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Using dead-reckoning to track movements and map burrows of fossorial species

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Abstract

Background Researching the movement patterns of fossorial animals and mapping of burrow systems presents a significant challenge due to the difficulty of direct observation and the limitations of most tracking systems to collect location fixes underground. A potential solution is using archival tags combined with dead-reckoning, a technique employed in nautical navigation to track animal movement underwater and through dense vegetation. However, this method has not yet been applied to the mapping of complex burrow systems in fossorial species. This study aims to test this approach using accelerometers and magnetometers attached to collars on black-tailed prairie dogs (*Cynomys ludovicianus*) The goal was to determine if 2D dead-reckoning, based on vectors derived from speed and heading data, could accurately track prairie dog movements and, by extension, map the structure of their burrows. To evaluate this method, we deployed 12 tags on wild animals and recorded acceleration and magnetometer data at 40 Hz and 16 Hz, respectively. These animals were allowed to move through artificial burrows comprised of plastic tubes of defined shape, before being released into the wild and tracked. The "tube runs" were used to validate 2D dead reckoning trajectory estimation. We compared the accuracy of five techniques for deriving speed: vectorial dynamic body acceleration (VeDBA), vectorial static body acceleration (VeSBA), step count, and constant speed.

Results Acceleration signals reliably indicated traveling behavior. Among the methods tested, the Vectorial sum of Dynamic Body Acceleration (VeDBA) proved to be the most accurate proxy for speed, with the smallest mean error (Fig. 5). Speed coefficients for VeDBA varied between runs (0.009 to 0.042) with this variation being the result of individual differences The animals moved at speeds ranging from 0.01 to 1.42 m/s. In addition, the 2D dead-reckoning process documented all turns (100%) in our plastic tunnel system and had a mean error of 15.38 cm over all test tunnel lengths of up to 4 m. This highlighted the potential for representing animal movements and the layout of burrows in free-roaming prairie dogs. We also determined that use of acceleration metrics identified 22 of 24 times (92%) when collared animals exited their burrows but only 4 or 6 times (67%) when they entered them.

Conclusions This work highlights the importance of dead-reckoning in studying space use by fossorial animals, essential for understanding how they interact with their environment, including vegetation and topography. Beyond environmental context, analyzing the specifics of animal movement—such as path tortuosity, speed, step lengths, and turn angles—is crucial for insights into species diffusion, foraging strategies, and vigilance.

Keywords Black-tailed prairie dog, Dead-reckoning, Fossorial, Burrows

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Background

Animal movement data are key to understanding behavioural ecology [1, 2], habitat use [3], animal energetics [4, 5], and disease ecology [6]. Conventionally, animal movement trajectories are constructed using sequential animal locations obtained using GPS [7], PTT or VHF telemetry [8]. However, these methods do not work or perform poorly in areas, where the telemetry or GPS signal cannot be transmitted, such as marine environments [9], and terrestrial habitats under thick vegetation or underground (e.g. [8, 10]). Researchers have trialled magneto-inductive tracking for European badgers (Meles meles) underground [11], but the method faced significant flaws. Signal interference from soil composition and environmental conditions, insufficient spatial resolution for complex setts, and the size and energy demands of the equipment limited its effectiveness. More generally, some researchers have used 'dead-reckoning', a process that uses information on animal heading (magnetometer), speed (accelerometer), and change in height/depth (barometer) to reconstruct movement paths by vectors [12, 13]. Examples of the use of dead-reckoning include diving seabirds [14], marine mammals [15, 16] and forest mammals [17] but there have been few attempts to uncover burrowing species complex underground systems [11]. We note that burrowing species also have a vertical component to their tunnels and so many of the challenges faced by 3D dead-reckoning of e.g. marine animals, will be applicable to fossorial species although presumably to a lesser extent. Previous studies of fossorial species' behaviour and movement primarily utilized accelerometer data to learn about underground speeds [18], behaviour [19, 20], and energy expenditures [18]. Despite its potential to reveal trajectories of animals inhabiting subterranean spaces, where conventional methods are ineffective, dead-reckoning, even in 2D, has never been applied to track the fine-scale movements of fossorial species except for a notable study by Link et al. [21]. These authors studied this approach for elucidating the movements of Brown rats (*Rattus norvegicus*) in the laboratory but did not take their system to the wild. Here, we test the application of 2D dead reckoning to reconstruct the trajectories of a fossorial species using a case study of black-tailed prairie dogs (*Cynomys ludovicianus*).

Among fossorial species, prairie dogs (*Cynomys* spp.) represent an ideal study species for evaluating the ability to use dead-reckoning to track subterranean movements. Represented by five species in North America, these relatively large (500–1500 g) ground squirrels are considered keystone species in grassland ecosystems due to their ability to alter grass composition and movement of soil by creating and maintaining complex burrow systems [22, 23]. Prairie dogs are capable of excavating burrow systems comprised of interconnected burrows of 10–30 cm in diameter to depths of up to 5 m below the surface [24, 25]. These colonial animals occur at high densities of 10–35 individuals per hectare and can create above-ground burrow entrances of up to 325 burrows per hectare within colonies that encompass thousands of hectares [24]. These colonies of prairie dogs provide a source of prey, landscape heterogeneity, and subterranean habitat that supports a host of dependent species, including the endangered black-footed ferret (*Mustela nigripes*) [23, 26]. Yet, despite the important ecosystem role prairie dogs serve in grassland communities, very little information has been acquired regarding the subterranean movements and behavior of these rodents, primarily due to the paucity of tracking technology capable of collecting underground data.

Here, we tested the use of dead reckoning to reconstruct the movements of black-tailed prairie dogs. Our aims are (i) to examine various speed metrics used to derive distance for the dead-reckoning analysis when prairie dogs move along burrows; (ii) to examine whether tri-axial accelerometer data can define when prairie dogs enter and exit their burrows and (iii) to collect data from numerous individuals within one area to map out the prairie dog burrow systems in two dimensions.

Methods

Study site

Data collection for this study was conducted from 16 to 25th August 2023 at American Prairie (AP), a privately-owned wildlife conservation area located in Phillips County, Montana, USA. AP is within the North American Great Plains region. The vegetation is dominated by mixed-grass grassland, which consisted of western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), and needle and thread (*Hesperostipa comata*) grasses mixed with silver sagebrush (*Artemisia cana*) and scarlet globemallow (*Sphaeralcea coccinea*), woolly plantain (*Plantago patagonica*), and American vetch (*Vicia americana*; [27]. The study site consisted of a 200 m by 200 m plot of a 288 hectare colony of black-tailed prairie dogs (*Cynomys ludovicanus*; longitude: − 107.7520, latitude: 47.7715, magnetic field intensity *ca.* 55,000 nT and inclination *ca.* 70° downward, though this varies over time slightly). Elevation within the study site ranged from 718 to 723 m. Although the abundance of prairie dogs was within this study site was not robustly determined, a cursory evaluation using visual observations suggested at least 50 individuals were present at the time of this study.

