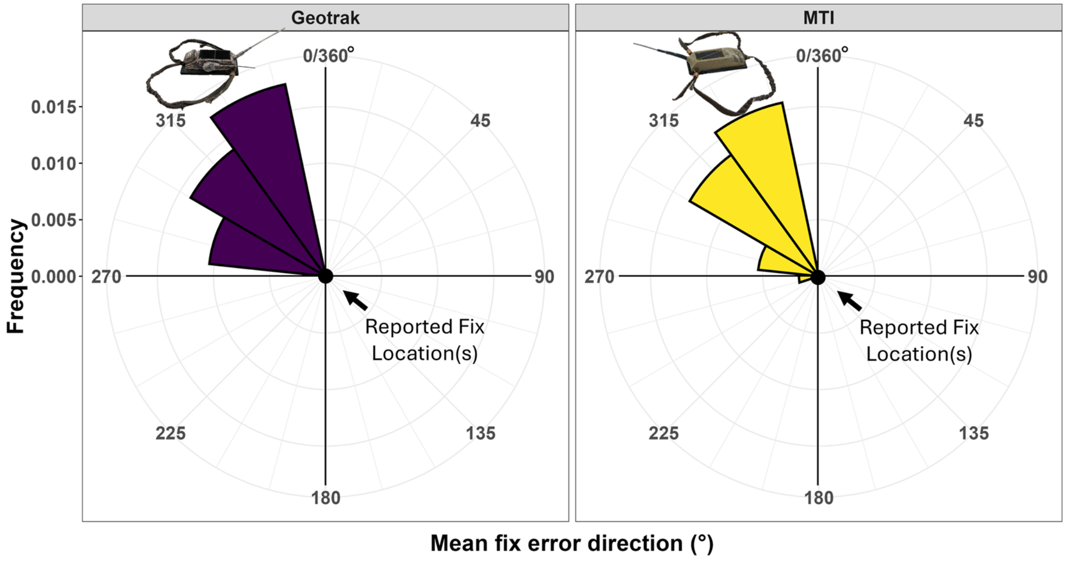

FIGURE 6 Mean fix error direction (in degrees) frequency from the registered fix location (reported point[s] provided by downloading GPS locations from Movebank, movebank.org) to the actual transmitter location on the ground, determined using empirical greater sage-grouse (*Centrocercus urophasianus*) nest location data in Utah and Wyoming, USA, between 2011 and 2019 (*n* = 92). We report the mean nesting fix error direction for each GPS company transmitter type (GeoTrak Inc. in purple, MTI = Microwave Telemetry Inc. in yellow).

