Environmental conditions and animal behavior influence performance of solar-powered GPS-GSM transmitters

Authors: Byrne, Michael E., Holland, Amanda E., Bryan, A. Lawrence, and Beasley, James C.

Source: The Condor, 119(3) : 389-404

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-16-76.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 119, 2017, pp. 389–404
DOI: 10.1650/CONDOR-16-76.1

RESEARCH ARTICLE

Environmental conditions and animal behavior influence performance of solar-powered GPS-GSM transmitters

Michael E. Byrne,[1a]* Amanda E. Holland,[1,2b] A. Lawrence Bryan,[1] and James C. Beasley[1,2]

[1] Savannah River Ecology Laboratory, University of Georgia, Aiken, South Carolina, USA
[2] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA
[a] Current address: School of Natural Resources, University of Missouri, Columbia, Missouri, USA
[b] Current address: Tunnel Loop Road, Grants Pass, Oregon, USA
* Corresponding author: mike.byrne013@gmail.com

Submitted April 15, 2016; Accepted March 20, 2017; Published May 31, 2017

ABSTRACT

Solar-powered GPS transmitters linked to the GSM cellular transmission system are a powerful new tool for avian research. Data collection can be researcher programmed or use dynamic fix (DF) rates that are automatically adjusted in accordance with battery charge. Lack of prior knowledge of fix (location) collection rates represents an obstacle to designing studies with transmitters that use DF rates. We assessed the quantity and quality of data collected by a commercially available DF transmitter. To assess fix collection rates, factors influencing fix collection rates, GPS accuracy, and the ability of transmitters to differentiate movement from nonmovement, we used a combination of controlled static tests at known locations, deployments on free-ranging Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), and motion tests. During static testing, transmitters often collected upwards of 500 fixes per day in open habitats with little cloud cover. Hourly fix rates varied, commonly reaching 1 fix min^{-1} at midday but dropping to 1 fix hr^{-1} at night. The numbers of daylight fixes collected during vulture deployments were greater on days with little cloud cover, positively correlated with increasing daily movement rates, and positively correlated with available daylight hours, likely due in part to increased solar radiation near the summer solstice. Mean horizontal GPS error was 7.8 m (± 12.2 m SD). Mean vertical error was 4.5 m (± 142 m) above true elevation. Speed records >0 km hr^{-1} were reliable indicators of movement provided a 3D fix was obtained. Overall, the transmitters that we evaluated provided large volumes of data, but the inability to control data collection schedules may prove problematic for some applications. DF solar-powered transmitters appear best suited for use with active species in open habitats, and least suitable for use with species that inhabit high latitudes year-round or spend considerable time under forest cover.

Keywords: animal location data, animal movement, *Cathartes aura*, *Coragyps atratus*, fix rate, GPS accuracy, telemetry

Las condiciones ambientales y el comportamiento animal influencian el desempeño de los transmisores GPS/GSM que funcionan con energía solar

RESUMEN

Los transmisores GPS que funcionan con energía solar y que se vinculan a sistemas de transmisión de celulares GSM son una nueva herramienta poderosa para las investigaciones ornitológicas. La colecta de datos puede ser programada por el investigador o usarse tasas de posicionamiento dinámico (PD) que son ajustadas de acuerdo con la carga de la batería. La falta de conocimiento previo de las tasas de colecta de las posiciones representa un obstáculo para diseñar estudios con transmisores de PD. Evaluamos la cantidad y calidad de los datos colectados con un transmisor de PD disponible comercialmente. Para evaluar las tasas de colecta de las posiciones, los factores que influencian las tasas de colecta, la exactitud del GPS y la habilidad de los transmisores para diferenciar movimiento de no movimiento, usamos i) una combinación de pruebas estadísticas controladas en ubicaciones conocidas, ii) individuos libres de *Coragyps atratus* y *Cathartes aura* dotados con transmisores, y iii) pruebas de movimiento. Durante las pruebas estáticas, los trasmisores usualmente colectaron más de 500 posiciones /día en ambientes abiertos con poca cobertura de nubes. Las tasas de posicionamiento por hora variaron, comúnmente llegando a 1 posición/minuto durante el mediodía, pero cayeron a 1 posición/hr a la noche. Las cantidades de posiciones con luz de día colectadas a partir de los buitres fueron mayores en los días con baja cobertura de nubes, lo que se correlacionó positivamente con los aumentos en las tasas de movimiento diario y con la disponibilidad de horas de luz, probablemente debido en parte al aumento de la radiación solar cerca del solsticio de verano. El error horizontal promedio del GPS fue 7.8 m (DE = 12.2 m). El error vertical promedio fue 4.5 m (DE = 142 m) por sobre la elevación verdadera. Los registros de velocidad $>$ 0 km/h son indicadores confiables de movimiento en la medida que se obtenga una posición 3D. En general, los transmisores que evaluamos brindaron grandes volúmenes de datos, pero la imposibilidad de controlar los esquemas de colecta de datos podría ser problemático para algunas aplicaciones. Los transmisores solares de PD parecen ser más adecuados para las especies activas en ambientes abiertos y menos adecuados para las especies que habitan altas latitudes todo el año o que pasan una parte considerable del tiempo bajo la cubierta del bosque.

Palabras clave: Cathartes aura, *Coragyps atratus*, datos de localización de animales, exactitud del GPS, movimiento de animales, tasa de localización, telemetría

INTRODUCTION

The use of Global Positioning Systems (GPS) has rapidly become the standard method for tracking wildlife when positional data of high spatial and temporal resolution are required. As technological advancements continually precipitate decreases in both the size and the cost of electronic components, the application of GPS technology to wildlife studies is continually expanding. The ability to transmit data remotely through networks such as the Argos satellite system and the Global System for Mobile Communications (GSM) cellular transmission system has facilitated application to highly mobile species for which transmitter retrieval or recapture is not logistically feasible, with the added benefit of allowing near real-time tracking of marked individuals. Among the recent developments in this arena are solar-powered GPS transmitters linked to the GSM system (hereafter, solar GPS-GSM units). Solar-powered units have the potential to remain active for several years, provided that the unit is not damaged, facilitating the collection of long-term datasets (e.g., Pérez-García et al. 2013, López-López et al. 2014, Pearse et al. 2016), and the GSM system provides a relatively cost-effective means of remotely transmitting high volumes of data. These benefits, combined with the reduction in weight afforded by the use of solar components in place of large batteries, make solar GPS-GSM units particularly well suited for avian research.

Two types of data collection are available for commercially available GPS-GSM units. With user-programmed transmitters, the researcher is responsible for programming when GPS fix (location) attempts are made. These units offer a flexible data collection schedule appropriate to specific research objectives. Additionally, the ability to collect GPS locations at regular time intervals is advantageous for many analyses of animal movement and habitat selection. One potential drawback, however, is that a limit is necessarily placed on the temporal resolution of data collection, as very high fix collection rates over long time periods run the risk of depleting battery life faster than it can be recharged. The second variety differs in that, rather than being programmed by the researcher, the fix collection schedule is dynamic and contingent on battery charge. Dynamic fix transmitters offer high GPS fix rates when conditions are favorable for maintaining a high battery charge, as well as long operating durations, at the expense of researcher control over data collection. While the promise of a high fix rate may be useful for fine-scale movement analyses, the lack of a priori knowledge of when and how often GPS fixes will be collected represents a serious obstacle to study design.

We assessed the performance of a dynamic fix transmitter across a suite of environmental and behavioral conditions. We evaluated transmitter performance in 3 ways. First, we conducted a series of static tests using motionless units placed under the forest canopy or in open fields. This revealed how much data was collected daily, diurnal variation in fix collection rates, the relationship between fix rate and battery charge, and variation between habitats. Additionally, static testing at known locations allowed us to quantify the spatial accuracy of GPS fixes in both horizontal and vertical dimensions. Although the horizontal accuracy of wildlife GPS transmitters has been the subject of many studies (D'eon and Delparte 2005, Lewis et al. 2007, Guthrie et al. 2011, Recio et al. 2011), vertical accuracy has rarely been considered. For birds, vertical accuracy is important for determining soaring altitudes (e.g., Avery et al. 2011) and for creating 3-dimensional utilization distributions (Tracey et al. 2014). Second, we assessed whether instantaneous speed estimates reported with GPS fixes, in the absence of more sophisticated accelerometry data, could be useful for differentiating whether a bird is moving or stationary. This may be helpful in behavioral studies, as well as when modeling movements and reconstructing tracks from temporally irregular data (Johnson et al. 2008). Finally, we analyzed the performance of transmitters deployed on free-ranging Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*). Because of the lack of researcher control over data collection, we were particularly interested in how the number of GPS fixes collected during daylight hours was influenced by cloud cover and vulture movements.

METHODS

Study Area

All static testing and vulture captures occurred in the Savannah River Site (SRS), a 78,000-ha limited-access former nuclear production and research facility operated by the U.S. Department of Energy (DOE) located near Aiken, South Carolina, USA (White and Gaines 2000). The SRS is located in the upper Atlantic Coastal Plain, and, as such, the topography is relatively flat, with elevation ranging from 30 m to 115 m above sea level (White and Gaines 2000). The landscape is primarily forested (∼94%), with ∼64% of the total area planted in loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and slash pine (*P. elliottii*) managed for timber production by the U.S. Forest Service (Workman and McLeod 1990). The remaining forest cover consists primarily of bottomland hardwood forests located along low-lying drainages and the Savannah River (Workman and McLeod 1990). Interspersed within the forest matrix are nuclear, industrial, and research facilities.

