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A framework for pre-processing individual location telemetry data for freshwater fish in a river section

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Abstract

Animal movement study often relies on individual tracking. The data scale (in time and space) varies according to the species, the environment where individuals live, or the exogenous processes that drive movement. To explore freshwater fish movement in rivers, fine-scale data are needed. Also, in rivers, recorded telemetry frequently shows missing data and location errors. The irregular time-steps, huge amount of data, environmental complexity (river section) and how fish move in such anisotropic environments undermine the use of statistical frameworks such as state-space models. To deal with these specificities, data pre-treatment can be required. We propose a generic method of telemetry data pre-processing, which can be transposed to other datasets. This framework includes interpolation to handle trajectories at fine time scales and performs data analysis within a state-space model. [We combined analyses on observed and simulated data at various interpola-](#)

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tion time-steps to choose the one that best preserves the general movement while reducing the total amount of data required. First, we directly compared raw and interpolated data, and the results of parameter inference of a simple state-space model using the interpolated data. The state-space model infers behavioural state based on speed and turning angle between successive locations in animal trajectories. We also included two additional variables computed from raw data: a quantitative indicator of the correspondence between the interpolated trajectory and the raw data, and the variance of turning angles of raw data within the interpolation time-step. We were finally able to determine the most appropriate time-step to obtain locations that were regularly spaced in time and to reduce the amount of data while maintaining the precision of the raw data. Computational time was reduced 12-fold by using a 30-second time-step to interpolate data simulated at 3-second intervals. The inclusion of the two variables derived from raw data compensated for the loss of information in interpolated trajectories and allowed more efficient discrimination between behaviours.

Keywords: Animal location data, Movement model, State-space model, Switching behaviour, Bayesian inference, Parameter estimation

1. Introduction

Movement is a key issue in animal ecology and has been the focus of increasing research, especially in aquatic ecology, in both marine and freshwater environments (Giuggioli and Bartumeus 2010, Lennox et al. 2017, Nathan et al. 2008). Movement influences many processes, at individual, population and community levels: habitat selection (Block et al. 2011, Capra et al. 2017), migra-

7 tion (Bultel et al. 2014, Drouineau et al. 2017, Tétard et al. 2016, Tétard et al. 2019),
 8 trophic dynamics (Lima 2002), spread of disease (Carraro et al. 2017, Jonsen et al. 2001,
 9 Pinder et al. 2005) and adaptability to climate change and extreme events
 10 (Boucek et al. 2017). The study of animal movement often relies on indi-
 11 vidual tracking. Recent technical progress has revolutionized such studies:
 12 the development of high-frequency tags enables high-frequency data col-
 13 lection at fine spatial resolution (Cagnacci et al. 2010, Hussey et al. 2015,
 14 Lennox et al. 2017). Tracking data at high temporal resolution are inval-
 15 able for species that are rarely static although staying in the same area.
 16 Location per hour, half-day or day provides information on individual move-
 17 ment within an animal’s living-range (e.g., within a region, or along a migra-
 18 tion route) over a long period of time rather than small quick displacements
 19 within or between local habitats (Capra et al. 2018, Donaldson et al. 2014).
 20 In contrast, tracking several locations per minute allow displacements to be
 21 described at fine scale, enabling precise investigations of suitable migratory
 22 conditions, habitat selection or behaviour choices at individual level (e.g.
 23 (Capra et al. 2017, Cooke et al. 2004, Tétard et al. 2019)). Telemetry data
 24 at a very fine time scale (of a few seconds) are being increasingly collected
 25 worldwide (Cooke et al. 2013, Hussey et al. 2015, Lennox et al. 2017). Po-
 26 sitions are generally estimated by triangulation, either by satellite or by
 27 multiple fixed receivers.
 28 Statistical modelling frameworks have been developed to analyse aquatic
 29 telemetry data (Whoriskey et al. 2019) by assessing and correcting posi-
 30 tion errors (Bergé et al. 2012, Roy et al. 2014), dealing with missing data
 31 (Woillez et al. 2016), inferring behaviour (Dorazio and Price 2019, Thiebault et al. 2018,