Biologgers

To map the movements of prairie dogs using dead-reckoning, we designed and created a collar-based attachment method for affixing a Daily Diary (DD; http://wildbytetechnologies.com/tags.html) circuit board to each animal (Fig. 1a). Our model of the DD was the 'Alice' version, which, within its housing (see below), measured 42 × 25 × 14 mm. The DD was powered by a 50 or 60 mAh rechargeable lithium battery, contained within a 3D printed Anycubic resin housing attached to the bottom of the collar. The collar was made using a strap of 15 mm width × 150 mm long biothane synthetic leather (The Strap Warehouse, Millersburg, Ohio, USA). The collar was fastened to the animal using a flat head bolt and nut attached using predrilled holes. Each collar also contained a solar powered GiPSy 6 GPS logger (TechnoSMart, Rome, Italy) and a second 100 mAh rechargeable lithium battery for the GPS. The GPS was not used in this study. The total weight of the collar and all components was ~ 16 g making up 1–2% of the species' body mass.

The DD consisted of a multi-sensor biologging unit [13, 28], comprising tri-axial accelerometers and tri-axial magnetometers. The unit was programmed to collect both acceleration (at 40 Hz) and magnetic field intensity (16 Hz) in all three orthogonal axes. The logger recorded the data on 128 kilobyte internal memory, allowing up to 8 days of continuous data. On the day of captures, the device was switched on and the DDs were calibrated by engaging them in a defined set of movements, conceived to provide proper three-dimensional coverage for the G- and M-spheres [29].

Animals captures and deployment

We capturedprairie dogs from 15 to 25 August 2023 using a matrix of 125 live traps (6 × 9 × 24 inches Tuffy 24; Tru Catch Traps, Belle Fourche, South Dakota, USA) distributed through our study site. We labelled and recorded the location of each trap using a hand-held GPS unit. We baited traps with sweet feed grains (MannaPro, St. Louis, Missouri, USA) and set traps open each morning and evening for a period of 4 h. We visually examined each trap once an hour to ensure captured prairie dogs were not exposed to high temperatures. We transported captured adult prairie dogs weighing > 800 g in the traps to nearby shade for processing (mean mass of the collared animals = 1.04 kg, range 0.80- to 1.68 kg). We recorded the weight, age, neck circumference, and sex of each animal we collared (Supplementary Information Table S1).

We briefly restrained each animal to attach the biologger collar. The orientation of the tags on the collars was set up such that the 3 acceleration axes corresponded to the main body axes of the animals (surge—*x*-axis, heave—*y*-axis and sway *z*-axis), although the collars could rotate so the heave and sway axes were effectively interchangeable. We then marked each animal using non-toxic hair dye along the back with a unique pattern for each individual. We returned the animal to the trap and monitored for approximately 15 min to ensure the collar remained in position and did not cause undesirable behavioral effects (i.e., excessive scratching or lethargy).

Before each collared prairie dogs was released, we performed a series of trials on them designed to provide fine-scale movement and location data over a verifiable path to compare the accuracy of the dead-reckoning process used in this study. We constructed "tube runs" by attaching straight and 90° elbow sections of 120 mm diameter, ventilated, and transparent plastic tubing

Fig. 1 Technology and apparatus used to assess dead-reckoning potential for prairie dogs. **A** Photo of the logging system deployed on prairie dogs; **B** with example of constructed tube run with trap connected

(Katee Product Inc, Chilton, WI, USA) together to create various shapes and configurations of total lengths between 1 and 3 m (Fig. 1b). We randomly choose the specific shape and configuration of each tube run used for each individual. We measured the length of each section of tube and the distance of ridges occurring at evenly spaced intervals of each section to reference the position of animal at approximately 10 cm accuracy as the prairie dog moved through the tube. We positioned each tube run such that one end was within 25 cm of the closest burrow to the location of capture of each animal. At the other end, we opened the door to the trap containing each collared prairie dog and allowed the animal to freely exit the trap and into the tube run. We recorded videos of the movement of each individual from the cage, through the tube run, and out into the burrow using smartphones held horizontally in hand while standing upright approximately 1 m from the tube run.

Camera traps

Across the study area, we deployed 87 motion-triggered cameras (Reconyx HyperFire 2, Reconyx, Holmen, WI, USA). We programmed the cameras to take 30-s videos with no delay anytime a motion was detected throughout the time period when collars were attached to prairie dogs. We positioned camera traps such that the field of view captured in recorded videos included all burrow entrances within approximately 20 m of the location at which the prairie dog was released after the collar was attached (Supplementary Information Fig. S1). We installed each camera at a height of 50 cm above the ground on a metal rebar stake positioned 2.0–2.5 m from the burrow entrance. Videos were recorded on a 32 gigabyte memory card. We replaced memory cards and camera batteries every 2–4 days to ensure sufficient memory and power.

To aid in the video review process described below, we recorded the location of each burrow within the field of view of each camera at 20 cm horizontal accuracy using a high-precision GPS receiver (Catalyst DA2, Trimble, Sunnyvale, CA, USA). We identified the position of each burrow in the recorded videos by recording ourselves holding a sign indicating a unique identification number while standing at each burrow.

Recaptures

After 5 days, we initiated efforts to recapture all collared prairie dogs using the same matrix of traps. We followed the same baiting and trap setting protocol as described above for recapturing all animals. Once a collared prairie dog was recaptured, and if the collar appeared intact, we performed a second tube run trial before removing the collar to increase our sample size on number of tube runs. In this case, the tube run was positioned between the trap containing the prairie dog and an empty trap at the other end positioned to safely contain the prairie dog after the animal moved freely through the tube run. We again recorded videos of the movement through the tube runs using smartphones. Once this second tube run was completed, we briefly restrained the prairie dog, removed the collar, and collected data on weight and condition of the animals. The animal was then released at the capture location.

Non-translocational movement

We examined the video footage and acceleration data to define 'non-translocational movement' (such as shaking or grooming) compared to 'traveling movement' (where the animals moved along their tunnels), because both may produce substantial acceleration signals. We reviewed the video footage to record the date, time, duration, and frequency of a set of non-translocation behaviors performed by collared prairie dogs (Supplementary Information Fig. S3, Table S2). Traveling was defined by smoothed VeDBA (smoothed across a second or 20 events) values. Any continuous movement less than five seconds or VeDBA smoothed < 0.25 g else was considered either non-translocational movement or resting. (Supplementary Information Fig. S2).

Dead-reckoning: comparing speed metrics

Within 2D dead-reckoning over short distances, as is the case in this study, heading estimates are expected to produce minimal deviation, because most solid state compasses are stated by the manufacturers to give heading to better than 2°. This is not true for speed estimates which are typically derived from acceleration proxies [30]. Dead-reckoning analysis was undertaken to produce paths consisting of 1 location per second for the prairie dogs by taking magnetometry data in tandem with the accelerometers to derive heading [12, 30] and assessing using several methods to derive speed, and, therefore, distance including; (i) vectorial dynamic body acceleration (VeDBA), (ii) vectorial static body acceleration (VeSBA), (iii) step count and (iv) constant speed. Each method is explained below:

VeDBA

VeDBA is the most common metric for speed for the dead-reckoning process [31] and calculated using;

$$VeDBA = \sqrt{(DBAX)^2 + (DBAY)^2 + (DBAZ)^2} \quad (1)$$

where DBA is the dynamic acceleration for the three axes (X, Y and Z). The dynamic acceleration was calculated by subtracting static acceleration (the raw acceleration smoothed with a running mean over 2 s [32] from the raw acceleration. This removes most of the gravitational influence the tag is undergoing to provide a metric that reflects the dynamism of animal movement [33]. Bidder et al. [31] regressed Overall Dynamic Body Acceleration (ODBA)—a metric that differs only marginally from VeDBA [34] against speed for 9 animal species on a treadmill and found good correlations (r^2 values between 0.74 and 0.99) for linear fits. We used this approach for our tunnel runs by calculating the speed of a run (the distance covered/time taken) and regressing it with the mean VeDBA for that run to derive speed vs VeDBA coefficients for a linear fit.