Transmitter Description

We tested Microwave Telemetry (Columbia, Maryland, USA) solar-powered GPS-GSM transmitters (model: GSM20-70) configured for backpack attachment. The dimensions of the transmitters that we tested were 9.7 cm (length) × 3.84 cm (width) × 2.54 cm (height), with a weight of 70 g. Two 4.5 cm × 1.2 cm solar strips were located on top of the unit. An onboard microprocessor managed the battery charge so that the unit could continue to collect and transmit data during nocturnal periods without depleting the battery. The transmitters were preprogrammed to dynamically adjust GPS fix rates so that rates increased during periods of high battery voltage and decreased during periods of low voltage. As of the time of writing there was no functionality to accommodate user-programmed GPS fix collection schedules. According to manufacturer specifications, daytime fix intervals varied from 1 min to 120 min contingent on battery voltage, while nighttime fix intervals ranged from 30 min to 240 min. The units were programmed to transmit data through the GSM system once daily. If GSM service was unavailable, data were stored onboard until the animal returned to a location in which GSM transmission was possible, with the ability to store up to 258,000 locations. Manufacturer estimates of GPS accuracy stated that, in the horizontal dimension, ∼87% of locations were expected to fall within 18 m of the true location, and, in the vertical dimension, ∼79% of locations were expected to have altitude measurements within 22 m of true altitude. Horizontal and vertical dilution of precision (HDOP and VDOP) measures were provided with each GPS fix. An instantaneous speed estimate in integer knots (kn) was also provided with each GPS location. Manufacturer specifications stated that speed estimates were accurate to ±1 kn when actual speed was >20 kn. An additional data file independent of GPS data that reported battery charge (V) and temperature (°C) was also provided with each daily GSM transmission.

Static Tests

We conducted a series of static tests to evaluate data collection rates and locational accuracy of GPS fixes under a number of environmental conditions. Each test consisted of placing 3 transmitters in the field to simulate conditions in which the transmitters might reasonably be assumed to operate given the size and generalized behavior of the large birds for which they were designed. The same 3 transmitters were tested at each site simultaneously, placed within 2 cm of each other. We conducted static tests at 5 sites, representing 3 environmental and behavioral treatments. At 2 sites, we placed the transmitters on the ground in an open field (0% canopy) to simulate a bird perched in an open area (hereafter, open treatment). At 2 sites, we placed the transmitters on the ground in a forested area with ∼70% canopy cover to simulate a bird perched on the ground under forest cover or in the lower levels of a tree (hereafter, forest treatment). To approximate the orientation of a transmitter attached to the back of a perched bird, we attached each unit to a wooden stake driven into the ground at a 45° angle with the transmitter ∼35 cm above ground. For consistency, the dorsal portion of the transmitter always faced south. Transmitters were placed in each test site at approximately midday and collected at midday 5 days later, giving the transmitters 4 full days in each site and 8 full days in each treatment. Tests in open and forest treatments occurred in November–December, 2014. To simulate a bird in flight (hereafter, flight treatment), we affixed each transmitter to the end of a 1.3-m wooden stake attached 11 m off the ground to a vertical wooden pole located in an open area. The stake was attached perpendicularly to the pole, so that the transmitter was located ∼1.2 m from the pole. Transmitters were oriented horizontally to the ground with a clear view of the sky. Logistical constraints prevented us from using 2 sites for this treatment, thus we allowed the transmitters to collect data in 1 site for 8 full days in February, 2015.

We quantified total atmospheric cloud cover daily during each static test. Cloud cover should negatively influence fix rate by limiting the sunlight reaching the transmitter, causing the transmitter to adjust its collection schedule accordingly to prevent excessive battery drain. We obtained cloud cover data from the European Center for Medium-Range Weather Forecasts (ECMWF) ERA-Interim global atmospheric reanalysis (http://www.ecmwf.int/en/research/climate-reanalysis/era-interim), which assimilates observations from a variety of sources and archives climatic data at a spatial resolution of 0.7° and a temporal resolution of 6 hr. We uploaded test site locations to Movebank (www.movebank.org) and used the *Env-DATA* system (Dodge et al. 2013) to obtain cloud cover at each site at hourly intervals on days during which tests occurred. Location-specific hourly estimates of cloud cover were obtained via bilinear interpolation from the ECMWF reanalysis dataset, and hourly values between sunrise and sunset were used to calculate mean daylight cloud cover.

Fix collection. We summed the total number of GPS fixes recorded, as well as the fixes recorded specifically during daylight hours (i.e. between sunrise and sunset), daily for each transmitter. To assess diurnal variation in fix acquisition rates, we summed the number of fixes reported hourly by each transmitter. To provide insight into the relationship between fix collection rate and battery charge, we calculated the mean charge value (V) reported hourly, and compared it with the associated number of GPS fixes collected for each hour.

GPS accuracy. All static test sites were $\leq$96 m from a National Geodetic Survey marker (it was not logistically possible to conduct tests at the exact locations of markers), and we used the relative height of the test units in relation to the nearest marker to derive true elevation (m above sea level) at each site. To determine the true location of each test site, we used the average of $\geq$100 locations collected with a WAAS-enabled (Wide Area Augmentation System) Garmin GPSMAP 62 (Garmin International, Olathe, Kansas, USA) handheld GPS unit (Oderwald and Boucher 2003). We measured the horizontal error of each GPS fix as the Euclidian distance between the GPS location collected by the test units and the true location. We measured the vertical error of each fix by calculating the difference between the elevation estimate of the GPS fixes and the true elevation of each test site; negative values represent error below the true altitude whereas positive values represent error above the true altitude. Centering vertical location error on 0 allowed us to elucidate whether there was any bias toward error above or below true elevation. We tested for variability in the spatial error of fixes collected by the 3 transmitters in both the vertical and horizontal dimensions in each treatment, and, on finding no significant difference between transmitters in any treatment (ANOVA, $P > 0.05$), pooled the data from all transmitters. For each treatment, we calculated the mean, standard deviation (SD), and range of GPS error in each dimension. Dilution of precision (DOP) measures have been suggested as a potential means of filtering inaccurate GPS locations (D'eon and Delparte 2005), although more recent studies have called into question the usefulness of this approach (Recio et al. 2011, Laver et al. 2015). To illustrate the relationship between DOP and GPS error for these transmitters, we plotted horizontal error and the absolute value of vertical error as a function of horizontal dilution of precision (HDOP) and vertical dilution of precision (VDOP), respectively.

Movement Tests

We tested whether the instantaneous speed estimates reported with the GPS fixes could be used to effectively differentiate whether a transmitter was moving or stationary when the fix was recorded, especially at low speed. On 2 cloudless afternoons, a researcher walked a path of known distance at a constant speed while holding a wooden stake with all 3 fully charged test units attached. The researcher held the stake so that transmitters were oriented parallel to the ground and ~1 m from their body. We calculated the average speed of each test walk and compared this with the speed estimates reported by the transmitters. We quantified success at detecting movement during test walks as the percentage of fixes with nonzero speed estimates. We quantified the rate at which transmitters erroneously assigned a movement speed to stationary transmitters as the percentage of fixes with nonzero speed estimates obtained during the static testing trials (described above).

Field Tests

We deployed units on 11 Turkey Vultures and 8 Black Vultures captured with cannon nets at wild boar (*Sus scrofa*) carcasses from June 17 to August 2, 2013, and 1 Black Vulture captured on April 23, 2014. We used data from these deployments to assess transmitter performance when applied to animals in the field. Transmitters were affixed via backpack harness using Teflon ribbon (Appendix Figure 8). All birds were released immediately after handling. Reported results represent tracking data collected through March 15, 2015.

Because we were interested in the number of useful fixes obtained, we filtered raw data before analysis using routine GPS data reduction criteria (Frair et al. 2010), with the goal of reporting the number of locations that would ultimately be used in an ecological study. We filtered locations by removing records with no available GPS fixes, records flagged as "negative altitude," "battery drain," or "low voltage," and all 2D fixes. We then applied a speed filter (McConnell et al. 1992) to remove locations associated with estimated mean minimum horizontal flight speeds $\geq$90 km hr^{-1}, a conservative cutoff speed for filtering outlier locations based on previous speed estimates of migrating Turkey Vultures (Mandel et al. 2008, Dodge et al. 2014). This had the effect of removing the most extreme outliers without also removing a large number of reasonable locations, a potential issue with filtering based on DOP metrics (Laver et al. 2015). To estimate height above ground, we calculated the difference between each postfiltered GPS location and elevation based on U.S. Geological Survey (USGS) 1/3 arc-second seamless digital elevation models (DEM; ~10 m^2 resolution; http://viewer.nationalmap.gov/).

