



Tools and Technology

Retained Satellite Information Influences Performance of GPS Devices in a Forested Ecosystem

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ABSTRACT Global Positioning System (GPS) units used in animal telemetry often suffer from nonrandom data loss and location error. GPS units use stored satellite information to estimate locations, including almanac and ephemeris data reflecting satellite positions at weekly and at <4-hr temporal scales, respectively. Using the smallest GPS collars (45–51 g) available for mammals, we evaluate how satellite information and environmental conditions affected GPS performance in 27 mobile trials, and field reliability during 56 deployments on Pacific marten (*Martes caurina*). We conducted trials in Lassen National Forest, California, USA, during March 2011–January 2012. We programmed GPS units to retain or remove satellite data (i.e., continuous or cold-start mode) before attempting a location (fix), thereby mimicking differing fix intervals. In continuous mode, fix success was 2.2× higher, was not influenced by environmental obstructions, and improved after a location with ≥4 satellites (3-D). In cold-start mode, fix success was negatively correlated with vegetation cover. Location error was lower for 3-D fixes. Censoring cold-start fixes with only 3 satellites (2-D) and 2-D locations prior to the first 3-D fix in continuous mode decreased location error by 91% and 55%, ensuring <50 m accuracy. The significance of previous fix success and reduced battery expenditure underscores the benefits of ephemeris data and short fix intervals. Only 66% of 56 units functioned upon delivery for field deployment. Once tested and deployed, 28% malfunctioned. This study demonstrates that GPS tests should use the same fix schedules as field deployments, and GPS data quality in dense cover improves with short fix intervals. Miniature GPS units are a promising tool, but the study design should be carefully considered. © 2015 The Wildlife Society.

KEY WORDS animal movement, carnivore, fix success, GPS, location error, *Martes americana*, *Martes caurina*, Telemetry Solutions.

Global Positioning System (GPS) telemetry has been used to collect location data from free-ranging animals with a high degree of precision and accuracy (Frair et al. 2010). Miniaturization of GPS unit has enabled researchers to use lightweight GPS collars (80–125 g) to study mammals as small as 2.5 kg (Blackie 2010, Recio et al. 2011, Brown et al. 2012, Adams et al. 2013). Smaller GPS collars (42–60 g) for mammals, available since 2009, have not been consistently effective (Thompson et al. 2012, Cypher et al. 2014). Limited battery life in lightweight GPS collars may increase malfunctions and reduce their functionality (Blackie 2010). Testing is needed because GPS failures and technical malfunctions can severely reduce performance, limiting sample size and data quality (Hebblewhite and Haydon 2010).

GPS error includes both location error and failed location attempts that result in missing data (Frair et al. 2010). GPS error can systematically bias resource-selection studies (Frair

et al. 2004, Visscher 2006), home range estimation (Horne et al. 2007), and evaluation of movement patterns (Hurford 2009). Minimizing bias due to GPS error and maximizing battery life are of utmost importance when considering use of GPS units, especially for these miniature sizes.

Although performance of any GPS device is affected by a range of environmental conditions and locations of available satellites (Grewal et al. 2007), GPS error is most often attributed to satellite signal obstruction due to vegetation, topography, or animal behavior (Frair et al. 2010). Failed location attempts are most often associated with dense canopy cover (Frair et al. 2010, Recio et al. 2011), and a combination of factors (e.g., canopy cover, topography) can explain increased location error (Recio et al. 2011). Furthermore, GPS error may be compounded by multiple obstructions (Augustine et al. 2011). These interactions may differ between study areas and collar brands, potentially explaining the wide range in fix success (successful GPS locations divided by the total attempts) and location error reported across studies (Lewis et al. 2007, Sager-Fradkin et al. 2007). GPS error also may be influenced by animal behavior through habitat preferences, antenna orientation, or whether animals rest or den in areas obstructed from

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satellites (e.g., burrows, cavities, buildings; D'Eon and Delparte 2005).

A largely unrecognized factor that may influence GPS error is the fix schedule, or duration between fix attempts. GPS error may be reduced and battery life increased, if the time between fix attempts is short enough to allow the GPS unit to retain 2 types of satellite information: almanac and ephemeris data (Singh 2006). Almanac data include coarse orbital parameters of satellites and are valid for several weeks (U.S. Department of Defense 2008, Tomkiewicz et al. 2010). Ephemeris data are precise satellite locations and are valid for 1–4 hr depending on the GPS unit and position of satellites on the horizon (Grewal et al. 2007, Tomkiewicz et al. 2010). Using simulations of GPS units 60% obstructed by vegetation, Augustine et al. (2011) predicted approximately 90% fix success at a 15-min fix interval but only approximately 50% at a 2-hr fix interval, presumably because of the declining relevance of the ephemeris data as satellites moved beyond the horizon. The influence of fix schedule on location error has not been evaluated.

