

METHODOLOGY

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Moving wildlife tracking forward under forested conditions with the SWIFT GPS algorithm

S. W. Forrest^{1*} , M. R. Recio² and P. J. Seddon¹

Abstract

The remote collection of animal location data has proliferated in recent decades, and higher-frequency data are increasingly available with battery-saving optimisations such as ‘snapshot’ algorithms that acquire GPS satellite data and post-process locations off-board. This is the first study to assess the effects of vegetation and topography on the fix success rate and location error of global positioning system (GPS) devices that use the SWIFT fix algorithm, developed by Lotek. To assess fix success rate (FSR—the proportion of successful fixes compared to the total number of attempts) and location error (LE), we conducted a stationary test at a predominately forested site on the South Island of New Zealand. The overall FSR was 83% ($\pm 15.3\%$ SD), which was affected strongly by canopy closure above 90%. Half of the locations were within 8.65 m of the true location, 79.7% were within 30 m, and 95% of locations were within 271 m. When 6 or more satellites were used, this reduced to 4.92 m and 18.6 m for 50% and 95%, respectively. Horizontal dilution of precision (HDOP), the number of satellites, and canopy closure all influenced location error. To field test the fix success rate of SWIFT GPS devices, we deployed them on forest-dwelling parrots with 2 and 3-h fix intervals, which showed similar FSR results to the stationary test when cavity-nesting individuals were removed (FSR mean \pm SD = $81.6 \pm 5.0\%$). The devices lasted an average of 147 days before depleting the battery, resulting in an average of 1087 successful fixes per individual at an average time of 9.38 s to acquire the GPS ephemeris, resulting in an average of 3.73 attempted locations per mAh of battery for PinPoint 350 devices. Our study provides a baseline for fix success rates and location errors under forested conditions that can be used for future SWIFT GPS tracking studies.

Keywords: SWIFT, GPS, Snapshot, Performance, Fix success rate, Location error, Stationary test, Canopy, Forest, Lotek

Background

Global Positioning System (GPS) technology has revolutionised wildlife tracking, allowing detailed coverage of an animal’s behaviour, for increasingly smaller species, and with reduced bias and thus much greater accuracy than conventional radio-tracking [1–5]. The technological developments that are enabling smaller animals to be tracked with higher frequency intervals are creating a ‘biologging revolution’ [5–7]. At the time of writing, GPS

devices weigh as little as 1 g, allowing tracking of animals as small as 20–33 g (5% and 3% weight limit, respectively). For larger animals, the decreased weight of modern GPS devices allows for the addition of other sensors such as accelerometers, proximity sensors, heart rate monitors, magnetometers, gyrometers, salinity and temperature sensors, and video cameras [3, 6, 7].

As the weight of the deployed GPS device is limited by the weight of the animal, the number of fixes that can be achieved by a given battery capacity is a primary consideration [8]. Solar panels are one solution to this issue, although for nocturnal or forest-dwelling species this may not be an option. For wildlife GPS devices without

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solar panels, battery life depends on a variety of factors including the interval of time between locations (fix interval), the method of data recovery, additional sensors, the design and manufacturer, and the algorithm used to determine locations [9, 10].

GPS devices use a trilateration process to determine their location based on data received from multiple satellites from one or several available satellite constellations, a process which typically occurs on-board the device. As a battery-saving optimisation, ‘snapshot’ algorithms rapidly acquire the GPS ephemeris (physical quantities including pseudorange, carrier phase, and Doppler of satellites in the sky), which can then be post-processed off-board to derive each location [10]. An example is Fastloc GPS, an algorithm which has greatly increased the applicability of GPS devices [11, 12]. Fastloc locations were initially developed for marine species that surface only briefly, but are typically less accurate than standard GPS locations [13]. A similar implementation of the GPS ephemeris snapshot technology is a ‘SWIFT fix’ algorithm for GPS devices, developed by the company Lotek (Lotek Wireless Inc, lotek.com), which is expected to deliver a greater number of location fixes for a given battery capacity. In a seabird tracking study that used equivalent Lotek PinPoint 120 GPS devices both with and without SWIFT fixes, the SWIFT fix devices attempted an average of 560 locations at a 15-min fix interval (range 96–1056 attempted locations) without depleting their batteries, whereas six of the equivalent standard-fixing tags depleted their battery after an average of 75.7 attempted locations with a 1-h fix interval (range 39–141 attempted locations) [14].

Despite advancements in both miniaturisation and algorithm efficiency, the performance of GPS devices is still influenced by both environmental and technical factors, and the physical limitations of devices. Environmental factors that obstruct GPS signals and lead to lower performance include vegetation and topography, while the technical factors affecting performance include the number of satellites available and their geometry in the sky. Physical limitations of the devices include the size and shape of the antenna and the algorithms used [15–19]. Common measures of GPS performance are the fix success rate (FSR)—the proportion of successful fixes compared to the total number of attempts, and the location error (LE)—the linear distance between the recorded fix and the true location of the device [18]. Fix success rates vary widely depending on the species being tracked and the landscape features present—for ‘standard’ GPS devices (GPS devices that process locations on-board) FSR can range from as low as 20% [20] to as high as 97% [21], but are typically in the range of 60–90% [17, 18, 22, 23]. Low fix success rates are often attributed to

vegetation that obstructs satellite signals, the movement and behaviour of the animal, and less so to topography [15, 17, 18, 20]. As fix success rates are affected by environmental conditions, the resulting locations can be systematically biased towards areas that are more likely to reliably fix locations reliably [15, 16].