Following outlier removal, we calculated the geographic mean of all GPS fixes during each 24-hr period for each vulture. We calculated the time of local sunrise and sunset for this location using the RAtmosphere package (Biavati 2014) in R (R Core Team 2014). This ensured that calculated day lengths were local to the area occupied by the vulture, allowing us to tally the number of usable diurnal GPS fixes obtained each day. To quantify environmental conditions, we first used the redisltraj function in the adehabitatLT package (Calenge 2006) in R to extract temporally regularized locations at 30 min intervals along GPS tracks. This helped to ensure that environmental data were collected consistently for all transmitters and that we obtained a measure of the environmental conditions experienced daily by each vulture, which would have been biased had we extracted environmental data associated with raw locations collected at irregular intervals. We recognize that there are more sophisticated methods of calculating temporally regularized locations, such as state-space models (Patterson et al. 2008), but, given the high temporal resolution of data collection, the coarseness of available environmental data, and the fact that this was not an ecological study per se, interpolation was sufficient for our purposes. We queried cloud cover data associated with each interpolated location using the *Env-DATA* system in Movebank, and calculated daylight cloud cover as the mean of all cloud cover estimates associated with interpolated positions occurring between sunrise and sunset.

To quantify vulture movement, we first created temporally discrete locations along each vulture's path at 10-min intervals between sunrise and sunset, again using the redisltra function in the adehabitatLT package. We considered a distance between a pair of consecutive interpolated locations $\geq$39 m, $\sim$3 SD from the mean horizontal telemetry error in the forest treatment (see Results), as evidence of movement. We calculated a metric of daily movement rate as the proportion of 10-min time steps classified as moving. We chose this metric, rather than distance between raw locations, because temporal irregularity in raw data collection would lead to biases. The use of interpolated locations does not ameliorate this issue entirely, but it does standardize the measure across days and individuals to provide an index of relative daily movement activity. Greater movement rates should correspond to increased daylight fix collection rates, as a flying bird presumably will increase sun exposure, thus facilitating battery charging.

Our goal was to model the number of daylight GPS fixes obtained as a function of vulture movement and environmental conditions, to see how each variable influenced data collection by a transmitter when deployed on an animal. Decoupling the influence of environment and behavior on fix rates is difficult because the 2 measures are potentially confounded. For example, is a greater fix rate a function of increased movement, or does collection of more data due to favorable environmental conditions allow us to detect movement more effectively? Conversely, is a low fix rate a result of low levels of movement, or does a low fix rate due to adverse environmental conditions decrease our ability to effectively detect movement? To control for environmental conditions when modeling daylight data collection from free-ranging vultures, we included only days on which daylight cloud cover was $\leq$10% (clear days) or $\geq$90% (cloudy days) in the analyses.

As the response variable was the count of GPS fixes obtained during daylight hours, we performed negative binomial regression in a generalized linear mixed model (GLMM) format using the lme4 package (Bates et al. 2015) in R. We chose negative binomial regression to account for overdispersion in the count data. Individual vulture ID was included as a random effect. Fixed effects included cloud condition, a discrete variable with "cloudy" as the reference condition, and daily movement rate as a continuous variable. Because the number of locations that can be collected in a day is limited by day length, we included the total minutes of daylight as an offset term. Also, to account for the fact that data collection may not be independent between successive days, we included the number of locations collected on the previous day as an additional fixed effect, which Hamel et al. (2012) illustrated was an effective way to account for autocorrelation in GLMMs.

We created a set of 3 a priori models which predicted that daylight fix rate would be a function of (1) cloud condition, (2) cloud condition and vulture movement, and (3) an interaction effect between cloud condition and vulture movement. The offset term and previous day's fixes were included in all 3 models. We analyzed the data from transmitters attached to each species separately and thus had 2 sets of models. We calculated Akaike's Information Criterion (AIC), and used ΔAIC (the difference in AIC from the top model) and Akaike model weights (w_i) to rank models and determine the most parsimonious model (Burnham and Anderson 2002). Following the recommendations of Arnold (2010), we calculated 85% confidence intervals (CI) for each parameter estimate and considered a parameter uninformative if the CI included 0.

RESULTS

Static Tests

Fix collection. A total of 16,576 records were collected across all treatments and test units during static testing, of which 0.01% were flagged as "no fix." A further 0.06% were flagged as "low voltage" or "battery drain" and provided no GPS locations, while 0.13% were flagged as "2D fixes" and provided horizontal positions but no vertical estimates. Fix rates varied considerably between treatments (Table 1). In particular, the number of fixes from the forest treatment was drastically lower than numbers from the other 2 treatments. Fixes obtained under forest cover were $\sim$8%, 6%, and 6% of those obtained in the open treatment for each of the 3 respective test units, and $\sim$6%, 4%, and 4% of

TABLE 1. Total number of GPS fixes reported by 3 GPS-GSM transmitters across 3 static treatments: on the ground in an open field (Open), on the ground under the forest canopy (Forest), and suspended 11 m above the ground in an open field to simulate flight (Flight). Daylight hr = total number of hours between sunrise and sunset during test periods. Daylight fixes (in parentheses) = total number of reported GPS locations between sunrise and sunset during test periods.

		Total fixes (Daylight fixes)		
Treatment	Daylight hr	Transmitter 1	Transmitter 2	Transmitter 3
Open	80.9	2,579 (2,376)	2,056 (1,926)	1,986 (1,819)
Forest	81.5	204 (120)	127 (67)	112 (58)
Flight	88.7	3,509 (3,298)	3,321 (3,059)	2,682 (2,437)

those from the flight treatment. The most fixes were obtained during the flight treatment for all test units. Longer day lengths during the flight treatment (February) compared with the open treatments (November and December) represent an important environmental difference between the treatments, which may partially account for the greater fix rates in the flight treatment. After accounting for differences in daylight hours (total fixes per hours of daylight) during test periods, the 3 test units collected ~19%, 35%, and 19% more locations during the 8 days in the flight treatment than in the open treatments.

In the open and flight treatments, daylight fix rates varied with cloud cover, with reduced fix rates as cloud cover increased (Figures 1A, 1C). This was not the case for the forest treatments (Figure 1B). The 3 test units often did not collect equal numbers of locations, despite being exposed to the same conditions, and appeared to exhibit different responses to changes in cloud cover (Figure 1). In

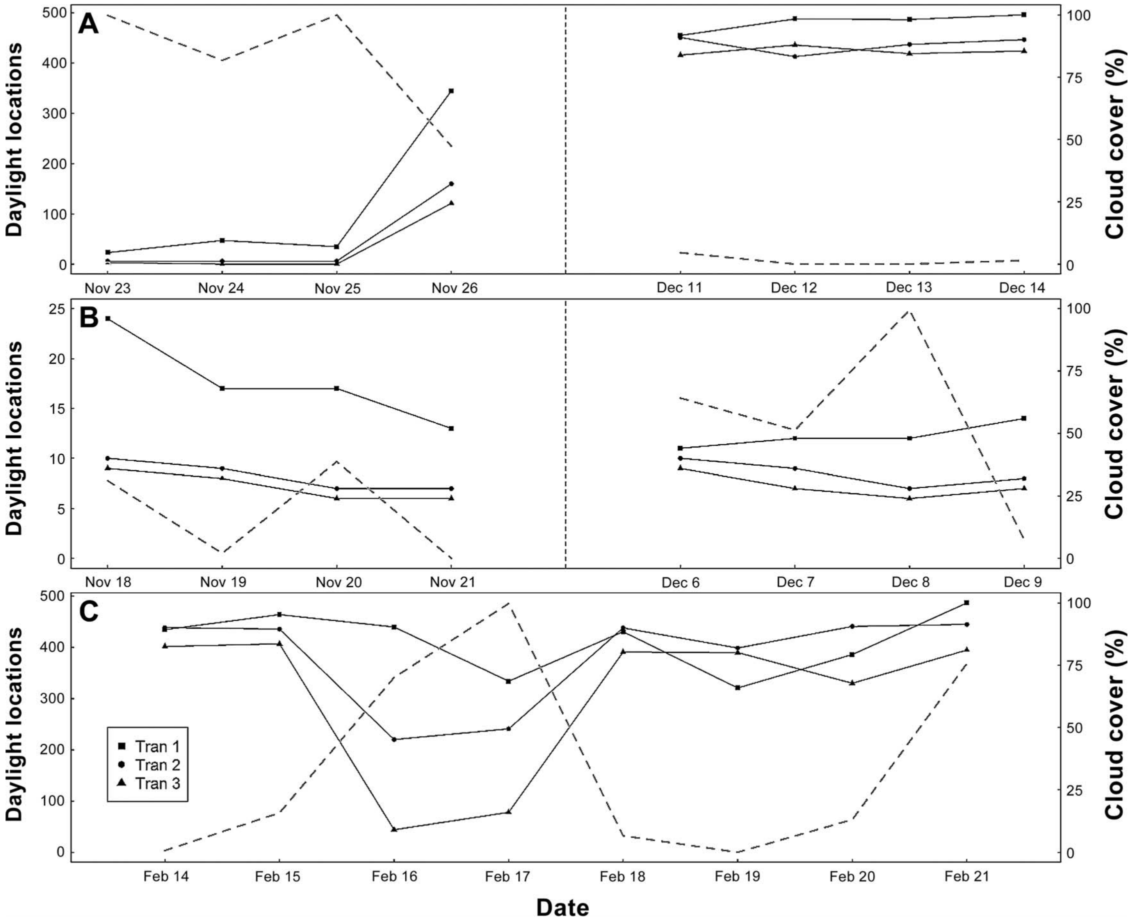


FIGURE 1. Total number of daylight fixes collected by 3 GPS-GSM transmitters in 3 static treatments: (**A**) on the ground in an open field, (**B**) on the ground under forest cover, and (**C**) suspended 11 m above the ground in an open field to simulate flight. The dashed line represents mean daily cloud cover (%). The 2 trials in treatments (A) and (B) are separated by a vertical dotted line.

