Animal Biotelemetry

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Dead-reckoning facilitates determination of activity and habitat use: a case study with European badgers (*Meles meles*)

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Abstract

Background Studies describing the movement of free-ranging animals often use remotely collected global positioning system (GPS) data. However, such data typically only include intermittent positional information, with a sampling frequency that is constrained by battery life, producing sub-sampling effects that have the potential to bias interpretation. GPS-enhanced 'dead-reckoning' of animal movements is an alternative approach that utilises combined information from GPS devices, tri-axial accelerometers, and tri-axial magnetometers. Continuous detailed information of animal movement, activity and habitat selection can then be inferred from finer-scale GPS-enhanced dead-reckoning. It is also a useful technique to reveal the minutiae of an animal's movements such as path tortuosity. However, examples of studies using these approaches on terrestrial species are limited.

Methods Collars equipped with GPS, tri-axial accelerometer, and tri-axial magnetometer loggers were deployed on European badgers, *Meles meles*, to collect data on geo-position, acceleration and magnetic compass heading, respectively. This enabled us to compare GPS data with calculated GPS-enhanced dead-reckoned data. We also examined space use, distances travelled, speed of travel, and path tortuosity in relation to habitat type.

Results Nightly distances travelled were 2.2 times greater when calculated using GPS-enhanced dead-reckoned data than when calculated using GPS data alone. The use of dead-reckoned data reduced Kernel Density Estimates (KDE) of animal ranges to approximately half the size (0.21 km^2) estimated using GPS data (0.46 km^2). In contrast, Minimum Convex Polygon (MCP) methods showed that use of dead reckoned data yielded larger estimates of animal ranges than use of GPS-only data (0.35 and 0.27 km^2, respectively).

Analyses indicated that longer periods of activity were associated with greater travel distances and increased activity-related energy expenditure. Badgers also moved greater distances when they travelled at faster speeds and when the routes that they took were less tortuous. Nightly activity-related energy expenditure was not related to average travel speed or average ambient temperature but was positively related to the length of time individuals spent outside the sett (burrow). Badger activity varied with habitat type, with greater distance, speed, track tortuosity, and activity undertaken within woodland areas. Analyses of the effects of varying GPS sampling rate indicate that assessments of distance travelled depend on the sampling interval and the tortuosity of the animal's track. Where animal paths

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change direction rapidly, it becomes more important to use dead-reckoned data rather than GPS data alone to determine space use and distances.

Conclusions This study demonstrates the efficacy of GPS-enhanced dead-reckoning to collect high-resolution data on animal movements, activity, and locations and thereby identify subtle differences amongst individuals. This work also shows how the temporal resolution of position fixes plays a key role in the estimation of various movement metrics, such as travel speed and track tortuosity.

Keywords Accelerometer, Magnetometer, GPS, Dead-reckoning, Vectorial dynamic body acceleration, Energy expenditure, Behaviour, Habitat

Background

Information on precise movements and behaviours of animals acquired using subject-borne loggers can provide important insights into resource and habitat use [1–5]. Understanding how animals utilise habitats is important for both conservation and wildlife management and can help elucidate critical current issues, such as predicting how environmental change may impact individual behaviour [1, 6, 7]. Recent studies using animal-borne loggers have advocated the combined deployment of GPS, tri-axial magnetometer, and tri-axial accelerometer data loggers to determine precise records of animal movement paths by the process of 'GPS-enhanced dead-reckoning' [8, 9]. Importantly, measured acceleration data can also be used to determine a proxy of activity-related energy expenditure, utilising metrics such as 'vectorial dynamic body acceleration' (VeDBA) [10], as well as providing behaviour profiles [11, 12]. Most studies employing GPS-enhanced dead-reckoning have focused on aquatic species such as pinnipeds [13–15], cetaceans [16–19] sea turtles [20] and other marine megafauna [21, 22]. Fewer studies have used the approach to investigate movement paths in terrestrial species (see [23] for validation in humans and domestic animals, [24] for examples in cattle and sheep, [25] for wild Eurasian beavers and [26] for African lions). Recently, dead-reckoning was used to determine movement paths of European badgers (*Meles meles*) [27, 28]. Critically, dead-reckoning provides seamless fine-scale (sub-second) resolution of animal movement, contrasting with the isolated use of GPS data, which are typically collected every few minutes at best. Therefore, animal paths calculated from GPS-enhanced dead-reckoned data tend to be more 'tortuous' (i.e., they follow the meandering course that an animal takes) and cover greater distances than those calculated from GPS-only data [8]. The current study extends previous work by exploring how GPS-enhanced dead-reckoned and GPS-only data provide different information on how animals use their habitat. We investigate how animals differ in terms of their time spent, their activity-related energy expenditure, and their travel speed as they traverse and utilise different habitat types, and how this information critically depends on GPS sampling rate and animal track tortuosity.

Methods

Study site and species

The study took place in a landscape of arable farmland, grazing pasture, recreational grassland, water bodies, and mixed deciduous and coniferous woodland centred on Woodchester Park, South-West England [29]. This area has been the location of a long-term study (initiated in 1975) of the resident badger population [30].

Trapping and collaring procedure

Badger capture and handling protocols at this site are well-established and have been described previously [30]. The animals collared as part of the present study were initially captured during routine trapping operations undertaken as part of this long-term study [30]. In brief, steel mesh traps baited with peanuts were deployed at badger main setts (entrances to burrow systems). Captured animals were then transported to a nearby facility where they were anaesthetised by intramuscular injection [31] prior to examination and collar fitting. Between June and August in 2014 and 2015 collars carrying GPS and tri-axial accelerometer and magnetometer loggers were initially fitted to 16 individuals (see below and Supplementary Information (SI) Figs. 1–3 for collar design). Collared individuals were then released the following morning. Four days later we initiated an additional trapping operation at all locations where the collared animals had been released, which was continued for 12 days by which time all collared animals had been recaptured. Collars were removed from recaptured animals and data were downloaded. Non-target (i.e., uncollared) animals were immediately released when traps were checked. All devices attached to the collars were recovered and none were obviously chewed. Of the 16 individuals that were initially collared, three accelerometer and magnetometer loggers and nine GPS loggers malfunctioned, possibly because of water ingress. Therefore, we could only undertake dead-reckoning calculations on five adult males and two adult females for which we had accelerometer, magnetometer and GPS data.

