

## RESEARCH ARTICLE

# Separating biological signal from methodological noise in home range estimates

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## Abstract

1. Space use is commonly estimated in animal ecology and has become a cornerstone of evidence-based conservation planning, with animal tracking increasingly used to underpin the designation of protected areas with high conservation value. However, tracking technologies and analytical methods may introduce biases in home range size estimates. We assessed these potential biases using simulated tracking data and published home range size estimates from empirical animal tracking studies.
2. We first simulated animal movement data and added published location error estimates for different technologies used for tracking sea turtles. Location data were analysed using common space use estimation methods (minimum convex polygon, fixed and autocorrelated kernel density estimation, biased random bridge and dynamic Brownian bridge movement model). Second, we reviewed home range size estimates obtained using different technologies to track hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) turtles to assess the relative impacts on home range estimates due to (i) tracking accuracy and (ii) analytical methods.
3. For both simulated data and empirical values of space use from the literature ( $n=90$  studies), relatively large home range estimates tended to be generated from lower resolution Argos tracking compared to higher-resolution Fastloc-GPS tracking. These findings reflect inaccuracies in location data providing spuriously large movements. For example, Argos and Fastloc-GPS home range size estimates for adult green turtles averaged 393 and 53 km<sup>2</sup> respectively ( $n=64$  and 39 individuals). For simulated data, biases introduced by tracking accuracy had a far greater impact on home range size estimation than the analytical method used, apart from when using autocorrelated kernel density estimation (AKDE) which compensated for positional error very well.
4. Our results suggest that in many cases, hawksbill and green turtles have relatively small home ranges (<10 km<sup>2</sup> and in some cases, <1 km<sup>2</sup>), with this picture of their limited space use only emerging through high-accuracy tracking. These general conclusions likely apply broadly across taxa and will impact attempts to

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assess patterns of home range sizes recorded for individuals across studies in different regions.

#### KEYWORDS

foraging, GPS, kernel analysis, marine turtle, satellite tracking, spatial ecology, utilisation distribution

## 1 | INTRODUCTION

Home range is a popular index of space use, defined as the area traversed by an animal for its regular activities of mating, foraging and caring for its young (Burt, 1943). The size of an animal's home range is influenced by various intrinsic and extrinsic factors including body size, metabolic requirements, food quality and availability (Chambault et al., 2020; Tamburello et al., 2015; Wood et al., 2017). In addition to such biological considerations, however, home range size estimates may also be affected by scientific decisions such as the tracking device technology and analytical methodology used to study space use (e.g. Börger et al., 2006; Thomson et al., 2017). For example, studies of space use by various taxa such as wild boar (Peris et al., 2020), baboons (Pebsworth et al., 2012) and reptiles (Silva et al., 2020) have reported that variable tracking technologies, analytical methods and sample size introduced methodological and analytical noise that led to over- or underestimated home range size estimates (Dwyer et al., 2015; Shimada et al., 2021; Signer et al., 2015). Therefore, it is important to be able to quantify the relative importance of biological signal versus methodological and analytical noise when assessing home ranges. Here, we consider these issues with respect to some widely used tracking technologies and analytical methods. In this way, we show some key considerations when comparing home range estimates across different studies.

Since the 1980s, satellite tracking has been used for many terrestrial, aerial and marine animals, most typically using the Argos satellite system (Fancy et al., 1988). This global system allows remote acquisition of animal location data and is used for species that range over broad areas. More recently, Argos satellite tracking has been supplemented with the relay of high-accuracy global positioning system (GPS) locations and a derivative of GPS, Fastloc-GPS (Kuhn et al., 2009). Unlike traditional GPS, which requires several seconds to generate a location estimate, Fastloc-GPS acquires high-accuracy location fixes within milliseconds, enabling GPS tracking technology to be used even for marine animals that surface briefly (Dujon et al., 2014). For animals with smaller ranges, tracking technologies might include very high frequency (VHF) radio (e.g. bats; Gottwald et al., 2022) and acoustic tracking for aquatic species (e.g. sharks, turtles; Lea et al., 2016). Satellite telemetry has led to the identification of space use patterns, species distributions and connectivity between habitats, often with strong conservation benefits (Crego et al., 2024; Katzner & Arlettaz, 2020; Kot et al., 2022). For example, in marine systems, information on space use patterns has led to the designation of marine protected areas (Sahri et al., 2022) and

approaches to reduce harmful interactions between humans and wildlife, such as boat strikes (Hays et al., 2019). It has been shown that less accurate tracking, for example, Argos compared to Fastloc-GPS, will lead to larger home range estimates (Martinez-Estevéz et al., 2021; Tanabe et al., 2023; Thomson et al., 2017).

Analytical approaches to process location data and estimate space use have evolved over the last 40 years. Minimum convex polygon (MCP; Mohr, 1947) is a traditional method that calculates home range as the extent of the smallest polygon without concave angles that contains the outermost locations and is still widely reported in comparative studies (e.g. Hardy et al., 2023; Wilson et al., 2020). Kernel density estimation (KDE; Worton, 1989) is commonly used to estimate the home range of an individual by calculating the probability that an animal occurred in a particular area over a specified period of time. Autocorrelated kernel density estimation (AKDE) builds on KDE and addresses common issues with animal location data such as autocorrelation and sampling biases (Fleming et al., 2015). Other commonly used analytical methods include biased random bridge (BRB), which relies on movement-based KDE via location interpolation (Benhamou, 2011), and the Brownian bridge movement model (BBMM; Horne et al., 2007), which estimates an animal's path using interpolation and accounts for time gaps and movement uncertainty. The dynamic Brownian bridge movement model (dBBMM) builds on BBMM by detecting behaviour changes, and both BBMM methods estimate an animal's occurrence distribution (rather than range distribution) by quantifying uncertainty in the movement path using likelihood statistics (Alston et al., 2022; Kranstauber et al., 2012). Unlike the traditional MCP and KDE methods, AKDE, BRB and dBBMM consider biological factors like behaviour and technical factors like location error that are known to influence animal movement and space use estimation.

