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Unexpectedly high precision of consumer-grade GPS units for small-scale animal movement studies

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Consumer-grade GPS units are a staple of modern field ecology, but the relatively large error radii reported by manufacturers (up to 10 meters) ostensibly precludes their utility in measuring fine-scale movement of small animals such as insects. Here we demonstrate that for data collected at fine spatio-temporal scales, these devices can produce exceptionally precise data on step-length and movement patterns of small animals. With an understanding of the properties of GPS error and how it arises, it is possible, using a simple field protocol, to use consumer grade GPS units to collect step-length data for the movement of small animals that introduces a median of 11 cm of error. Such small errors make these inexpensive units useful for measuring insect and other small animal movements on small to intermediate scales on budgets that are orders of magnitude lower than the survey-grade units used in past studies. As an additional advantage, these units are much simpler to operate and insect or other small animal trackways can be collected more quickly than either survey-grade units or more traditional ruler / gird approaches.

Unexpectedly high precision of consumer-grade GPS units for small-scale animal movement studies

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Abstract: Consumer-grade GPS units are a staple of modern field ecology, but the relatively large error radii reported by manufacturers (up to 10 meters) ostensibly precludes their utility in measuring fine-scale movement of small animals such as insects. Here we demonstrate that for data collected at fine spatio-temporal scales, these devices can produce exceptionally precise data on step-length and movement patterns of small animals. With an understanding of the properties of GPS error and how it arises, it is possible, using a simple field protocol, to use consumer grade GPS units to collect step-length data for the movement of small animals that introduces a median of 11 cm of error. Such small errors make these inexpensive units useful for measuring insect and other small animal movements on small to intermediate scales on budgets that are orders of magnitude lower than the survey-grade units used in past studies. As an additional advantage, these units are much simpler to operate and insect or other small animal trackways can be collected more quickly than either survey-grade units or more traditional ruler / gird approaches.

Subjects Behavioral Ecology, Landscape Ecology, Animal Movement, Insect Ecology.

Keywords Animal tracking, Movement ecology, Insect movement, Tracking methods, *Euphydrays*, Checkerspot butterflies, Butterfly movement.

Introduction

Movement ecology is developing into an important sub-discipline of ecology. This new field has developed for several reasons. First, animal tracking technology has become relatively inexpensive, light, and reliable, and tracking devices are becoming available for a broader range of species (Cagnacci et al., 2010; Block et al., 2011), with some technologies even permitting tracking of large insects (Osborne et al., 1999; Chapman et al., 2011). Second, while this technological revolution has been taking place, or perhaps because of it, population and behavioral ecologists are becoming increasingly aware of the importance of understanding movement. Movement processes are key in the maintenance of metapopulation genetic diversity and population viability, intra- and interspecific interactions, predator-prey relationships, connectivity of animal subpopulations, and they often figure prominently in conservation plans (Hanski, 1999; Dover & Settele, 2009; Knowlton & Graham, 2010; Morales et al., 2010; Costa at al., 2012; Fagan et al., 2013). Along with the development of tracking technologies and increased interest in animal movement, advances in computing have allowed the development of powerful statistical models that can fit the complex time-series of animal movements to robustly address a wide range of ecological questions (e.g. Blackwell, 2003; Jonsen et al., 2005; Breed et al., 2012; Mcclintock et al., 2013).

Although much of the new tracking data measure movement on broad spatial and temporal scales, movement measured at smaller scales is relevant to an animal's overall behavioral repertoire, kinematics, and physiology (*Goldbogen et al., 2006; Weimerskirch et al. 2006; Niato et al., 2010*). In the early years of movement ecology, insects were preferred study organisms for understanding movement at these small scales. Insects are small, often abundant, and many have local movements that are easy for a human observer to follow and observe.

Moreover, a careful human observer is unlikely to alter the behavior of an insect being followed,

where similar strategies would be extremely disruptive if applied to vertebrates (*Kareiva & Shigesada*, 1983; Galen & Plowright, 1985; Haddad, 1999; Schultz & Crone, 2001; Morales, 2002). These convenient properties made insects common choices for many classic early movement ecology studies (*Kareiva & Shigesada*, 1983; Odendall et al., 1989; Turchin, 1998).