Here, we evaluate the effectiveness of the smallest GPS collar commercially available for mammals (42–52 g) as part of a study of movement of a small carnivore, Pacific marten (*Martes caurina*; 0.5–1.2 kg), formerly the American marten (*M. americana*), in western North America (Dawson and Cook 2012). Martens are associated with dense forests with multilayered canopies (Spencer et al. 1983) and rest in highly obstructed areas, such as tree cavities, long enough to reduce or eliminate the usefulness of ephemeris data. These characteristics are similar to mammals with the lowest reported GPS collar-fix rates: fishers (*Pekania pennanti*; 25–38%; Thompson et al. 2012) and wolverines (*Gulo gulo*; 46%; Mattisson et al. 2010). To infer the accuracy of GPS data collected using these collars on free-ranging marten, we conducted a controlled experiment with repeated mobile trials (GPS unit was actively moving) using a test GPS collar within known marten home ranges. First, we compared the degree to which retention of ephemeris and almanac data affected fix success in forested patches that differed in overhead cover. Second, we modeled how environmental obstruction, retained satellite information, or the combination of factors influenced fix success. We used predictions to evaluate how fix success differed during active movement by martens (continuous mode) or after emerging from an obstructed rest site or den (when ephemeris data would no longer be valid, cold-start mode). Third, we assessed performance and accuracy by testing whether time to estimate locations and location error differed in each mode. Lastly, we evaluated whether miniature GPS collars (cumulatively, the GPS, very-high-frequency, and ultra-high-frequency radiotransmitter components) were an effective tool for studying forest-associated mammals of <1 kg.

STUDY AREA

We conducted trials in Lassen National Forest, California, USA, during March 2011–January 2012. The study area was mountainous, with elevations ranging from 1,500 m to

2,100 m. Forest stand types included red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole (*Pinus contorta*), or mixed conifer.

We stratified the landscape into 3 forest-patch classifications that we predicted would influence marten occurrence and GPS performance. ‘Complex’ stands had structurally diverse understories and overstory canopy cover ranging from 35% to 68% ($48.2\% \pm 1.6\%$, $\bar{x} \pm \text{SE}$) as estimated with a moosehorn coverscope (Fiala et al. 2006). ‘Simple’ stands had been subjected to a variety of forest management activities that reduced understory complexity and branches near to the ground and resulted in overhead canopy cover between 15% and 48% ($26.3\% \pm 2.1\%$). ‘Open’ stands included areas with little or no overstory canopy cover ($3.2\% \pm 0.9\%$, 0–14%).

MATERIALS AND METHODS

We evaluated 48-track-channel JP-18S4 GPS receivers (FMO Electronics, Langewiesen, Germany) within Quantum 4000 Enhanced Micro-Mini GPS collars (Telemetry Solutions, Concord, CA; hereafter, ‘GPS.’) We tested these units in 2 forms: 1) a test unit with a rechargeable battery; and 2) marten-deployed collars. The test and marten-deployed units contained identical GPS components and software. At each fix attempt, we programmed the GPS to collect satellite information for a maximum of 120 s and then stay on for an additional 30 s.

We manually programmed the test unit to estimate locations in 2 modes: continuous and cold start. Continuous mode is comparable to standard GPS collar settings where almanac and ephemeris data are retained after downloading from satellites and can include 3 fix conditions: hot, warm, or cold start (Grewal et al. 2007, Tomkiewicz et al. 2010). A ‘hot start’ fix can be acquired in <1–8 s, depending on the unit, if both almanac and ephemeris data are retained and there are ≥ 3 connected satellites. A ‘warm start’ fix can be acquired within 25–35 s if only almanac data are retained with ≥ 3 connected satellites. A ‘cold-start’ fix could be acquired in 25–35 s if neither almanac nor ephemeris data are available with ≥ 3 connected satellites. Expected time to fix with a cold, warm, or hot start is similar among modern multichannel GPS units (Tomkiewicz et al. 2010). We manually programmed test receivers to remain in ‘cold-start’ mode for selected trials. We used cold-start mode to simulate a GPS on an animal that routinely uses obstructed areas for longer than 4 hr and predicted that mode would have the lowest fix success and highest location error.

Mobile Trials

We used mobile GPS testing to determine how satellite information influenced fix success in different patch types. In mobile trials, we moved a test unit through the environment to simulate the movements of a marten; the test unit was attached to a saline-filled water bottle to simulate proximity to an animal’s body (Frair et al. 2010). We attached 4 strings between the bottle and a cross made of plastic pipe, similar to the handle used for marionette puppets. The string length was such that the GPS unit was at the height of a marten-sized mammal (approx. 20 cm from the ground) when held

by the tester, who manipulated the cross to simulate the bounding movement expected from martens and moved the device from one side of their body to the other to minimize blocking satellites.