The interaction between tracking resolution of Fastloc-GPS vs. Argos location data and commonly used analytical methods for home range estimation has not yet been considered. Following theoretical considerations for how tracking resolution and analytical method impact space use estimation using simulated data, we then explore empirical home range estimates across studies of two commonly tracked species, hawksbill (*Eretmochelys imbricata*; Ei) and green turtles (*Chelonia mydas*; Cm). The hard shells of Cheloniid species facilitate transmitter attachment, and their pantropical distribution and conservation dependence means that tracking studies are available from many parts of the globe, which are increasingly used in the designation of marine protected areas (e.g. Davies et al., 2021; Hays et al., 2019). Both species inhabit productive but

vulnerable foraging habitats such as coral reefs and seagrass beds (Christianen et al., 2023; Hoenner et al., 2015) and variations in their spatial behaviour can inform the need for ecosystem protection (Hardy et al., 2023). We consider how these data can be directly compared to assess global patterns of home range size for broadly distributed species.

## 2 | MATERIALS AND METHODS

### 2.1 | Data simulation

To quantify and compare variation in home range size estimation that can arise due to tracking technology and analytical method, we simulated movement data based on the Ornstein–Uhlenbeck foraging (OUF) Gaussian process (Fleming et al., 2014a, 2014b; Uhlenbeck & Ornstein, 1930), a correlated random walk that accounts for autocorrelation and generates movement tending toward a central location (e.g. Noonan et al., 2019), resembling behaviour at foraging grounds. Data were generated using the `simulate` function from package `ctmm` (Calabrese et al., 2016) in R version 4.2.3 (R Core Team, 2023) for 10 distinct individuals to ensure computational feasibility whilst obtaining reasonable estimates of variability. We chose an isotropic model (equal movement in all directions), and movement variance was set to 200,000 m<sup>2</sup> in order to generate realistic home range sizes (<4 km<sup>2</sup>) based on published estimates using Fastloc-GPS locations (Hardy et al., 2023; Hays et al., 2021). We based the other model parameters on results extracted from publicly available tracking datasets for foraging hawksbill ( $n=5$ ; Hays et al., 2021) and green ( $n=5$ ; Hardy et al., 2023) turtles, ensuring realistic autocorrelation parameters for position and velocity. The resulting autocorrelation values were 126,000 s (35 h) for the home range crossing time, a measure of long-term spatial autocorrelation, and 3300 s (55 min) for the velocity autocorrelation time, which reflects short-term consistency in movement direction and speed (mean values,  $n=10$ ). Times were similar across species (Table S1).

The number of simulated locations ( $n=1441$ ) was selected to achieve a sampling duration of 6 months to emulate typical mean tracking durations (e.g. Maurer et al., 2024; Shaver et al., 2013) and transmission frequency (one location every 3 h, see Hays et al., 2021) for sea turtles. Timestamps (range: 01/01/2024 00:00:00–29/06/2024 00:00:00) were generated using the R package `lubridate` (Grolemund & Wickham, 2011).

To generate mock tracking datasets from our simulated animal movement data, we added randomly generated, independent location errors for each location fix drawn from bivariate ( $x$  and  $y$ ) normal distributions typical of Fastloc-GPS and Argos data. The spatial error estimate used for Fastloc-GPS was 70 m (i.e. mean=0 m, SD=29 m, 95% of locations with  $\geq 6$  satellites, Dujon et al., 2014). For Argos tracking data, each positional fix is assigned a location class (LC) based on the number of messages received and the estimated positional accuracy, with four or more messages required for standard locations (LC 3, 2, 1, 0, spatial accuracies ranging from

<250 m to >1500 m) and auxiliary locations assigned in the case of fewer than four messages (LC A and B, spatial accuracy unknown) (CLS, 2016). Argos tracking data for sea turtles can often be dominated by LC B owing to their brief surfacing pattern; two levels of accuracy were therefore simulated for mock Argos datasets to reflect typical filtering criteria used in empirical studies (often determined by the number of high-quality locations available): high accuracy (LC 3, 2, 1, A; spatial error: 2500 m, SD: 1000 m) and low accuracy (LC 3, 2, 1, 0, A, B; spatial error: 10000 m, SD: 6000 m). Spatial error was assigned according to independent tests of location accuracy (Hays et al., 2001; Witt et al., 2010).

### 2.2 | Home range estimation using simulated data

We calculated the 50% and 95% utilisation distribution (UD), commonly referred to as the 'core' and 'full' home range, for each mock tracking dataset (Fastloc-GPS, Argos high-accuracy and Argos low accuracy for each simulated animal) using each of the following analytical methods: (1) MCP, (2) fixed KDE, (3) AKDE, (4) BRB and (5) dBBMM (see Supporting Information: Extended methods). We used the area encompassing 95% of simulated animal locations as a theoretical reference area against which 95% UDs calculated from each mock tracking dataset were compared, using the following formula (see Noonan et al., 2019):

$$\text{reference area} = -2 * \log(0.05) * \pi * \text{movement variance}$$

### 2.3 | Comparison of published home range estimates for hawksbill and green turtles

We searched for peer-reviewed literature on foraging home ranges of hawksbill and green turtles on Web of Science and Google Scholar between 16 January 2023–12 March 2023, and again on 17 February 2024 to update the list, using a combination of keywords: ((*Eretmochelys imbricata*) OR *Chelonia mydas*) OR ("hawksbill" OR "green") AND "turtle") AND ("home range" OR "space use") AND ((*foraging* OR *feeding*) AND ("ground" OR "site")) (1980–2024). We examined available studies for information on methods and metrics of home range sizes. We conducted backwards and forward searches by scanning the reference lists of shortlisted papers and checking articles that had cited the shortlisted papers. We excluded studies that did not provide either mean values or data for individual turtles, used recapture distance to measure habitat use or focused on migration or the inter-nesting period.