When successful fixes are taken, the precision cannot be calculated from animal deployments, as the true location of the animal is not known. Therefore, it is informative to quantify the distribution of expected location errors when the true location of the device is known, such as through a stationary test. Location errors for standard GPS devices typically average 10–30 m, with 50% of values typically falling within 5.5–20 m (circular error probability—CEP 50%), and 95% of values (CEP 95%) typically falling within 20–80 m, although outlier locations in the order of several kilometres can also occur [15, 18, 19, 24–26]. Location errors are influenced by many factors that obstruct or obscure satellite signals. Vegetation obstructs signals and can mean the GPS device connects with fewer satellites, which consequently provides poorer geometries to calculate locations. Topography can also obstruct signals and lead to multi-pathing due to signal reflection on hard surfaces. Visible satellites that are nearer to each other in the sky typically result in larger measurement errors compared to satellites that are further apart, which is quantified as the dilution of precision (DOP) [15, 18, 19]. Among DOP estimators, the horizontal dilution of precision (HDOP) is an indicator of the precision of latitude and longitude values. Although HDOP indicates a likelihood of obtaining a more accurate location, previous studies have found that HDOP is a poor indicator of location accuracy (R^2 ranging from 0.14 to 0.18) [18, 19]. Thus, it has been concluded that DOP metrics should not be relied upon as an indicator of accuracy, nor as a variable with which to filter the data [15, 18, 19]. GPS manufacturers often also have proprietary error metrics, such as eRes for Lotek devices with SWIFT fixes, which provide an indication of error.

As GPS devices that use SWIFT fixes differ from standard GPS devices in their processing of locations, it is important to ascertain baseline fix success rates and accuracy, so that these improvements in technology can be assessed. To address the lack of stationary testing for GPS devices with SWIFT fixes, we assessed lightweight GPS devices with SWIFT fixes in a range of canopy closure and topographic conditions. Our objectives were to: (1) assess the effect of environmental factors (obstruction due to vegetation and topography) on the fix success rate of lightweight GPS devices using a SWIFT fix algorithm; (2) assess the effect of environmental and technical factors—number of satellites, HDOP, and eRes (proprietary error metric) on location error; (3) investigate the

distribution of these errors, and discuss whether technical factors should be used to filter data; (4) assess the fix success rate when tags were deployed on a forest-dwelling endemic New Zealand parrot—the kākā (*Nestor meridionalis*).

Materials and methods

GPS devices and their placement

To investigate the fix success rate (FSR) and precision of locations, we assessed the performance of nine Lotek PinPoint VHF 350 SWIFT GPS devices (18.4 g) in a stationary test in varying canopy and topography conditions (Additional file 1: Fig. S1). These devices have a short whip antenna (~5 cm) and allow a maximum of 12 s to acquire the GPS satellite constellation ephemeris. If the device has not acquired sufficient satellite data within this time, it will time-out and register a failed fix. To investigate FSR for the intended purpose of the devices, we deployed the above SWIFT GPS devices on the South Island subspecies of an endemic New Zealand parrot, the kākā (*Nestor meridionalis meridionalis*). For the stationary test, devices were placed within Orokonui Ecosanctuary near Dunedin, New Zealand (−45.770°S, 170.596°E). Orokonui Ecosanctuary is a 307-ha ring-fenced, predator-free sanctuary comprising open exotic grassland, open forest (*Kunzea ericoides* and *Eucalyptus regnans*), regenerating native broadleaf forest (e.g. *Fuchsia excorticata*, *Griselinia littoralis*, *Melictyus ramiflorus*), and remnant native Podocarpaceae forest. Several predator-sensitive species that are threatened in New Zealand have been translocated to Orokonui, including kākā. Eleven sites were selected to be representative of New Zealand forest conditions, with a range of vegetation canopy closures, composition, and stand ages. One device was placed at each site, with two devices used twice. All stationary test locations were at sites of kākā presence confirmed by using VHF telemetry.

We set the devices for an acquisition rate of one-hourly fixes, which were left for 43 h, as the GPS constellation orbital period is c. 11 h 58 min, resulting in more than 3 complete satellite constellation cycles during a 36-h period [19, 27]. The units were attached horizontally on the upper side of a branch at breast height. Location data were recorded on on-board memory, with the capability of remote download via an ultra high frequency (UHF) link, and included date, time, latitude, longitude, altitude, number of satellites, HDOP, eRes, and temperature.

GPS device performance

Fix success rate (FSR) was calculated for each site by dividing the number of successful fixes by the total number of fix attempts. We quantified the accuracy of the GPS unit as the location error (LE), which was calculated

as the shortest distance on the WGS84 ellipsoid between the known location of the GPS unit deployed, determined using a handheld GARMIN GPSmap 60CSx (accuracy of <10 m for 95% of locations) that was ground-truthed by satellite map matching of known landmarks, and the location that was recorded by the Lotek GPS unit (R package ‘geosphere’; [28]). To assess accuracy and compare between sites, we calculated the median (\bar{x} LE), and the 75% and 95% quantiles.

Canopy closure

We quantified obstruction due to vegetation by measuring canopy closure, defined as the proportion of sky hemisphere that is obscured by vegetation when viewed from a single point [29]. Canopy closure ranges from 0 (no obstruction) to 1 (complete obstruction). To quantify canopy closure, we used a Fujifilm XT-2 with an 18–55 mm F2.8–4 lens to take perpendicular vertical photographs at each test location, which we then aggregated and binarised using open source editing software (details in Additional file 1, and see Additional file 1: Fig. S2 and Fig. S3) [30]. We quantified the percentage of sky visible to the camera as a proportion of white to black pixels as an approximation of canopy cover.