During mobile trials, we collected data in continuous and cold-start modes using a paired design. We first created meandering transects approximately 2 km long with predetermined start and end points. Half of the transects were completely within a single patch type (i.e., complex, simple, open), while the other half traversed roughly equal amounts of each patch type in a random order. We walked or skied along each transect with the GPS in a randomly chosen mode. At the end of that track, the GPS was reset to the alternative mode and we retraced our path. This ensured that data collected in both modes reflected similar conditions and time periods (within 2.5 hr). We assumed satellite availability and configuration would be similar within that period.

We compared GPS fixes from the test device with a tracklog collected using a Bluetooth Garmin® 10x GPS (Garmin International Inc., Olathe, KS) positioned approximately 2 m above the ground at a scheduled fix rate of 15 s. We scheduled the test unit to take fixes at the same 5-min interval as the marten-deployed collars. The tracklog was considered the reference position, and location error for the test unit was calculated as the Euclidean distance between the 2 corresponding spatial coordinates (test unit and tracklog) collected at the closest time. The error from the Garmin 10x was estimated to be <10 m (Garmin 2006), whereas location error from low-quality fixes on GPS collars may exceed 500 m; thus, the paired design of our study allowed standardized comparison of relative error between modes.

Environmental Covariates

We examined the potential for interaction between vegetation and topography and satellite information during mobile trials because we predicted those factors would explain most variation in fix success. We collected geo-referenced environmental data along our transects every 5 min, but offset the collection by 2.5 min from the test device to ensure the GPS unit was moving when it attempted a fix. Even though user-collected environmental data were offset by as much as 100 m within the 2.5-min interval, the relative homogeneity of the patches chosen for our trials likely reduced the associated error. Topographic obstruction was represented by aspect, elevation, and satellite obstruction from topography. We calculated the number of available satellites at the mobile trial location and time using Trimble Planning software version 2.9 (Trimble Navigation Limited, Sunnyvale, CA). We calculated aspect and elevation in ArcGIS version 10.0 using a publically available 10-m-resolution digital elevation model (Bowen et al. 2010). We represented aspect by the variables northness [$\cos(\text{aspect} \times \pi)/180$] and eastness [$\sin(\text{aspect} \times \pi)/180$] (Zar 1999). Topographical obstruction was determined with 'sky view factor' (SVF), a parameter corresponding to the amount of visible sky limited by topography. We used the program Sky-View Factor using the maximum number of calculated angles (64) and a range of 30 pixels (Ošti et al. 2010, Zakšek et al.

2011). Complete satellite view (100%) indicated no obstruction due to topography. Our values for SVF ranged between 79% and 100% during our mobile trials; the study area had a SVF range between 57.2% and 100%, similar to other GPS tests (see Hansen and Riggs 2008). We estimated vegetation obstruction categorically by patch type following our GIS map and canopy cover averaged from measurements recorded along the track.

GPS Performance and Modeling Fix Success

First, we compared fix success between patch types using a 2-way factorial Analysis of Variance, adjusting with Tukey's Honestly Significant Difference to correct for multiple comparisons. We also calculated the risk ratio of a fix between all combinations of patch types (e.g., open vs. complex) in each GPS mode (Grimes and Schulz 2008).

We used generalized linear mixed-models with a logit-link to assess whether the probability of fix success was influenced by patch type or topographical obstruction (both cold-start and continuous mode), retained satellite information (continuous mode), or the combination of obstruction and satellite information (continuous mode). We represented topographical obstruction with SVF, elevation, and aspect. To describe whether satellite information was retained, we used binary variables indicating the presence or absence of previously acquired locations (previous fix) or previously acquired 3-D fix (≥ 4 satellites, previous 3-D fix). Track identity was retained as a random factor within each model using package lme4 (Bates et al. 2013) in Program R (R Foundation for Statistical Computing, Vienna, Austria), because each track presumably experienced a unique combination of environmental effects. We used an information theoretic approach with Akaike's Information Criterion (AIC) to evaluate candidate models (Burnham and Anderson 2002), and used package MuMIn (Barton 2013) to average model coefficients from candidate models ($\Delta\text{AIC} < 4$; Burnham and Anderson 2004) and calculated mixed-model R^2 estimates (Nakagawa and Schielzeth 2013) to evaluate relative model fit.