A VeDBA threshold or window method [12, 33] assumes that low-values of VeDBA occur when animals are not travelling, e.g. standing, sitting or lying, or extremely high, short-term (<5 s) VeDBA values when animals shake themselves or roll rapidly. Thus, to identify travelling, we implemented a Boolean rule that highlighted when VeDBA values lay within thresholds. We then implemented dead-reckoning when these conditions were met. These window values are presumed to vary between species and tag attachment [35] so travelling behaviour should be ground-truthed with observations when possible. In the case of prairie dogs, this threshold was set between 0.1 and 1.5 g following observation of the tube runs undertaken by the animals following release.

VeSBA

VeSBA incorporates all three acceleration axes like VeDBA, but instead removes the dynamism highlighted by VeDBA out of the animal movement. However, we have noted that, although VeSBA is particularly valuable when animals have high centripetal acceleration (such as occurs during cornering [36], it also appears to increase with speed. VeSBA is derived via;

$$VeSBA = \sqrt{(SBAX)^2 + (SBAY)^2 + (SBAZ)^2} \tag{2}$$

where SBA is the static acceleration in the three axes (X, Y and Z), calculated by running a running mean smoothing window over two seconds across each acceleration axis [32]. We used a VeSBA window approach in the same way as we did for VeDBA (see above) but used a different threshold to define movement, since the derivations of VeDBA and VeSBA are fundamentally different.

Step definition

One of the most obvious delineators of traveling behaviour and speed is the identification of steps (or strides), assuming they can be defined within the tag data. A particular form of analysis based on a Boolean method, the Lowest Common Denominator (LoCoD) approach, can be used to define individual steps within an animal's movement [37]. This approach looks for specific changes and defined patterns in acceleration signals, that occur during movement, that are predictable with each step, and which only occur during traveling behaviour. In the use of the LoCoD approach, we attempted to identify and quantify steps (Fig. 2) and then used a step count to construct a step count vs speed relationship coefficient to quantify distance for dead-reckoning. For this, the step count per meter of tunnel run was regressed against speed for all runs. To implement this, the tube-run videos were synchronized with their respective DD data to define the sensor-dependent features of steps. Following this, we produced an algorithm within the Daily Diary Movement Trace (DDMT) software [28], which implemented the LoCoD method, and searched for steps within any prescribed animal movement data [37]. For prairie dogs, we calculated the jerk (=rate of change of acceleration) between x-axis data points that were 0.075 s apart (corresponding to the time for 3 points to occur). The quantification of steps had two conditions, where the jerk surpassed 0.2 g/s, and VeDBA smoothed (across a second) was higher than 0.25 g. To mark individual steps, a blind spot was implemented following identification of a step so that strides were only marked once despite having variable stride lengths [37]. Our optimal blind spot lasted 5 sequential events (0.125 s).

Constant speed

The last method tested as a proxy for speed was estimating a constant speed. The metric was taken from the mean speed value from each tube run. The constant speed in this case would be the distance between the first and last verified point divided by the time taken to complete the tube run.

Assessing different speed methods and accuracy using observed tube runs

To evaluate if 2D dead-reckoning analysis might be viable for fossorial animals whose movement is constricted by the burrows, we processed the data from the tube run by examining the recorded videos frame by frame to determine 'true' location on a second-by-second basis (position determined to the nearest 10 cm). First, we used video editing software (Adobe Premiere Pro, Adobe, San Jose, CA, USA) and reviewed the video at 100 frames per second, from there we could locate the position of the prairie dog, and specifically, the collar worn by the prairie dog, at 1-s intervals beginning from the start of each video. We replicated the configuration of each tube run to scale in QGIS version 3.24 by creating a vector

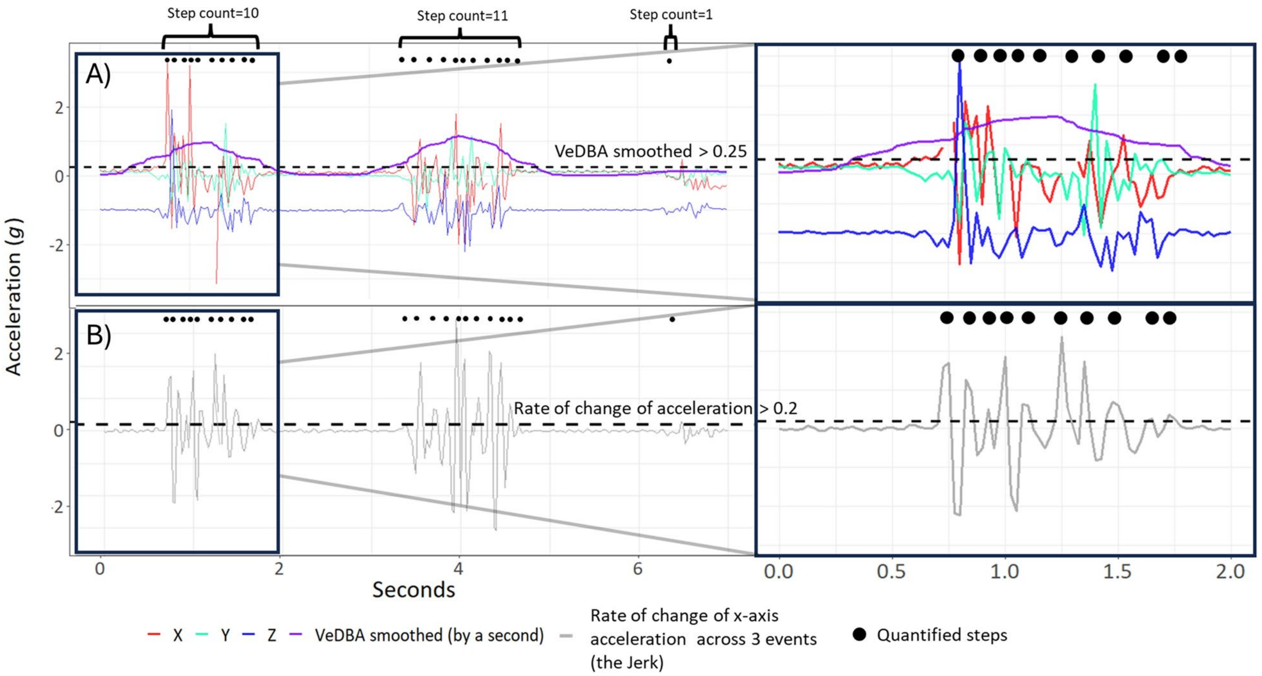

Fig. 2 Step detection in Prairie dog movement. **A** Raw acceleration signals in x-, y- and z-axes, recorded on a Prairie dog during locomotion within a tube run, from which VeDBA can be calculated. **B** Surge in x-axis acceleration. One step was detected each time two conditions were simultaneously verified: (1) VeDBA smoothed (by 1 s) > 0.25 g and (2) rate of change surge in x acceleration (the jerk) > 0.2 g. Acceleration taken from 1 individual during movement/stepping within a tube run. The data shown is 12 s

shapefile including the dimensions and arrangement of each segment of tube. We then created a point shapefile, where points placed along the replicated tube runs in our vector shapefile matched the position of the prairie dog within the tube run at each 1-s interval as observed in the videos. We labeled these 'true' locations with the interval number to be used for assessing the accuracy of the dead-reckoning of the movement path of each animal through the tube run.