Topographic obstruction

To quantify the obstruction of satellite signals due to the topography, we measured the amount of sky not impeded in the hemisphere above the horizon, termed the sky view factor (SVF). SVF values of 0 indicate that the sky above a point is completely obstructed (e.g. in a cave), whereas a value of 1 indicates the sky is completely open (e.g. on top of a mountain). We calculated SVF from a 15-m resolution Digital Elevation Model of New Zealand [31]. The R package ‘horizon’ was used to quantify the amount of topographic obstruction at 32 angles up to a distance of 3000 m [32, 33]. Stationary test locations were overlaid and cell values at these points were used in analyses (Additional file 1: Fig. S4). The range of sky availability for the test locations ranged from 0.913 to 0.989 (mean \pm SD = 0.958 \pm 0.022).

Statistical analysis

We used a multimodel inference and model averaging approach to assess the influence of vegetation and topography (environmental predictors) on fix success rate (FSR), and to assess the influence of the environmental predictors, as well as horizontal dilution of precision, the number of satellites and eRes (technical predictors) on location error (LE) [34, 35]. We assessed all combinations of the predictors. For both analyses, we included the stationary test location as a random factor to account for the non-independent location fixes taken at each site [36]. We

used a model-selection approach to rank models based on Akaike's Information Criterion corrected for small sample size (AICc), also calculating the Akaike weight [34, 37]. To determine averaged predictor coefficients we used a full-model-average calculation, which averages over all models in proportion to their Akaike weight, rather than only the models in which the predictor appears—this is to prevent biasing the averaged predictor coefficient away from zero [34, 35]. Predictors were considered significant if the model-averaged confidence intervals did not overlap with 0. Model fit was assessed using pseudo-R-squared (hereafter R^2) for mixed-effects models, and the value reported is the marginal R^2 , which compares the model with fixed factors against a null model containing only the random factors [38–40]. R^2 is typically considered a measure of a model's ability to explain variation within the dataset, so we considered the explanatory power of each predictor variable as the R^2 value for models that contained solely that predictor variable (and the random factor of 'site') [18, 34, 38]. Both generalised linear and linear mixed models were fitted using the 'lme4' package in R [41], and the model-selection process was implemented using the 'MuMIn' package [40]. For both fix success rate and location error analyses, correlation between predictors was checked using variance inflation factors (VIF—all parameters were below 2), and all models were checked for overdispersion [42].

Fix success rate (FSR)

For FSR we used a binomial generalised linear mixed model (GLMM) to evaluate the influence of the canopy closure and sky view factor. To be directly comparable, both variables were scaled by centering and dividing by 2 standard deviations. In total, four models were fitted to FSR, which resulted from all the combinations of the two fixed factors, including a global model with both variables, and a null model without any predictor variables.

Location error (LE)

For location error, we used a linear mixed model (LMM) to assess the influence of canopy closure, sky view factor, horizontal dilution of precision (HDOP), the number of satellites, and eRes on the natural logarithm of linear error (LE_{\log} —to meet assumptions of normality). Due to the different scales of the predictor variables of LE in the LMM, and to make them directly comparable, we scaled all predictor variables by centering and dividing by 2 standard deviations. In total 32 LMMs were fitted to LE, which is all combinations of the five fixed factors including the global and null models. Models were run with and without a very large outlier to assess the outlier's influence, but the results did not fundamentally change, and the presented results include all data.

Case study with kākā (*Nestor meridionalis*)

To assess the fix success rate of GPS devices with SWIFT fixes when deployed on animals, we attached 10 SWIFT GPS devices to kākā, which are forest-dwelling parrots endemic to New Zealand (Additional file 1: Fig. S5 and Fig. S6). Kākā typically occupy areas with dense canopy, and forage both in the canopy and on the ground [43, 44], and are therefore considered a suitable test species for forested conditions. We fitted nine Lotek PinPoint GPS VHF-350 devices with SWIFT GPS fixes (PP350—18.4 g with 350 mAh battery) and one Lotek PinPoint GPS VHF-450 device with SWIFT GPS fixes (PP450—19.1 g with 450 mAh battery) to the kākā using a backpack harnesses with a weak-link [45]. The PP350 were set to fix a location every 3 h, and every 2 h for the PP450, which was the same device design but with a larger battery. Both devices had VHF radio-beacon capabilities, which was enabled at 40 pulses per minute (ppm) for a 4-h window each day to locate the kākā; UHF capabilities to download the data to a Lotek PinPoint Commander unit, which was enabled for a 10-h window each day; and a three-axis accelerometer, which recorded an overall dynamic body acceleration (ODBA) value once per minute for the full tracking period.

Results

Fix success rate

The fix success rate (FSR) ranged from 56 to 100% between sites ($\mu\text{FSR} \pm \text{SD} = 83.3\% \pm 15.3\%$). FSR decreased with increasing canopy cover, although successful fixes remained above 90% until canopy closure exceeded 0.9, after which the FSR decreased sharply (Fig. 1). The top-ranked model included only canopy closure, and the second-ranked model included canopy closure and sky availability (Table 1). The full model-averaged coefficients indicated a negative and significant relationship for FSR in relation to canopy closure (increasing canopy closure resulted in less successful fixes) ($\beta_{\text{canopy}} = -4.66$, 95% CI [-7.02 to -2.30]) (Fig. 1) and that topographic obstruction had a negative but weak relationship with FSR ($\beta_{\text{SVF}} = -0.12$, 95% CI [-1.16 to 0.47]) (Table 2). The model containing canopy cover alone (with site as a random factor) had an R^2 of 0.424, and the model with sky view factor alone had an R^2 of 0.024.