32 Vermard et al. 2010), and investigating the influence of the environment on
 33 individual movements (Bestley et al. 2013, Drouineau et al. 2017, Patterson et al. 2009).
 34 State-space modelling is one of the useful existing statistical frameworks
 35 for animal movement analysis (Dorazio and Price 2019, Jonsen et al. 2003,
 36 Joo et al. 2013, Patterson et al. 2008).
 37 Most animal movement studies have focused on large terrestrial or marine
 38 species, e.g. (Andersen et al. 2017, Bailey et al. 2008, Franke et al. 2006,
 39 Hedger et al. 2008, McClintock et al. 2012) which move in a wide and open
 40 environment, few have dealt with freshwater organisms. Telemetry data for
 41 anisotropic, irregular environments, such as large rivers, show some speci-
 42 ficities (Cooke et al. 2013). Firstly, triangulation is made difficult by ground
 43 irregularities and the presence of vegetation, causing frequent signal loss. Sec-
 44 ondly, the precision of triangulation varies in space (Bergé et al. 2012). And
 45 thirdly, the anisotropic closed conditions of hydrographic networks are spe-
 46 cific limitations on animal movement (Quaglietta and Porto 2019, Sutherland et al. 2015)
 47 and complicate the trajectory analysis. Fish navigation is known to be influ-
 48 enced by physical cues such as current fields and physical obstacles (e.g., [dams](#)
 49 or river banks) (Goodwin et al. 2014) leading to highly orientated navigation
 50 which does not fulfil the isotropy assumption usually applied in open environ-
 51 ments. The second major issue is the temporal and spatial scales at which fish
 52 movement is characterised. Telemetry studies of freshwater fish generally fo-
 53 cus on seasonal movement, e.g. (Dorazio and Price 2019, Fraley et al. 2016,
 54 Koehn and Nicol 2016, Muhlfeld 2012), and modelling frameworks are rarely
 55 applied to analysing individual movements at fine scales. However, such
 56 fine-scale data and corresponding analytical methods are critical to study-

57 ing small-scale foraging movements of fishes within their home range, which
58 (Dingle 1996) called "station keeping" movement, in contrast to migration
59 over large distances.

60 The combination of environmental limitations, which entail irregularities in
61 signal recording, and fine spatial and temporal scale has three main conse-
62 quences. Firstly, irregular time-steps have to be handled. Secondly, analysing
63 the huge amount of data generated requires great computer power, which
64 may lead to a trade-off between reducing computing time and not degrading
65 fine-scale data quality. And thirdly, the consideration of entire individual
66 trajectories from the beginning to the end of the recording period is not al-
67 ways necessary; a certain number of trajectories spaced in time can also be
68 used to explore individual behaviour.

69 To deal with irregular time-steps, an appropriately longer time-step can be
70 chosen, coupled with interpolation, if necessary, to deal with any missing
71 data. Increasing the time-step generally reduces the rate of missing data
72 while also reducing the amount of data to be analysed. However, it impairs
73 overall precision compared to the raw dataset, and may impact ecological in-
74 terpretations based on these trajectories. In this paper, we propose a generic
75 method of data processing to accurately infer individual behaviours from
76 trajectories at fine temporal and spatial scales. Analysis was performed at
77 different time-steps and compared so as to select the most appropriate one:
78 *i.e.*, the one that preserved the general movement while efficiently discrimi-
79 nating between behaviours (here, slow and fast movements). To this end, we
80 directly compared the raw and interpolated data, and compared the results of
81 the parameters inference of a simple state-space model with the interpolated

82 data. We did not deal with location error, as our aim was to infer indi-
83 vidual behaviour based on observed movement rather than reconstruct the
84 exact individual trajectories. Moreover, usual correction methods are based
85 on an isotropy assumption (*i.e.*, that there is no favoured direction within
86 the space, and animal navigation consequently depends only on behaviour
87 and not on environmental characteristics such as flow fields around physical
88 obstacles), which is not fulfilled here.

89 To illustrate this approach, we used telemetry data for individual fish col-
90 lected in the Rhône River at 3-second intervals (Capra et al. 2017). The
91 initial objective of the study was to infer the relationships between fish be-
92 haviour and hydraulic conditions through analysis of fish movements. In this
93 context, we used a state-space model to discriminate fish behaviours. For
94 that, raw fish location data (hereafter referred to as "raw data") must be
95 pre-processed. While maintaining the precision of the raw data, gaps be-
96 tween locations must be dealt with so as to obtain regularly time-spaced
97 data.