The 'great circle distance' distance between the tube run location and the dead-reckoned location was calculated (using the Earth's radius of 6371 m) via the following equation:

$$Distance = arc\cos(\sin Lat_{DR} \cdot \sin Lat_{TR} + \cos Lat_{DR} \cdot \cos Lat_{TR} \cdot \cos(Lon_{TR} - Lon_{DR})) \cdot 6371.103 \quad (3)$$

where $\mathrm{Lat_{DR}}$ is the latitude of the departure point, $\mathrm{Lat_{TR}}$ is the latitude of the target point, $\mathrm{Lon_{DR}}$ is the longitude of the departure point, $\mathrm{Lon_{TR}}$ is the longitude of the target point, all measured in radians, and 6371.103 is the approximate radius of the Earth (in km) [38]. This calculation was carried out using the package 'fossil' within R [39]. The same package was used to calculate animal travel speed.

Defining entering a burrow, moving underground, and burrow depth

To map out the prairie dog burrow system, underground movement needs to be defined. We used the tube runs and camera trap video footage synchronised with the acceleration data to derive a LoCoD-based method (see above) to quantify when animals entered burrows. We used the videos recorded using the array of camera traps we deployed to identify the time, location, and movement (entering a burrow or exiting a burrow) of our collared prairie dogs. We reviewed each video and recorded the time stamp and the location using the burrow identification process described above, each time a collared prairie dogs were observed entering or exiting a burrow. We identified individual

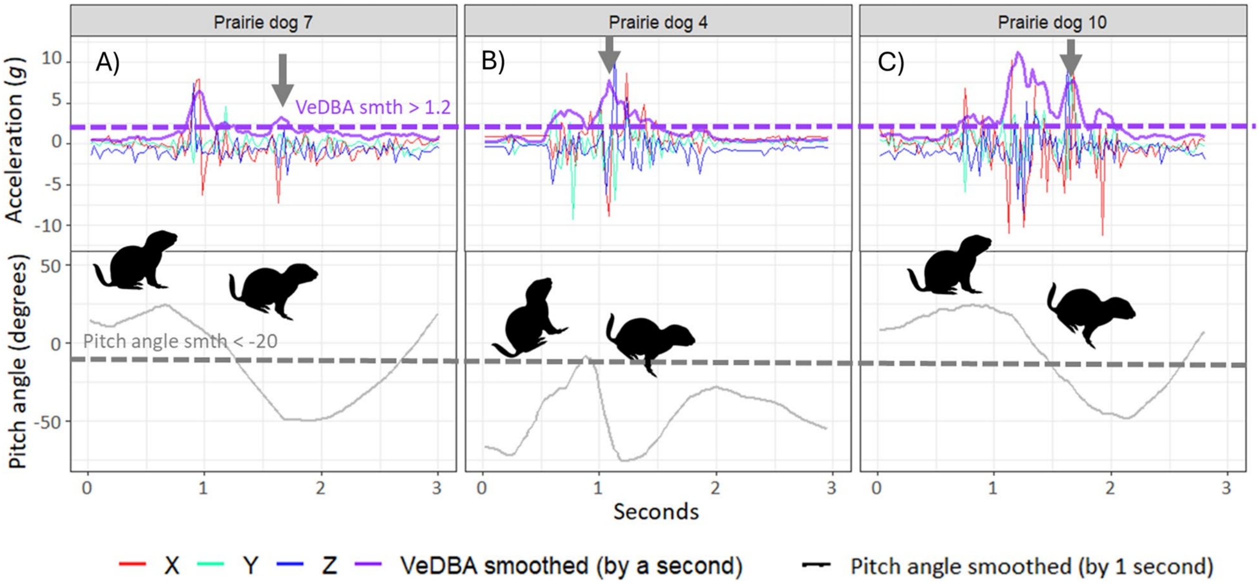

Fig. 3 Identification of burrow entry by prairie dogs: tri-axial acceleration data, smoothed VeDBA, and smoothed pitch angle for three example prairie dogs descending into their burrows. Each individual is represented by a unique letter. The gray arrows indicate instances, where both conditions of the dual criteria are met, and "entering the tunnel" is identified within the acceleration trace. Behaviour was categorized using video footage after a tunnel run or camera trap footage and each panel (A, B, C) represents a different instance of this behaviour

prairie dogs based on the unique dye-mark given during capture.

The rule for entering a burrow used was; when the animal pitch angle (derived from the acceleration x channel [32]) smoothed (using a running mean across 1 s of data) was less than − 20° and VeDBA smoothed over 0.5 s was greater than 1.2 g, then 'mark as a descent into a burrow' (Fig. 3).

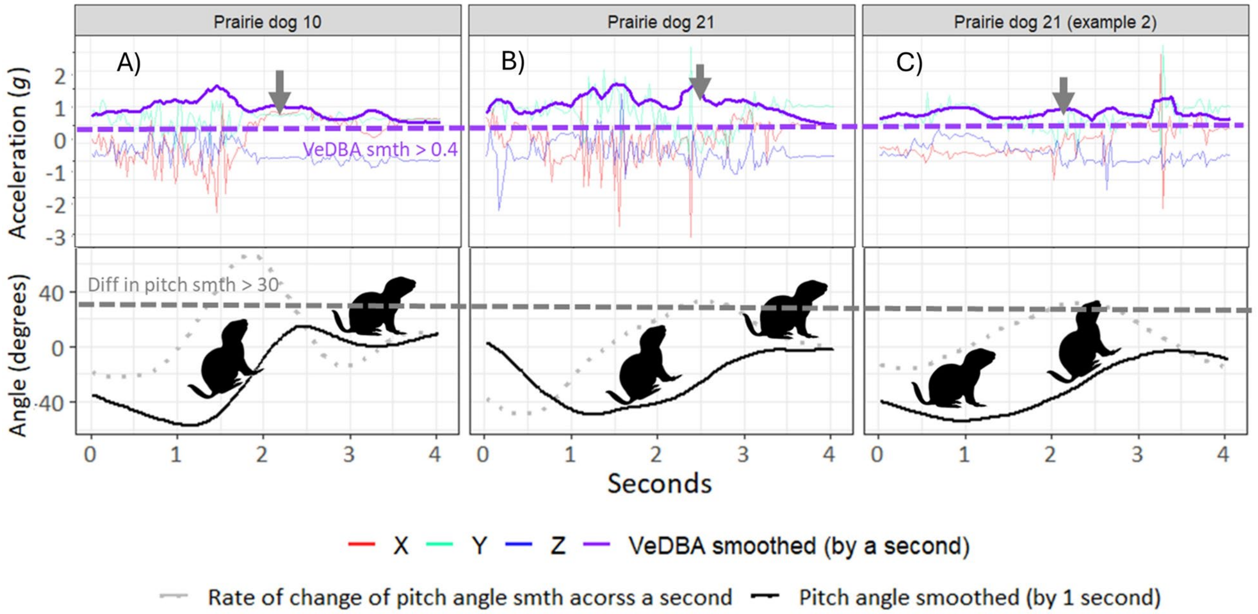

Fig. 4 Identification of burrow entry by prairie dogs: tri-axial acceleration data, smoothed VeDBA, and smoothed pitch angle for three example prairie dogs descending into their burrows. Each individual is represented by a unique letter. The gray arrows indicate instances, where both conditions of the dual criteria are met, and "exiting the tunnel" is identified within the acceleration trace. Behaviour was categorized using video footage from camera trap footage and each panel (A, B, C) represents a different instance of this behaviour