Location error

The distribution of location errors was strongly positively skewed (Fig. 2); with 50% of the locations falling within 8.65 m of the true location, 79.7% within 30 m and 95% of values within 271 m. 2.3% of all locations exceeded 1 km. When 6 or more satellites were used, 50% of the locations fell within 4.92 m and 95% of locations fell within 18.6 m

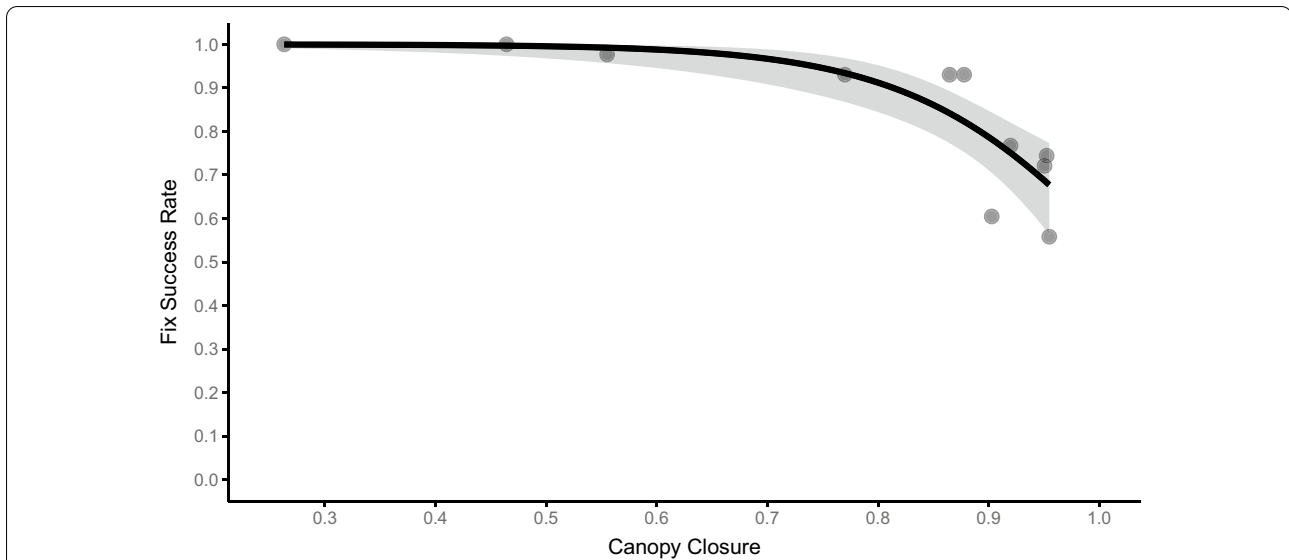


Fig. 1 Fitted binomial generalised linear mixed model of the proportion of successful fixes (FSR) as a function of canopy closure. Sky availability due to topography was also included as a fixed-effect, and the stationary test location was included as a random effect. Pseudo- R^2 was 0.401

Table 1 Models fitted to fix success rate (FSR) of GPS units tested in stationary sites ($n = 11$) under varying habitat and topographic conditions

Rank	Model parameters	R^2m	k	AICc	$\Delta AICc$	ω
1	Canopy closure	0.424	3	359.62	0	0.66
2	Canopy closure + sky view factor	0.407	4	360.97	1.36	0.34
3	Null	0.000	2	378.25	18.6	0.00
4	Sky view factor	0.024	3	379.01	19.4	0.00

R^2m is the theoretical marginal pseudo- R^2 , k is the number of parameters, AICc is the corrected Akaike Information Criterion, $\Delta AICc$ is the difference in corrected Akaike Information Criterion between the top model and the i th model, and ω is the Akaike weight

Table 2 Coefficient estimates and confidence intervals for scaled predictor variables included in LMM model selection, ordered by the magnitude of the coefficient estimate

Predictor variable	2.5% CI	Estimate	97.5% CI	R^2m
Canopy closure	-7.02	-4.66	-2.30	0.424
SVF	-1.16	-0.12	0.47	0.024

Confidence intervals that did not overlap 0 were considered significant and are shown in bold. R^2m is the marginal R -squared for the model that contained only that predictor variable

(Table 3). The topographic obstruction had an average between sites of 95.8% ($\pm 0.02\%$ SD), and canopy closure had an average of 77.0% ($\pm 23.6\%$ SD) (Additional file 1: Table S1).

Model selection revealed eight models that were within an $AICc < 10$ (Table 4, full output in Additional file 1: Table S2). The top-ranked model included HDOP, the number of satellites, and canopy closure.

The second-ranked model included HDOP, the number of satellites, and sky view factor. The full model-averaged coefficients suggested that the magnitude of location errors (LE_{log}) was influenced significantly by HDOP (larger HDOP resulted in larger errors: $\beta_{HDOP} = 0.956$, 95% CI [0.733 to 1.178]—Fig. 3) and the number of satellites (more satellites resulted in smaller errors: $\beta_{satellites} = -0.907$, 95% CI [-1.234 to -0.579]) (Table 4, Fig. 4 and Additional file 1: Fig. S7). Denser canopy closure resulted in larger errors ($\beta_{canopy} = 0.507$, 95% CI [-0.333 to 1.348] Additional file 1: Fig. S8), and explained the most variation in the dataset when considered as the sole predictor ($R^2 = 0.256$) (Table 5). There were weak relationships between sky view factor (SVF) and eRes (Additional file 1: Fig. S9). The R^2 for the model with canopy closure as the sole predictor was the largest with 0.256, followed by satellites with 0.191, HDOP with 0.133, SVF with 0.126, and eRes with 0.029.