For each study, we extracted information on tracking technology used, location data filtering parameters, analytical method, foraging site (or approximate location; if available), species, life stage, sex and estimated home range size (mean  $\pm$  SD) as 50% and 95% UDs or 100% MCPs, as well as sample size and seasonal/diel variation. For comparisons of estimated space use across published home range sizes, we categorised tracking technology by Fastloc-GPS, Argos-only, acoustic and radio.

After finding that Argos data tended to overestimate home range size, we selected Fastloc-GPS-derived estimates for tests of difference in space use patterns among life stage groups and between the two species, in order to better reveal underlying patterns without added noise from varying location accuracy. We ran these tests of difference on published Fastloc-GPS-derived estimates using a single metric—KDE (95% KDE UD, hereafter 'KUD') was selected for comparisons across life stages and between species because it was the most frequently used analytical method in the reviewed literature, providing adequate sample size.

## 2.4 | Data analysis

All analyses were performed in R version 4.2.3 (R Core Team, 2023). To assess the accuracy of tracking technologies and analytical methods in estimating home ranges, we measured bias in full home range size estimates derived from our mock tracking datasets using each method. To do this, we calculated bias as the difference between the estimated 95% UD and the reference area.

Literature-gleaned data were checked for normality using the Shapiro–Wilk test and for homogeneity of variance using the Levene test (95% KUDs and 100% MCPs for Fastloc-GPS, Argos and acoustic tracking technologies, and Fastloc-GPS-derived 95% KUDs of hawksbill and green turtles for each life stage). Non-parametric tests were used to compare groups owing to non-normally distributed data.

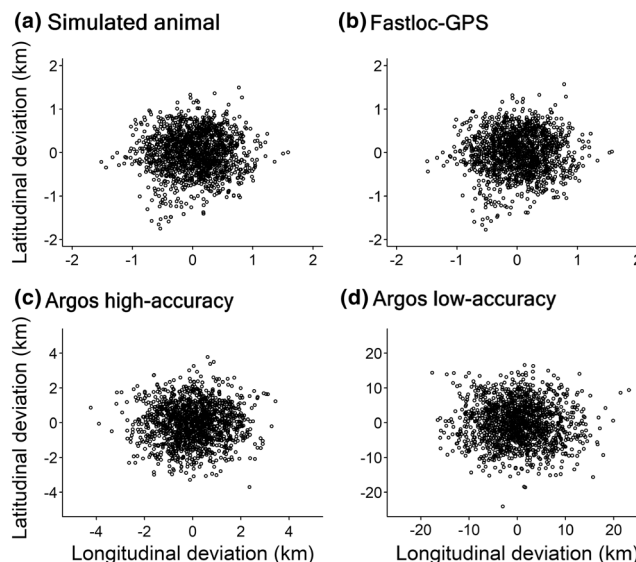
We used the Kruskal–Wallis test and a post hoc pairwise Wilcoxon test adjusted with Bonferroni correction to compare home range estimates of individual turtles from the literature across tracking technologies for each species and each estimator (95% KUD and 100% MCP). We then used the Mann–Whitney *U*-test to compare Fastloc-GPS 95% KUD estimates for individual turtles between independent groups, that is across life stages for each species and between the two species to check for space use patterns.

## 3 | RESULTS

### 3.1 | Home range estimation using simulated animal movement data

The 95% reference area for each simulated animal was 3.76 km<sup>2</sup> (Figure 1). The reference area was the same across all ten simulations because this is set by the movement variance parameter.

Tracking accuracy generally had far greater impact on home range size estimates than analytical method, except for AKDE (Figure 2, Figure S1). For example, Argos data increased bias by orders of magnitude relative to Fastloc-GPS data (Fastloc-GPS mean  $\pm$  SD: 0.1  $\pm$  0.3 km<sup>2</sup>; Argos high accuracy: 20.9  $\pm$  13.5 km<sup>2</sup>; Argos low accuracy: 769  $\pm$  466 km<sup>2</sup>), while most of the analytical methods (except AKDE) had relatively modest impact by comparison (Figure 2). In contrast to the other methods, AKDE compensated for variable accuracy



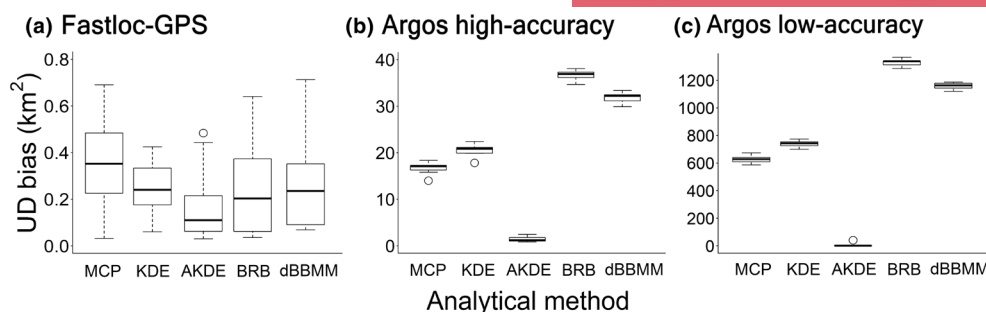
**FIGURE 1** Example of (a) simulated animal movement locations and (b–d) corresponding mock tracking locations incorporating typical error estimates associated with (b) Fastloc-GPS and (c, d) Argos tracking technology, assuming high and low filtering based on location class (c: 3, 2, 1, A; d: 3, 2, 1, 0, A, B). Note the difference in scale between panels.

in simulated movement data, giving much closer size estimates across tracking technologies than the other methods (Fastloc-GPS with AKDE: 3.7  $\pm$  0.2 km<sup>2</sup>; Argos high-accuracy with AKDE: 2.4  $\pm$  0.5 km<sup>2</sup>; Argos low accuracy with AKDE: 8.3  $\pm$  12.9 km<sup>2</sup>).