Location error was reported for each mode and patch type, and we used data permutation and a Wilcoxon–Mann–Whitney test with a Bonferroni adjustment for multiple comparisons to assess whether location error differed between patch types (Hothorn et al. 2008). The number of satellites acquired during a location can dramatically influence precision (Lewis et al. 2007), so for each mode we graphically depicted 2-dimensional (2-D) and 3-dimensional (3-D) locations, which require 3 and ≥ 4 satellites to obtain a fix, respectively. Battery life is a limiting factor for small collars, and we report time to fix (TTF) in each mode. We tested for differences in TTF between modes with data permutation and a Wilcoxon–Mann–Whitney test.

Field Data Collection with Miniature GPS Collars—Marten Case Study

Marten GPS collars contained an identical GPS system as our test unit, but also contained an ultra-high-frequency (UHF) unit for remote downloading of GPS data and a very-high-frequency (VHF) transmitter to locate the collar.

Expected GPS and UHF battery life with continuous data collection was 11 or 14.3 hr, depending on battery size (i.e., 0.50- or 0.66-sized AA lithium battery), which equated to a minimum of 307 or 399 expected fix attempts, respectively. For marten collars, we chose the same schedule as the test unit for evaluating movement paths, providing an estimated minimum of 26 to 33 hr of data collection depending on battery size. To increase battery life, we set GPS collars to attempt fixes only when activity sensors (accelerometers) recorded movement (Brown et al. 2012), to avoid fix attempts when the animal was resting in obstructed locations.

We tested marten-deployed collars at 2 stages: as delivered from the manufacturing company and after marten deployment. Upon receipt from the manufacturer, we tested the GPS with our mobile trial methods in a large field with no topographical obstruction and at low elevation (1,380 m) for a minimum of 25 minutes (4–6 fixes). On more than one occasion, we observed that collars would function during stationary tests, but not when the collar was in motion, which was often attributable to poor wiring and required refurbishment by the manufacturer. We considered the GPS acceptable if it obtained ≥ 1 fix with ≥ 4 satellites (3-D) that was accurate within 50 m. We tested the VHF with an R-1000 receiver (Communication Specialists, Orange, CA) and attempted to remotely download data. If all systems worked, we considered the GPS collar functional. We recaptured martens 10–21 days after GPS deployment, and considered the VHF functional if we received a signal within 30 kHz of the original frequency and if battery life exceeded 60% of battery expectancy. We estimated battery life, the total amount of time the GPS was recording data, by adding TTF for each GPS fix attempt. We report success overall and during the first and last 9-month periods of our study because we

worked continuously with the manufacturing company to improve collar design and testing before shipment.

We captured and processed martens using methods approved by Oregon State University's Institute for Animal Care and Use Committee (Permit: 3944, 4367) and California Department of Fish and Wildlife Memorandum of Understanding with a Scientific Collecting permit (Permit: 803099–01). Global Positioning System deployments on martens were performed under anesthesia (Mortenson and Moriarty 2015), and all efforts were made to minimize suffering and discomfort. We followed recommendations by the American Society of Mammalogists (Sikes et al. 2011) and used capture techniques that minimized spread of potential diseases (Gabriel et al. 2012).

RESULTS

We completed 27 mobile tracks with the test unit; 19 were paired with cold-start and continuous modes and 8 were in continuous mode only. Track length was ≥ 1 km ($\bar{x} \pm SE = 2,317 \pm 145$ m) and the average duration was 55 min (55 ± 1.3 min). We obtained an average of 14 fix attempts/track ($SE = 0.7$) and 234 total fix attempts in cold-start and 366 in continuous modes.

Fix Success

Fix success was higher in continuous (83.1%) than cold-start (37.1%) mode (Fig. 1). The GPS was $2.2\times$ more likely to obtain a fix in continuous mode than cold-start mode ($\chi^2 = 128.78$, $P < 0.01$) and 1.2 – $6.6\times$ more likely to obtain a fix in continuous mode between patch types (Fig. 1).

Fix success for trials remaining within a single patch type differed from trials that spanned all patch types, particularly in continuous mode and complex patch types ($\chi^2 = 17.88$, $P < 0.01$). We experienced an average $44\% \pm 25\%$ fix success in complex patches ($n = 95$ attempts, 6 trials) in continuous