As contemporary movement ecology study systems, insects have fallen out of favor. Electronic tracking tags are now small enough to be deployed on a wide range of small mammals, birds, and fishes, and virtually all mammals larger than 10 kg. Once deployed, these tracking tags can monitor movements for weeks, months, and sometimes years virtually without effort. The relative ease and large quantity of data produced from tagging technologies, as compared to the labor intensive methods used in the classic insect movement studies, has vastly broadened the size spectrum of model taxa in movement ecology. With the exception of a few robust species (*Kissling et al., 2014*), insects are not able to carry such tags and are unsuitable for such tagging protocols.

However, there remains interest in understanding how insects and other animals too small to affix tracking tags move and use space. If an organism's movements are very small and constrained, they can be effectively captured with video cameras (*Noldus et al., 2002*). For animals that mix both small (centimeter-scale) and large (meter-scale) movements together, common in many flying insects (*Schultz & Crone, 2001; Severns & Breed, 2014; Breed et al., 2015*), video methods are usually unworkable because the animals will quickly move out of frame. There have been some successful attempts to track insects by affixing tags to them, most notably harmonic radar (*Osborne et al., 1999; Ovaskainen et al., 2008; Kissling et al., 2014*). Harmonic radar, however, is only viable for the very largest, strongest fliers such as bees, dragonflies, and some butterflies. The radar systems also require line-of-sight detection and a powerful and expensive radar unit, and for many insect species the attached harmonic radar

antennae physically interfere with flight (*Kissling et al., 2014*). Thus, for the majority of insects, traditional manual tracking remains the most practical approach in the field. These approaches require observers to follow individual insects, and place markers, usually pin flags, behind the animal as it moves. Marked locations are subsequently measured using a tape, laser range finder, pre-installed reference grid or similar on-the-ground measurement methods (*Turchin, 1998*). Such methods are often extremely labor intensive, and accurate locations across the landscape are limited by the boundaries of the reference grid.

In the past 20 years, hand-held GPS units, in parallel with the aforementioned tracking technology, have greatly improved in quality and these devices are now a common piece of field gear for nearly all field ecologists. The reported error on these units usually ranges from 3 to 10 meters. Researchers needing centimeter-scale accuracy often required to study insect movement have instead opted to use survey-grade GPS base units with hand-held receivers. These systems commonly cost \$20000 -\$40000 USD, require dedicated training, and often propriety software to run. Moreover, these systems are cumbersome compared to consumer grade GPS units and difficult to operate in the field. By comparison, consumer-grade GPS units sell for a few hundred dollars and promise accuracy no better than 3 meters. Ostensibly, this low precision should be too coarse for insect tracking studies, but these relatively inexpensive GPS units have become considerably more accurate and precise over the last decade. More importantly, the nature of the error reported by the devices and manufacturers is misunderstood (Arnold & Zandbergen, 2011). For many movement questions, the precision of these consumer grade devices may in fact be extremely high and appropriate for collecting movement data on centimeter scales.

Here, we demonstrate the unexpectedly high accuracy of consumer grade GPS units for the measurement of insect movement by presenting and analyzing data from two grassland associated checkerspot butterflies, *Euphydryas phaeton* and *E. editha taylori*. We discuss how to achieve the degree of GPS accuracy suitable for insect movement studies, and the counter-intuitive data collection method which favors the use of the inexpensive, consumer grade GPS over the considerably more expensive professional units.

Methods

As part of a larger study on butterfly movement and ecology, we used consumer-grade GPS units to track two species of checkerspot butterfly in two geographically distinct regions, *Euphydryas phaeton* (Baltimore checkerspot) and *Euphydryas editha taylori* (Taylor's checkerspot). We used consumer grade GPS units in this instance because survey grade units were not available. Both species occupy open, graminoid-dominated habitats, one in eastern (*E. phaeton*) and the other in western (*E. e. taylori*) North America. Populations of these two butterflies have relatively recently, within the last 30-120 years, adopted *Plantago lanceolata* (English plantain), an exotic species to North America (*Cavers et al., 1980; Wolff & Schaal 2002*), as the primary larval host plant (*Danby, 1890; Stamp, 1979*).

Butterfly tracking and GPS accuracy. We tracked female checkerspots at a total of four sites, two in Massachusetts for *E. phaeton* (the Bullit Reservation, near Asheville, MA and Stevens-Coolidge Place, North Andover, MA) and *E. e. taylori* was tracked on two privately owned sites near Corvallis, Oregon (see Severns & Breed, 2014 for details). Butterflies were tracked through open grasslands and wetlands of moderate scale (~0.8 to 20 ha) that were bordered by closed-canopy forest matrix.