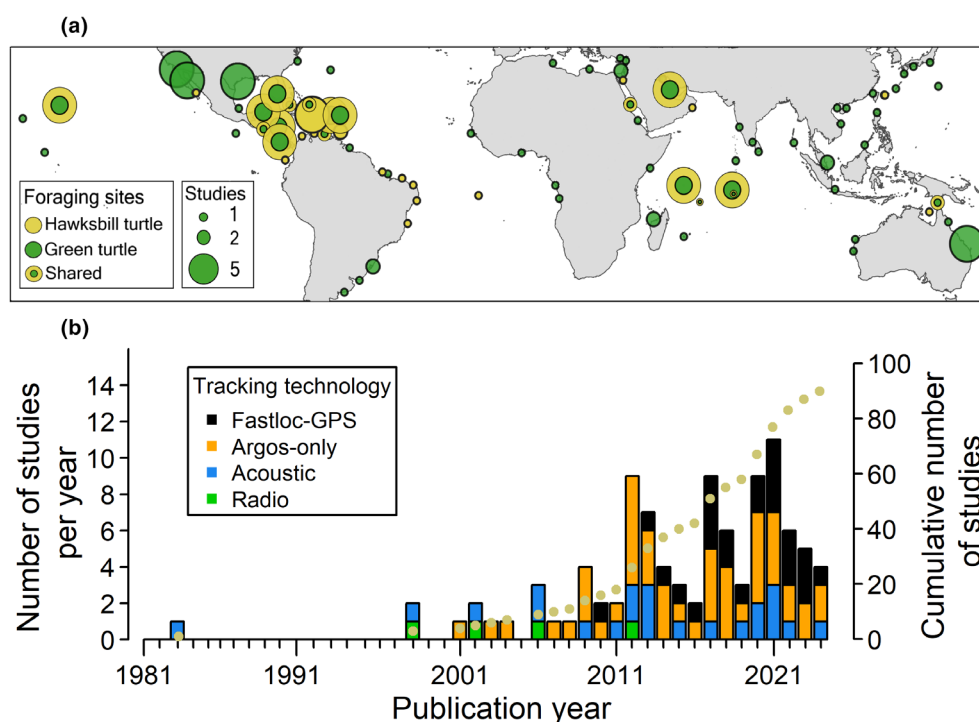
Full home range estimates for simulated Argos data (1.3–1368 km<sup>2</sup>) were often substantially larger than those for simulated Fastloc-GPS data (3.1–4.2 km<sup>2</sup>; Figure S2, Table S2), the largest difference per simulated individual being 438 times the Fastloc-GPS estimate (1338 km<sup>2</sup> Argos low accuracy cf. 3.05 km<sup>2</sup> Fastloc-GPS, BRB and dBBMM estimates respectively, simulated animal 7). Within each tracking technology, estimates across the four methods excluding AKDE fell within a comparable range, varying by at most a factor of around two. AKDE accounted for low accuracy in the simulated data very successfully, producing size estimates close to the reference area for Argos low-accuracy data—up to 495 times smaller than the other methods (Table S2). Methods often performed inconsistently across tracking technologies; dBBMM and BRB produced the largest estimates with Argos tracking data but gave relatively small estimates for Fastloc-GPS data (Figure 2).

### 3.2 | Published home range estimates of hawksbill and green turtles

We found 90 studies that reported home range sizes for hawksbill (Ei: *n* = 30) and green turtles (Cm: *n* = 60) at their foraging grounds (Figure 3, Tables S3 and S4) in the Atlantic (*n* = 47), Pacific (*n* = 24) and Indian (*n* = 17) Oceans and in the Mediterranean Sea (*n* = 2). The country accounting for the highest number of studies was the United States (*n* = 24), followed by Australia (*n* = 10) and Mexico



**FIGURE 2** Bias—the difference between the 95% utilisation distribution (UD) derived using five analytical methods from simulated data representing (a) Fastloc-GPS, (b) Argos high-accuracy and (c) Argos low-accuracy tracking data and the reference area. Tracking accuracy inflated full home range size estimates by orders of magnitude, while most analytical methods had a more modest impact (namely minimum convex polygon, MCP; fixed kernel density estimation, KDE; autocorrelated kernel density estimation, AKDE; biased random bridge, BRB; and dynamic Brownian bridge movement model, dBBMM). AKDE compensated for lower-accuracy data, giving size estimates close to the reference area for Argos data. Note the variation in y-axis scales.



**FIGURE 3** (a) Number of foraging home range studies on hawksbill ( $n=30$ ) and green turtles ( $n=60$ ) in 43 countries across the world. (b) Hawksbill and green turtle home range studies by year and by tracking technology. Bars indicate the number of studies; yellow circles show the cumulative number of studies. See [Tables S3](#) and [S4](#) for details.

( $n=6$ ) (Figure 3a). Overall, 41 studies included home range estimates for adult sea turtles (Ei:  $n=15$ ; Cm:  $n=26$ ), 34 for juvenile turtles (Ei:  $n=10$ ; Cm:  $n=24$ ), 11 for subadults (Ei:  $n=4$ ; Cm:  $n=7$ ) and 10 for mixed life stages (Ei:  $n=2$ ; Cm:  $n=8$ ). The number of studies published yearly has grown over time, with the use of Fastloc-GPS tracking technology increasing in the last decade (Figure 3b).