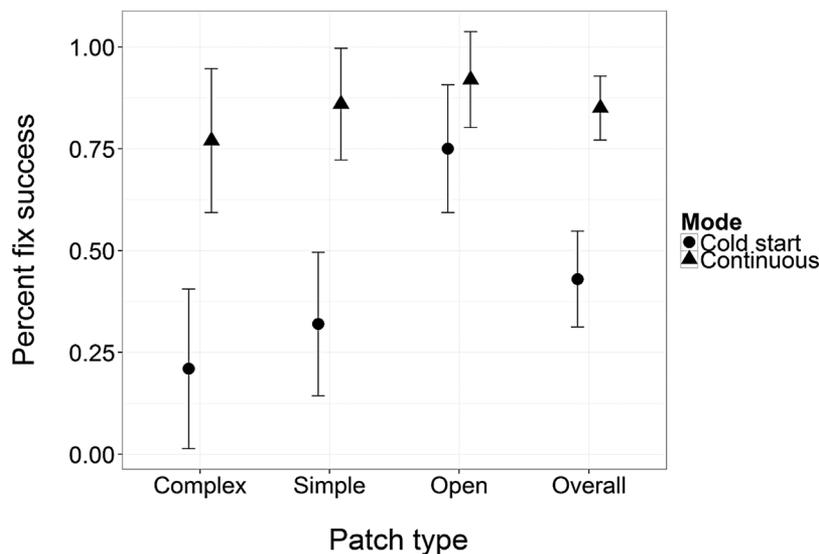


Figure 1. Fix success for miniature GPS collars deployed on Pacific marten differed with (continuous mode, triangles) and without (cold-start mode, circles) satellite information (ephemeris and almanac data). Fix success was measured in 27 mobile GPS trials in Lassen National Forest, California, USA (March 2011–January 2012), including 19 paired trials in both modes. Average fix success and 95% confidence intervals (bars) differed significantly between modes in all patch types but those without canopy cover (open).

Table 1. Mean fix success rates (\bar{x}) and standard error (SE) from trials conducted in Lassen National Forest, California, USA (March 2011–January 2012) of miniature GPS units deployed on Pacific marten in complex, simple, and open patch types were dependent on the trial type. We completed trials completely within a single patch type ('only,' 10–14 fix attempts) and from one patch type into another (3–5 fix attempts) to mimic an animal moving among patches.

GPS direction	Continuous				Cold start			
	Trials	Fix attempts	Fix success (\bar{x})	Fix success (SE)	Trials	Fix attempts	Fix success (\bar{x})	Fix success (SE)
Complex								
Complex only	6	62	44.3	24.5	3	32	0	0
Simple to complex	4	16	93.5	12	4	16	17.5	11.8
Open to complex	4	35	100.0	0	3	20	13.3	14.4
Simple								
Simple only	5	46	86.0	13.3	5	54	3.7	3.3
Open to simple	2	16	61.5	15.4	3	19	42.1	12.7
Complex to simple	0				0			
Open								
Open only	4	43	95.7	2.9	4	45	82.2	9.1
Simple to open	0				2	6	100.0	0.0
Complex to open	1	12	100.0	0.0	0			

mode if the unit initiated within the dense forest cover. In contrast, fix success in complex patches was >93% if the GPS was initiated in either open or simple patches prior to entering the dense canopy (Table 1). The GPS was unable to obtain a fix in either cold-start or continuous mode for the duration of 3 independent trials conducted entirely within complex patch types, suggesting a strong influence of satellite information on fix success.

Variables influencing fix success differed between continuous and cold-start modes (Table 2). In continuous mode, fix success increased with a previous fix in 3-D (previous 3-D fix), but we observed inconsistent relationships with vegetation obstruction where fix success was positively correlated with complex and open patches and negatively correlated with simple. In contrast, fix success in cold-start mode was negatively affected by increased vegetation cover and this was the only competitive model (Table 2).

Location Error and Time to Fix

Location error did not differ between continuous and cold-start mode when accounting for number of satellites and patch type (Table 3). Average location error was less for 3-D fixes ($\bar{x} \pm SE = 28.0 \pm 6.1$ m) than 2-D fixes (586.8 ± 64.0 m, $t = 8.7$, $df = 82$, $P < 0.001$). Most (88%) of 3-D fixes were

within 30 m and 97% were within 100 m of the true location (Fig. 2A). Thus, 3-D fixes were accurate regardless of fix interval, previous 3-D fix, or mode. However, satellite information (mode) strongly influenced error of 2-D fixes (Table 3). In cold-start mode, location error for 2-D fixes ranged from 198.0 m to 2,097.7 m. In continuous mode, 2-D fixes ranged between 11.8 m and 1,772.4 m from the reference location and 2-D fixes with a previous 3-D fix in continuous mode had a median location error of only 30 m (Fig. 2B). In cold-start mode, censoring fixes with 3 satellites (2-D) decreased average location error by 91%; in continuous mode, cold-start censoring 2-D locations prior to the first 3-D fix decreased location error by 55% and ensured that all locations were accurate to within 50 m.