Female checkerspots were selected opportunistically and tracking of selected individuals began immediately. Butterflies were followed, usually keeping a distance of 1-2 meters and GPS locations were recorded every 15 seconds for 15 minutes for *E. phaeton* and every 20 seconds

for 20 minutes for *E. e. taylori* with a consumer-grade, Garmin eTrex Venture HC. We enabled the WAAS setting (wide area augmentation system) on each unit, which enables greater accuracy through real time corrections using multiple satellite and on-the-ground reference stations (*Arnold & Zandbergen, 2011*).

We used two closely related methods for measuring movement tracks. First, we used the traditional method of recording a movement path by placing pinflags at each location and when butterflies remained at the same position for more than one time step, recorded the number of time steps at that position. When the observation period ended we revisited each pin flag and recorded a GPS waypoint. This requires two trips around the trackway, one to place the flags while the butterfly is moving and another to take a waypoint after the flags have been placed.

Alternatively, we collected waypoints in real time, at each time step while the individual was being tracked. When individuals were alighted this was done by positioning the GPS unit above the individual at a distance that did not affect behavior, usually about a meter. While in flight, a position was taken directly behind the individual, along the flight path it had just made. Because pin flags were not used the course does not need to be revisited twice, which is less labor intensive and caused less trampling damage to habitat as compared to the pin flag approach. In practice, collecting waypoints while tracking did not appear to induce any more abnormal behavior than the more traditional pin flag method, though care must be taken not to hold the GPS unit such that it casts a shadow on the tracked butterfly.

In many cases we were able to follow individuals for the entire prescribed observation interval of 15 or 20 minutes, but occasionally individuals could not be followed or were otherwise lost, so some tracks were shorter in duration than others. Flight of both species may be cut short by sudden bouts of inclement weather, abruptly causing butterflies to become completely still. To account for these issues, we employed rules for aborting behavioral

observations if butterflies entered a protracted bout of resting during the observation period. If we observed 5 minutes of continuous inactivity we terminated the tracking effort for that individual and another was selected (either immediately if the weather permitted, or when weather improved). Tracking occurred when the weather conditions were ideal for buttery flight, in full or nearly full sun, and between 1000 hrs to 1700 hrs.

At every time step we recorded behavioral information, enabling the construction of behavioral budgets (reported in *Severns & Breed, 2014; Breed et al., 2015*). However, the behavioral data also indicated whether the tracked individual moved or did not move during a particular time step. For our analysis, this is key, because a GPS location was collected at every time step regardless of whether the butterfly moved. This enabled us to compare actual butterfly movements to "null" movements for the tracks where a GPS position was collected at every time step. "Null" movements are apparent moves made according to the GPS data, but through our direct observations, we know that no movement actually took place. Thus, the null moves are strictly attributable to GPS error. This allowed us to sort the steps represented by each consecutive GPS location into those representing movement and those representing only GPS error. We then compared the step-lengths in butterfly pathways where the individual moved (true steps) to the step-lengths where there was no movement (null steps). We used these errors to estimate the signal to noise ratio in the movement pathways and the patterns associated with the error over time (direction and magnitude).

Results

We found that with respect to the scale of real butterfly step-lengths, GPS error was very small, with the average null step-length being 0.378 m and a median null step-length of 0.11 m. 37% of null steps were 0.0 m, 80.3% of null steps were less than 0.25 m and 94.8% of null steps were

less than 1 m. The results are summarized in Table 1 with examples of the contributions to displacement by null steps and real steps for 4 *E. phaeton* tracks in Fig. 2. Th relatively large mean of null step-lengths was due to a handful of very large erroneous steps. Real steps (across both species) had mean and median lengths of 3.14 m and 2.12 m, respectively. Comparing means, the signal to noise ratio was 8.4, while the signal-to-noise ratio of the median, a better estimate of central tendency, was 19.3.