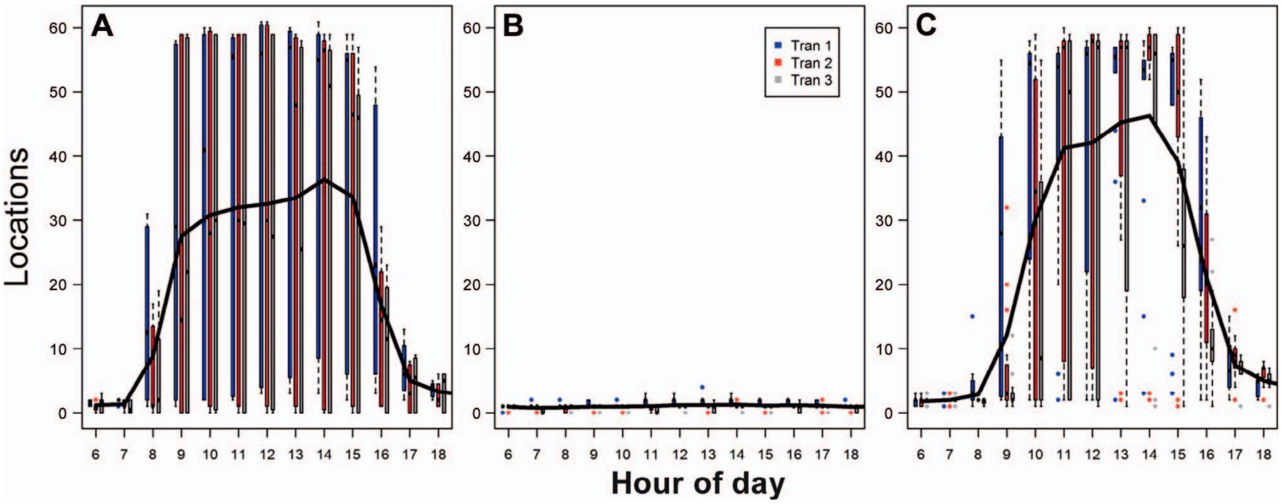


FIGURE 2. Boxplots of the number of GPS locations collected hourly by 3 GPS-GSM transmitters in 3 static treatments: (**A**) on the ground in an open field, (**B**) on the ground under the forest canopy, and (**C**) suspended 11 m above the ground in an open field to simulate flight. Colored lines represent the interquartile range (IQR), small black squares within the IQR show the median, whiskers indicate the range, and dots are outliers. The black line shows the hourly mean of all transmitters combined.

total, transmitter 1 collected the most locations in all treatments, and transmitter 3 the fewest (Table 1). The variable response to cloud cover was best illustrated during the flight treatment when cloud cover began to increase on the 3rd day (Figure 1C). On this day, the 3 transmitters collected 440, 220, and 44 daylight locations. Transmitter 3 collected 0 locations over a 2.9-day period (1247 hours on November 23 to 1029 hours on November 26, 2014) during the 1st open treatment trial due to low battery voltage. We obtained ~1 fix every 2 hr during daylight for transmitters 1 and 2 during this period, which coincided with the units being placed in an open field on an overcast day after 4 days under canopy cover (Figure 1).

We observed clear temporal variation in hourly fix rates across the 24-hr cycle in open and flight treatments (Figures 2A, 2C), with hourly fix rates peaking in the midafternoon. It was not uncommon for transmitters to collect close to 60 locations hr^{-1} at these times on days with little cloud cover. In open and flight treatments, hourly fix rates decreased markedly at night, with an average of 1.0 and 1.7 locations collected hourly from 2000 to 0500 hours. In forest, the number of hourly fixes was uniformly low in all hours, and no test unit collected >4 locations during any hour of the day, regardless of weather conditions (Figure 2B).

Mean hourly battery voltage ranged from 3.6 to 4.1 V. When battery voltage was <3.95 V, the number of hourly fixes recorded was <10, but fix rate increased dramatically at higher voltages (Figure 3). As an example of the relationship between variation in battery charge and fix rate, Figure 4 represents an hourly time series of mean battery voltage and number of locations collected by transmitter 2 during 3 consecutive days in the flight treatment. The midday peaks in data collection correspond to the hours of highest battery charge, which also correspond to the times when the sun is at its highest point in the sky and solar radiation is strongest. Battery voltage decreased rapidly in the late afternoon, as did fix collection rates, and continued to drop through the night until reaching a low around dawn the next day.

GPS accuracy. Mean horizontal error (Euclidean distance) of GPS fixes for all treatments combined was 7.8 m (± 12.2 m SD; range: 0.3–875.0 m), and mean vertical error was 4.5 m (± 142 m SD, range: –142 to 9,325 m). Mean vertical error was slightly biased toward overestimating true elevation. Precision was lower in the vertical dimension, although the SD may have been inflated as a result of 18 outlier locations with error >1 km above true elevation. In the vertical dimension, 93% of locations were within the range of 22 m below to 22 m above true elevation, exceeding the accuracy reported by the manufacturer. Similarly, horizontal accuracy exceeded manufacturer reports, with 96% of locations within 18 m of the true location. Habitat influenced accuracy, as GPS locations in the forest treatment were generally less accurate in both dimensions than locations collected in the open and flight treatments (Table 2). Mean GPS error was similar between the open and flight treatments in both dimensions (Table 2, Figure 5), although 85% of the largest vertical outliers (>100 m above true elevation) were recorded in the flight treatment. Surprisingly, the relationship between DOP metrics and GPS error indicated that the largest GPS errors were associated with small DOP values (<3) in both the horizontal and vertical dimensions (Figure 6).

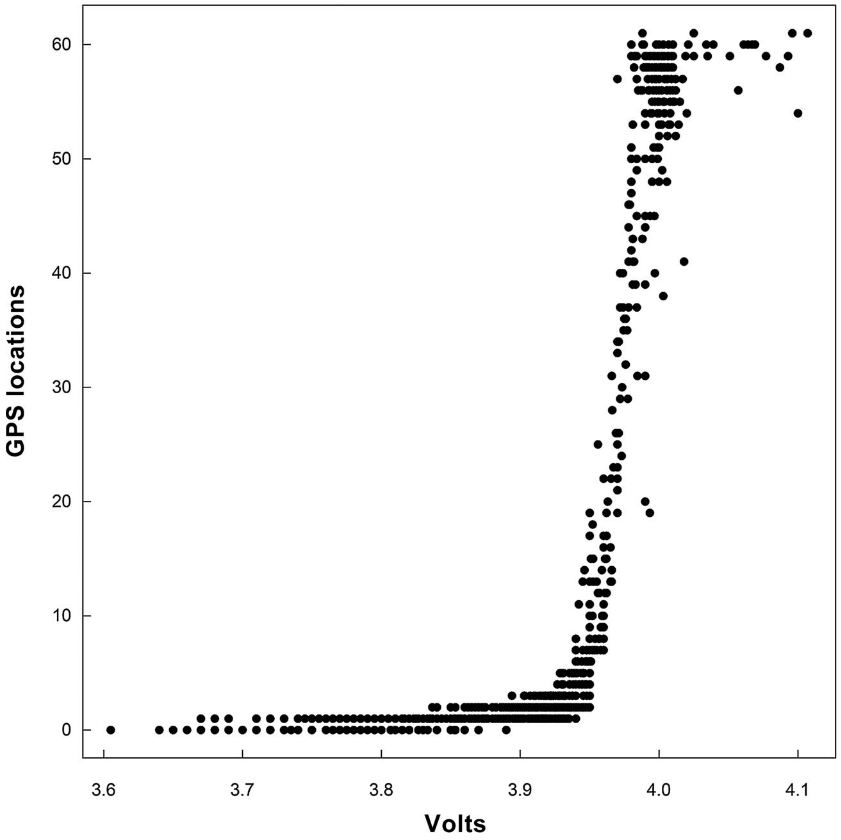


FIGURE 3. Hourly mean battery voltage and number of GPS locations collected for 3 GPS-GSM transmitters during 24 days of static testing on the ground in open fields, under forest cover, and suspended 11 m above the ground in an open field. Results are for all 3 transmitters combined.