Time to fix was significantly less in continuous than cold-start mode (39.6 ± 1.9 and 91.2 ± 3.2 s, respectively; $Z = 11.9$, $df = 86$, $P < 0.01$). Within continuous mode, TTF was significantly less when there was a previous fix: 38.4 ± 1.3 and 83.6 ± 4.2 s with and without previous fixes, respectively ($Z = 10.3$, $df = 119$, $P < 0.01$). There was no difference in TTF between cold-start mode and fixes in continuous mode that lacked a previous fix ($Z = -1.4$, $df = 202$, $P = 0.15$), which emphasizes increased efficiency of the GPS with previous satellite information.

Table 2. Model selection results for linear mixed models of fix success for mobile miniature GPS units deployed on Pacific marten operating with (continuous mode) and without (cold-start mode) satellite information, including differences in Akaike Information Criterion (ΔAIC), degrees of freedom (df), and model weight (w_i). We conducted trials in Lassen National Forest, California, USA (March 2011–January 2012). Predictor variables included a previous successful location or 3-D location (previous fix, previous 3-D fix, continuous mode only), satellite view factor (SVF), aspect as represented by northness and eastness (Zar 1999), elevation, patch type (i.e., open, simple, complex), and the 'track' or mobile path taken as a random effect.

Mode	Model name	df	ΔAIC	w_i
Continuous	Previous 3-D fix	3	0.00	0.63
	Previous 3-D fix + patch type	5	1.04	0.37
	Previous fix	3	24.36	0.0
	Patch type	4	37.73	0.0
	Intercept	2	44.39	0.0
	Patch type + SVF + northness + eastness + elevation	8	45.33	0.0
	SVF + northness + eastness + elevation	6	55.58	0.0
	Previous 3-D fix + SVF + northness + eastness + elevation	7	56.08	0.0
	Cold start	Patch type	4	0.00
Patch type + SVF + northness + eastness + elevation		8	18.6	0.0
Intercept		2	23.7	0.0
SVF + northness + eastness + elevation		6	63.0	0.0

Table 3. Location error for miniature GPS units deployed on Pacific marten in cold-start versus continuous modes as estimated from mobile GPS trials conducted in Lassen National Forest, California, USA (March 2011–January 2012), with number of fix attempts (n), mean (\bar{x}) and standard error (SE) in meters (m), test statistic (Z), and P -value after a Bonferroni correction (P) differentiating between the 2 modes and fix type within patch type.

Patch type	Fix type	Cold start			Continuous			Z	P
		n	\bar{x} (m)	SE	n	\bar{x} (m)	SE		
Open	2-D	11	1,311.9	158.0	7	982.0	227.9	0.95	0.370
	3-D	44	30.9	7.0	93	38.8	19.3	1.59	0.110
	No	19			3				
Simple	2-D	8	889.8	191.6	14	536.4	166.0	1.43	0.170
	3-D	17	17.8	7.7	95	22.0	4.6	2.17	0.030
	No	72			17				
Complex	2-D	3	951.2	73.1	39	239.2	40.3	2.76	<0.001
	3-D	4	19.5	6.1	56	21.5	2.4	0.24	0.830
	No	56			42				
Combined	2-D	22	1,109.2	111.5	60	395.2	61.1	4.93	<0.001
	3-D	65	26.7	5.2	244	28.3	7.6	0.47	0.640
	No	147			62				