Discussion

To understand why we found such small errors and reconcile these findings with the larger error radii reported by GPS units, it is important to understand that these errors are fundamentally different from those reported by GPS units and the manufactures. Error reported by GPS units are relative to fixed positions on the surface of the earth. Here we are interested in the contribution of error to animal movement step-lengths, which are recorded by two GPS locations taken in quick succession (15 or 20 seconds, in this case). The reason errors are so small has to do with the "slow-varying" nature of GPS error, where by, on short time scales, error residuals are highly autocorrelated. This means that the underlying movement steps, even when very small, will faithfully represent movement because the starting and ending GPS locations are displaced from the surface of the earth with approximately the same direction and magnitude. If the error residuals of the starting and ending GPS locations are the same, the underlying movement step will be correct. The slow-varying nature of GPS error and high autocorrelation of residuals is well illustrated by Arnold and Zandbergen (2011), who carefully examine the nature of error in consumer grade GPS units.

Our experiments with tracking accuracy using consumer grade, hand-held GPS units have some important implications. First, the accuracy and precision of the step-lengths was

considerably better than manufacturer states in our purpose of measuring movement. Similar conclusions were reached by the US Federal Aviation Administration and National Transportation & Safety Board with respect to the waypoints themselves. In 2008, they reported the real 95% confidence intervals using the WAAS (Wide Area Augmentation System) augmented GPS units (now standard on most consumer grade GPS units) were on the order of 0.5 to 1.0 meter (*FAA*, 2008). The nominal error for WAAS augmented GPS units is 7.6 m. However, this 7.6 m error radius is actually the mandated upper bound of the WAAS system. It is likely that, given the reliance on GPS systems of navigation and surveying, GPS manufacturers overstate error to protect themselves against liability.

In our data, error introduced to step-lengths by consecutively collected GPS points were generally < 0.25 m and the signal to noise ratio was between 9:1 and 20:1, depending upon how it was calculated. Both checkerspot butterflies made moves that averaged just over a meter, with many steps that were much shorter. Compared to the scale of movement that the tracked butterflies made during flight, GPS noise had minimal (though not negligible) impact on the movement pathway. Our ability to quantify butterfly movements and to detect differences in movement patterns between and within the two checkerspot species was high, and it was extremely easy to detect even subtle difference in movement (reported elsewhere: *Severns & Breed, 2014; Breed et al., 2015*).

There are some elements of our sampling protocol that were likely key in obtaining highly precise results. First, observation intervals were short; 15 and 20 seconds. These intervals are considerably shorter than the satellite drift error process that affects GPS accuracy, with autocorrelation dissipating to zero after about 15-30 minutes - though we note that changes in error autocorrelation can sometimes be abrupt when consecutive positions are fixed using a different constellation of GPS satellites. Second, adult butterflies were only active under warm,

calm, clear, and atmospherically settled days, optimal conditions for acquiring satellites and minimizing GPS error. Furthermore, the butterflies we tracked live in open meadows, so multipath error (reflected signals) was likely minimal. Both sites were also in North America, where WAAS network coverage is 100%. These factors likely enabled the GPS units to produce more accurate locations than could be expected beneath a forest canopy or in canyons, for example. Consequently, the high precision and otherwise slow drift GPS error (usually introduced by ionospheric interference) resulted in the extremely high quality results.

From our results, we cannot conclusively determine the time interval at which the GPS error residuals will no longer correlated. But, given the nature of ioniospheric distortion, observation protocols that use intervals up to 1 minute and perhaps 2 will likely produce results similar to our 15-20 second time intervals. Longer time steps would not be recommend unless meter-scale accuracy is acceptable. Finally, as track locations are recorded in-person (as opposed to remotely through an electronic tag), we highly recommend that the observer take ancillary behavioural notes, indicating if a step occurred and approximately how long that step was, in order to ground truth the step lengths collected. These notes were key for us, as without records of butterfly behavior from standard behavioral observations, it would not have been possible to assess how well the GPS units performed.

Although slow drift error will introduce only a small amount of error to individual steps, it will shift entire tracks in one direction and / or slightly distort whole tracks. However, almost all relevant behavioral information is preserved with the consumer grade GPS units, and because the scale of the error is still relatively small (a meter or so using the WAAS system), habitat usage patterns will be well represented. True centimeter scale accuracy, such as that produced by survey grade GPS units, would likely only be required if two conditions are in place: 1) all features in the landscape to which an animal might respond are known at centimeter-scale

accuracy (such as individual flower blossoms or host plant locations) and 2) animals actually respond to resources only at these scales and not the larger scales that might be produced by habitat edges.