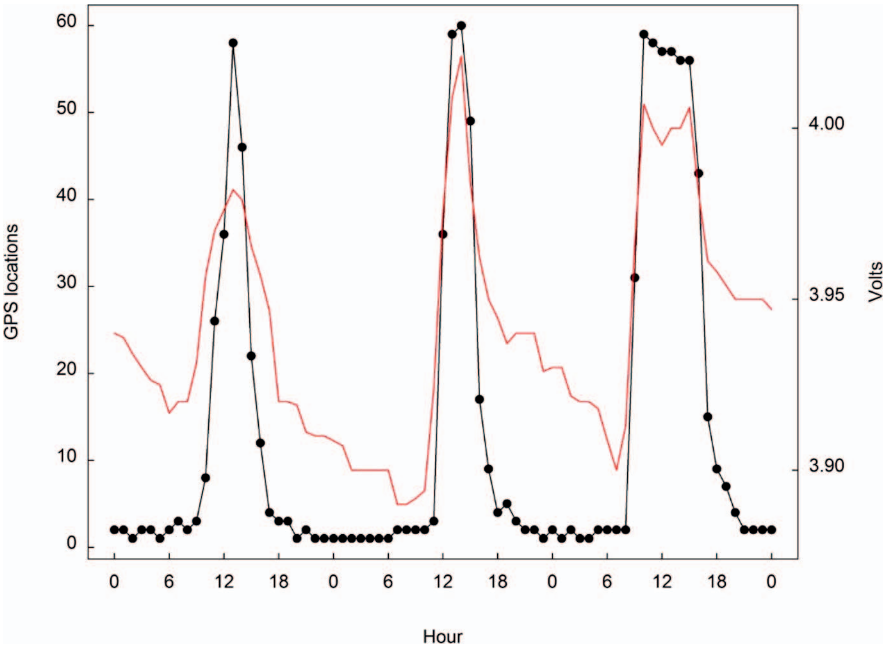


FIGURE 4. Time series of the number of hourly GPS locations collected (black line and circles) and battery voltage (red line) for a 70-g Microwave Telemetry (Columbia, Maryland, USA) solar GPS-GSM transmitter over a 3-day period during a static test of transmitter performance using a motionless unit suspended 11 m above the ground in an open field.

TABLE 2. Mean and standard deviation (SD) of GPS telemetry error (m) for location fixes collected by 3 GPS-GSM transmitters across 3 static treatments: on the ground in an open field (Open), on the ground under the forest canopy (Forest), and suspended 11 m above the ground in an open field to simulate flight (Flight).

		Error (mean ± SD)	
Treatment	Number of GPS fixes	Horizontal	Vertical
Open	6,554	6.3 ± 11.8	3.7 ± 134.6
Forest	443	17.3 ± 13.7	10.3 ± 17.6
Flight	9,334	8.4 ± 12.1	4.8 ± 151.0

Movement Tests

Test walk 1 took place between 1328 and 1436 hours EST (1.13 hr) on May 6, 2015. During this time the 3 test units collected 61, 59, and 51 locations, of which 100% indicated that the transmitter was moving (speed >0 integer knots [kn]). The researcher walked at a pace of ~2.5 kn during this test, and the median GPS speed value was 2 kn (range: 1–3 kn). Test walk 2 took place between 1149 and 1245 hours EST (0.93 hr) on May 7, 2015. During walk 2 the transmitters reported 13, 30, and 56 locations, of which 13 (100%), 21 (70%), and 54 (96%) indicated that the transmitter was moving. The researcher walked at a pace of ~3.1 kn during test walk 2; the median GPS speed value was 2 kn (range: 0–3 kn). Transmitter 1 reported a GPS fix every 1 min for the first 13 min of walk 2, then did not report again until 10.8 hr later. All locations reported by transmitter 2 during walk 2 with speed values of 0 kn were 2D fixes.

Of the GPS locations collected during static testing, a small percentage reported speeds >0 kn, corresponding to 0.16%, 0.09%, and 0.18% for each of the 3 test units, respectively. Erroneous speeds (>0 kn) recorded during static tests ranged from 1 to 199 kn, 62% of which were 1 kn. All erroneous static test speeds >1 kn were associated with large errors in vertical GPS accuracy (>1 km).

Field Tests

Of the 20 transmitters deployed on vultures, 3 stopped reporting within 24 hr of deployment. It is not known if these cases were the result of transmitter malfunction or attachment failure, resulting in the transmitter being dropped in a location with limited sunlight or no GSM reception. The remaining 17 transmitters reported well, with 14 still reporting data at the end of the study. Both species traveled well outside the immediate tagging area. On average, filtering removed <1% of raw locations for both species and, in total, 1,898,426 GPS locations were retained. Units returned a mean of 203.6 (Black Vultures) or 257.3 (Turkey Vultures) usable locations per day. Although it was common for several thousand postfiltered locations to have elevation estimates below the digital elevation model (DEM) value at that location, the overall percentage of postfiltered locations with negative height estimates was <1% for all transmitters (maximum = 0.15%). Caution is required when interpreting negative height values, as error in the DEM or the GPS location can result in a negative value when a bird is on the ground. Performance reports for all deployed units can be found in Appendix Table 5.

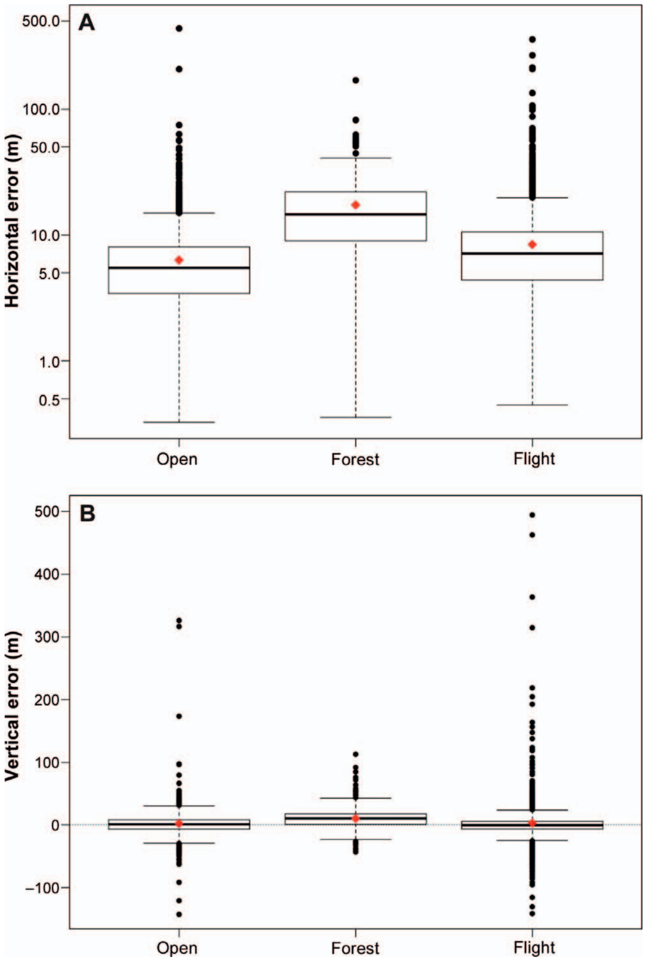


FIGURE 5. (**A**) Horizontal error and (**B**) vertical error of GPS locations collected by 3 GPS-GSM transmitters in 3 static treatments: on the ground in an open field (Open), on the ground under the forest canopy (Forest), and suspended 11 m above the ground in an open field to simulate flight (Flight). Note the log scaling of the *y*-axis in (A). Red diamonds indicate mean displacement, thick black lines represent the median, boxes show the interquartile range, whiskers indicate the range, and circles are outliers. Vertical error is represented as the distribution of error from true elevation; the dotted line at 0 represents no vertical error.

The top performing model for daylight fix rates differed between species. For units deployed on Turkey Vultures, the model that included an interaction effect between cloud cover and daily movement had overwhelming

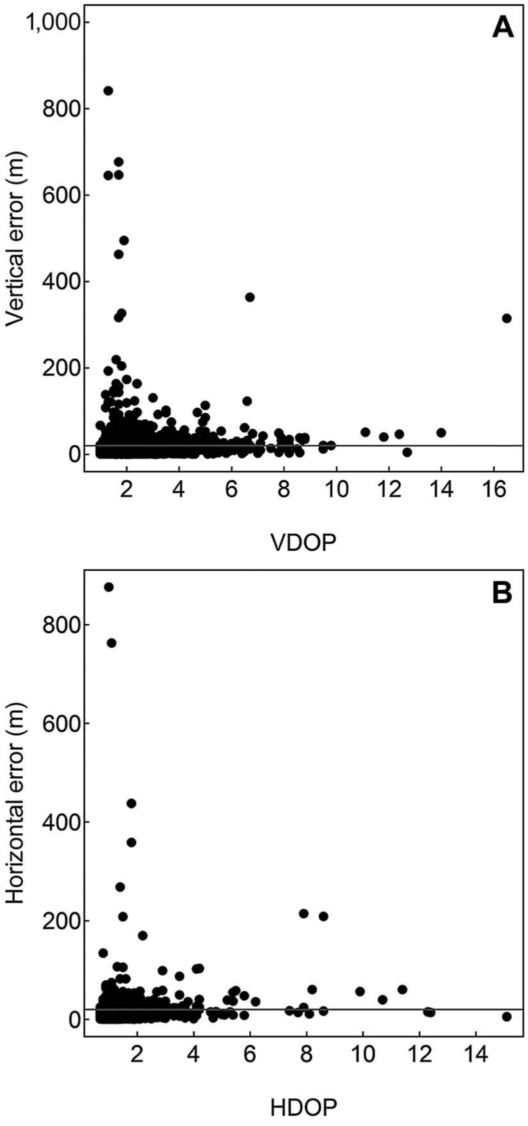


FIGURE 6. Relationship between (**A**) vertical GPS error (absolute value) and vertical dilution of precision (VDOP), and (**B**) horizontal GPS error and horizontal dilution of precision (HDOP) for GPS locations obtained by 3 GPS-GSM transmitters during static testing of transmitter performance using motionless units on the ground in open fields, on the ground under the forest canopy, and suspended 11 m off the ground in a field. For reference, the horizontal line represents error = 20 m.