Logger deployment and dead reckoning

Tri-axial accelerometer and tri-axial magnetometer data loggers were set to record continuously at 25 and 5 Hz, respectively. The loggers were built into a single device (X8m-3, Gulf Coast Data Concepts, LLC, Waveland, MS, USA) which was attached to a leather collar [32]. Collars were also fitted with a GPS logger (i-gotU GT-120; Mobile Action Technology, Inc., Taiwan), which was programmed to record a locational fix once every five minutes between 20:00 and 07:00. Further details of logger setup, programming and deployment are described in the SI.

The calculation of movement tracks by GPS-enhanced dead-reckoning has been described in detail previously (e.g., 23, 24, 26). In brief, static acceleration [33] was used to calculate body pitch and roll. This was then used to set magnetometer outputs which accounted for the angle at which the device was attached to the badger so that the longitudinal axis of the animal corresponded to that of the device [34]. The animal heading (degrees) was then calculated using the measured logger pitch and roll in tandem with the magnetometer data. The speed of travel was estimated from the acceleration metric 'vectorial dynamic body acceleration' VeDBA, which is a function of activity-related energy expenditure, and therefore speed of locomotion [23, 35, 36]. GPS-enhanced dead-reckoning calculations were undertaken in Framework4 (v2.6) software [24] as previously described [23]. The resultant data outputs comprised latitude and longitude geo-positions at the sampling frequency of the collected acceleration data (25 Hz). Data were then used to determine track tortuosity by calculating the differences in compass heading between each calculated dead-reckoned point, (i.e., the difference in angle between the vectors of subsequent points at 25 Hz).

Data screening

Data were selected for dead-reckoning calculations by manually inspecting the accelerometer data for each badger during each night and only using periods when locomotion (i.e., traversing distance) occurred [27]. The GPS location for the sett at which each badger was trapped and subsequently released was included as the first location point for each badger. Often GPS fixes were only obtained once the badger had left the sett due to the inability of the logger to obtain a location fix whilst animals were underground, or poor coverage for other reasons, such as being under trees, resulting in an average fix success rate of 64.2% across all nights of data (see SI Table 1).

Space use

To explore how individuals utilised the landscape, the areas they ranged over during the period of data recording ('short-term ranges') were expressed as 95% kernel density estimates (KDE; derived using the '*adehabitatHR*' package with 'reference' bandwidth applied (version 0.4.19) [37] and '*PBSmapping*' (version 2.73.0) [38] package in R [39]). We also present estimates of short-term ranges determined using 95% Minimum Convex Polygon (MCP) to allow for comparison with other studies. Separate estimates of short-term ranges were calculated for the entirety of an individual's measurement period from the GPS-only data and from the GPS-enhanced dead-reckoned data to allow the two methods to be compared. Relationships between short-term ranges, average nightly distances travelled, and activity-related energy costs were examined (Table 1, model 1 and SI Table 2). Activity was determined by summing nightly VeDBA measured at 25 Hz, and averaging across the nights a badger was monitored.

Distances travelled

The distances individuals travelled per night were determined using the locational GPS-enhanced dead-reckoned data recorded at 25 Hz. The sum of the distance between sequential geo-location points was calculated in R (RStudio version 4.1.2) using the '*geosphere*' package (version 1.5–14) [40]. Distances travelled using GPS-only locational data were calculated in the same way. Dead-reckoned distances travelled were assessed in relation to the duration of nightly activity; the sum of the VeDBA values for a particular night (as a measurement of nightly activity); the mean speed individuals travelled per night (measured in ms^{-1} as the total distance travelled per night, divided by the duration of activity); and, the sum tortuosity per night (measured as the nightly sum of the change in compass heading between sequential geolocation points). These factors were included as covariates in generalized linear mixed models (GLMMs) (lme4, version 1-27.1) [41] with distance travelled as the dependent variable. Badger identity was included in the models as a random effect to account for repeated measures within individuals, and the best fit final model was selected based on the lowest Akaike information criterion corrected for small sample sizes (AICc) (bbmle version 1.0.24) [42] using stepwise deletion (Final model see Table 1, model 2. Full models considered see SI Table 3) [43].

Activity

To investigate potential determinants of badger activity, variation in nightly summed VeDBA (as the dependent variable) was examined in relation to average nightly

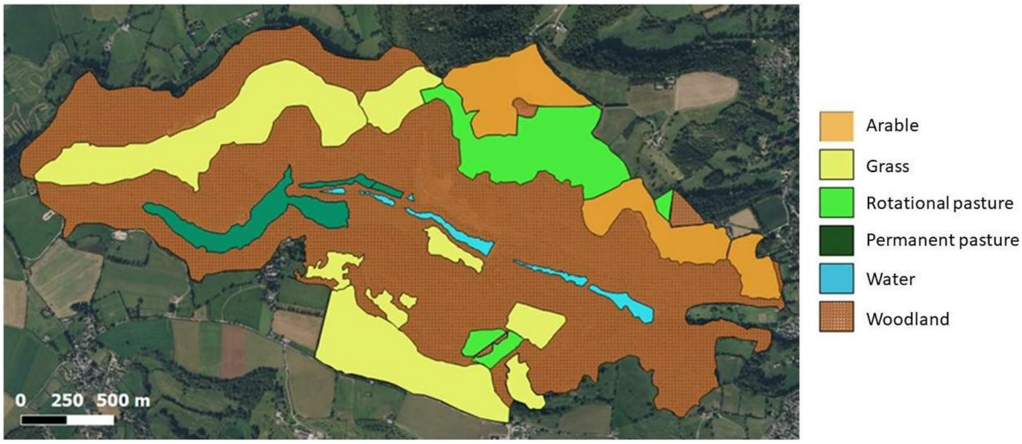

Fig. 1 Woodchester Park study site showing the various habitat types within. 'Arable' is shown as *orange* shading; Recreational grassland ('Grass') as *yellow*; Pasture as *light green* ('Rotational pasture') and *dark green* ('Permanent pasture'); water features ('Water') as *blue* and 'Woodland' as dappled *brown* shading

Table 1 Final best-fit general linear (GLM) and general linear mixed models (GLMM) examining variation in area use, nightly travel distances, and activity as determined using GPS-enhanced dead-reckoned data