For insects and other animals moving on small to medium scales in the field which can be followed by an observer without affecting behaviour (e.g. *Potts & Lewis, 2014; Potts et al., 2014*), consumer grade GPS units offer a remarkably inexpensive and easy way to collect movement data with sub-meter accuracy and movement studies can be conducted with little upfront cost. It is important to understand how GPS error operates on step-length data, and the errors we report do not represent error in position relative to the surface of the earth, which may still be large. Precision mapping of actual geographic locations and the boundaries of landscape elements (sub-meter accuracy) may be more labor intensive than recording movement tracks and care must be taken if precise geographic position is required. If precisely measuring step-lengths, orientations, and movement behavior of insects or other small animals though time is the study goal, as is often the case in movement ecology, consumer grade GPS units are likely to be a viable alternative to much more expensive, survey-grade, base units and rovers.

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Literature Cited

Arnold LL, Zandbergen PA. 2011. Positional accuracy of the wide area augmentation system in consumer-grade GPS units. *Computers & Geosciences* **37**: 883–892.

Blackwell P. 2003. Bayesian inference for Markov processes with diffusion and discrete components. *Biometrika* **90**:613–627.

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR,

Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP. 2011. Tagging of Pacific Pelagics: Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90.

Breed GA, Costa DP, Jonsen ID, Robinson PW, Mills-Flemming J. 2012. State- space methods for more completely capturing behavioral dynamics from animal tracks. *Ecological Modelling* **235**:49–58.

Breed GA, Severns PM, Edwards AM. 2015. Apparent power-law distributions in animal movements can arise from intraspecific interactions. *Proceedings of the Royal Society of London Interface* **12**:10140927.

Cagnacci F, Boitani L, Powell RA, Boyce MS. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 2157–2162.

Chapman JW, Drake VA, Reynolds DR. 2011. Recent insights from radar studies of insect flight. *Annual Review of Entomology* **56**:337–356.

Costa DP, Breed GA, Robinson PW. 2012. New insights into pelagic migrations: implications for ecology and conservation. *Annual Review of Ecology, Evolution, and Systematics* **43**:73–96.

Dover J, Settele J. 2009. The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation* **13**:3–27.

FAA (Federal Aviation Authority), 2008. Wide-Area Augmentation System performance analysis report. Report No. 24. Federal Aviation Authority, William J. Hughes Technical Center, NSTB/WAAS T&E Team.

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, LaDage L. 2012. Spatial memory and animal movement. *Ecology Letters* **16**:1316–1329.

Galen C, Plowright RC. 1985. Contrasting movement patterns of nectar-collecting and pollen-collecting bumble bees (*Bombus terricola*) on fireweed (*Chamaenerion angustifolium*) inflorescences." *Ecological Entomology* **10**:9–17.

Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology* **209**:1231–1244.

Haddad NM. 1999. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* **153**:215–227.

Hanski I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* **87**:209–219.

Jonsen ID, Flemming JM, Myers RA. 2005. Robust state-space modeling of animal movement data. *Ecology* **86**:2874–2880.

Kareiva PM, Shigesada N. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* **56**:234–238.

Kissling DW, Pattemore DE, Hagen M. 2014. Challenges and prospects in the telemetry of insects. *Biological Reviews* **89**:511–530.

Knowlton JL, Graham CH. 2010. Using behavioral landscape ecology to predict species' responses to land-use and climate change. *Biological Conservation* **143**:1342–1354.

McClintock BT, Russell DJ, Matthiopoulos J, King R. 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. *Ecology* **94**:838–849.

Morales JM. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *The American Naturalist* **160**:531–538.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010. Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:2289–2301.

Naito Y, Bornemann H, Takahashi A, McIntyre T, Plötz J. 2010. Fine-scale feeding behavior of Weddell seals revealed by a mandible accelerometer. *Polar Science* **4**:309–316.

Noldus LP, Spink AJ, Tegelenbosch RAJ. 2002. Computerised video tracking, movement analysis and behaviour recognition in insects. *Computers and Electronics in Agriculture* **35**:201–227.

Odendaal FJ, Turchin P, Stermitz FR. 1989. Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia* **78**:283–288.

Osborne JL, Clark SJ, Morris RJ, Williams IH, Riley JR, Smith AD, Reynolds DR, Edwards AS. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* **36**:519–533.