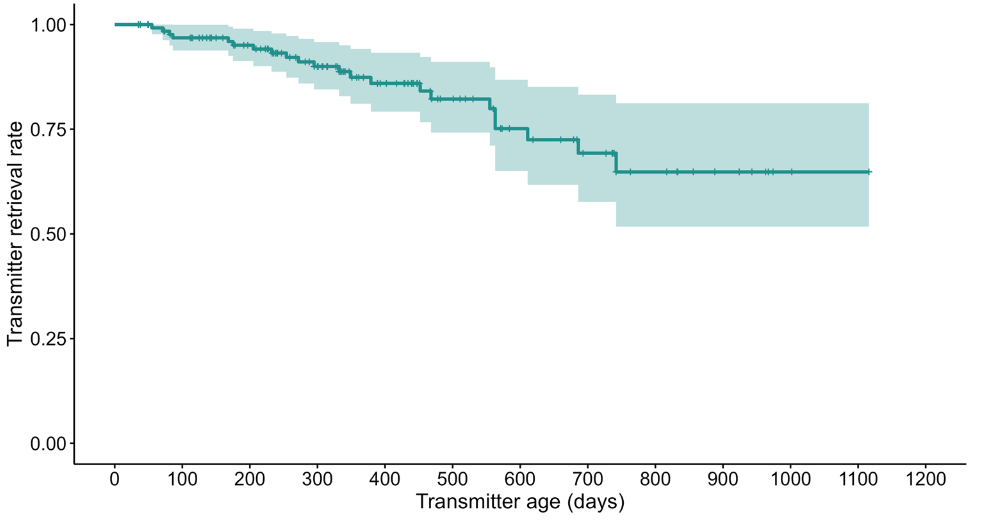

FIGURE 7 Transmitter retrieval rate (inverse to loss rate) probability by transmitter deployment age (days) for all transmitters regardless of company (GeoTrak Inc. and Microwave Telemetry Inc.) deployed on greater sage-grouse (*Centrocercus urophasianus*) in Utah and Wyoming, USA, between 2011 and 2019 (*n* = 266 transmitters).

mean from the nest location than MTI. There was no difference in performance between the 2 companies' transmitters for the transmitter loss, daily nest fix inefficiency conditional model, and nesting precision models. For nest accuracy precision, latitude and days nesting best explained the observed variation. When transmitters are in a fixed location (e.g., the sage-grouse is nesting, dead, or the transmitter has fallen off), the transmitter can be expected to be located in the NW direction from the fix locations reported from GPS data.

Upon retrieval from the field, transmitters returned to the respective manufacturer for refurbishment produced better efficiency in their subsequent deployment than those cumulatively redeployed. The improved performance post-refurbishment was evident through the daily fix and expected day gap analyses, where new and refurbished transmitters outperformed cumulatively deployed transmitters. For some GPS manufacturers, refurbishing can cost less than a third of the cost of a new transmitter (Keith LeSage, GeoTrak Inc, personal communication), presenting an economical option for researchers. One factor that could have affected the lowered performance of cumulatively redeployed transmitters is storage between deployments; storage was not standardized across the 3 universities' projects. We found no publications comparing the fix efficiency between new, refurbished, or cumulatively deployed GPS transmitters.

Both transmitters functioned worse during winter than in other seasons. Lower winter performance in solar-powered GPS transmitters is due to a combination of low solar radiation with fewer hours of sunlight and sage-grouse behavior, where they spend more time amongst higher sagebrush canopy cover and often will create burrows in the snow (Connelly et al. 2011b). Canopy or vegetation cover is inversely related to fix error (Frair et al. 2010) because it affects the available open sky (Forin-Wiart et al. 2015). Thus, topography (Ironside et al. 2017), ground (for fossorial/torpor species; McMahon et al. 2017), and buildings (for urban species; Adams et al. 2013) can lower GPS performance. Additionally, researchers typically reduce the number of fixes in winter to conserve battery. However, this may be counterproductive and lead to compounded reduced performance given the lower solar radiation and increased time between fixes (fix interval). Programming transmitters to collect 15–25% more fixes than needed and decreasing the fix interval (Hofman et al. 2019; see Forin-Wiart et al. [2015] on cold start and warm start GPS information) in all seasons may counteract low rates of fix acquisition (Cain et al. 2005, Forin-Wiart et al. 2015, Jung et al. 2018). To prevent habitat selection bias, researchers provide recommendations on accounting for fix errors, as even 10% of missing locations can lead to poor inference (Frair et al. 2004, Nielson et al. 2009, Webb et al. 2013, Christin et al. 2015).

Latitude explained much of the variation in performance for some of the nesting analyses. Other research has found differences in GPS performance and latitude, where transmitters on species that inhabited higher latitudes during the summer solstice performed better (Jung et al. 2018). A greater array of Argos satellites with increasing latitude may explain this relationship, in addition to the increased solar radiation present during the summer months (Christin et al. 2015, Jung et al. 2018). However, Jung et al. (2018) also found that transmitters in high latitudes during the winter months performed worse than those in latitudes closer to the equator due to the lower solar radiation and less-direct sunlight. Our results provide additional support for the effects of latitude on functionality.