98 2. Material and methods

99 2.1. Case study

100 Bergé et al. (Bergé et al. 2012) collected telemetry data on freshwater
101 fish in the Rhône River using the HTI ([https://www.innovasea.com/fish-](https://www.innovasea.com/fish-tracking/)
102 [tracking/](https://www.innovasea.com/fish-tracking/)) acoustic fixed telemetry system. Our system includes a set of
103 pre-positioned hydrophones used to detect ultrasounds emitted by acoustic
104 tags (frequency of 307 KHz). Tags signals that allow the identification of
105 the tag, and precise positioning of the tag through a triangulation process

provided that the signal is detected by at least 3 hydrophones (hydrophones were all connected to a single controller and synchronized with UTC time to improve the triangulation). Further details are provided in Berg et al. (Bergé et al. 2012).

Locations of 94 individuals of various species were tracked for 3 months at a time interval of 3 seconds. The dataset suffered from the usual defects affecting tracking data. Firstly, individuals were not systematically located every 3 seconds during the 3 months of the experiment. There were two types of gap in the data: large gaps, in which the individual signal was lost for several minutes to several days, and small gaps where the individual signal was lost for a few 3-second periods (*i.e.*, 3 seconds to a few minutes). A second defect was specific to the triangulation process of the HTI system: some successive locations form artefactual "star-shaped" trajectories (Appendix A, Figure A1). Though this type of star-shaped pattern is specific to the triangulation process, it is more generally one of the types of location error besetting most tracking studies. The fine time-scale data may also incur a specific problem: when an individual is static or moving very slowly, its successive locations can be tracked as being as distant as when it is moving faster, due to triangulation error.

2.2. Proposed data pre-processing

Three pre-processing steps were performed on the raw data. The first was the choice of a time-step p . The second dealt with the large gaps between certain successive locations. For this, we considered using a threshold s equal to twice the time-step p , in order to split the trajectory in two while avoiding interpolation in-between points that were too far apart in time. If the dura-

tion between two successive locations $(x, y)_i$ and $(x, y)_{i+1}$ (x and y denoting
 the spatial coordinates and i the [index](#) of the location) is greater than s ,
 then these two locations are assumed to belong to two distinct independent
 trajectories. The raw data for a given trajectory are denoted hereafter as the
 "support of the trajectory". The third step consisted in the linear interpo-
 lation of new locations within each trajectory according to the time-step p
 to deal with missing data within each trajectory. Interpolations were carried
 out using the *move* R package (Kranstauber and Smolla 2008).
 We tested 6 interpolation time-steps (with the associated s threshold): 30, 60,
 120, 180, 240, and 300 seconds, denoted by p_k , $k \in [1, 6]$. In order to test the
 different means of pre-processing the raw data, 16 of the 731 trajectories of
 individual European catfish (*Silurus glanis*) were selected. European catfish
 were chosen because this species included well-tracked individuals presenting
 numerous locations, and thus longer trajectories than for other species.
 The complete trajectories can comprise three general patterns: (i) [travelling](#)
 (T), in which the individual moves over a long distance, where start and end
 locations are distant from one another; (ii) [stationary](#) (S), where locations
 are concentrated within a short perimeter (potentially "star-shaped") with
 start and end locations nearby; and (iii) a [mixed pattern](#) (B , for "bi-type")
 where a stationary move follows a long move or vice versa. Four trajec-
 tories of each for the stationary and travelling types, and 8 trajectories for
 the mixed type were selected for the test dataset. Two examples of each
 trajectory type at each time-step are shown in Figure 1.