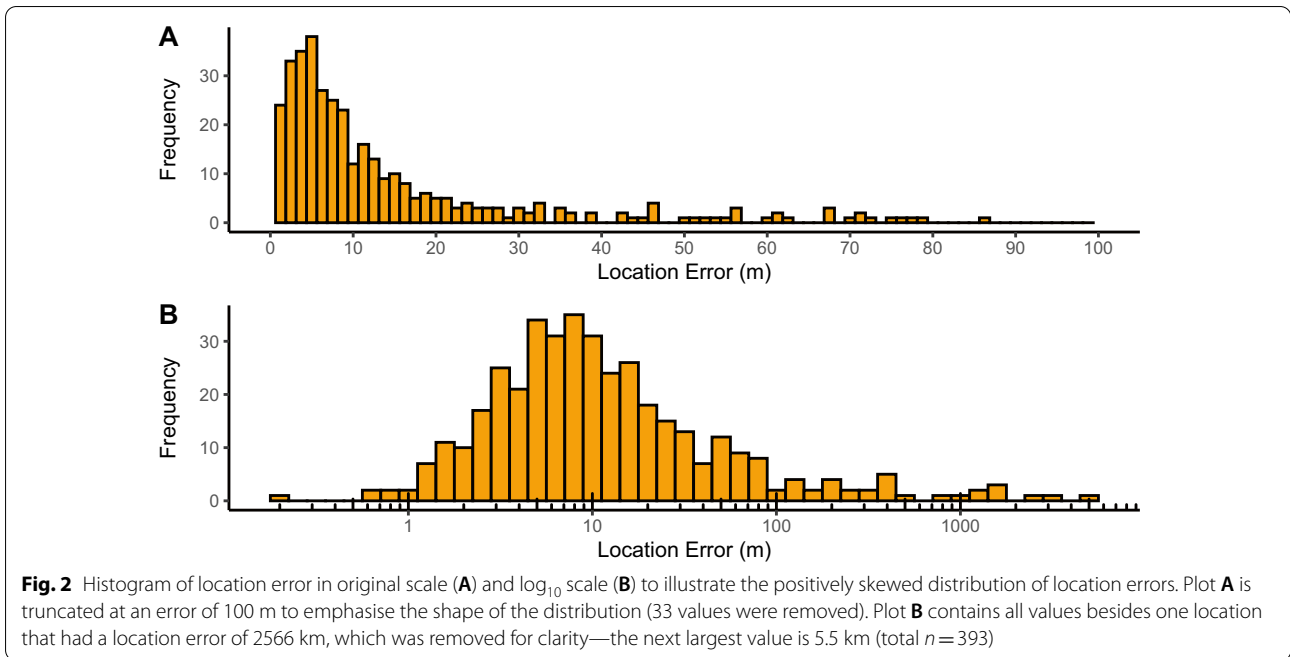


Table 3 Median and frequency percentiles for location errors for a given number of satellites in a stationary test in varying vegetation and topographic conditions

Satellites	<i>n</i>	Proportion	50% (xLE)	75%	95%
3	59	15.0%	38.5	204	2739
4	86	21.8%	18.2	38.1	251
5	85	21.6%	9.4	20.5	75.3
6	87	22.1%	6.9	10.8	23.7
7	62	15.7%	4.0	7.2	14.6
8	15	3.8%	3.3	5.5	6.5
All	394	100%	8.65	21.6	271

The proportion is the percentage of locations derived from a given number of satellites, and xLE is median location error