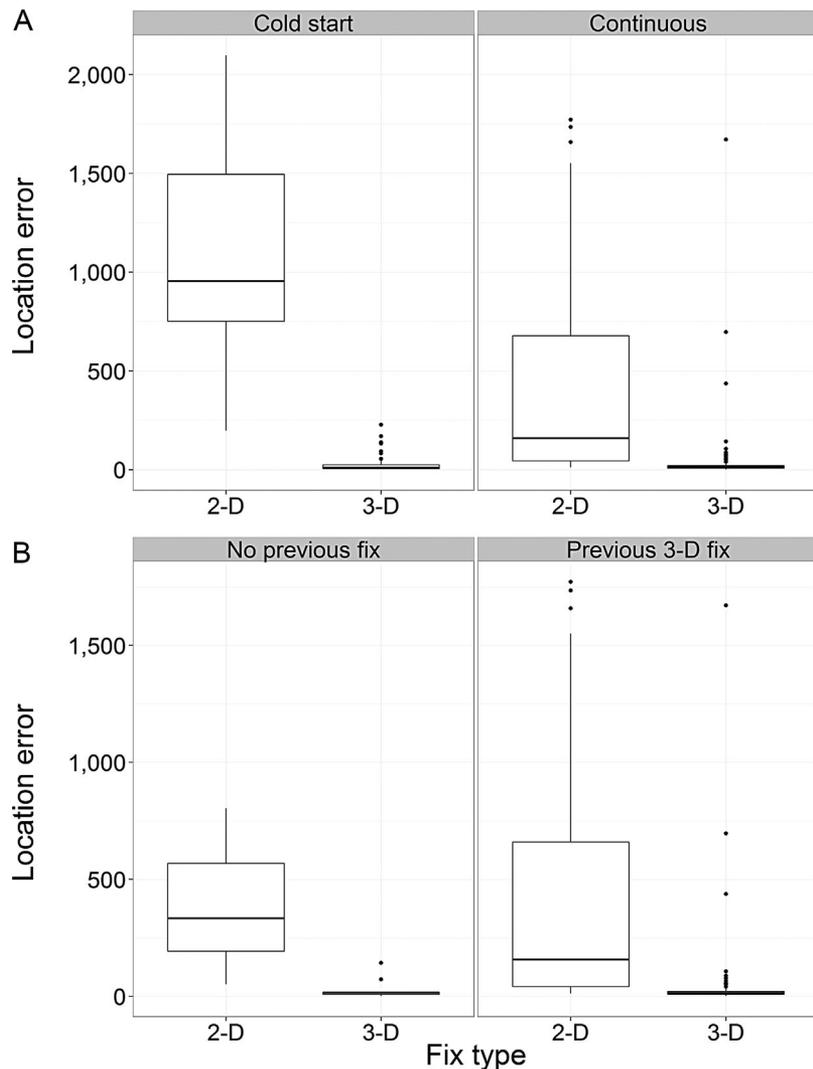


Figure 2. Location error of miniature GPS collars deployed on Pacific marten for 2-D and 3-D fixes between modes and with previous 3-D fixes depicted with box-plots (medians and quartiles shown). Global Positioning System location error for (A) 2-D and 3-D fixes differed in both cold-start (ephemeris and almanac data not available) and continuous (ephemeris and almanac data available) mode; and (B) location error in continuous mode differed with and without a previous 3-D fix during 27 mobile GPS trials in Lassen National Forest, California, USA (March 2011–January 2012).

Field Data Collection with Miniature GPS Collars

New or refurbished GPS collars direct from the company ($n=56$) functioned 66% of the time on initial testing. Malfunctions at that time occurred with the GPS (27% of all collars), VHF (7%), and/or UHF (18%) systems. Following collar deployment on martens, 72.5% (total deployments = 42) functioned. Malfunctions during deployments included GPS (20% of all collars) and/or VHF (12.5%) failure. The UHF could not be tested due to insufficient battery power.

We obtained 6–681 fixes during marten collar deployments (285.1 ± 30.1 fixes). We collected GPS data on martens for 0.1–9.8 days and experienced an average fix success of $66.4\% \pm 2\%$. Of the fixes obtained, 50–92%/collar deployment were 3-D locations ($79\% \pm 2\%$). Average fix success improved from 10% in the first 9 months to 60% in the last 9 months ($n=4$ and 7 deployments, respectively). Average total battery life, summed across all periods when the collar was attempting a fix, was 9.9 ± 1.3 and 11.0 ± 0.9 hr for the 0.50 and 0.66 AA battery sizes. We had premature battery failure in 40% of marten collars.

DISCUSSION

This study may be the first to experimentally evaluate the influence of ephemeris and almanac data on GPS error. Although field-deployed collars would not be set in cold-start mode, manually reprogramming the GPS to erase all satellite information allowed us to gauge expectations for GPS data collected with long fix intervals or for free-ranging animals that rest in obstructed areas for prolonged periods, after which ephemeris data would need to be collected anew. Obstruction from vegetation affected fix success most strongly in cold-start mode, which may explain why vegetation cover has little to no effect on fix success when the duration between fixes is short (e.g., this study, Lewis et al. 2007, Recio et al. 2011, Quaglietta et al. 2012, Adams et al. 2013). In complex patches with dense forest cover and a multistory canopy, the GPS devices we used were $6.6\times$ less likely (11% vs. 69% fix success) to obtain a fix when in cold-start mode than when in continuous mode. Fix success rates $<50\%$ may be typical in areas with vegetation obstructions and fix intervals greater than the interval for which ephemeris data are valid (i.e., 1–4 hr; Sager-Fradkin et al. 2007, Blackie 2010, Ott and van Aarde 2010). Our controlled experiment suggests that the combination of vegetation obstruction and lack of satellite information imposes substantial GPS bias on many data sets.

Overall fix success in continuous mode was 83%, which was less than (Cargnelutti et al. 2007) or comparable to other studies in forested environments (Jiang et al. 2008, Recio et al. 2011). In continuous mode, fix success was most affected by retained satellite information and was only weakly influenced by vegetation obstruction. Importantly, this suggests the negative influence of vegetation cover on GPS data may be reduced with a short fix interval. In cold-start mode, as expected, fix success decreased with vegetation obstruction. However, the negative effects of vegetation during our study were less than reported by Augustine (2010), where the influence of topographical obstruction and

vegetation obstruction accounted for 79% of the variation in fix success during stationary tests.