Model no.	Response	Fixed effects	AICc	Marginal R^2	Conditional R^2	Final model effects	χ^2	*df*	*p*
1	Area use	Average distance + Average sum VeDBA	7.557	–	–	**Average distance**	20.311	1	**<0.001**
						Average sum VeDBA	4.389	1	**0.036**
2	Distance travelled per night	Sum VeDBA + Average speed*Sum tortuosity + Hours + Average temperature	470.932	0.958	0.975	**Sum VeDBA**	7.339	1	**0.007**
						Speed	52.740	1	**<0.001**
						Sum tortuosity	5.404	1	**0.020**
						Hours	3.340	1	0.068
						Average temperature	2.770	1	0.096
						Speed:Sum tortuosity	5.161	1	**0.023**
3	Sum VeDBA per night	Hours + Average speed + Sum tortuosity	584.064	0.681	0.753	**Hours**	51.238	1	**<0.001**
						Average speed	0.018	1	0.893
						Average temperature	0.125	1	0.726
4	% Time spent (sqrt transformed)	Habitat	512.235	0.592	0.595	**Habitat**	162.163	3	**<0.001**
5	Distance travelled	Habitat	627.361	0.510	0.510	**Habitat**	71.742	3	**<0.001**
6	Average VeDBA per second	Habitat	345.158	0.155	0.502	**Habitat**	20.587	3	**<0.001**
7	Average speed (log transformed)	Habitat	109.676	0.248	0.580	**Habitat**	38.949	3	**<0.001**
8	Average tortuosity per second (sqrt transformed)	Habitat	439.677	0.256	0.354	**Habitat**	26.361	3	**<0.001**

Model numbers (1–8) are shown, alongside the dependent 'response' variable (and relevant transformations). Independent variables ('fixed effects') are shown with an asterisk (*) denoting an interaction between variables and a plus sign (+) denoting main effects. AICc represents the Akaike information criterion values corrected for small sample sizes, which were used to select the final best-fit model. Marginal and conditional R^2 values are noted. Final model effects are shown, with corresponding Chi-squared statistic (χ^2), degrees of freedom (*df*), and probability value (*p*). Significant *p* values are shown in bold. Model 1 was a GLM examining variation in area use during the collared period using Kernel Density Estimate (KDE). Models 2 and 3 were GLMMs examining GPS-enhanced dead-reckoned travel distances and sum VeDBA per night, respectively, with Badger ID included as a random effect to account for repeated measures from individuals. Models 4–8 were also GLMMs with Badger ID included as a random effect, and examined variation in time spent, distance travelled, and activity (VeDBA, speed, and tortuosity) in different habitats

speed of travel, average nightly summed tortuosity, the duration of nightly activity, and average nightly ambient temperature [44] as recorded by a local weather station [45]. As before, the best fit final GLMM was selected based on AICc values following stepwise deletion (See Table 1, model 3 for final model, and SI Table 4 for full models).

Habitat type categorisation

Habitat types were digitised from Google Earth satellite imagery using arcGIS version 10.2.1 (ESRI, California, USA), verified by ground-truthing, and projected onto a British National Grid map (OSGB 1936). Habitat types were defined as 'Arable', (farmland used to grow crops), 'Pasture' (permanent and part-time rotational pasture used to graze animals), 'Recreational Grassland' (grass areas used by members of the public for exercise and leisure), and 'Woodland' (mature stands of deciduous, coniferous, and mixed coniferous and deciduous trees) (Fig. 1).

Variation in badger activity across habitat types

Dead-reckoned tracks were overlaid onto the habitat type map (Fig. 1), and the times that badgers entered and departed from each habitat type were recorded. This enabled the time spent in different habitats (calculated as a percentage of the time a badger was active) to be determined on a nightly basis for all individuals. The time spent in different habitats was also determined using GPS-only data, by calculating the percentage of GPS fixes occurring in each habitat per night. Distances that individuals travelled, their average speed, average VeDBA per second (i.e., relative activity), and average tortuosity per second within different habitats were also determined. We then examined differences in behaviour and activity relative to habitat type using separate GLMMs (Table 1, models 4–8). Post-hoc pairwise comparisons were conducted between habitats via least-squares means (*emmeans* 1.7.1-1) with Tukey adjustment (SI Tables 5–8, 10) [46]. Variation in GPS-only and GPS-enhanced dead-reckoned measurements of the proportion of time spent, average speed, and average tortuosity in different habitats was examined via GLMMs (SI Table 11, models 1, 3, and 5). Where GPS-only and GPS-enhanced dead-reckoned measurements differed significantly, post-hoc pairwise comparisons were conducted via least-squares means with Tukey adjustment (SI Tables 13–14). Variation in GPS-only measurements of time spent, average speed, and average tortuosity between different habitats was also examined via GLMMs (SI Table 11 models 2, 4, and 6), with post-hoc pairwise comparisons conducted via least-squares means with Tukey adjustment where appropriate (SI Table 15).

Effect of GPS sampling rate on variation between GPS and dead-reckoned data

The difference in distance travelled when estimated using GPS data alone versus GPS-enhanced dead-reckoned data depends on sampling interval and the real track tortuosity of the animal in question [8, 47]. For example, if an animal changes direction often and rapidly, then GPS-enhanced dead-reckoned data will be useful to identify such tortuous tracks. GPS sampling rate (and hence sampling interval) is often limited by battery life, and so battery size (itself dictated by animal size) often limits the quantity of data that can be recorded. Clearly, as the GPS sampling rate approaches that of the dead-reckoned data, the calculated distance travelled derived from GPS-only data will increase, hence decreasing the added value of the combined approach. But, the scale and extent of movement tortuosity (of the animal's track) will be pivotal in changing the ratio of GPS-only calculated distance to the GPS-enhanced dead-reckoned distance. As an animal's tracks become more tortuous, the added value of dead-reckoning increases.

A simple model illustrates this concept. Here, animal movement is simulated by allocating a random (but constrained) distance between step lengths within animal tracks. This reveals the extent to which even random movement produces variability in track tortuosity over the track length (Fig. 2A). Importantly, such variability in track tortuosity profoundly affects the calculated distance travelled between fixes (effectively the distance per unit time, i.e., the animal's speed). As an animal's track becomes less tortuous or straighter, (simulated here by adding a directional component to the north–south distances travelled, Fig. 2B), then the calculated dead-reckoned distance becomes more similar to the measured GPS-only distance travelled. When an animal's tracks become even less tortuous (with an even greater directional component Fig. 2C), the differences in the ratio between GPS-enhanced dead-reckoned and GPS-only distances travelled reduce further and, in our example case, disappear. Note the differences between dead-reckoned and GPS-calculated distances become more extreme as the frequency of the GPS points decreases. Our case to illustrate this compares GPS-only sampling rates of one per 10, 100 and 1000 dead-reckoned points. If there are 1000 dead-reckoned points with each point determined once per second, this is equivalent to 16.67 min, which is similar to a 'real-life' GPS sampling regime of once every c.15 min, hence one GPS fix per 1000 dead reckoned points represents a likely scenario.