No significant relationships were observed in the expected hazard rate for transmitter loss. Sage-grouse studies depend on the reliable longevity and retrieval of GPS transmitters, especially for population vital rates related to female sage-grouse, where some exhibit long lifespans and nest for several years in a row (Connelly et al. 2011a). Transmitter functionality spanning the entire life of the study species is crucial for elucidating valuable information across multi-year studies as this reduces the recapture cost and potential stress to the animal (Baker et al. 2013). Microwave Telemetry and GeoTrak state that the expected functionality for these 22-g transmitters is up to 3 years. Thus, researchers can utilize either transmitter and expect similar retrieval rates from the field.

We could not determine the best predictors to explain the daily nest-fix inefficiency variation. The variation in daily nest fix inefficiency might be explained by individual nesting behavior. Research has noted the variation in yearling (the sage-grouse age class group designating the age between the first breeding season and second breeding season [Connelly et al. 2011a]) incubation behavior compared to adults, where yearlings spend more time away from their nests (Coates and Delehanty 2008). Further exploration of female incubation behavior (e.g., nest recession) may be equally informative (Dudko et al. 2019). After exploring age and individual behavior, decreasing the scale at which we evaluate nesting GPS efficiency from daily to individual fix levels may yield further insights. However, this scale might not be biologically informative. Other variables playing a critical role that we did not include are satellite array (Sager-Fradkin et al. 2007, McMahon et al. 2017), temperature (Schlippe Justicia et al. 2018), and weather (Jung et al. 2018, Schlippe Justicia et al. 2018), and, thus, further exploration of this relationship is needed.

Our analysis provides performance assessments of MTI and GeoTrak's 22-g, solar-powered GPS-Argos transmitters deployed on sage-grouse over various environmental conditions in both nesting and nonnesting periods. Researchers studying sage-grouse or species under similar environmental conditions could consult manufacturers on battery drain trade-offs with increased fix acquisition for solar-powered transmitters. In addition to exploring other variables related to study species and environment, researchers should perform further testing with transmitters produced after 2019, as some manufacturers have improved hardware and software, and lighter-weight, solar-powered transmitters (~12 g) have become available (e.g., GeoTrak Inc.). Stationary tests as controls for performance should be employed within an experimental design framework simultaneously with real-time telemetry studies on free-ranging study animals to isolate transmitter-related variables from variables related to the environment or deployment on the animal (e.g., behavior, plumage or fur covering, solar panel or antenna orientation when mounted on the animal; Blackie 2010, Byrne et al. 2017). Accurately accounting for known fix errors inherent in GPS data improves the inference at which researchers can understand free-ranging animal individual- and population-level space use, behavior, demographics, predator-prey dynamics, and human-wildlife conflicts (Latham et al. 2015).

CONSERVATION IMPLICATIONS

Cumulatively redeployed transmitters consistently exhibited the worst performance. The analytical products derived from data garnered from species of concern are often closely scrutinized (e.g., legal conflicts between governing agencies and private entities, landowners, or special interest groups), and any bias or lowered inference can lead to poor legal or management decisions. We recommend refurbishing transmitters following each deployment, if possible, to retain the highest efficiency in these transmitters. Better performance can be expected in the summer months at higher latitudes than at lower latitudes but, conversely, worse performance can be anticipated in the winter months.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All sage-grouse were captured and marked in accordance with approval from respective agency and educational institutions: Utah State University IACUC permit numbers were 2322, 2439, 2560, 10111, 10175, 11161; Brigham Young University IACUC permit numbers were 100302, 110301, 050301, 080402; and University of Wyoming IACUC permit numbers were 03132011, 03142011, 20140128JB0059, and 20140228JB00065. University of Wyoming research was approved by Wyoming Game and Fish Department (Chapter 33 Permits 800 and 801) and Montana Department of Fish, Wildlife and Parks (Scientific Collector's Permits, 2013e072, 2014e037, and 2015e76).

DATA AVAILABILITY STATEMENT

The Utah Division of Wildlife Resources owns the data used for this research from Utah State University and Brigham Young University that support the associated research findings. Restrictions apply to the availability of these data, which were used under license for this research. Data from the University of Wyoming are also available, depending on permission.

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SUPPORTING INFORMATION

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