Location data were collected using Fastloc-GPS ( $n=24$  studies), Argos ( $n=48$ ), acoustic ( $n=22$ ) and radio transmitters ( $n=4$ ) (Figure 3b). One study used observations reported by SCUBA divers via a smartphone GIS application (Baumbach et al., 2019). In studies that used Argos tracking, filtering of location data ranged from no

filtering (LC 3, 2, 1, 0, A, B, Z;  $n=2$ ), low filtering (LC 3, 2, 1, 0, A, B, or 3, 2, 1, A, B;  $n=30$ ), medium filtering (LC 3, 2, 1, 0, or 3, 2, 1, 0, A;  $n=5$ ) to high filtering (LC 3, 2, 1, or 3, 2, 1, A;  $n=7$ ). The most widely used analytical methods for home range estimation were MCP ( $n=30$ , 1983–2024) and KDE ( $n=65$ , 1998–2024), with several studies using both ( $n=18$ , 2002–2023). KDE analyses used different types of smoothing (e.g. fixed,  $n=32$ ; adaptive,  $n=1$ ) and bandwidths (least squared cross validation, LSCV,  $n=16$ ; the Gaussian reference function  $href$ ,  $n=10$ ; plug-in  $h$ ,  $n=10$ ; ad hoc,  $n=4$ ). While traditional MCP and KDE methods continue to be widely used, studies increasingly adopted new methods: localised convex hull ( $n=4$ ,



TABLE 1 Home range size varies with tracking technology for hawksbill and green turtles.

HR estimator	Tracking technology	Hawksbill turtle HR (mean $\pm$ SD, range) km <sup>2</sup>	Number of individuals (number of studies)	Green turtle HR (mean $\pm$ SD, range) km <sup>2</sup>	Number of individuals (number of studies)
95% KUD	Fastloc-GPS	11.5 $\pm$ 25.50, 0.01–96.90	28 (5)	27.70 $\pm$ 135, 0.09–931.01	72 (8)
	Argos-only	204 $\pm$ 194, 38.70–861	48 (5)	540 $\pm$ 1081, 0.17–5148	135 (16)
	Acoustic	0.56 $\pm$ 0.34, 0.07–1.26	15 (2)	6.60 $\pm$ 9.42, 0.73–53.40	164 (8)
	Radio	NA	NA	3.15 $\pm$ 2.72, 0.84–8.5	6 (1)
100% MCP	Fastloc-GPS	8.20 $\pm$ 7.10, 1.10–19.00	8 (2)	4.66 $\pm$ 8.30, 0.01–45.75	30 (4)
	Argos-only	3726 $\pm$ 5860, 1.96–27,001	33 (5)	3024 $\pm$ 11,738, 0.10–92,734	68 (10)
	Acoustic	0.66 $\pm$ 1.07, 0.05–4.04	17 (1)	7.21 $\pm$ 8.89, 0.06–39.08	41 (5)
	Radio	0.36 $\pm$ 0.17, 0.15–0.55	6 (1)	NA	NA

Note: Tracking datasets with higher estimated accuracy (acoustic and Fastloc-GPS) resulted in small home range sizes relative to those with lower estimated accuracy (Argos). See [Tables S3](#) and [S4](#) for more details.

Abbreviations: HR, home range; KUD, kernel density estimation utilisation distribution; MCP, minimum convex polygon.

2012–2019), BRB ( $n=5$ , 2016–2024), Autocorrelated KDE ( $n=4$ , 2019–2024) and dBBMM ( $n=1$ , 2024).

### 3.3 | Comparison of published space use estimates for hawksbill and green turtles

Published home range size estimates using 95% KUD and 100% MCP for individual turtles of both species varied significantly between tracking technologies, specifically Argos and acoustic, and Argos and Fastloc-GPS data, but not between acoustic and Fastloc-GPS estimates ([Tables 1](#) and [2](#)). Fastloc-GPS studies recorded 95% KUD home range estimates  $<40\text{km}^2$  across life stages for both species ( $n=12$  out of 14 studies, range: 0.15–193.9 km<sup>2</sup>), whereas Argos-derived 95% KUD estimates were often  $>50\text{km}^2$  for green turtles ( $n=10$  out of 17 studies, range: 4.8–5148 km<sup>2</sup>) and  $>100\text{km}^2$  for hawksbill ( $n=6$  out of 7 studies, range: 48.7–8474.5 km<sup>2</sup>; [Figure 4a](#)). Only one example combined Argos data with AKDE, giving a home range estimate of 198 km<sup>2</sup> (Hardin et al., 2024).

There were significant differences in home range size estimates of adults and juveniles of the two species (Fastloc-GPS; Ei:  $U_{17}=85$ ,  $p<0.05$ ; Cm:  $U_{49}=648.5$ ,  $p<0.05$ ). Juveniles were recorded occupying mean home ranges  $<4\text{km}^2$  (Ei:  $3.01 \pm 5.06\text{km}^2$ ,  $n=11$ ; Cm:  $1.97 \pm 1.94\text{km}^2$ ,  $n=19$ ), while adults had larger home range sizes of  $28.60\text{km}^2$  ( $\pm 37.70$ ,  $n=10$ ) and  $53.40\text{km}^2$  ( $\pm 187$ ,  $n=39$ ) for hawksbills and green turtles respectively. Subadult life stages were excluded due to insufficient data. Between the two species, there was no significant difference in the home range sizes of adults ( $U=190$ ,  $p=0.91$ ) or juveniles ( $U=118$ ,  $p=0.58$ ).