Results

Comparison of GPS-only versus GPS-enhanced dead-reckoned estimates of area use

When comparing 95% Kernel density estimates (KDE) of area use, GPS-only data provided larger measurements than dead reckoned data (0.46 ± 0.41 and 0.21 ± 0.15 km^2, respectively, $w = 28$, $p = 0.016$). Conversely, when examining minimum convex polygon (MCP) estimates of area use, dead-reckoned data provided larger measurements than GPS-only data (0.35 ± 0.22 vs. 0.27 ± 0.15 km^2,

$w = 27$, $p = 0.031$) (Fig. 3A–C). Examination of dead-reckoned derived KDE estimates of area use indicated that larger area use was associated with greater average nightly travel distances ($\chi^2 = 20.311$, $p < 0.001$), and greater average activity, as measured by sum VeDBA ($\chi^2 = 4.389$, $p = 0.036$ (Table 1, model 1).

Distances travelled per night

Distances travelled per night were significantly greater when they were calculated using GPS-enhanced dead-reckoned data than when using GPS-only data (9.03 ± 4.8 and 4.17 ± 1.77 km, respectively, $w = 406$, $p < 0.001$, Fig. 4, Table 1, model 2). Individuals that were active outside the sett for longer periods of time travelled greater distances ($\chi^2 = 4.095$, $p = 0.043$) and had higher summed VeDBA ($\chi^2 = 7.339$, $p = 0.007$) than those that spent more time in the sett. There was also a significant interactive effect of average travel speed (ms^{-1}) and the summed tortuosity per night ($\chi^2 = 5.702$, $p = 0.023$) on nightly distance travelled. At low speeds, there was little effect of path tortuosity on distance travelled, but at higher travel speeds, low tortuosity was associated with greater dead-reckoned distances (Fig. 5).

Activity

Activity, measured as the summed VeDBA during a particular night, was greater on nights when individuals were active for longer periods of time ($\chi^2 = 51.238$, $p < 0.001$), but was not associated with average overnight ambient temperature ($\chi^2 = 0.123$, $p = 0.476$) or average travel speed ($\chi^2 = 0.018$, $p = 0.893$) (Table 1, model 3).

Variation in activity with habitat type

There was no significant difference between GPS-only and GPS-enhanced dead-reckoned measurements of time spent in different habitats ($\chi^2 = 0.078$, $p = 0.994$, Fig. 6A, SI Table 11, model 1). Examination of GPS-enhanced dead-reckoned data indicated there were significant differences in the proportion of time badgers spent in different habitats ($\chi^2 = 162.163$, $p < 0.001$, Table 1, model 4). A greater percentage of active time per individual was spent in woodland (mean 68.26 ± 25.16%) than in any other habitat (Fig. 6A). Individuals also spent more time during their nightly excursions on pasture than on arable land (mean 15.996 ± 23.264% and mean 3.168 ± 8.354%, respectively). Dead-reckoned travel distances also varied significantly with habitat ($\chi^2 = 71.742$, $p < 0.001$), with badgers travelling greater distances in woodland than in any other habitat (Fig. 6B).

Average VeDBA per second, speed (ms^{-1}), and tortuosity per second all varied with habitat ($\chi^2 = 20.587$, $p < 0.001$, $\chi^2 = 38.949$, $p < 0.001$, $\chi^2 = 26.361$, $p < 0.001$, respectively. Table 1 models 6–8, Fig. 7). Post-hoc analyses revealed that badgers were more active and travelled at greater speeds in woodland than in any other habitat, with the exception of pasture (Fig. 6C, D respectively, S1 Tables 7 and 8). The comparison of average travel speed between woodland and pasture marginally failed to reach significance ($p = 0.052$). The overall average speed of travel across all habitats was 0.32 ± 0.65 ms^{-1} (average speed range 0.17–1.04 ms^{-1}) with the single highest speed of 7.53 ms^{-1} occurring in woodland (SI, Table 9). Woodland was also the habitat where individuals travelled in the most tortuous paths. (Fig. 6E, SI Table 10). Use of GPS-only data or GPS-enhanced dead-reckoned data produced different results when speed and tortuosity were compared between habitats (see Supplementary Information for comparisons).

(See figure on next page.)

Fig. 2 Examples of animal movements generated assuming constant step duration but variable step length. Three scenarios are shown whereby the straight-line step taken in any direction is specified as into East–West and North–South vectors using standard trigonometry. Scenario **A** shows random movement (where distances travelled both East–West and North–South per step (in metres) were randomly selected to be between −10 and +10), **B** shows random movement but with a directional component (distances travelled East–West were randomly selected to be between −10 and +10 while distances travelled North–South were randomly selected to be between −10 and +12) and **C** shows random movement with a highly directional component (distances travelled East–West were randomly selected to be between −10 and +10 while distances travelled North–South were randomly selected to be between −10 and +20). The *left-hand panes* show examples of the track simulations while the *middle panes* show the distances travelled according to whether the distance is determined by adding the cumulative distance between GPS points or the cumulative distance between dead-reckoned points and according to how often the GPS position is taken relative to that of the dead-reckoned position. In the *middle* panes, y-axes represent calculated distance travelled; x-axes represent the straight-line distance between the first and last of 10 points and the cumulative distance between 10 points ('One GPS per 10 DR points'), the straight-line distance between the first and last of 100 points and the cumulative distance of 100 points ('One GPS per 100 DR points') and the straight-line distance between the first and last of 1000 points and the cumulative distance between 1000 points ('One GPS per 1000 DR points'). The *right-hand panes* show the ratios of GPS-only to GPS-enhanced dead-reckoned distances for the various scenarios (note difference in y-axis scale for *right hand panel* in **A**–**C**). *Error bars* denote standard deviations of path lengths (*middle panes*) and ratios of path lengths (*right hand panes*) which were sampled 1990, 1900 and 1000 times, respectively for 10, 100 and 1000 DR points, respectively