The quantification for exiting a burrow utilized a differential channel, where the rate of change of pitch angle, smoothed across 1 s, was calculated across a second. The rule had two conditions which had to be fulfilled for the behaviour to be classified as an 'exit'. First, the difference in smoothed pitch angle had to be > 30°/s and, second, the smoothed VeDBA (smoothed across half a second) had to be > 0.4 g (Fig. 4). We noted that burrow exits always took > 0.5 s and that some transient behaviors, such as standing up, could cause false positives. We removed these by eliminating all burrow exits identified by our two conditions (above) that lasted less than 0.5 s. (Supplementary Information Fig. S3, Table S2).

Applying dead reckoning to 'free-roaming' data

We took horizontal animal movement to map out the burrows defined by the dead-reckoned movements of individuals starting from above ground verified points. We defined verified points as times when the true above ground location of the prairie dog could be determined, because the animal appeared in the camera trap array at a recorded burrow. The dead-reckoned paths were then filtered based on where the prairie dogs had entered the burrow located at each verified point. All spatially relevant underground locations were super-imposed onto one another to estimate the location of underground burrows. A combination of DDMT [28] and R [39] with the 'ggamp' package was used to visualise and map out the burrows. Revisit and residence time analysis was conducted using the 'recurse' package. A 1-m radius circle was moved along the dead-reckoned underground track, and a 'revisit' was recorded whenever the animal left and then re-entered the circle. In addition, if the animal remained within the circle, the total time spent at that location was accumulated.

Results

Dead-reckoning: comparing speed metrics

Out of the 18 prairie dogs we collared as part of this study, we obtained DD data from 12 individuals that could be used for dead-reckoning (Supplementary Information Table S1). Comparing the different speed methods using DD data obtained from 23 tube runs from these animals of up to 4 m in length, we found the VeDBA metric the best proxy for speed (Supplementary Information Fig. S4. Accordingly, VeDBA also gave location accuracy within a 20 cm margin of error for 75% of the time across all tube runs. The other methods; Step definition, VeSBA and constant speed had higher levels of error within the desired 20 cm error margins occurring 52%, 42% and 42% of the time across all tube runs, respectively (Fig. 5, Supplementary Information Fig. S5). Speed coefficients varied between runs (0.009 to 0.042 when VeDBA was used for speed (Supplementary Information Table S3) with this variation being the result of individual differences. We suspect that such differences were due to variable collar attachment between individuals, especially tightness, which was hard to standardize [35].

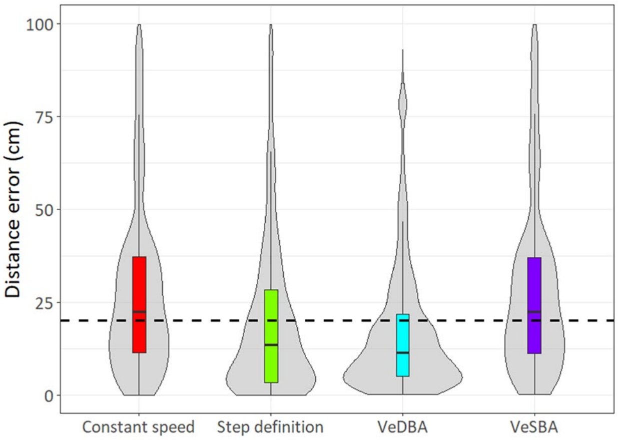

Fig. 5 Comparison of various proxies for speed in DD tag-equipped Prairie dogs—box-whisker plot layed over a violin plot using the distance errors based on various speed estimates (constant speed, step definition, VeDBA and VeSBA—see text) derived from prairie dogs moving along specified tubes up to 4 m long before entering their burrow. Data are all positions taken from 23 tube runs across 12 individuals. The whiskers of the boxplot indicate the upper and lower limits, while the edges of the box represent the upper and lower quartiles. The central line denotes the median, and outliers are not displayed

All prairie dog tube runs were visualised by overlaying the verified points of their positions over the dead-reckoned points with VeDBA being used for speed (Fig. 6). The 2D dead-reckoned estimates of position mostly matched well (15.38 cm mean error), with the largest errors due to quick movements (39.76 cm largest error). Estimation of tube run underperformed when animals speed exceeded 0.38 m/s (see Supplementary Information Fig. 5). The mean tortuosity, calculated as the ratio of the straight-line distance between the start and end points of the tube run to the total path length, was 0.71. The mean positive acceleration (rate of change of speed) of the animals moving through the tube was 0.11 m s^{-2}.

Defining entering a burrow

Our metric for detecting when a prairie dog entered the burrow system (Fig. 3) successfully identified 22 out of 24 burrow entrances. However, it was less effective at detecting when the animals exited, correctly identifying 4 out of 6 exits (Fig. 4). The tube runs allowed us to