TABLE 3. Model selection results for the full candidate model set of negative binomial generalized linear mixed-effects models of the number of daylight fixes collected by GPS-GSM transmitters deployed on Black Vultures ($n = 8$) and Turkey Vultures ($n = 9$) from June 17, 2013, to March 15, 2015, as a function of cloud cover (Cloud) and daily vulture movement rate (Movement). An offset term for day length (total minutes of daylight) and a fixed effect for the number of daylight fixes collected on the previous day were included in all models. We report the number of parameters (K), the difference in Akaike's Information Criterion (AIC) relative to the smallest value (ΔAIC), Akaike model weight (w_i), and model deviance.

Model	K	ΔAIC	w_i	Deviance
Black Vulture				
Cloud + Movement	6	0.00 [a]	0.72	16,393.7
Cloud*Movement	7	1.88	0.28	16,393.6
Cloud	4	391.70	<0.01	16,789.4
Turkey Vulture				
Cloud*Movement	7	0.00 [b]	>0.99	20,222.8
Cloud + Movement	6	54.40	<0.01	20,279.2
Cloud	4	544.70	<0.01	20,771.5

[a] AIC = 16,405.7.
[b] AIC = 20,236.8.

support (w_i >0.99; Table 3). The top model for units deployed on Black Vultures included cloud cover and daily movement, but with no interaction effect (Table 3). Although the Black Vulture model that included the interaction had a ΔAIC value <2 (Table 3), the 85% CI of the interaction parameter estimate encompassed 0, signifying that it was uninformative. All parameters included in the top performing models for units deployed on both species were informative (Table 4). Autocorrelation function plots of residuals indicated that incorporation of the previous day's fix rate sufficiently accounted for temporal autocorrelation in all cases. The standard error of the random effect of individual vultures in the top model was 0.16 for Black Vultures and 0.06 for Turkey Vultures.

For both species, daylight fix rates were greater on clear days (≤10% cloud cover) than cloudy days (≥90% cloud cover), and increased as daily movement rates increased (Table 4). To illustrate the relationship between explanatory variables and daylight fix rates, we used the fixed

TABLE 4. Parameter estimates and 85% confidence limits of fixed effects from top performing negative binomial generalized linear mixed models (Table 3) of the number of daylight fixes collected by GPS-GSM transmitters attached to Black and Turkey vultures from June 17, 2013, to March 15, 2015, during clear (≤10% cloud cover) and cloudy (≥90% cloud cover) days.

Parameter [a]	β	85% CL
Black Vulture		
Cloud condition	0.992	0.929, 1.054
Previous	0.002	0.002, 0.003
Movement	1.997	1.798, 2.195
Turkey Vulture		
Cloud condition	1.711	1.572, 1.850
Previous	0.002	0.002, 0.002
Movement	3.314	3.097, 3.531
Movement*Cloud condition	−1.560	−1.858, −1.262

[a] Cloud condition = categorical value representing a clear vs. a cloudy (reference) day; Previous = the number of daylight fixes collected on the previous day; Movement = the proportion of interpolated 10-min daylight time steps with displacements >39 m.

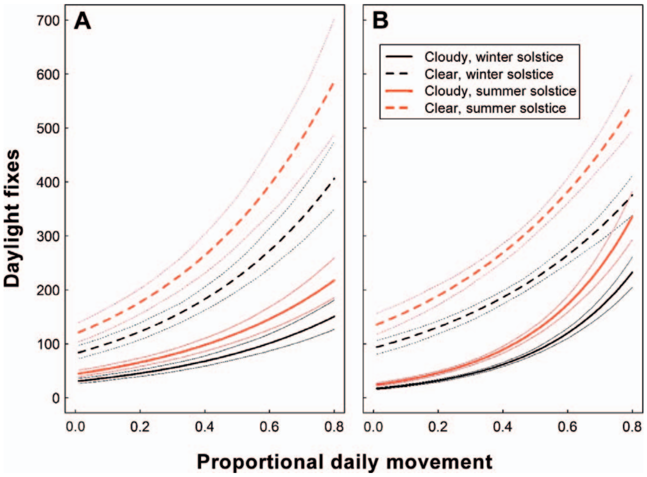


FIGURE 7. Model-predicted estimates and 95% confidence intervals for the number of daylight fixes collected by GPS-GSM transmitters attached to (**A**) Black Vultures and (**B**) Turkey Vultures as a function of daily movement rate during clear ($\leq$10% cloud cover) and cloudy days ($\geq$90% cloud cover). Red lines indicate conditions associated with summer solstice (14.4 daylight hr) and black lines conditions of winter solstice (9.9 daylight hr) for Aiken, South Carolina, USA. The previous day's fixes were held constant at 175.

effects estimates from the top performing model for each species to predict the expected number of daylight fixes as a function of proportional daily movement in both clear and cloudy conditions during the summer solstice (14.4 hr of daylight) and winter solstice (9.9 hr of daylight) at the tagging location (SRS), holding the previous day's fix count at 175 GPS locations (Figure 7). Model predictions indicated that, for both species, for any given cloud cover condition, more fixes would be expected during the summer solstice; however, more fixes could be expected during the winter solstice if conditions were clear than during a cloudy summer solstice (Figure 7). In all cases, expected daylight fix rates increased with daily movement rates. As a result of the interaction effect, for units deployed on Turkey Vultures, greater daily movement rates caused a more rapid increase in daylight fixes during cloudy conditions than clear conditions (Figure 7).

DISCUSSION

Data Collection Rates

The transmitters that we tested in this study were capable of collecting large volumes of data, but data collection rates were highly variable, both between days and on an hourly scale within days. Ultimately, data collection rates were tied to battery charge, which itself was a function of the amount and intensity of solar radiation reaching the solar panels and the size and capacity of the battery. Both static tests and deployments on wild vultures illustrated that factors that influenced the amount and duration of solar radiation reaching the units—habitat, environmental conditions, and animal behavior—played a role in how much data was collected.

Under clear conditions with unobstructed sun exposure, fix rates commonly reached the manufacturer-specified maximum of 1 location min^{-1} during afternoon hours when battery charge was highest, but dropped considerably to $\leq$1 location hr^{-1} at night. For strictly diurnal species, the reduction in data collection during nocturnal periods may not be of much consequence from a behavioral perspective. However, even diurnal species may engage in important behaviors (e.g., foraging) during dawn and dusk periods, coinciding with the daylight hours when fix rates are lowest. Researchers need to decide if the decrease in temporal resolution during these periods is acceptable for their specific objectives. While a number of methodologies have been developed in recent years to analyze movement data collected at irregular intervals (e.g., Horne et al. 2007, Patterson et al. 2008, Gurarie et al. 2009), many analyses are greatly simplified by data collected at regular time intervals. Even complex state-space models that are designed to deal with temporal irregularity may misidentify behavioral states when considerable or systematic gaps exist in the time series (Breed et al. 2011).

Fix rates were uniformly low at all hours under canopy cover. The influence of habitat on hourly data collection rates carried over into total daylight fix rates. Transmitters were able to collect up to 500 GPS locations between sunrise and sunset on clear days in open and flight treatments, but no unit collected >25 daylight locations when under forest cover. While daylight fix rates varied according to cloud cover conditions in open and flight treatments, cloud cover had no discernable influence on daylight fix rates in the forest treatment. Canopy cover limits the amount of sunlight reaching the solar panels and likely leads to a necessary reduction in fix rate to avoid complete battery drain. This may have implications for habitat selections studies of species that use forested habitats, as a systematic habitat- and behavior-related bias in GPS fix rate may lead to biases in estimates of habitat use if not accounted for. Frair et al. (2010) provide an extensive review of potential methods to correct for such biases and the benefits and considerations associated with each.

Data from free-ranging vultures indicated that animal movement, cloud cover, and the time of year affected daylight collection rates. Daylight fix rates were positively correlated with movement rates for both species, and we suspect that this was the result of increased solar exposure when flying, which facilitated battery charging. Interestingly, the influence of movement on daylight fix rate was stronger in cloudy conditions than clear conditions for transmitters deployed on Turkey Vultures, but there was no such interaction observed for transmitters on Black Vultures. That the top models explaining daylight fix rate were different between species suggests that inherent differences in behavior and habitat use between species may translate to differences in transmitter performance, even when operating in similar weather conditions.

More fixes were expected during the summer than the winter solstice. In summer, day length is longer, and the maximum angle of the sun above the horizon (solar elevation) at solar noon is higher. In our example, noon solar elevation on the summer and winter solstices was 80.1° and 33.2°, respectively. The combination of longer days and higher solar elevation results in more hours of sunlight as well as higher-intensity solar radiation over a proportionally longer portion of the day. These conditions should be more favorable to battery charging rates, leading to elevated fix collection rates during the day. Additionally, daylight fix rates of transmitters deployed on free-ranging vultures were influenced by the previous day's fix rate, potentially as a result of temporal correlation in environmental conditions and animal behavior, or carryover effects on battery charge from one day to the next.