154 2.3. Validation criteria

155 To compare the interpolated trajectories using the different time-steps p_k ,
 156 several criteria were considered.

157 2.3.1. Computed variables

158 Two variables were computed to quantify the consistency between the
 159 raw data and each interpolated trajectory. They showed different patterns
 160 according to the type of trajectory, and were computed to see how they
 161 varied according to time-step. The two additional variables, denoted by U_1
 162 and U_2 , concerned speed and turning angles respectively. For a trajectory j
 163 associated with time-step p_k , let $(x, y)_{n_j \times p_k}$, $n_j \in [0, N_j]$ (with N_j the total
 164 number of locations in the trajectory j) be the n_j^{th} location in the trajectory.
 165 Considering the support of the trajectory j , let $i \in [0, I_{n_j}]$ be an index for
 166 raw data locations, denoted by $(x, y)_{i_{n_j}}$, between time $n_j \times p_k$ and $(n_j + 1) \times p_k$
 167 of the trajectory locations and $\theta_{i_{n_j}}$ the angle between the locations $(x, y)_{i_{n_j}}$,
 168 $(x, y)_{(i+1)_{n_j}}$ and $(x, y)_{(i+2)_{n_j}}$.
 169 For a time-step p_k and a total time $n_j \times p_k$ of the trajectory j , $U_{1_{k, n_j}}$ and
 170 $U_{2_{k, n_j}}$, are defined as follows:

$$U_{1_{(k, n_j)}} = \frac{d((x, y)_{n_j \times p_k}, (x, y)_{(n_j + 1) \times p_k})}{\sum_{i=0}^{I_{n_j} - 1} d((x, y)_{i_{n_j}}, (x, y)_{i_{n_j} + 1})} \quad (1)$$

171 where $d(X_1, X_2)$ represents the covered distance between locations X_1 and
 172 X_2 . U_1 is thus the ratio between the covered distance according to the
 173 interpolated data and the covered distance according to the raw data, within
 174 the interpolation time-step. U_1 represents a quantitative indicator of the

175 correspondence between the interpolated trajectory and the raw data: the
 176 higher U_1 , the better the fit.

$$U_{2(k,n_j)} = \text{var}(\theta_{i_{n_j}}) \quad (2)$$

177 where $i \in [0, I_n]$ and $\text{var}(X)$ denotes the variance of X . U_2 is thus the
 178 variance of turning angles of raw data within the interpolation time-step. If
 179 the variance is small, the trajectory is rectilinear within the interpolated time-
 180 step and little information is lost. However, a large variance may indicate a
 181 star-shaped pattern, especially if associated with a low U_1 .

182 2.3.2. State-space modelling

183 We developed a state-space model based on (Morales et al. 2004) to dis-
 184 criminate between the different individual behaviours in the 16 selected tra-
 185 jectories. Model parameters were estimated independently for each time-step,
 186 so as to assess variations in parameter estimates according to the time-step.
 187 Results for each time-step were also compared with and without adding U_1
 188 and U_2 , to see whether behaviour discrimination was improved by including
 189 these two variables.

190 *Model definition.* Model states correspond to the succession of fish behaviours
 191 at each time increment, with two possible behaviours: "Resting" (denoted by
 192 R), which corresponds to slow or erratic movements, and "Moving" (denoted
 193 by M), which corresponds to fast, oriented movements. We assumed con-
 194 stant behaviour switching probabilities between successive time increments.
 195 The observation model links the state at time t to corresponding movement
 196 variables (*i.e.*, speed between two locations and turning angles between two

197 moves) (Morales et al. 2004). Low mean speed and high turning angles vari-
 198 ance are taken to characterise "Resting" behaviour, whereas high speed and
 199 mean turning angles around 0° are taken to characterise "Moving" behaviour.
 200 "Resting" behaviour is expected to predominate in "Stationary" trajectories,
 201 "Moving" behaviour in "Travelling" trajectories. The model is written as fol-
 202 lows:

203 Transition matrix

$$M_q = \begin{pmatrix} q_{R \rightarrow R} & 1 - q_{R \rightarrow R} \\ 1 - q_{M \rightarrow M} & q_{M \rightarrow M} \end{pmatrix} \quad (3)$$

204 State equation

$$z_t \sim \mathcal{B}(M_q[z_{t-1}]) \quad (4)$$

205 Observation model

$$\begin{aligned} y_{v_t} &\sim \mathcal{G}(a[z_t], \lambda[z_t]) \\ y_{\phi_t} &\sim \mathcal{WC}(b[z_t], \rho[z_t]) \end{aligned} \quad (5)$$