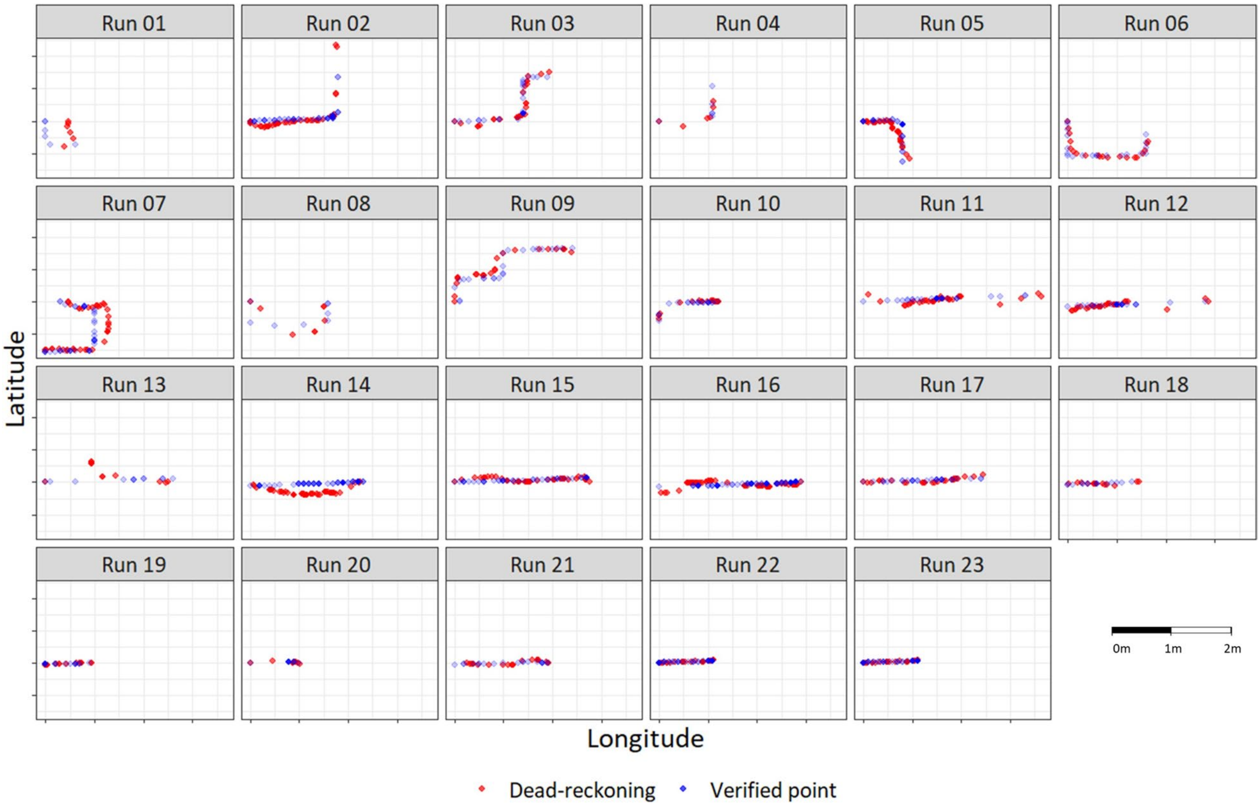

Fig. 6 Dead-reckoned tracks from Prairie dogs accord well with tunnel architecture—comparison of dead-reckoned paths with verified points during prairie dog movement through transparent pipes used to simulate burrows (see text). Data taken from 23 tube runs across 12 individuals

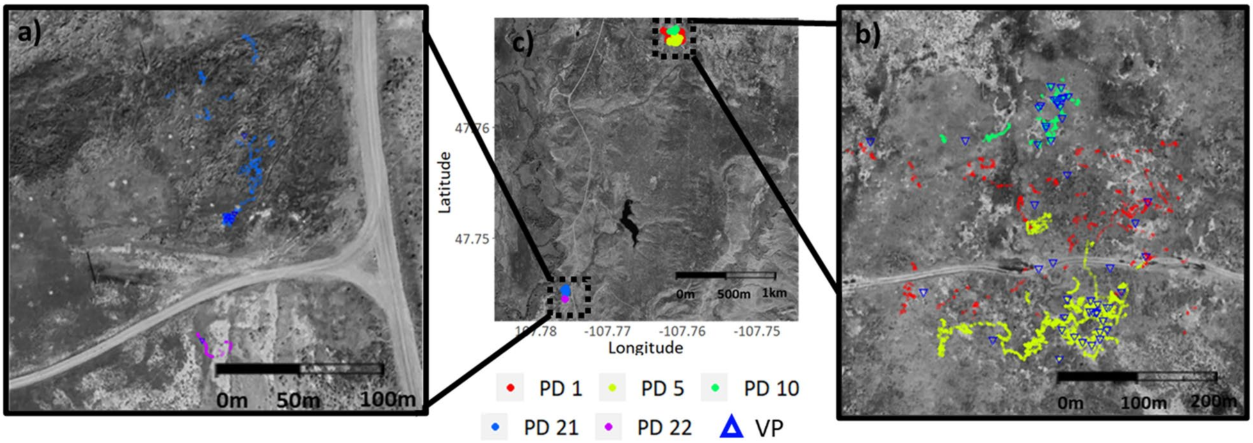

Fig. 7 Prairie dog burrow architecture as deduced by 2D dead-reckoning—location of prairie dog burrows as deduced using dead-reckoning on 5 individuals with (**a**) Prairie dog 4 and 5 shown in blue and purple, respectively, tagged at the 'Enrico' study site, (**b**) locations of prairie dogs 1, 2 and 3, shown in red, yellow and green, respectively, with individuals tagged at the 'Box elder' study site. **c** shows how both sites are situated within American Prairie. Data shown is a total of 31 h across 5 individuals

validate our method for defining movement under controlled conditions (Fig. 2). We only included animals that did not display behaviors that could move the tag during the tube runs, such as shaking and grooming so our experimental protocol did not account for non-translocational movement.

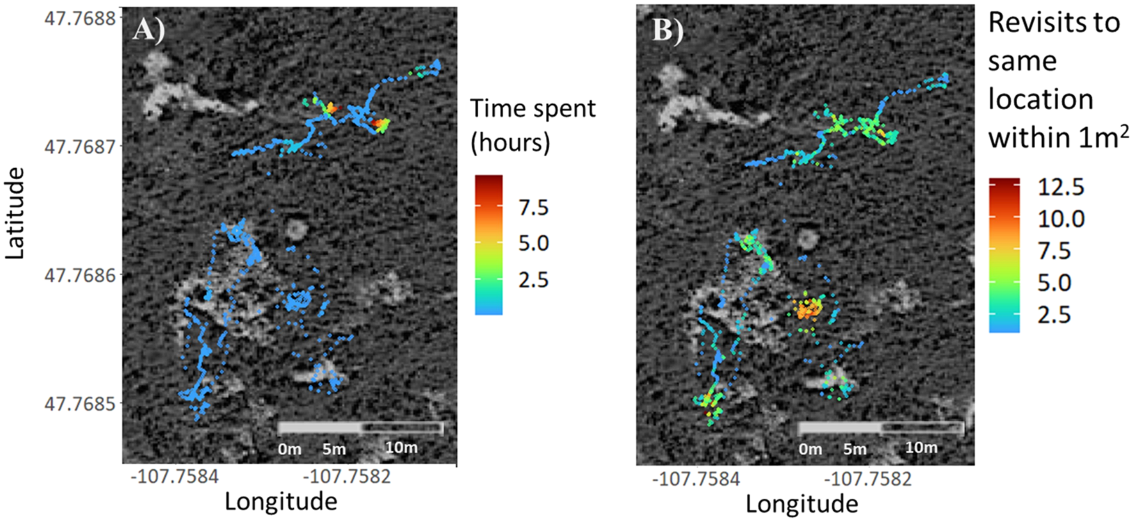

Fig. 8 Detail in Prairie dog burrow architecture as deduced by 2D dead-reckoning—location of prairie dog burrows as deduced using dead-reckoning on 1 individual (**a**) shows the total time spent according to location and (**b**) shows the number of revisits within 1 m^2 of particular sites. Data shown is a total of 20 h. The individual selected for this analysis is was prairie dog (PD) 7

Applying 2D dead reckoning to 'free-roaming' data

We plotted 31 h of underground movements for 5 individuals within 2 h of a verified point (Fig. 7), a period where we considered that dead-reckoned errors would be manageable and at least well defined in time. Across these individuals, we successfully mapped out 382 m of burrows with further analysis showing a ~ 1% space shared with space use of 4.78 km^2 with a max burrow length of 10 m (Fig. 7). Revisit analysis indicated the time spent in various location pockets underground and how regularly the burrows were used and is illustrated in Fig. 8 for one individual.