Ovaskainen O, Smith AD, Osborne JL, Reynolds DR, Carreck NL, Martin AP, Niitepõld K, Hanski I. 2008. Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. Proceedings of the National Academy of Science 105:19090–19095.

Potts JR, Lewis MA. 2014. How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society B: Biological Sciences* **281**:20140231.

Potts JR, Mokross K, Stouffer PC, Lewis MA. 2014. Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. *Ecology and Evolution* 4:4578–4588.

Schultz CB, Crone EE. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* **82**:1879–1892.

Severns PM, Breed GA. 2014. Behavioral consequences of exotic host plant adoption and the differing roles of male harassment on female movement in two checkerspot butterflies. *Behavioral Ecology and Sociobiology* **68**:805–814.

Turchin P. 1998. Quantitative Analysis of Movement: Measuring and modeling population redistribution in plants and animals. Sinauer Associates, Sunderland, MA.

Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F. 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. *Oecologia* **146**: 681–691.

Tables

Table 1. Comparison of null steps (butterfly was directly observed to not move) and real steps (butterfly was directly observed to move) as measured by consumer-grade GPS units.

Statistic	Null Steps	Real Steps
Number (N)	2830	1228
Median (m)	0.111	2.12
Mean (m)	0.378	3.14
Number = 0	1042 (36.8%)	21 (1.7%)
Number < 0.25 m	2275 (80.3%)	144 (11.7%)
Number < 1.00 m	2684 (94.8%)	358 (29.1%)
Number < 3.00 m	2759 (97.5%)	739 (60.1%)
Number $> 10.0 \text{ m}$	20 (0.7%)	75 (6.1%)

Figures

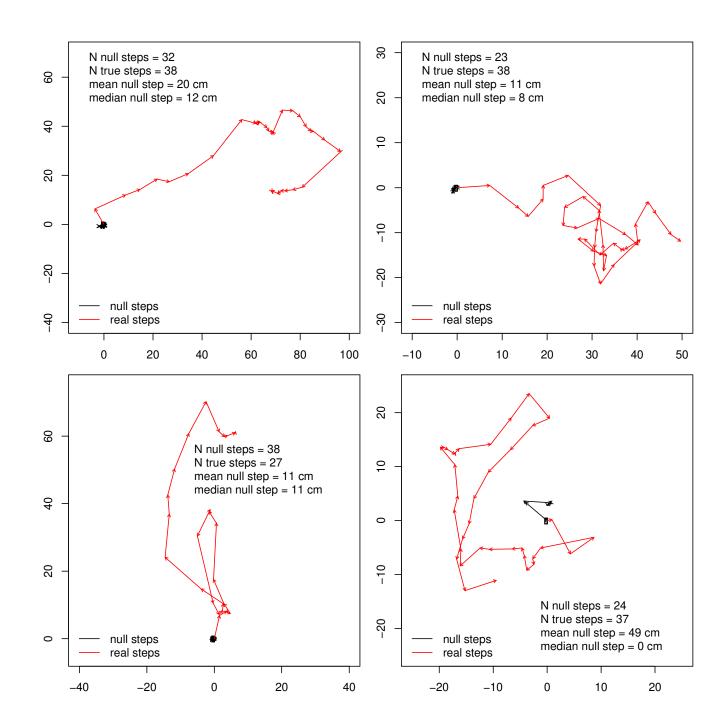


Figure 1. Four example butterfly tracks, the starting points are set to 0 and the scale is in meters. The red tracks show the true steps connected, while the black tracks connect the null steps for comparison.

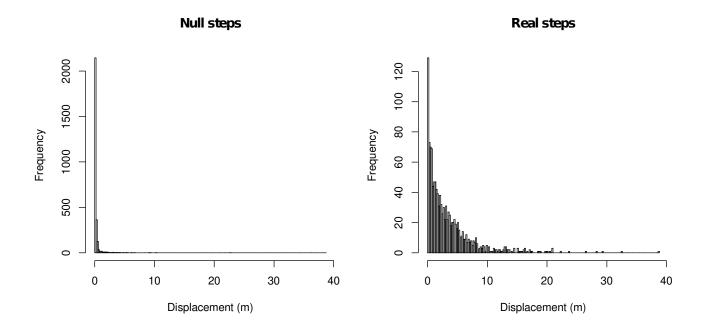


Figure 2. Histograms of null steps (left) and true steps (right).