206 with $q_{R \rightarrow R}$ and $q_{M \rightarrow M}$ being the probability of maintaining resting, or
 207 moving, behaviour following resting, or moving, behaviour, and z_t being the
 208 behaviour at time t (R or M). Concerning the data, y_{v_t} is the observed speed
 209 between $t - 1$ and t , and y_{ϕ_t} is the observed turning angle between $t - 2$ and
 210 $t - 1$ and $t - 1$ and t . Concerning the parameters, $a[z_t]$ and $\lambda[z_t]$ describe the
 211 speed for behaviour z at time t and $b[z_t]$, and $\rho[z_t]$ describes the turning angle
 212 for behaviour z at time t . \mathcal{B} , \mathcal{G} and \mathcal{WC} represent the Bernoulli [distribution](#),
 213 the Gamma [distribution](#) and the Wrapped Cauchy [distribution](#), respectively.
 214 Given that U_1 and U_2 allow integration of information derived from the raw
 215 data independently of the interpolation, two models were tested to determine

whether taking into account of U_1 and U_2 improved the model's behaviour discrimination. The first (hereafter, "Model 1") included only variables from interpolated data (observed speed and observed turning angles). In the second (hereafter, "Model 2"), U_1 and U_2 were added to the variables, the observation model becoming as follows:

$$\begin{aligned} y_{v_t} &\sim \mathcal{G}(a[z_t], \lambda[z_t]) \\ y_{\phi_t} &\sim \mathcal{WC}(b[z_t], \rho[z_t]) \\ U_{1_t} &\sim \text{Beta}(\alpha[z_t], \beta[z_t]) \\ U_{2_t} &\sim \mathcal{N}(\mu[z_t], \sigma[z_t]) \end{aligned} \tag{6}$$

with $\alpha[z_t]$ and $\beta[z_t]$ being the parameters describing U_1 for behaviour z at time t , $\mu[z_t]$ and $\sigma[z_t]$ being the parameters describing U_2 for behaviour z at time t . *Beta* and \mathcal{N} represent for the Beta distribution and the normal distribution, respectively.

Computation. Bayesian inference was used to fit the model to the data: *i.e.*, the trajectories obtained for each time-step p_k . A single model was fitted for all selected trajectories at once. Prior distributions were defined summarising all available information on each parameter (Appendix B, Table B1). Markov Chain Monte Carlo (MCMC) computations were performed using JAGS software and the *rjags* R package (Plummer 2009, R Core team 2018). A total of 10,000 iterations were performed as a burn-in phase, and inference was based on 20,000 additional iterations for each of the three independent chains (with different initiations). The Gelman and Rubin tests (Gelman and Rubin 1992) were used to check the convergence of the estimation process. The computation times for the different time-steps p_k were compared. The estimated behaviour at each time-step was recorded from the

237 MCMC iterations. For each location, the credibility of resting and moving
 238 behaviours was calculated, as the mean of the behaviours estimated for all
 239 the MCMC iterations. We also calculated the mean duration of maintain-
 240 ing each behaviour (*i.e.*, the expected value of the geometric distribution
 241 with switching probability, multiplied by the time-step), with the medians
 242 and 95% credibility intervals of the posterior distributions for both switching
 243 probabilities.

244 Twelve fits of the models were performed for all 16 selected trajectories: one
 245 with Model 1 and one with Model 2, for each of the 6 tested time-steps. We
 246 also performed 2 additional fits using all the individual trajectories: one with
 247 Model 1 and one with Model 2, for the time-step which appeared to be the
 248 most appropriate after checking the various criteria. As convergence might
 249 not be reached for a simple model with two behaviours (Morales et al. 2004),
 250 we also tested similar models (without and with U_1 and U_2) including a third
 251 intermediate behaviour.

252 *Simulated data analysis.* A Markov chain of 10,000 behaviours was simu-
 253 lated with fixed transition probabilities ($q_{R \rightarrow R} = 0.99$ and $q_{M \rightarrow M} = 0.97$)
 254 using Model 1. Each point in the chain stands for a theoretical location of
 255 the individual and, for each point, a speed and a relative angle was derived
 256 from the distributions of speeds and relative angles of each behaviour (with
 257 the following fixed parameter values for speed and turning angles distribu-
 258 tions: $a_1 = 0.1$, $a_2 = 1.5$, $\lambda_1 = 10.5$, $\lambda_2 = 5$, $b_1 = 3.15$, $b_2 = 0$, $\rho_1 = 0.3$
 259 and $\rho_2 = 0.9$). Then, for each chain point, a theoretical location was cal-
 260 culated. Thus, we obtained a series of 10,000 locations associated with a
 261 behaviour. The theoretical time-step of this trajectory was 3 seconds. The