Revisits by animals moving along the same path can also help define the architecture of the burrow, refining estimates (Fig. 9, [40]).

Discussion

While dead-reckoning is well documented for aerial, aquatic and (above ground) terrestrial species [10, 41, 42], there are substantial unknowns in fossorial animals. These unknowns include the extent to which traveling behaviour can be reliably identified and how good metrics for speed, such as VeDBA [12], apply to animals whose movement is constrained within burrows. This is

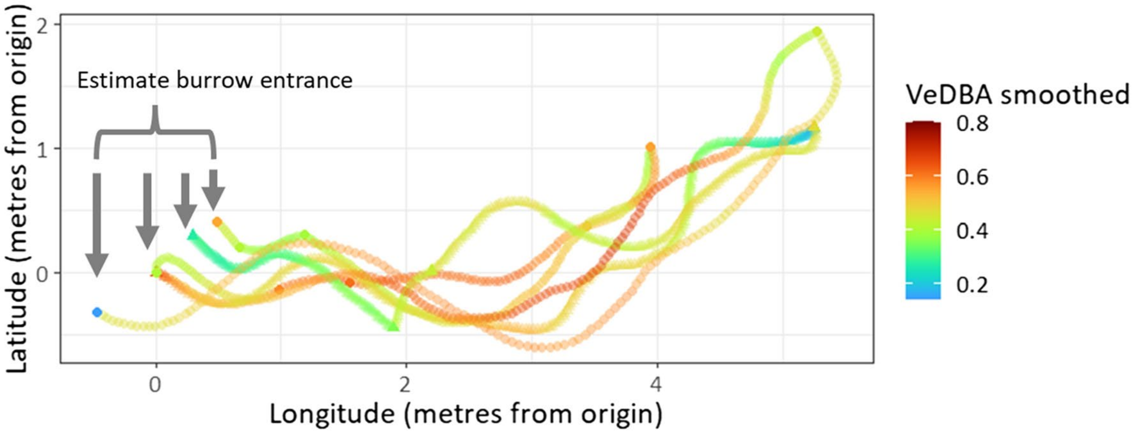

Fig. 9 Superimposed dead-reckoned tracks can help define Prairie dog burrow architecture—multiple superimposed tracks of a single Prairie dog moving down one burrow path with respect to a single verified position (a camera) to illustrate how multiple tracks may function together to provide a more precise estimate of burrow space. Data shown is a total of ~ 4 min. The individual selected for this analysis is was prairie dog (PD) 7

a first attempt to determine the movement of a fossorial species while underground, and in the process, we derive information on the structure of the burrows.

Speed proxies

We examined four metrics as proxies for speed and found that VeDBA produced a lower mean and maximum error than the other three methods (Fig. 5). However, our defined burrow runs may be overly generous to the VeDBA metric, since individuals using our system either moved or were stationary, not engaging in any non-movement activity, such as scratching, that produces an appreciable VeDBA signal. Nonetheless, the value of VeDBA as a speed metric has been stressed in the literature for terrestrial animals [12, 30], and it is encouraging that it also seems to work well underground. However, we did not explicitly examine what happens to VeDBA when prairie dogs went around a corner and this is a subject that needs further study. It is complex, because many animals reduce speed during cornering, especially when speeds are high, not least because cornering requires more power for any given speed [43]. As a possible clue to speed during moving round corners, VeSBA has been cited as more useful for indicating high speed cornering at least [31, 44], although our attempts to use it as a general speed proxy showed it to be markedly worse than VeDBA (Fig. 5). Whether cornering or not, in any case the movement speed of prairie dogs in the burrows seems to be generally less than 0.15 m/s, where any VeSBA signal is likely to be minimal. Constant speed underperformed too, even though, for prairie dogs, the expectation was that, in the confined space of the burrow, the speed would change little. However, within our tube run experiments, the rodents displayed a range of speeds (0.01 m/s to 1.42 m/s) that immediately indicate the extent of errors. In a laboratory study on rats, Link et al. [40]successfully used 'pseudo-step counts' (a single peak in the heave acceleration corresponding to four footfalls) to determine distance traveled for their dead-reckoning study. Similarly, we considered step definition in our approach, because steps obviously equate to distance but animals have increases in speed accompanied by increases in stride frequency which is also tied to stride length, confounding any linear interpolation [45, 46]. In our work, the mean error using this metric, although less than VeSBA or constant speed values, was higher than for VeDBA (Fig. 5). We assume that this is due to prairie dogs changing both step frequency and stride length with speed, as do many mammals [47]. If the conditions for this were precisely defined for prairie dogs, step frequency could still be potentially used to derive speed. More work is needed to elucidate this. It may also be that the ventral mounting of the DD on the collar meant that the unit occasionally touched the ground during travelling, putting in false steps and reducing the accuracy of the approach. Finally, it may be that step resolution would be increased at higher sampling frequencies, because the waveform produced by the steps becomes clearer. Again, more work is needed to address this.

Burrow use detection and non-travelling movement

Our starting point for mapping burrow use was detection of descent into the burrow system using the change in pitch. Although our work with the wild prairie dogs meant that the cameras could identify when the animals descended into their burrow system, it is unrealistic to assume under most field deployments that a camera could monitor every burrow entrance. As such, it is important to be able to identify when the prairie dogs enter and exit their burrows. Our Boolean rule involving pitch performed well during the descent analysis, accurately quantifying 92% of the observed free-roaming entries captured by camera trap footage, indicating minimal missed entries. In addition, from the limited observations of other above-ground behaviors (number of observation = 1195, individuals = 7), no behavior was incorrectly flagged as a burrow entry. Exit from the burrows was less reliable, presumably because exiting animals take a variable length of time to ascertain if it is safe, which affects the rate of change of pitch. Tags incorporating light sensors and/or barometric pressure sensors would probably make entrance and exit definition more reliable.

Any estimate of prairie dog movement using dead-reckoning needs to be able to differentiate between non-translocational body movement, such as shaking or scratching, and genuine travel. Since the animals in our tube runs only engaged in either travel or being stationary, our protocol could not assess this. However, observations of animals in camera trap footage and the field indicate that such non-translocational movements are very transient, rarely lasting more than 5 s (Supplementary Information Table S3). Such transient movements can easily be identified and precluded using Boolean rules on the acceleration data [37, 48]. Ultimately, unless these behaviours occur frequently, their transient nature means that they would not cause substantial deviations in dead-reckoned paths.

2D dead-reckoning for fossorial animals

This work indicates that 2D dead-reckoning has substantial potential for tracking fossorial species, providing information on their speeds and movements, and providing two dimensional location estimates when the animal is beneath the surface. This is illustrated by the detail provided by the high-resolution paths derived using sub-second acceleration data, even though verified points may be up to 2 h apart (Fig. 7). Importantly, high temporal resolution does not necessarily equate with high spatial resolution. In this regard, previous work has shown the importance of verified points, and the frequency with which they should be taken, on dead-reckoned location estimates [49]. This frequency, which need not take just the form of GPS fixes [49], varies with animal lifestyle and is critical for minimizing errors. Typically, these verified positions need to occur every 3 h in terrestrial animals [41].