## 4 | DISCUSSION

We have shown here, through theoretical considerations and analysis of empirical data collected across studies, that the accuracy of tracking likely introduces far more variability into animal home

range size estimates than the analytical methods used to process the data. This is an important finding when the goal is to synthesise data from across studies to make regional or global comparisons of space use. AKDE provided excellent compensation for low accuracy in simulated animal movement data; however, only a single example in the literature for hawksbill and green turtles used AKDE with Argos data. The accuracy of different tracking technologies, such as Fastloc-GPS and Argos, is often well known (e.g. Douglas et al., 2012; Dujon et al., 2014; Thomson et al., 2017) but is usually not considered explicitly in tracking studies. We conceptualised this issue by considering simulated animal movement data and the likely pattern of locations that would be received from Fastloc-GPS and Argos transmitters. This type of conceptualisation of location error has been considered before, for example, when developing procedures to reliably estimate the speed of travel from low-quality Argos tracking (Hays et al., 2001).

A broad range of analytical methods are routinely used to assess space use, such as MCP (Mohr, 1947), KDE (Worton, 1989), AKDE (Fleming et al., 2015), BRB (Benhamou, 2011) and dBBMM (Kranstauber et al., 2012). Home range estimates are known to vary depending on the analytical method used. For example, AKDE estimates of jaguar home ranges in South America were up to 5 times larger than KUD estimates (Morato et al., 2016), while home range estimates for hawksbill turtles in Florida were 10–30 times larger when using MCP than KDE (Wood et al., 2017). However, we provide evidence that these differences are much smaller than the impact of location accuracy of tracking technologies, except for AKDE which gave home range size estimates close to the reference area even for low-accuracy mock tracking datasets.

Our results suggest that home range estimates from Argos tracking are often likely gross overestimates of an animal's true space use. This limitation of Argos tracking has sometimes been recognised (see Martinez-Estevéz et al., 2021) but is often not considered (see Hawkes et al., 2012). Argos tracking provides several benefits that make it an extremely popular option, including global coverage and no recapture requirement, and also has the advantages of lower cost and power

TABLE 2 Comparison of home range size estimates between tracking technologies for hawksbill and green turtles.

Species	Estimator	Kruskal–Wallis			Technology comparison	Pairwise Wilcoxon test	
		<i>H</i>	<i>df</i>	<i>p</i>		<i>n</i>	<i>p</i>
Hawksbill turtle	95% KUD	63.84	2	<0.05	Argos versus Acoustic	63	<0.05
					Argos versus Fastloc-GPS	76	<0.05
					Acoustic versus Fastloc-GPS	43	0.16
	100% MCP	43.17	2	<0.05	Argos versus Acoustic	50	<0.05
					Argos versus Fastloc-GPS	41	<0.05
					Acoustic versus Fastloc-GPS	25	<0.05
Green turtle	95% KUD	161.37	2	<0.05	Argos versus Acoustic	309	<0.05
					Argos versus Fastloc-GPS	209	<0.05
					Acoustic versus Fastloc-GPS	228	1
	100% MCP	52.22	2	<0.05	Argos versus Acoustic	109	<0.05
					Argos versus Fastloc-GPS	98	<0.05
					Acoustic versus Fastloc-GPS	71	0.06

Note: Significant values ( $p < 0.05$ ) are indicated in bold.

Abbreviations: KUD, kernel density estimation utilisation distribution; MCP, minimum convex polygon; *n*, total number of individuals.

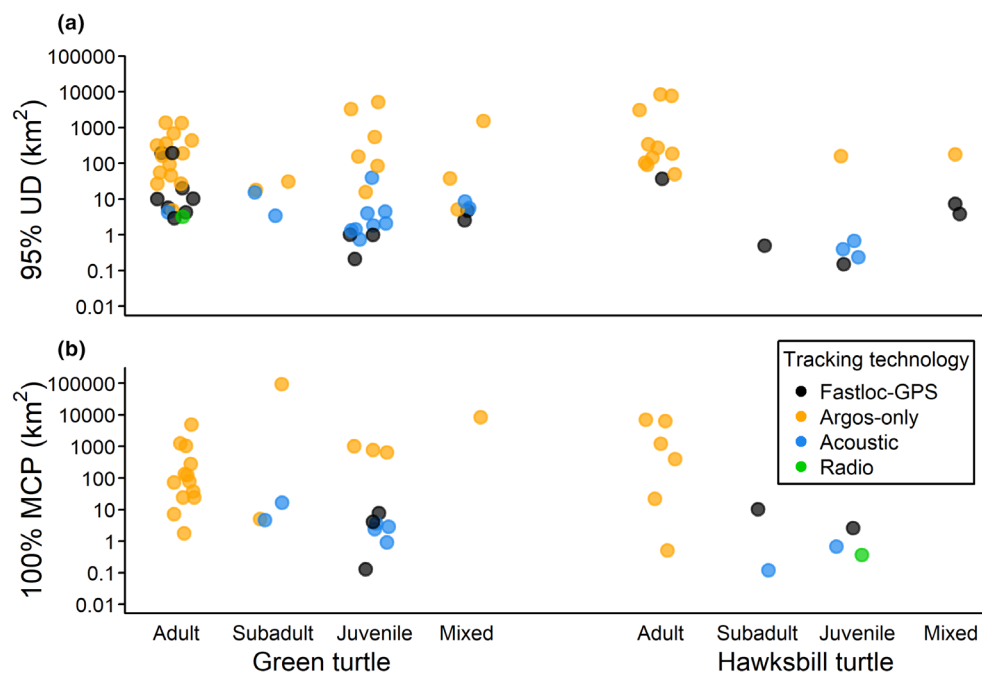


FIGURE 4 Published home range estimates of hawksbill and green turtles at their foraging sites by life stage, tracking technology and analytical method, reported as (a) 95% kernel density estimation utilisation distribution (KUD) and (b) 100% minimum convex polygon (MCP). Home range estimates using 95% KUD  $< 10 \text{ km}^2$  were reported in 71% of Fastloc-GPS studies across life stages of both species and  $< 1 \text{ km}^2$  in 36% of the studies, while only 8% of Argos studies resulted in estimates  $< 10 \text{ km}^2$ .