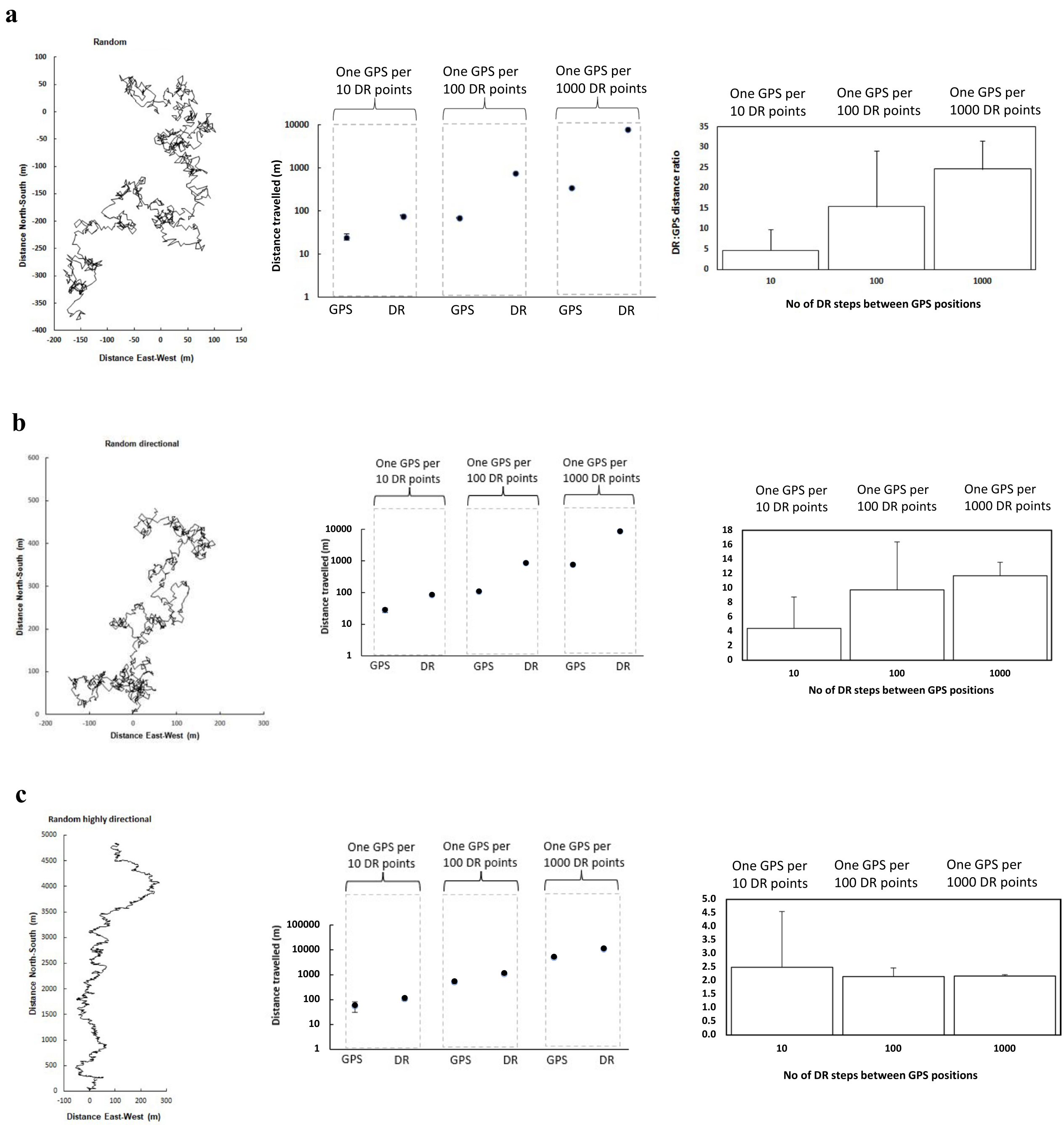

Fig. 2 (See legend on previous page.)

Discussion

This study aimed to show how the use of GPS-enhanced dead-reckoned data could be used in addition to GPS-only data to provide detailed information on animals' movements, activities and space use. In particular, we aimed to examine how Eurasian badgers, in a high-density population, utilise various aspects of their habitat, how active they were in various locations, and how they negotiated the landscape, either travelling fast or undertaking more tortuous paths. In addition, we were interested in exploring how the frequency of GPS points affects the variation between GPS-only and GPS-enhanced dead-reckoned data.

In terms of space utilization, use of GPS-enhanced dead-reckoned data produced smaller estimates of area use than use of GPS-only data, when calculated as 95%