We find it is more appropriate to talk about verified points that should occur after specific distances rather than times, because it is in the process of moving that errors accumulate. Our data on the general activity patterns from the accelerometer data of the collared prairie dogs used in this study indicate that they spend ~ 27% of their time traveling. If their traveling speed is approximately ~ 0.1 m/s, a 2-h window for determining movements amounts to a distance of approximately 720 m. However, it is pessimistic to assume that during such movement, the animals continually travel along new trajectories, as do many non-fossorial animals [30, 41]. Instead, fossorial animals are constrained to their burrows and so are likely to be back-tracking in a matrix that is more akin to a city street system than it is to overground movement of animals which may choose to move in any direction. In this respect, the more localised the burrow system, the more constrained the movements of its inhabitants will be. Therefore, we thus suggest that dead-reckoning the movements of fossorial species can benefit in accuracy from the spatial restriction that the burrows impose. The constraints of the burrows can also be used to refine estimates of the burrow positions in space. A single, or multiple, animals departing from a verified position in one burrow matrix, will have limited choice of movement. Many individuals (or the same individual) will use the same path so that, if tracks are superimposed, the multiple routes can be used to construct a more accurate picture of the underground network (Figs. 8, 9) [40]. In addition to this, we suggest that unusual features within defined burrow sections, such as a point at which the burrow almost doubles back on itself, can be used as verified positions (once the location of this feature has been defined by multiple individual tracks—see above). This point was highlighted by Link et al. [40] in an inertial measurement unit study on rats. Thus, there may be circumstances, where individuals of fossorial species can have their locations 'verified' even if they do not surface to trigger the standard verified position system (camera traps in our case).

Our dead-reckoning calculations produced only 2D paths (burrows), although there is a vertical element to them, with some prairie dog burrows descending to 5 m [25]. While we used animal pitch to identify when prairie dogs descended into their burrows and hinted at its potential to map burrow systems in 3D, we believe that the method described here may not provide the necessary accuracy. This is because the variation in pitch over time during movement is likely to produce large errors if the tunnels slope gently. Further testing is required to draw any definitive conclusions. However, the combination of pitch with barometric pressure as measured onboard the DD (some sensors can resolve height to within 10 cm) could be a very powerful approach for taking the burrow system into three dimensions. Variable burrow height also introduces errors in our 2D dead-reckoning, because dynamic body acceleration metrics such as VeDBA and ODBA change with slope, even at constant speed [31], so steeper slopes within the burrows can confound our speed, and, therefore, distance, estimates. Nonetheless, given their horizontal extent, further research is needed to validate the transition from 2 to 3D mapping of prairie dog burrows to ensure the accuracy of dead-reckoned tracks.

Although our approach gives some information of the movements of prairie dogs in their burrows, it is naïve to assume that we can map out all the connections in their underground complexes using this method. Notably, we can only apply this approach to the parts of a burrow systems actually used by collared animals as unused burrows or portions of burrows will be excluded during mapping initiatives based purely on animal movements. Including more collared individuals, and for longer periods of time, should increase the likelihood of including greater portions of the burrow network in mapping using this technique. Likewise, independent mapping methods, such as ground penetrating radar, would improve the resolution (as well as helping correct for dead-reckoning errors). Ground penetrating radar has been shown to be a powerful methodology for elucidating spaces underground [50, 51] but it does not work under all conditions [50] and gives no information on the function of burrows. In this respect, it is helpful that the dead-reckoning protocol described here uses accelerometers, because these sensors are used widely to determine and quantify animal behaviour, including sleeping, feeding, fighting etc. [29, 52, 53]. As such, the combination of location via dead-reckoning with behaviour should give important information regarding the extent to which particular behaviours are associated with specific spaces and perhaps even indicate how many individuals occupy the underground spaces simultaneously. This can also be combined with information on revisits and time spent resting in defined spaces (e.g. Figure 8). It is not known the extent to which Prairie dogs use chambers for specific activities, such as sleep or food storage, although chamber differentiation has been described for other fossorial mammals [54]. Allocation of time to chambers has particular value in consideration of disease transmission, such as sylvatic plague [55, 56].

Next steps

We consider that determining the depth of prairie dog burrows is an important next step. Depth is of interest as likely plays a crucial role in regulating temperature fluctuations [57] and influencing oxygen flow, both of which are presumed to impact the overall quality of the underground environment.

The system that we tested used cameras to provide verified points, which proved effective. However, cameras cannot be reliably used to cover all burrow entrances occurring within a prairie dog colony and camera data is time consuming to assess. Another method that might prove simpler is using rare earth magnets at intervals above the burrows (assuming that the burrow position is known with respect to the surface). Such magnets would produce a spike in the vectorial sum of the magnetometer data as the animals passed them, defining that position [11]. Indeed, the use of variously strong magnets, which will produce a correspondingly large vectorial sum peak, might also help refine this approach. Otherwise, animals could be fitted with GPS or VHF units on their collars, although tests would have to be carried out to determine if the systems provide the necessary accuracy.

Conclusions

Overall, this work underpins the importance of dead-reckoning as a solution for examining space use in fossorial animals. This is relevant for understanding how the animals relate to environmental space (as e.g. determined by vegetation surveys [58, 59] and topography, etc. [60, 61]). However, the specifics of the paths taken by animals themselves (tortuosity [62], speed [44, 63]), step lengths [64] and turn angles [5, 65], etc.) are also important for understanding a suite of animal movement issues, such as species' diffusion [4], food location strategies [66, 67] and vigilance [68, 69]. However, the work on immovable burrows has further value in providing a template for 'city' construction. As with humans, we expect the burrow network developed by prairie dogs to reflect the needs of their society, incorporating needed attributes, such as ventilation, high-speed sections, escape from predator sections, aggregation spots, storage and sleeping spots, providing a comprehensive network that caters for the complex needs of their hidden societies.

Abbreviations

AP	American Prairie
DD	Daily diary
DDMT	Daily diary movement trace
GPS	Global position system
LoCoD	Lowest common denominator
mAh	Milliampere
PTT	Platform transmitting terminals
VHF	Very high frequency
3D	Three dimensions

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-025-00408-2.

Additional file 1.

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Author contributions

J.R. and J.B. and R.P.W. and H.S. contributed to the conception, J.R. and J.B. and I.N. contributed to design of the work, J.R. and J.B. and I.N. and H.S. contributed to acquisition and analysis of data J.R. and J.B. and I.N. and R.P.W. contributed to interpretation of data. J.R. drafted the work.

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Availability of data and materials

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

This study was conducted in accordance with the [name of the relevant guidelines or ethical standards, e.g., "Ethical Principles of Animal Experimentation"]. Ethical approval for this research was obtained from the Smithsonian Institution's Animal Care and Use Protocol under approval number SI-23012. All necessary permits were acquired for the described field studies, and the animals involved were handled according to the guidelines established by Smithsonian Institution's Animal Care and Use Protocol SI-23012 and Montana Fish, Wildlife, and Parks Scientific Collector's Permit # 2024-022-W. Where applicable, written consent was obtained from all participants or their legal guardians prior to inclusion in the study.

Consent for publication

All authors consent to the publication of this manuscript.

Competing interests

The authors declare no competing interests.

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