usage than Fastloc-GPS tracking (Witt et al., 2010). However, a key message from our theoretical considerations is that to compare home range sizes across studies, a good starting point is to exclude Argos tracking and focus on high-accuracy Fastloc-GPS tracking, unless AKDE sees broader adoption in future studies. Such analyses synthesising data from across studies may be increasingly important to determine biological factors influencing animal space use. For example, there are concerns that in some parts of the world, high densities of

adult green turtles following population recoveries may lead to overgrazing of seagrass meadows, on which this species feeds (Christianen et al., 2023; Gangal et al., 2021). Comparisons of space use patterns using high-accuracy tracking may provide an approach to identifying the occurrence of such habitat destruction (Hardy et al., 2023; Hays et al., 2024). While local productivity and ecosystem health are expected to influence home range size, varying among sites and regions, we show that the much larger influence of tracking accuracy

will obscure any such pattern until sufficient high accuracy (Fastloc-GPS) datasets are available to contrast habitat use across regions using comparable datasets, unless data are shared for re-processing using AKDE and further testing using empirical data provides results consistent with those from our simulated assessments.

Once across-study comparisons are distilled down to those using high-resolution tracking (e.g. Fastloc-GPS), the next stage to allow inter-comparison of results is to consider the magnitude of the differences in home range sizes likely introduced by the analytical methods. For example, our theoretical considerations suggest that BRB and dBBMM analyses provide relatively high estimates of space use when used with Argos data, around 350 times larger than the reference area, and 500 times larger than AKDE estimates. Studies on elephants and terrestrial reptiles found that dBBMM analysis reduced type I and type II errors compared with MCP and KDE (Silva et al., 2018; Wilson et al., 2020) and BRB performed better than KDE and MCP in estimating chimpanzee home ranges in Gabon (Martínez-Íñigo et al., 2021). Notably, these studies collected data using radio and GPS devices, suggesting that these movement models perform better relative to other estimators when location accuracy is high—as reflected in our analysis of simulated datasets. It is crucial to note, however, that dBBMM estimates an animal's occurrence distribution rather than its range distribution and that this distinction is important. An occurrence distribution is based on likelihood statistics, has radically different properties and responds differently to increased sampling frequency, which will reduce uncertainty and produce smaller estimates (Alston et al., 2022). While dBBMM has been used to predict home range in the past, the recommendation is that this estimator is intended to answer different ecological questions and should be regarded as distinct from home range estimators, particularly as continuing improvements in tracking technology allow sampling at increasingly high frequencies (Alston et al., 2022).

Our analysis showed that AKDE produced home range size estimates that are comparable to conventional methods such as MCP and KDE for simulated Fastloc-GPS data. This has also been shown for empirical data where AKDE home range size estimates of Perth red foxes (*Vulpes vulpes*) recorded using GPS closely aligned with those of MCP (Kobryn et al., 2023). Furthermore, AKDE estimates for our simulated Argos high- and low-accuracy datasets were similar to those of Fastloc-GPS, indicating the method's efficacy in accounting for varying levels of telemetry error (Fleming et al., 2020). Beyond error correction, AKDE offers advantages by addressing key statistical assumptions. Traditional approaches like MCP and KDE assume locations are independently and identically distributed (IID), while the newer approaches of BRB and dBBMM incorporate Brownian motion (BM) as the underlying movement process. In contrast, AKDE enables selection of the optimal movement model from multiple candidate processes including IID, BM and OUF (Fleming et al., 2015). Our findings underscore the robustness of AKDE in accounting for variable location accuracy when generating estimates of animal space use.

With our simulated Fastloc-GPS data, home range estimates across analytical methods differed by less than a factor of two, although this might be expected to vary with patterns of space use.

So, where Fastloc-GPS has been used, across studies we might expect that differences in home range estimates greater than twofold might reflect real differences between regions, rather than different methodologies. For example, for juvenile green turtles tracked using Fastloc-GPS, the mean home range size was 24 km<sup>2</sup> in Florida compared with 0.21 km<sup>2</sup> in the South-West Indian Ocean (Chambault et al., 2020; Wildermann et al., 2019), suggesting that the difference in home range estimates could be linked to biological factors. Similarly, the mean home range size of adult hawksbill females was 1.39 km<sup>2</sup> in the Torres Strait (Barr et al., 2021) compared with 37 km<sup>2</sup> in the Gulf of Carpentaria due to the use of large offshore foraging grounds by some turtles (Hoenner et al., 2015). Such comparisons in home ranges of different populations recorded using high-accuracy Fastloc-GPS technology would indicate that extrinsic factors influencing space use such as habitat characteristics may require conservation attention.

The results of our comparison of home range estimates from the literature are consistent with our findings from theoretical considerations. Generally, high home range estimates were provided by studies for all life stages that used Argos tracking, for example, 5148 km<sup>2</sup> for a juvenile green turtle in the South China Sea (Ng et al., 2018) and 6289 km<sup>2</sup> for adult female hawksbills in the Caribbean (Hawkes et al., 2012). These home range estimates are likely gross overestimates due to noise from low-accuracy tracking. State space models (SSMs) have been recommended for animal tracking data to correct location inaccuracies introduced by Argos technology (Jonsen et al., 2005). Eight out of forty-five Argos tracking studies describing hawksbill and green turtle 95% KUD home ranges in the last 20 years have used SSMs to ameliorate tracking inaccuracy, but only one resulted in a mean home range estimate <100 km<sup>2</sup> (Hart et al., 2017), and three gave estimates >1000 km<sup>2</sup> (e.g. Metz et al., 2020; Sloan et al., 2022). Despite these limitations, Argos tracking has great value for determining migratory destinations (e.g. Maurer et al., 2022) and establishing connectivity between regions (e.g. Attum et al., 2014). Argos-only data should not be used to derive home range size estimates unless AKDE is used to compensate for location accuracy, although this has not yet been tested using real tracking data. Overinflated space use estimates are likely to dilute the actual protection afforded across the estimated range of a species, as conservation measures must be balanced with human access to marine resources. High-accuracy tracking can highlight restricted hotspots of space use where the strictest conservation efforts could be enforced.