Based on our results, researchers may expect to obtain the greatest daylight fix rates for active species in temperate latitudes close to the summer solstice. Ideal species for study with transmitters with dynamic fix programming may be migratory species that move to high latitudes in the spring and summer months, then move to lower latitudes in winter. In the tropics, researchers may expect high daylight fix rates year-round, assuming that the study species allows the transmitter regular access to an unobstructed view of the sky, either through flight behavior or use of open habitats. Application is likely somewhat limited for species that remain at high latitudes year-round as fix rates may be expected to drop considerably during winter periods. We assessed the largest model available from Microwave Telemetry. Transmitter weight is closely tied to battery size, and larger batteries are able to hold a charge longer than small batteries. As such, the fix collection rates of smaller models may be more sensitive to changes in environmental conditions, such as cloud cover, that affect the ability of the unit to charge.

We were unable to rigorously test GSM capabilities, but note that transmission of data via the GSM system worked very well; updates were received from transmitters during static tests once daily during all testing periods, and very rarely (<1% of the time) did transmitters on vultures provide data reports >24 hr apart. The GSM system is a cellular communications network and requires the transmitter to be within range of the coverage area in order to transmit data. Thus, researchers using GSM transmitters should expect less frequent transmissions in areas with poor coverage.

GPS Accuracy

Our static testing indicated that GPS locations were quite accurate on average, with 93% of locations within 22 m of true elevation and 96% within 18 m of true horizontal position. Accuracy was influenced by habitat, however, with mean spatial error increasing when units were under forest cover. Habitat structure often influences GPS accuracy, and increased error under forest cover has commonly been reported for other GPS wildlife tracking devices (Dussault et al. 1999, Cargnelutti et al. 2007, Lewis et al. 2007, Hansen and Riggs 2008, Guthrie et al. 2011). Presumably this is due to canopy cover reducing GPS reception, resulting in fewer satellites being used to estimate a location. Ornithologists using this technology to study species in forested habitats must account for this variability when studying habitat use and selection, for example by ensuring that the resolution of habitat data used in analyses is not greater than expected GPS error. Although our study area was relatively flat, previous studies have found that topography can influence GPS accuracy in a similar manner (Cain et al. 2005); researchers working in rugged terrain are advised to investigate the effect of topography on GPS accuracy in their study region.

We found that the greatest GPS errors were associated with relatively small HDOP and VDOP values. Although earlier studies have suggested that screening GPS data by removing locations with DOP values above an arbitrary cutoff may effectively remove outliers and reduce mean location error (D'eon and Delparte 2005, Lewis et al. 2007), more recent work has demonstrated that, since the removal of GPS Selective Availability, DOP is less reliable for identifying large GPS errors (Recio et al. 2011, Laver et al. 2015), and that screening based solely on DOP may come at the cost of removing many accurate locations with little gain in error reduction. We advise against filtering based solely on DOP values and suggest that any screening incorporate multiple conditions or, ideally, take a model-based approach to identifying unacceptable location error, sensu Laver et al. (2015). We suggest that this applies to all modern GPS telemetry technology and not just the transmitters that we tested.

Movement Identification

Our results suggest that speed estimates reported with GPS locations may be useful indicators of activity, even for individuals moving slowly, provided that a 3D fix is obtained. Obtaining these data from GPS tags can reduce the need for additional accelerometer packages, which add weight and can increase costs to birds (Chivers et al. 2016). Additionally, our static tests revealed a very low rate of incorrect movement assignments (<1%). Visual inspection of vulture movement paths indicated high correspondence between apparent movements and speed values (for an example of a portion of a Black Vulture track, see Appendix Figure 9). This could be useful for constructing behavioral models of avian movement. For example, for marine mammals, wet-dry sensors that identify haul-out behavior have been included as covariates in movement path reconstruction models to identify times when the animal was stationary (Johnson et al. 2008). Similarly, dive record data has been incorporated into multistate models based on locational data to identify foraging state (McClintock et al. 2013). Speed estimates reported with GPS locations could similarly be incorporated into models along with locational data for behavioral analysis. However, these data are not appropriate for fine-scale investigations into flight type and energetics, as might be gained from dedicated accelerometers (e.g., Williams et al. 2015) or units that can be programmed to collect GPS data continuously at very high resolution (0.5–1.0 min intervals) during specific times of interest (e.g., Katzner et al. 2015).

Solar-powered GPS-GSM units provide unprecedented opportunity to study fine-scale movement behavior of birds, potentially allowing research into fundamental questions of movement ecology that have previously been logistically impossible (Bridge et al. 2011). However, researchers must be aware of the factors that influence the quality and quantity of data acquisition to optimize study design. We hope that our results will serve as a practical source of information for ecologists designing studies using solar GPS-GSM tracking. Regardless of the tracking device used, we suggest that researchers conduct controlled testing prior to deployment of any tracking device to test for variability between individual units, to quantify location error specific to conditions in their study site, and to understand the conditions that may influence data collection rates.

ACKNOWLEDGMENTS

We thank Mark Edwards and Malcolm Squires for technical assistance during static tests.

Funding statement: Funding was provided by the U.S. Department of Agriculture Animal Plant Health Inspection Service National Wildlife Research Center and the U.S. Department of Energy under award number DE-FC09-07SR22506 to the University of Georgia Research Foundation. None of the funders had any input into the content of the manuscript, nor required their approval of the manuscript before submission or publication.

Ethics statement: All capture and handling procedures were approved under the University of Georgia Institutional Animal Care and Use Protocol number A2013 02-004, and U.S. Geological Survey Bird Banding permit number 22002.

Author contributions: M.E.B., A.E.H., and J.C.B. conceived the idea, design, and experiments; all authors performed the experiments and conducted research; M.E.B. and A.E.H. developed and designed the methods; M.E.B. analyzed the data; and all authors wrote the paper.

LITERATURE CITED

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Avery, M. L., J. S. Humphrey, T. S. Daughtery, J. W. Fischer, M. P. Milleson, E. A. Tillman, W. E. Bruce, and W. D. Walter (2011). Vulture flight behavior and implications for aircraft safety. The Journal of Wildlife Management 75:1581–1587.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Biavati, G. (2014). RAtmosphere: Standard atmospheric profiles. R package version 1.1. https://CRAN.R-project.org/package=RAtmosphere

Breed, G. A., D. P. Costa, M. E. Goebel, and P. W. Robinson (2011). Electronic tracking tag programming is critical to data collection for behavioral time-series analysis. Ecosphere 2: art10.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski (2011). Technology on the move: Recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Cain, J. W., III, P. R. Krausman, B. D. Jansen, and J. R. Morgart (2005). Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926–934.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Cargnelutti, B., A. Coulon, A. J. M. Hewison, M. Goulard, J.-M. Angibault, and N. Morellet (2007). Testing Global Positioning System performance for wildlife monitoring using mobile collars and known reference points. The Journal of Wildlife Management 71:1380–1387.

Chivers, L. S., S. A. Hatch, and K. H. Elliott (2016). Accelerometry reveals an impact of short-term tagging on seabird activity budgets. The Condor: Ornithological Applications 118:159–168.

D'eon, R. G., and D. Delparte (2005). Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

Dodge, S., G. Bohrer, K. Bildstein, S. C. Davidson, R. Weinzierl, M. J. Bechard, D. B. Barber, R. Kays, D. Brandes, J. Han, and M. Wikelski (2014). Environmental drivers of variability in the movement ecology of Turkey Vultures (*Cathartes aura*) in North and South America. Philosophical Transactions of the Royal Society B 396:20130195.

Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski (2013).

The environmental-data automated track annotation (*Env-DATA*) system: Linking animal tracks with environmental data. Movement Ecology 1:3.

Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot (1999). Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27:965–972.

Frair, J. L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N. J. DeCesare, and L. Pedrotti (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B 365:2187–2200.

Gurarie, E., R. D. Andrews, and K. L. Laidre (2009). A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:395–408.

Guthrie, J. D., M. E. Byrne, J. B. Hardin, C. O. Kochanny, K. L. Skow, R. T. Snelgrove, M. J. Butler, M. J. Peterson, M. J. Chamberlain, and B. A. Collier (2011). Evaluation of a Global Positioning System backpack transmitter for Wild Turkey research. The Journal of Wildlife Management 75:539–547.

Hamel, S., N. G. Yoccoz, and J. Gaillard (2012). Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. Methods in Ecology and Evolution 3:731–742.

Hansen, M. C., and R. A. Riggs (2008). Accuracy, precision, and observation rates of Global Positioning System telemetry collars. The Journal of Wildlife Management 72:518–526.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis (2007). Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Johnson, D. S., J. M. London, M.-A. Lea, and J. W. Durban (2008). Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215.

Katzner, T. E., P. J. Turk, A. E. Duerr, T. A. Miller, M. J. Lanzone, J. L. Cooper, D. Brandes, J. A. Tremblay, and J. Lemaître (2015). Use of multiple modes of flight subsidy by a soaring terrestrial bird, the Golden Eagle *Aquila chrysaetos*, when on migration. Journal of the Royal Society Interface 12: 20150530.

Laver, P. N., R. A. Powell, and K. A. Alexander (2015). Screening GPS telemetry data for locations having unacceptable error. Ecological Informatics 27:11–20.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling (2007). Effects of habitat on GPS collar performance: Using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

López-López, P., C. Garćia-Ripollés, and V. Urios (2014). Food predictability determines space use of endangered vultures: Implications for management of supplementary feeding. Ecological Applications 24:938–949.