Deployment on kākā

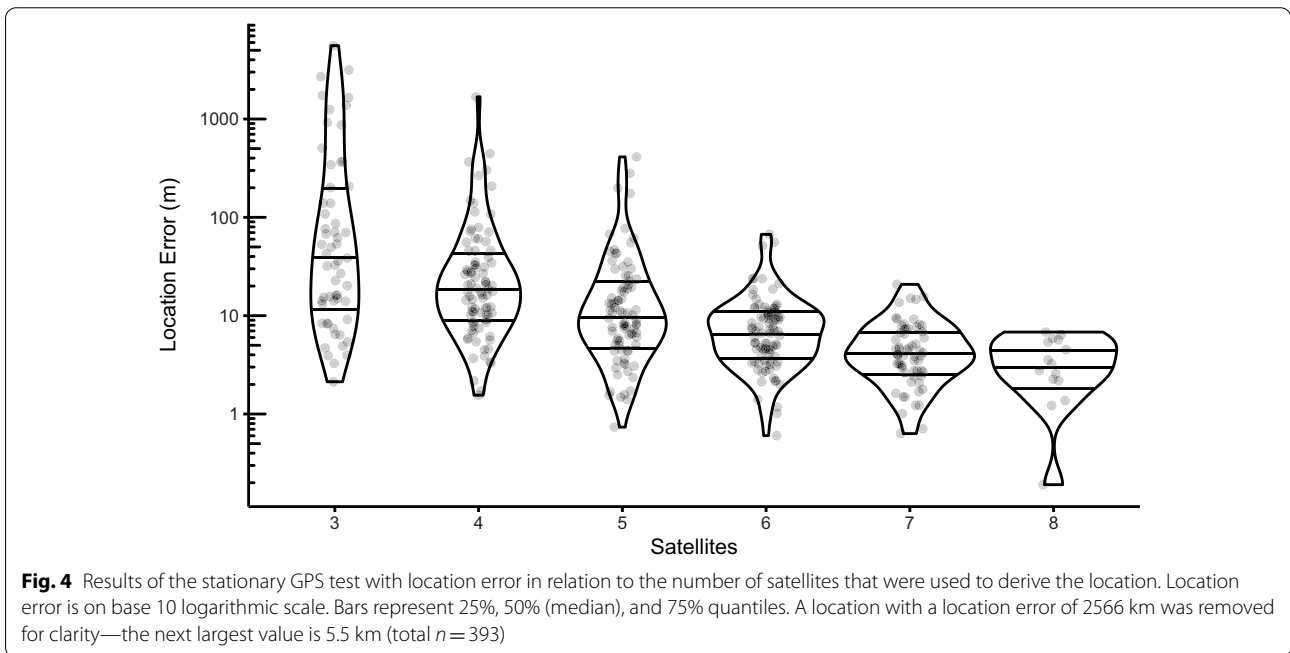
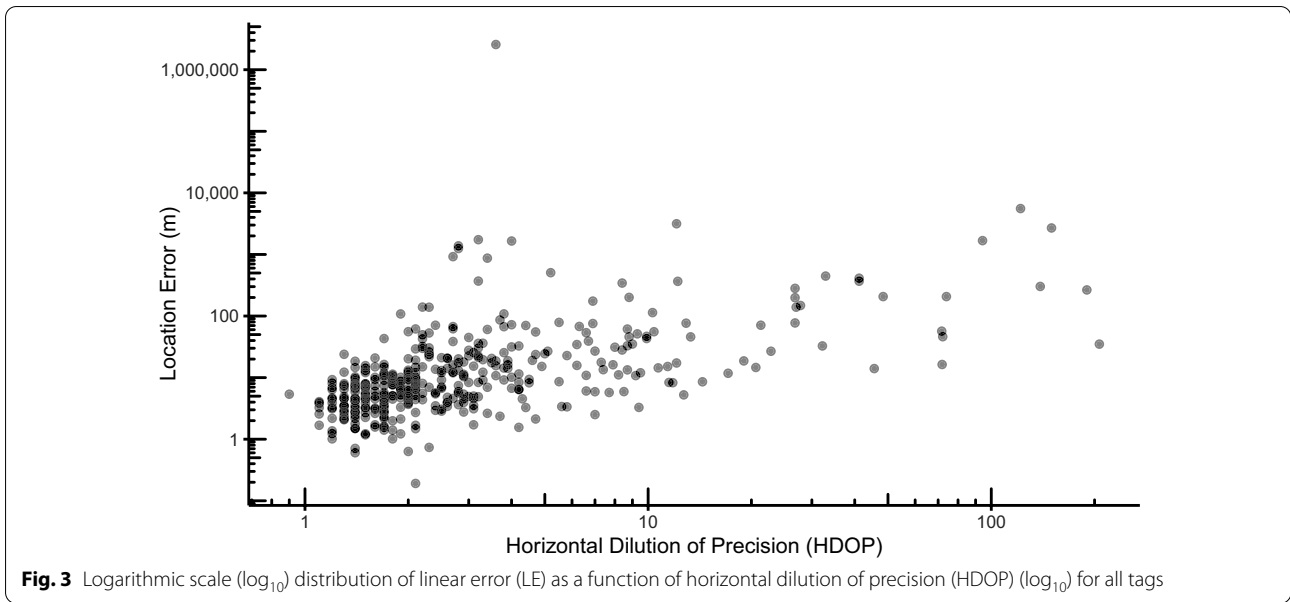
The SWIFT GPS device deployment on kākā ranged in duration from 111 to 163 days (mean = 144 ± 16 days SD), and gathered between 725 and 1257 successful fixes

for each individual for the PP350 tags (mean = 1016 ± 168 successful fixes SD), and 1727 fixes for the PP450 tag (Table 6) before the battery was exhausted [46]. The average time to acquire the GPS ephemeris for all individuals and all locations was 9.38 s. The resulting fix success rate (FSR) varied from 63.9 to 90.2% (mean = 78.4 ± 8.2% SD between individuals). Two of these individuals (45509 and 45511 in Table 6) nested in tree cavities, which resulted in several months where FSR dropped below 10%. When these two kākā were removed, the average FSR for the remaining 8 individuals was 81.6% (± 5.0% SD). In total, there were 10,755 successful location fixes from 13,590 attempts for ten individuals, providing an average of 2.90 successful locations and 3.73 attempted locations per mAh of battery for the PP350, and 3.83 successful locations and 4.56 attempted locations per mAh of battery for the PP450.

Table 4 Models with AICc < 10 (full table in Additional file 1: Table S2) fitted to the natural logarithm of location error (LElog) for GPS devices tested in stationary sites ($n = 11$) under varying habitat and topographic conditions

Rank	Model parameters	R ² m	<i>k</i>	AICc	ΔAICc	ω
1	HDOP + satellites + canopy closure	0.381	6	1307.67	0	0.27
2	HDOP + satellites + SVF	0.36	6	1307.73	0.06	0.26
3	HDOP + satellites + canopy closure + SVF	0.396	7	1308.36	0.69	0.19
4	HDOP + satellites	0.286	5	1309.16	1.49	0.13

Explanatory variables are the canopy closure due to vegetation, sky view factor due to topography (SVF), horizontal dilution of precision (HDOP), the number of satellites used to derive the fix, and a proprietary eRes metric. R2m is the theoretical marginal pseudo-R2, *k* is the number of parameters, AICc is the corrected Akaike Information Criterion, ΔAICc is the difference in corrected Akaike Information Criterion between the top model and the *i*th model, and ω is the Akaike weight