As expected from theoretical consideration, high-accuracy Fastloc-GPS tracking revealed generally small home ranges across life stages. For example, Wood et al. (2017) showed that the mean space use of six subadult hawksbill turtles in Southeast Florida was 0.49 km<sup>2</sup>, that is these turtles maintained very small foraging areas. Similarly, six adult hawksbills in Australia were reported to occupy a mean home range of 1.38 km<sup>2</sup> (Barr et al., 2021). High-accuracy Fastloc-GPS data can also reveal inter-individual variability in space use such as described by Gredzens et al. (2014) and Tanabe et al. (2023), where most adult green turtles occupied small home range sizes except one turtle in each case that was transient and occupied multiple foraging



sites. These high-resolution studies often reveal a diel pattern in space use by turtles. For example, Hays et al. (2024) reported that the mean distance between the centre of day versus night areas occupied was around 1.57 km for 32 green turtles across different foraging grounds. Such studies, along with direct observations, are revealing that ideal foraging areas for sea turtles likely provide both good forage availability as well as protection (e.g. caves or other structures) where turtles have a lower risk of predation (Smulders et al., 2023). Using space use estimates from Fastloc-GPS tracking studies, our review indicates that home range sizes vary between juvenile and adult green turtle populations. For example, immature green turtles in the Chagos Archipelago occupied a mean home range of 1.13 km<sup>2</sup> (Hays et al., 2021), whereas post-nesting green turtles tagged in Chagos occupied a mean day home range of 20 km<sup>2</sup> at their respective foraging grounds spread across the Western Indian Ocean (Christiansen et al., 2017). High-accuracy tracking can clarify differences in space use strategies across life stages and lead to a better understanding of habitat use patterns across regions and species.

While our findings allow more informed comparisons of existing home range estimates from across different studies, an important point to note is that data-sharing and archiving raw data in freely available repositories such as Movebank ([www.movebank.org](http://www.movebank.org); Kranstauber et al., 2011) will facilitate meta-analysis of location data to determine patterns in space use across the globe. Examples of data deposition in Movebank are already starting to appear (Hays et al., 2021, 2024). The benefits of collaboration and data-sharing are also evident in recent global examinations of movement patterns for particular taxa that are driving informed conservation decisions (e.g. Queiroz et al., 2019; Womersley et al., 2022). While processing raw tracking data from across studies in a consistent manner is ultimately the best data analysis solution, there will always be published studies where the raw data are unavailable. It is in these cases that we emphasise our key message of appreciating the impact of location accuracy when estimating animal space use.

Our study provides evidence that tracking technologies introduce far greater variation in home range size estimates than the analytical methods used on the data they collect. High-resolution technologies like Fastloc-GPS provide reliable estimates of fine-scale space use of animals, while Argos tracking is effective for recording broad movements like migratory paths. These differences can influence decisions in spatial planning and are particularly relevant for global conservation initiatives such as the 30×30 Biodiversity Target 3 of the Kunming-Montreal Global Biodiversity Framework (WWF & IUCN WCPA, 2023), or in designating areas for species and habitat protection such as Important Shark and Ray Areas (ISRAs; Kyne et al., 2023). Where sufficient animals have been tracked, high-accuracy tracking can allow the strictest conservation measures to be applied where they are most needed, rather than diluted across larger areas that may reflect location inaccuracy rather than animal space use. We emphasise that method selection is crucial for obtaining reliable ecological insights that can guide evidence-based management strategies.

## AUTHOR CONTRIBUTIONS

Nicole Esteban, Graeme C. Hays, and Kimberley L. Stokes conceived the study. Nupur Kale compiled and analysed data supported by Kimberley L. Stokes. All authors contributed critically to the manuscript text and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no financial or competing interests.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data and code available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.31zcrjf0b> (Kale et al., 2025).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Example space use estimates showing core (50% utilisation distribution, UD; yellow) and full home ranges (95% UD; green) generated from simulated Fastloc-GPS (a–e), Argos high-accuracy (f–j), and Argos low-accuracy (k–o) datasets using (a, f, k) Minimum Convex Polygon, (b, g, l) Kernel Density Estimation, (c, h, m) Autocorrelated Kernel Density Estimation, (d, i, n) Biased Random Bridge, and (e, j, o) dynamic Brownian Bridge Movement Model. Simulated animal locations are shown in black. Note the variation in axis scales between the tracking technologies (panel rows).

**Figure S2.** Home range estimates derived using five analytical methods from simulated data representing (a, d) Fastloc-GPS, (b, e) Argos high-accuracy and (c, f) Argos low-accuracy tracking. Red dotted line indicates the reference area used by the simulated animal (3.76 km<sup>2</sup>).

**Table S1.** Autocorrelation parameters extracted from publicly available Fastloc-GPS datasets: home range crossing time (positional autocorrelation) and velocity autocorrelation time.

**Table S2.** Mean home range size estimates using 50% and 95% utilisation distributions (UDs) from simulated datasets resembling commonly used tracking technologies, analysed with Minimum Convex Polygon (MCP), Kernel Density Estimation (KDE), Autocorrelated Kernel Density Estimation (AKDE), Biased Random Bridge (BRB), and dynamic Brownian Bridge Movement Model (dBBMM).

**Table S3.** Global home range size estimates of green turtles (*Chelonia mydas*) from the literature, grouped by tracking technology and life stage.

**Table S4.** Global home range size estimates of hawksbill turtles (*Eretmochelys imbricata*) grouped by tracking technology and life stage.

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