The likelihood of fix success in continuous mode was strongly increased ($50\times$ greater) when the GPS obtained a previous 3-D fix. As observed in our trials, fix success in a particular patch type may depend on the unit's initial location. In complex stands, we observed 0% fix success if the unit was activated within the stand and 96% fix success if a location and thus accurate ephemeris data were obtained before entering the complex patch. This difference was more dramatic than location error reported previously (DeCesare et al. 2005), and implies that inferences from GPS tests should only be applied to free-ranging deployments with the same fix interval as the test (Cain et al. 2005, Augustine et al. 2011). Collars with fix intervals >4 hr will likely have reduced fix success compared to either stationary and mobile trials with shorter fix intervals (Sager-Fradkin et al. 2007, Thompson et al. 2012).

Another consideration for future studies was that retained satellite information also decreased TTF, thus saving battery power. The average TTF in continuous mode was 56 s less than in cold-start mode. This difference was similar to TTF in continuous mode without a previous fix. Short fix schedules improve median TTF (Ryan et al. 2004), and decreasing TTF will inevitably increase battery life, although very short fix schedules may not be appropriate for many studies. Importantly, we observed TTF often exceeding 90 s without a previous fix in complex patch types. This surpasses standard settings of many GPS collars, and prematurely shutting off the GPS would reduce fix success and data quality.

Average location error in our study was strongly reduced by 1) eliminating 2-D fixes from data sets with long fix intervals or periods without satellite information, and/or 2) eliminating all 2-D fixes after a series of failed fixes until a 3-D fix was obtained. As demonstrated in previous studies (Lewis et al. 2007, Ott and van Aarde 2010), removing all 2-D fixes results in data loss and further biases data (Cargnelutti et al. 2007). However, in cold-start mode mimicking fix intervals >4 hr, every 2-D fix was inaccurate (>198 m). High location error compounds bias caused by $<60\%$ fix success (Frair et al. 2004, Nielson et al. 2009), and errors >800 m were observed in $>15\%$ of 2-D data in cold-start mode. In continuous mode, following a successful location in 3-D suggesting that accurate satellite information was obtained, 95% of locations, including 2-D fixes, were accurate within 50 m.

Although fix success was not strongly influenced by patch type or topographical obstruction when almanac and ephemeris data were available, these factors influence GPS performance especially for animals spending long periods under obstructions, and should be considered in wildlife research. For instance, bias from large location error in fixes lacking valid ephemeris data may erroneously suggest that an animal utilized an area outside its preferred habitat, and negatively affects interpretation for habitat specialists (Visscher 2006), such as the Pacific marten. Therefore, if attempting fine-scale analyses of habitat use, we would consider removing all 2-D locations when fix intervals exceed the period where ephemeris data are useful (>4 hr).

Researchers with different goals will need to establish the appropriate trade-off between fix schedules and length of collar deployment, but this study suggests that short fix intervals can reduce GPS error by retaining satellite information and can increase the amount of data collected on mobile, free-ranging, small mammals associated with areas of vegetation cover. We suggest that maximizing satellite information to increase fix success may be achieved by pulsing multiple fix attempts in sequence (e.g., 1 fix attempt every 10 min for 30 min or 1 fix attempt every hour for 3 hr); however, we did not directly test efficiency with differing schedules. Shorter fix intervals likely will not help GPS error caused by substantial topographic obstruction (Augustine et al. 2011). Future researchers should consider both mobile and stationary trials, stratified by vegetation cover and topographical obstruction (satellite view factor) within the study area of interest, prior to deploying GPS collars. Most importantly, because of the rapidly changing nature of ephemeris data, researchers should not extrapolate findings from GPS tests that use a dramatically different fix interval from their proposed study. The trade-off between collar life and accuracy of locations resulting from a particular fix interval must be carefully balanced depending on the scale of the analysis in question, especially when using miniature units.

Malfunctions are expected from small collars (Blackie 2010, Cypher et al. 2014), and as seen here, 34% of our collars malfunctioned upon receipt. We strongly recommend testing all components thoroughly before field deployment. Following initial testing, our fix success in deployments on free-ranging martens was fairly high (66%), especially considering that martens are associated with dense forest cover. This success seems largely attributable to the short fix interval. However, the accelerometer-based fix schedule that we used to reduce fix attempts when animals were resting (Brown et al. 2012) likely contributed to increased fix success. Despite observed malfunctions, the miniature GPS collars provided reliable data and are a promising tool for small mammal research.

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