Discussion

We have provided the first performance assessment of GPS devices with SWIFT fixes under forested conditions to inform future wildlife tracking studies. Our results indicate that the SWIFT GPS devices performed well under all but very dense canopy, with an average FSR between 11 stationary test sites of $83.3 \pm 15.3\%$ SD, and an FSR for non-nesting South Island kākā (*Nestor meridionalis meridionalis*) of $81.6 \pm 5\%$ SD. The similarity between the stationary test and the field test results

suggests that the stationary test locations were representative of kākā habitat, which is typically native New Zealand forest [43, 47], although as a volant species locations might have been taken when the kākā were flying above the canopy. Topographic obstruction had little measurable effect on FSR, although a narrow range of topographic conditions were available in the study area, and topography will likely be more important in more mountainous areas [24]. The FSR is within the range of standard GPS units deployed on wild animals; for Sirtrack devices on

Table 5 Coefficient estimates and confidence intervals for scaled predictor variables included in LMM model selection, ordered by the magnitude of the coefficient estimate

Predictor variable	2.5% CI	Estimate	97.5% CI	R ² m
HDOP	0.733	0.956	1.178	0.133
Canopy closure	−0.333	0.507	1.348	0.256
Satellites	−1.234	−0.907	−0.579	0.191
SVF	−0.932	−0.254	0.424	0.126
eRes	−0.108	0.012	0.132	0.029

Confidence intervals that did not overlap 0 are shown in bold. R²m is the marginal R-squared for the model that contained only that predictor variable

the same species FSR can range from an average of 64.8% (range 24.7–74.0%) [22] to 90.8% (range 86.4–94.1%) [23]. For other manufacturers and species, FSR values are typically in the range of 60–90% [17–19].

Despite the shorter satellite signal acquisition window afforded by the SWIFT algorithm compared to standard GPS devices; most locations were still accurate. The median location error for all locations of 8.65 m was similar to standard GPS fixes (5.5–20 m), although the 95% location error of 271 m was larger than that for standard GPS fixes (20–80 m) [18, 19, 26]. The SWIFT location errors were reduced substantially when six or more satellites were used (4.92 m and 18.6 m for 50% and 95%, respectively). These locations were more accurate than Fastloc locations, of which 50% of values fell within 36 m and 95% within 724 m when four satellites were used, which reduced to 18 m and 70 m for 50% and 95% when 6 or more satellites are used [13].

However, a significant advantage of Fastloc GPS devices is that they acquire GPS ephemeris data in 10 s of milliseconds, compared to 5–12 s for SWIFT GPS devices, and will therefore be more suitable for briefly surfacing marine animals. This is a domain where Fastloc GPS devices have been widely applied with great success [48, 49], and where SWIFT GPS devices will have little utility. Fastloc devices also process and compress signals on-board the tag, which can then be transmitted over the Argos network [50]—which is not currently a feature for SWIFT GPS devices. An additional consideration when using GPS devices that post-process locations is their inability to use geo-fencing, as the GPS device is not aware of its own position.

Similarly to fix success rate, the precision of locations was also influenced by canopy closure, with increasing median errors at higher canopy closure values, and a larger number of outliers when canopy closure was above 0.90. The poor explanatory power of technical factors such as horizontal dilution of precision and the number of satellites echoes previous studies that have expressed caution in evaluating the accuracy of a location based on these factors alone [15, 18, 19]. However, the more accurate locations do result from a greater number of satellites, with 95% of location errors being less than 18.6 m when 6 or more satellites were used (41.6% of all locations, *n* = 164). The proprietary eRes metric did not appear to provide any value for assessing the accuracy of a location.

The field testing on kākā suggests that SWIFT fix devices likely have greater battery efficiency than standard fix devices, although battery capacity is dependent on

Table 6 Performance of GPS units deployed on 10 kākā at Orokonui Ecosanctuary

Kākā				GPS unit performance		
ID	Sex	Age	Origin	Days	<i>n</i>	FSR
45505	<i>M</i>	1	<i>Orokonui</i>	140	1727	0.84
45506	M	10	Orokonui	148	1003	0.78
45507	M	5	Captive	162	1128	0.81
45508	F	1	Orokonui	163	1257	0.90
45509	F	3	Orokonui	128	725	0.64
45510	F	2	Orokonui	111	828	0.73
45511	F	2	Orokonui	138	803	0.67
45512	M	3	Captive	157	1108	0.83
45513	M	10	Captive	149	1034	0.80
45514	F	8	Orokonui	143	1142	0.83
Mean		4.5		144	1076	0.78
±SD		3.6		16	285	0.08
Mean without nesting individuals						0.82
±SD without nesting individuals						0.05

Days—number of data collection days; *n*—number of successful fixes; FSR—fix success rate (proportion of successful fixes/failed fixes). Cavity-nesting females are shown in bold, and the PinPoint 450 device with a larger battery and shorter fix interval is shown in italics

many factors, and information such as battery capacity in mAh is rarely reported in the literature, making comparison difficult. The PP350 devices tested in this study averaged 3.73 attempted locations per mAh, and the PP450 device had 4.56 attempts/mAh, which is similar to 4.67 attempts/mAh by PP120 devices with SWIFT fixes in [14], and 4.95 attempts/mAh by PP50 devices with SWIFT fixes in [51]. A comparable estimate for standard GPS fix devices is 0.63 attempts/mAh for Lotek PinPoint 120 devices [14]. Other estimates of attempts/mAh range from 0.10 to 1.29 for low-cost custom-built standard fix devices weighing 84–240 g [52–54].