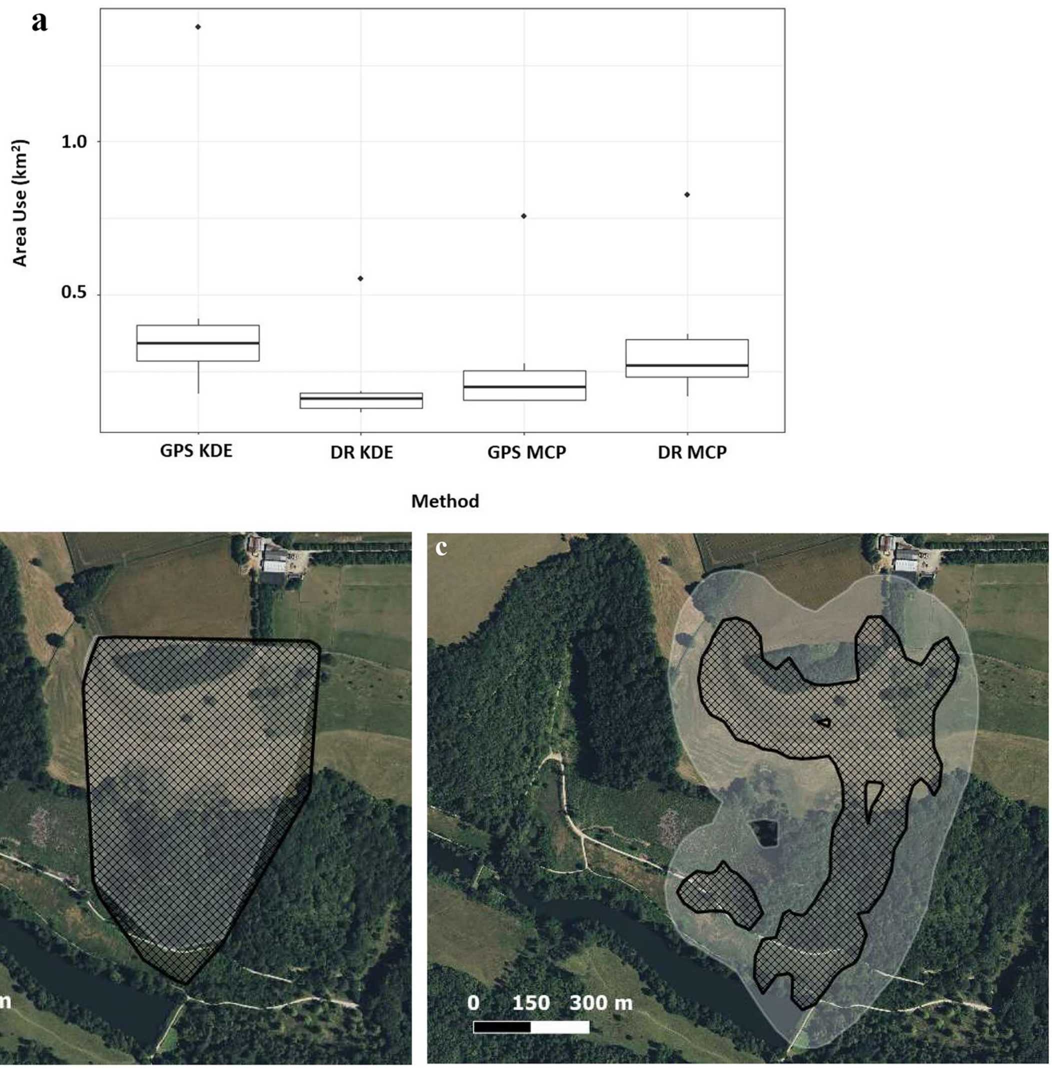

Fig. 3 Measurements of area use by badgers obtained using different methodologies. **A** shows measurements of area use by all seven badgers obtained via 95% Kernel Density Estimate when calculated using GPS data ('GPS KDE'), and GPS-enabled Dead-Reckoned data ('DR KDE'), and via 95% Minimum Convex Polygon when calculated using GPS data ('GPS MCP') and GPS-enhanced dead-reckoned data ('DR MCP') across all nights of collaring. The *black horizontal line* represents the median, with the upper and lower quartiles represented by the top and bottom of each bar, respectively. The whiskers (*vertical black lines*) extend to the smallest and largest values no more than 1.5 times the inter quartile range. Outlying values beyond the extent of the whiskers are denoted as individual points. **B** illustrates differences in area use for one individual badger as determined using 95% Minimum Convex Polygons calculated using (i) GPS data (represented by light grey shading) and (ii) GPS-enhanced dead-reckoned data (denoted as a *black hatched area*) which measured 0.153 and 0.168 km^2, respectively. **C** shows 95% Kernel Density Estimates for the same individual calculated using (i) GPS data (*light grey* shading) and (ii) GPS-enhanced dead-reckoned data (*black hatched area*) which measured 0.291 and 0.120 km^2, respectively

Kernel Density Estimates. Conversely, when 95% Minimum Convex Polygons were derived, the use of dead-reckoned data produced larger estimates of area use than using GPS-only data did. This contrasts with previous work [27] which found no significant difference in estimated range size between the two methods (using the same 95% MCP calculation) in a medium density population. Clearly badgers use space differently in different landscapes, perhaps with more utilisation of core areas at higher densities. This highlights the importance of using both appropriate space-use calculation methods and sufficiently high-resolution data to examine badger movement patterns accurately.

Whilst previous studies of badgers have made use of tri-axial accelerometery and proxies for energy expenditure [48–51], only two have determined badger movements using GPS-enhanced dead-reckoning, both using the same medium density (2.47 individuals per Ha) rural population

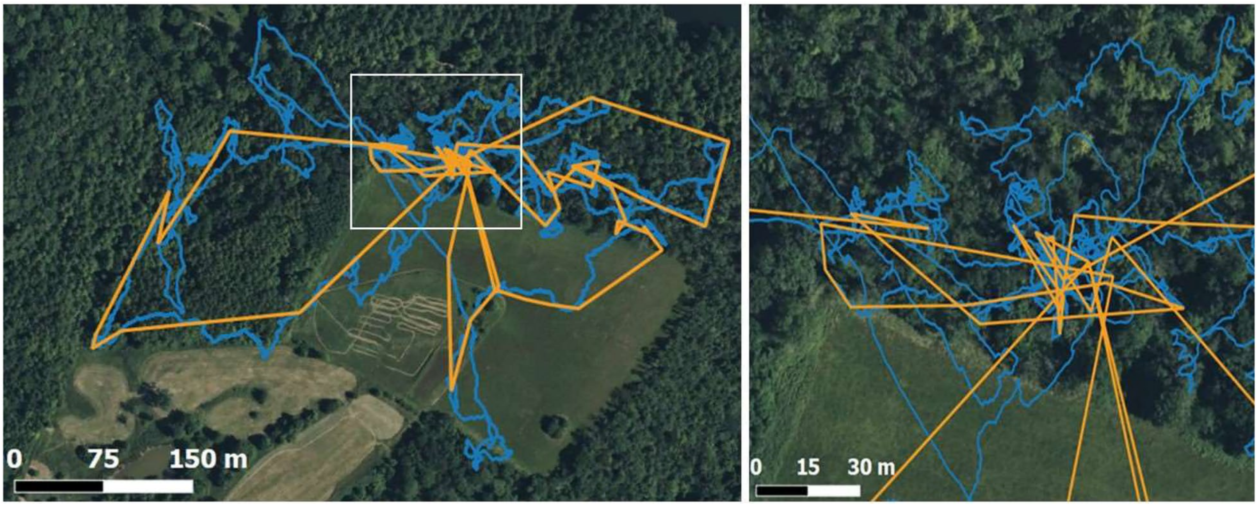

Fig. 4 Comparison of one night's movement for an individual badger according to GPS data (*orange*) and GPS-enhanced dead-reckoned data (*blue*). The *left*-hand panel shows a full night's data over a period of 6 h, 52 min, 52 s. The GPS-only track, based on 67 locational fixes (a fix success rate of 81.7%) measured 3.97 km, whilst the GPS-enhanced dead-reckoned track measured 10.93 km for the same period. A woodland area around the badger's sett is highlighted by a *white rectangle*, with the *right*-hand panel showing an expanded version of this area, highlighting the comparison of GPS-only and GPS-enhanced dead-reckoned derived movement

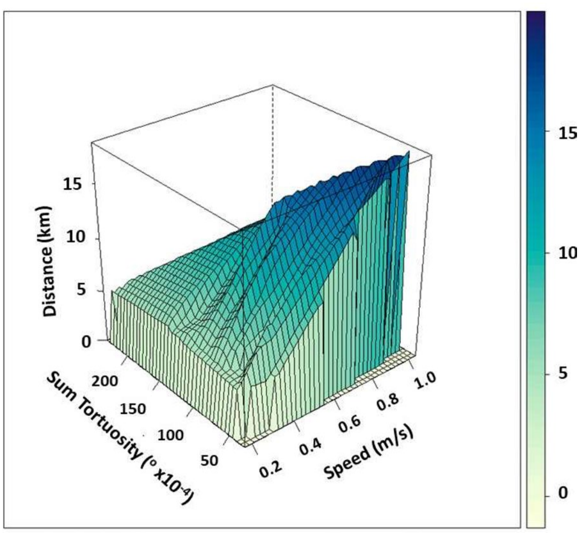

Fig. 5 Wireframe surface plot of the interaction between sum tortuosity (degrees) and average speed of travel (m/s) in relation to GPS-enhanced dead-reckoned (DR) distance travelled per night (km). The plot indicates that at low average speed, tortuosity has little effect on distance travelled, but the greatest distances travelled are associated with low tortuosity and high speeds