Mandel, J. T., K. L. Bildstein, G. Boher, and D. W. Winkler (2008). Movement ecology of migration in Turkey Vultures. Proceedings of the National Academy of Sciences USA 105:19102–19107.

McClintock, B. T., D. J. F. Russell, J. Matthiopoulos, and R. King (2013). Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology 94:838–849.

McConnell, B. J., C. Chambers, and M. A. Fedak (1992). Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science 4:393–398.

Oderwald, R. G., and B. A. Boucher (2003). GPS after Selective Availability: How accurate is accurate enough? Journal of Forestry 101:24–27.

Patterson, T. A., L. Thomas, C. Wilcox, O. Otvaskainen, and J. Matthiopoulos (2008). State-space models of individual animal movement. Trends in Ecology & Evolution 23:87–94.

Pearse, A. T., D. A. Brandt, and G. L. Krapu (2016). Wintering Sandhill Crane exposure to wind energy development in the central and southern Great Plains, USA. The Condor: Ornithological Applications 118:391–401.

Pérez-García, J. M., A. Margalida, I. Afonso, E. Ferreiro, A. Gardiazábal, F. Botella, and J. A. Sánchez-Zapata (2013). Interannual home range variation, territoriality and overlap in breeding Bonelli's Eagles (*Aquila fasciata*) tracked by GPS telemetry. Journal of Ornithology 154:63–71.

R Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://ww.R-project.org/

Recio, M. R., R. Mathieu, P. Denys, P. Sirguey, and P. J. Seddon (2011). Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. PLoS ONE 6:e28225.

Tracey, J. A., J. Sheppard, J. Zhu, F. Wei, R. R. Swaisgood, and R. N. Fisher (2014). Movement-based estimation and visualization of space use in 3D for wildlife ecology and conservation. PLoS ONE 9:e101205.

White, D. L., and K. F. Gaines (2000). The Savannah River Site: Site description, land use, and management history. In Avian Research at the Savannah River Site: A Model for Integrating Basic Research and Long-Term Management (J. B. Dunning, Jr., and J. C. Kilgo, Editors). Studies in Avian Biology 21:8–17.

Williams, H. J., E. L. C. Shepard, O. Duriez, and S. A. Lambertucci (2015). Can accelerometry be used to distinguish between flight types in soaring birds? Animal Biotelemetry 3:45.

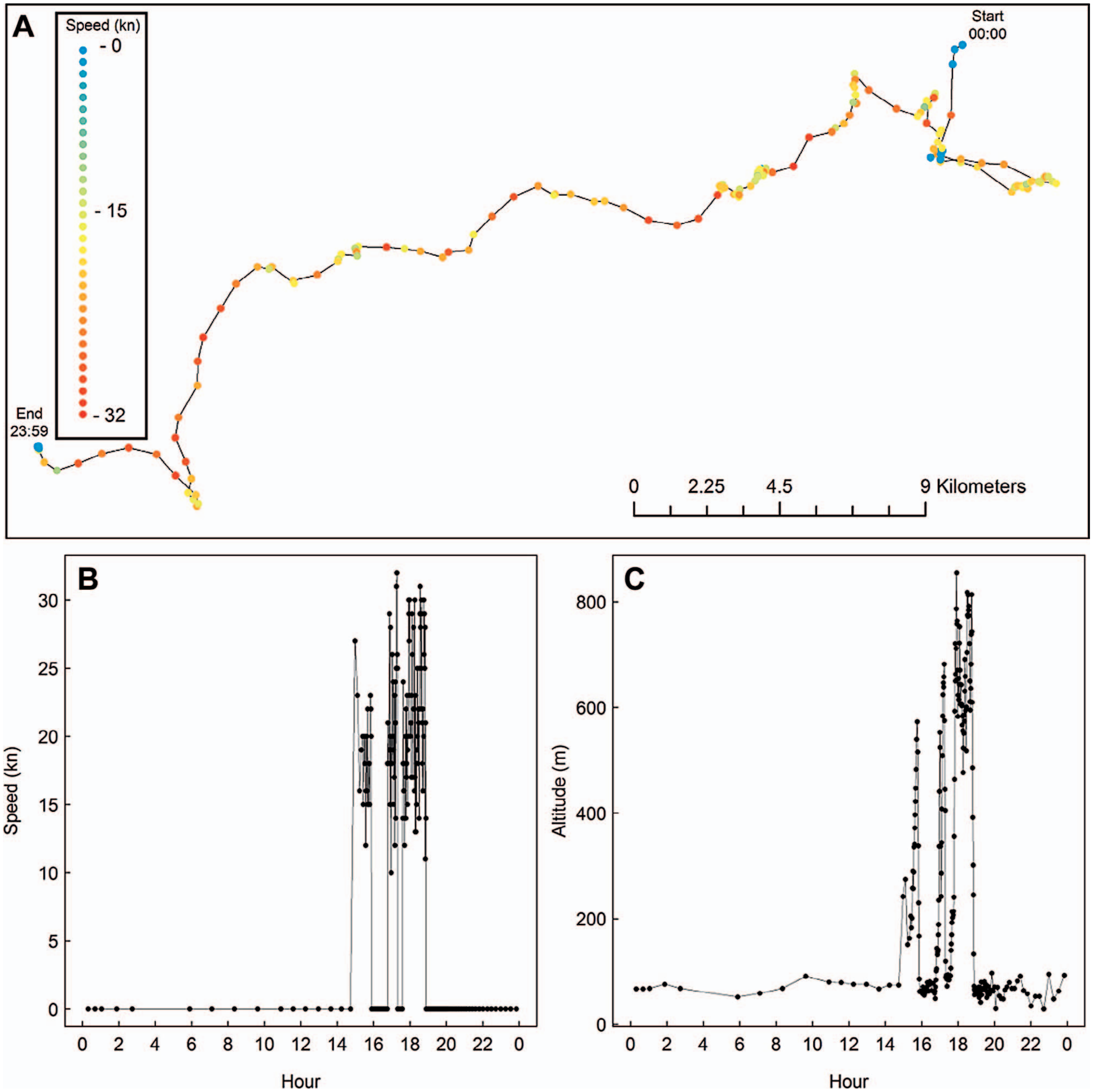
Workman, S. W., and K. W. McLeod (1990). Vegetation of the Savannah River Site: Major community types. Technical Report SRO-NERP-19, Savannah River Ecology Laboratory, Aiken, SC, USA.

APPENDIX TABLE 5. Performance summary for 20 Microwave Telemetry (Columbia, Maryland, USA) solar-powered GPS-GSM transmitters attached to Black (BV) and Turkey vultures (TV) in South Carolina, USA, from June 17, 2013, to March 15, 2015, including total days at liberty (DAL); transmitter fate (Fate); total number of reported locations (Reports); number of reports flagged as no fix (NF), 2D fix (2D), negative altitude (–Alt), battery drain (BD), or low voltage (LV); number of useful locations after raw data processing (Post); and the number of postprocessed locations with altitude estimates below ground level (–Ht).

ID	Species	DAL	Fate [a]	Reports	NF	2D	−Alt	BD	LV	Post	−Ht
161	BV	620	Active	92,473	46	258	161	2	0	91,314	7,140
162	BV	633	Active	140,388	58	405	256	0	0	138,275	10,884
164	BV	0	Missing	0	0	0	0	0	0	0	0
165	BV	633	Active	96,136	654	315	134	0	0	94,665	9,245
167	BV	365	Missing	102,537	5	82	70	0	0	101,660	4,236
168	BV	328	Active	61,733	24	167	131	0	0	61,120	8,893
174	BV	318	Active	68,229	78	165	93	0	2	67,426	5,534
175	BV	590	Active	133,958	44	201	169	0	0	132,632	13,202
177	BV	446	Drop	96,043	287	375	135	0	0	94,636	13,520
163	TV	627	Active	190,847	37	324	132	0	0	189,084	12,116
166	TV	593	Active	133,327	10	188	143	1	1	130,978	1
169	TV	1	Missing	223	0	0	0	0	0	221	9
170	TV	1	Missing	145	0	1	0	0	0	140	6
171	TV	636	Active	158,859	28	237	162	0	0	157,657	19,212
172	TV	618	Active	164,435	8	136	141	0	0	163,256	14,169
173	TV	627	Active	194,890	14	153	118	0	0	192,668	9,013
176	TV	614	Active	136,850	5	149	139	1	6	135,914	12,707
178	TV	326	Active	90,949	2	90	64	0	0	90,025	5,213
179	TV	592	Active	148,578	28	200	136	0	0	147,457	14,570
180	TV	177	Missing	41,625	2	90	52	0	0	40,256	2,464

[a] Active = unit still transmitting as of March 15, 2015; Missing = communication with unit lost; and Drop = unit detached from bird and recovered.

APPENDIX FIGURE 8. Example of a solar-powered GPS-GSM transmitter (Microwave Telemetry, Columbia, Maryland, USA) attached to a Turkey Vulture.



APPENDIX FIGURE 9. Example of data recorded by a GPS-GSM transmitter attached to a Black Vulture during a 24-hr period, showing (**A**) the track taken by the bird in South Carolina, USA, color-coded by instantaneous speed estimates reported with each location, as well as (**B**) the time series of speed estimates, and (**C**) altitude estimates.