Global Positioning System (GPS) devices with SWIFT fixes and similar ‘snapshot’ algorithms show promising potential, even in heavily vegetated areas, although ~20% of locations might have errors greater than 30 m, which should be considered when planning a study using this technology. Occasionally location errors up to several kilometres can occur in SWIFT fix datasets, but these are usually straightforward to filter out using species-specific movement capabilities. For migratory species with sparse location fixing schedules, it would be harder to correctly identify erroneous locations in order to remove them. For this we recommend a method that incorporates the observed behaviour of the animal and the number of satellites, such as in Shimada et al. [55].

As GPS devices become smaller and lighter to track increasingly smaller species, innovative use of algorithms such as those that acquire the GPS ephemeris will increase unit deployment time and location frequency [56, 57]. An increase in efficiency will enable the collection of richer data from additional sensors including accelerometers, proximity sensors, heart rate monitors, and video cameras. When combined with powerful computational approaches that can accommodate multiple data streams such as hidden Markov models [58], state-space models [59, 60], and machine learning methods [61, 62], finer-scale and subtler behaviours might be identified, providing more comprehensive insights into animal behaviour, movement and ecology [3, 5–7].

Conclusions

The primary improvement of SWIFT fixes compared to standard GPS devices is a battery-saving optimisation that reduces energy consumption, allowing users either to extend the length of deployment, or to increase the location frequency. The fix success rate of SWIFT GPS devices was found to be similar to standard GPS devices, even in dense canopy, although ~20% of locations may have location errors greater than 30 m. As performance is dependent on the environmental conditions present at the study site, it is recommended to test any GPS devices under expected study conditions prior to deployment on animals.

Abbreviations

GPS: Global Positioning System; FSR: Fix success rate; LE: Location error; CEP: Circular error probability; DOP: Dilution of precision; HDOP: Horizontal dilution of precision; CC: Canopy closure; SVF: Sky view factor; AIC: Akaike Information Criterion; AICc: Corrected Akaike Information Criterion; LMM: Linear mixed model; GLMM: Generalised linear mixed model.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-022-00289-9>.

Additional file 1: Figure S1. The ten Lotek GPS devices (18.4–19.1 grams) that were used in a stationary test and to collect GPS location data of the forest parrot kākā. These devices used a SWIFT fix algorithm. The shorter antenna is for receiving satellite data, and the longer antenna is for VHF and UHF communication. One PinPoint VHF 450 tag (foreground) was used, which had a larger battery and lighter and more flexible antenna than the 9 PinPoint VHF 350 tags used. **Figure S2:** Perpendicular canopy closure photographs superimposed with a transparency of 50% to illustrate alignment and increased photograph coverage of the sky. **Figure S3:** Three vertically-taken canopy closure photographs (panel ‘a’) of varying canopy cover that have been binarised (panel ‘b’) using the free and open-source software program Krita. Only a single photograph is shown for clarity, but percentages are the result of the average of two perpendicular photos. 45508, 45510 and 45507 are the ID numbers of the devices. (Table S1). **Figure S4:** Study area showing the sky view factor calculated using the ‘horizon’ package (Van Doninck 2018). The Orokonui Ecosanctuary fence is shown as a black line, and the stationary test locations are shown as red points. Sky view factor values at the test locations ranged from 0.920 to 0.989. **Figure S5:** Kākā (*Nestor meridionalis*) with a GPS device fitted using a backpack harness with a weak-link [45]. The shorter aerial is used for receiving GPS signals, and the longer aerial is for VHF and UHF transmission. **Figure S6:** Kākā with GPS device in-situ at a supplementary feeding station. Smaller antenna is for connection to satellites for GPS, and longer antenna is for VHF and UHF communication. **Figure S7:** Cumulative distributions of location error for a given number of satellites. Values for a given number of satellites are listed in Table 5. **Figure S8:** Results of the stationary GPS test with location error in relation to canopy closure at each site. Location error is on the base 10 logarithmic scale. Bars represent 25%, 50% (median), and 75% quartiles. **Figure S9:** Logarithmic scale (log10) distribution of Linear Error (LE) as a function of eRes (proprietary error metric for SWIFT fixes) for all tags. **Table S1:** Stationary test results of Lotek GPS units that used a SWIFT fix algorithm and were tested in kākā (*Nestor meridionalis*) habitat in Orokonui Ecosanctuary, New Zealand, ordered by ascending mean canopy closure (CC). SVF is the proportion of sky that is unobstructed due to topography. CC is the mean canopy closure due to vegetation calculated from two photographs taken perpendicularly. FSR is the Fix Success Rate, and $\bar{x}LE$ is the median of location error for each tag. **Table S2:** Models with AICc < 10 fitted to the natural logarithm of location error (LElog) for GPS devices tested in stationary sites (n = 11) under varying habitat and topographic conditions. Explanatory variables are the canopy closure due to vegetation, sky view factor due to topography, horizontal dilution of precision (HDOP), the number of satellites used to derive the fix, and a proprietary eRes metric. R2m is the theoretical marginal pseudo-R2, k is the number of parameters, AICc is the corrected Akaike Information Criterion, $\Delta AICc$ is the difference in Akaike weight between the top model and the *i*th model, and Ω is the Akaike weight.

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Author contributions

SWF, MRR and PJS conceived the idea for the study; SWF performed the analyses and wrote the manuscript; MRR provided feedback on the analyses and manuscript, and PJS provided feedback on the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The stationary test dataset generated and analysed during the current study is available in the GitHub repository, [<https://github.com/swforrest/SWIFT-GPS-Test.git>]. The kākā deployment dataset generated and analysed during the current study is not publicly available until publication of further papers.

Ethics approval and consent to participate

This study was conducted with approval from the University of Otago Animal Ethics Committee under the Animal Use Protocol AUP-18–237.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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