[27, 28]. Magowan et al. [27] examined the movement and habitat interactions of two badgers and demonstrated how GPS-enhanced dead-reckoned tracks revealed specific details of area use, with badgers apparently seeking out key areas such as field margins and hedgerows. Analyses of these tracks also showed that badgers travelled 2.2 times further than GPS-only data would have suggested. In a subsequent study, using the same population, but over a longer time period, Redpath et al. [28] came to a similar conclusion. This is supported by the current results, in which use of GPS-enhanced dead-reckoned data reveals that badgers moved greater distances (by a factor of 2.2) than would be indicated by GPS-only data. One aspect to note is that collars (carrying the loggers) had to be retrieved to access acceleration data, which in our case involved capturing non-target animals. Whilst this might not be an issue with a study population of badgers that are frequently trapped, different methods of logger retrieval might be appropriate for more sensitive or harder-to-capture species, such as automated drop-off collars, although these devices also have their issues [52].

Examination of the effect of GPS sampling rate on the variation between GPS-only and GPS-enhanced dead-reckoned data in our simulation shows, unsurprisingly, that distances calculated by dead-reckoning are always greater than those derived from temporally sparser GPS fixes (Fig. 2), and that the differences become more extreme as the GPS-positional fixes become sparser. However, as the animal track becomes more directional, the difference between GPS-enhanced dead-reckoned and GPS-only distance travelled reduces (Fig. 2A–C). Thus, the degree of tortuosity in animal tracks profoundly affects the extent to which GPS data accurately represents distances covered and movement speed. In short, distance and speed measurements are fundamentally affected by sampling interval and the overall effect that this will have

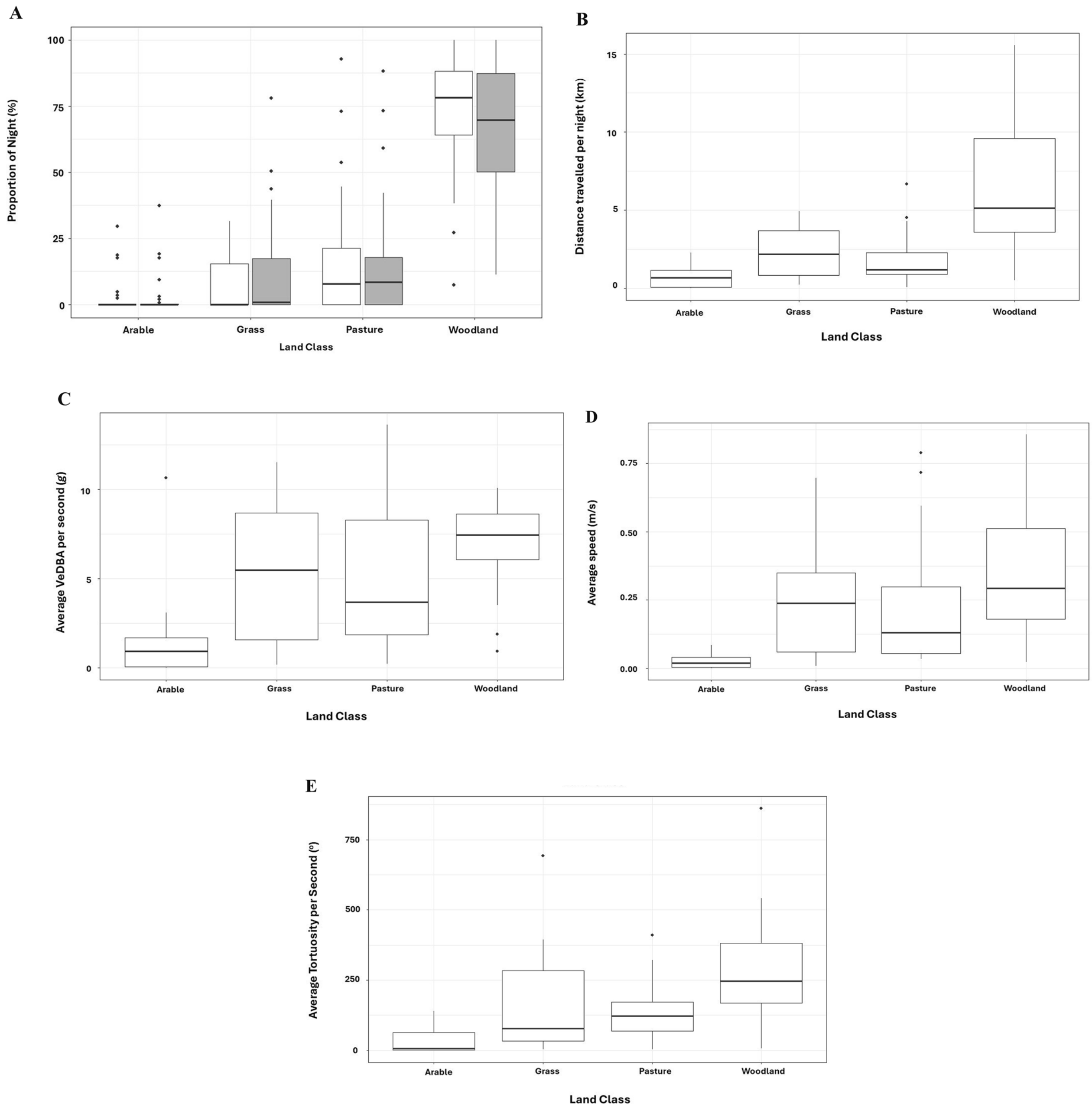

Fig. 6 Variation in badger activity with habitat 'Arable', 'Grass', 'Pasture', and 'Woodland'. **A** Proportion (%) of active time per night spent in each habitat by seven individuals. The proportion of time spent in each habitat according to GPS-only data is shown in *white*, with GPS-enhanced dead-reckoned data represented by *grey boxplots*. **B** GPS-enhanced dead-reckoned distance travelled per night (km) within each habitat. **C** Average summed VeDBA per second (*g*), **D** average speed (m/s), **E** average sum tortuosity (degrees per second) per night within each habitat. The *black horizontal lines* represent the median, with the upper and lower quartiles represented by the *top* and *bottom* of each bar, respectively. The whiskers (*vertical black lines*) extend to the smallest and largest values no more than 1.5 times the inter quartile range. Outlying values beyond the extent of the whiskers are denoted as individual points

depends on the characteristics of the track (specifically the scales at which tortuosity occurs). This means that we cannot expect many GPS-only derived track characteristics to be directly comparable over the duration of a given track if the animal engages in locomotion at varying tortuosities. This is not the case with dead-reckoned data which can be collected at a frequency that measures the nuances of an animal's movements. All this gives perspective to the current badger data but also highlights what must be a general trend.

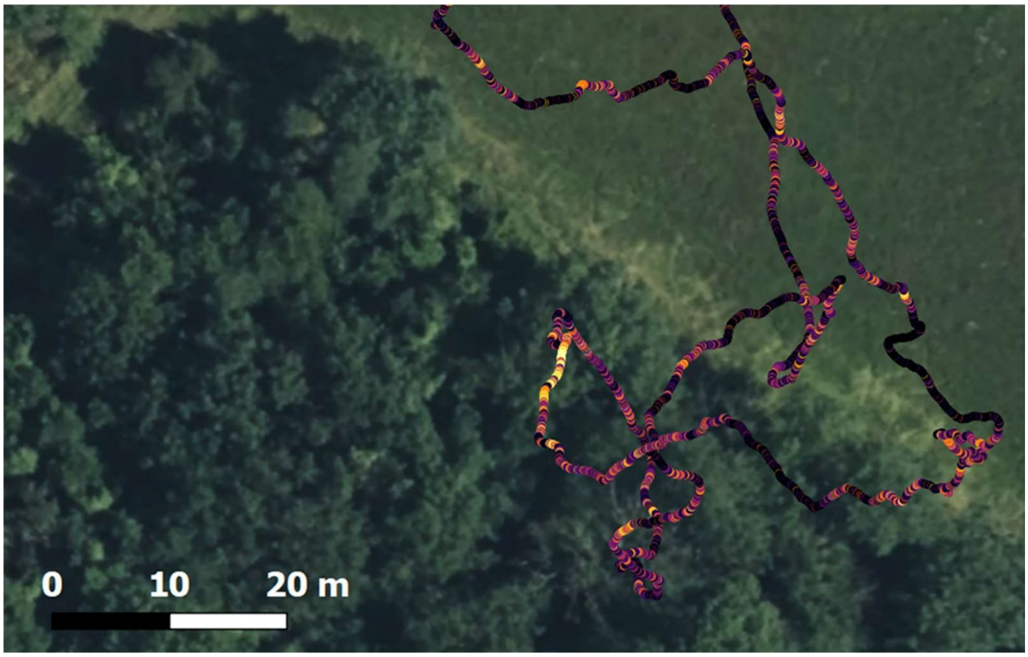

Fig. 7 Example VeDBA changes with an animal's track over different habitats. VeDBA is visualised on a colour gradient, with lower VeDBA values being denoted by *lighter yellow* colours and higher VeDBA values shown in *dark purple*. In this instance, the badger travelled from a recreational grassland area into a woodland area and back. Within the grass area, the apparently longer stretches of higher VeDBA (indicating increased activity-related energy expenditure) may relate to badgers travelling at speed and in a more direct path, whereas in the woodland area the GPS-enhanced dead-reckoned track is more tortuous

If an animal does engage in locomotion creating paths at varying tortuosities, this also results in variation in the accuracies of the measurements of landscape utilization by individuals, not only in the time spent in each habitat, but also the activity undertaken when GPS-only data is used. Although badgers often use well-trodden paths when they travel between locations (e.g., setts, latrines), which likely constrains some of their nightly path tortuosities, our study animals spent most time and were most active (as determined by summed VeDBA per minute) in woodland. However, there was no effect of ambient temperature on activity [48, 49, 53]. Presumably this is because ambient temperature did not vary sufficiently across the measurement period in the current study to substantially affect activity. Activity varied with habitat, with more vigorous activity and more tortuous tracks occurring within woodland (Figs. 6, 7). This might be indicative of increased activity in food-rich patches [32, 54], or indeed greater social interaction at and near the sett (which is more likely to be in woodland). Speed of travel also varied amongst different habitats, with woodland and pasture associated with greater speeds. Clearly, understanding the precise relationship between VeDBA, speed, and track tortuosity will help interpret such area-specific behavioural patterns, and for this, the implications of any gait change with speed will also need to be considered [55, 56, 57] examined badger movement patterns in a Mediterranean landscape and suggested that track tortuosity was likely to be related to the distribution of food [57]. This may be the case in the current study, but confirmation would require examining other behaviours associated with each location and habitat such as scent-marking and visiting latrine sites as well as social interactions that might be potential drivers of track tortuosity.

Overall, it is evident that GPS-enhanced dead-reckoned data has the potential to provide detailed information on how badgers, and other species, utilise and interact with their environment. Our results also show that use of GPS-enhanced dead-reckoned data will indicate that animals utilise specific areas of the surrounding habitat, range further, and travel further than use of GPS-only data would suggest. Moreover, the benefits of GPS-enhanced dead-reckoning include measurements of fine-scale information, providing precise estimates of speed, track tortuosity and activity, which can be associated with precise position, and which have been shown to be significantly affected by the resolution of data used in their determination. The implications of this work lie far beyond single species and single environment studies insofar as these methods will be useful to ascertain how species utilise their environment, what activities they undertake at specific locations, and crucially, what measurement resolution is needed.

Abbreviations

GPS	Global positioning system
VeDBA	Vectorial dynamic body acceleration
OSGB	Ordinance survey of Great Britain
Hz	Hertz
KDE	Kernel density estimate
MCP	Minimum convex polygon
DR	GPS-enhanced dead-reckoning
GLMM	Generalised linear mixed effects model
GLM	Generalised linear model

Supplementary Information

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Supplementary Material 1.

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Author contributions
DMS, NJM and RJD conceived the initial study and oversaw the project and fieldwork. KB, DMcC, RJD and DMS conducted fieldwork and data collection. SS, KB, RPW, SM and DMS analyzed the data. SS, KB, SM, DMS and NJM prepared the initial manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
All work on animals described here was conducted under Home Office Project Licence 60/4285 and was subject to internal ethical review at the Animal and Plant Health Agency.

Competing interests
The authors declare no competing interests.

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