pre-processing described in the Section 2.2 was applied: for the 6 tested time-steps, the simulated trajectory was interpolated, speeds and turning angles were calculated, as well as the two additional variables U_1 and U_2 . Then, we estimated the parameters of Model 1 (with speeds and turning angles only) and Model 2 (with speeds, turning angles and the two additional variables U_1 and U_2) for each time-step and for the raw trajectory. Computation time was recorded and, when the model converged, the goodness of fit between the simulated and inferred behaviours was computed. For the 3-second trajectory (raw simulated data), inferred and simulated behaviours were compared directly. For the interpolated trajectories, first we computed the mean of the simulated behaviours between two locations within the time-step, then the root mean squared error for all the behaviours of the trajectory were calculated, comparing for each location the mean simulated behaviour and the inferred one. To compare results between time-steps, the root mean squared error was divided by the number of locations in the interpolated trajectory.

3. Results

3.1. Influence of the time-step between interpolated locations on behaviour inference

3.1.1. General correspondence of interpolated trajectories and raw data

Superimposition of raw data and interpolated trajectories is (for convenience) shown for 6 typical trajectories out of the 16 studied trajectories in Figure 1. For bi-type 1 and the two stationary trajectories, the interpolated trajectories did not show any major differences in overall movement between

time-steps. However, the duration of the trajectories increased with the time-step, which was expected because of the increasing threshold separating two distinct trajectories, whereas the number of locations decreased. On the contrary, for bi-type 2 and the two travelling trajectories with the most changes in direction, the interpolated trajectories did not show any major differences for time-steps below 60 seconds, but diverged from the raw data for the four longer time-steps (120, 180, 240 and 300 seconds).

3.1.2. Additional variables

The ratio between covered distance from interpolated and raw data, namely U_1 , showed a similar pattern for all types of trajectory and for all time-steps (Figure 2a). As expected, U_1 decreased with increasing time-step, due to shorter covered distance in interpolated data. In the 5 time-steps longer than 30 seconds, the difference in U_1 between the three types of trajectories was greater than in the first time-step (30 seconds). Likewise, the variance of turning angles within the interpolation time-step, namely U_2 , showed a pattern similar to U_1 (Figure 2b).

3.1.3. Modelling results

Parameter estimation. The MCMC algorithm consistently converged according to Gelman and Rubin diagnostics for each simulation performed with the 16 selected trajectories. For all parameters, posterior distributions were narrower than prior distributions. The narrowness of the posterior distributions suggests that sufficient information was available from the data to accurately estimate the model parameters. Overall, there were progressive differences between parameter estimates with increasing time-step (Figure 3). However,

the posterior distributions of the first two time-steps (30 and 60 seconds) differed strongly from those of the other four time-steps, all of which were quite similar.

The mean of speed distributions of resting behaviour a_R decreased with increasing time-step, because of decreasing estimated travel distance in the interpolated trajectory. Mean turning angle distributions b_R and b_M were constant for all time-steps. The modes of U_1 (the ratio between the covered distance from the interpolated and raw data, within the interpolation time-step) distributions α_R and α_M decreased with increasing time-step, because the longer the time-step, the lower the fit between interpolated trajectory and raw data. Mean U_2 for moving behaviour μ_M increased with increasing time-step, where the turning angles were more acute (*e.g.*, travelling trajectories in Figure 1). Mean U_2 for the resting behaviour μ_R was similar for all time-steps.

Concerning the transition probability of maintaining resting behaviour $q_{R \rightarrow R}$, posterior distributions were similar for the four longer time-steps (120 to 300 seconds), with a median value around 0.975. For the second tested time-step (60 seconds), the median of the posterior distribution was lower (around 0.95), and much lower for the shortest time-step of 30 seconds (around 0.88). Concerning the transition probability of maintaining moving behaviour $q_{M \rightarrow M}$, posterior distributions were similar for the two longest time-steps of 240 and 300 seconds, with a median value around 0.90, and for the 30, 120 and 180 second time-steps, with a median value around 0.87. For the 60 second time-step, the median value of the posterior distribution was higher (around 0.93).

335 *Inferred behaviours.* Behaviours were highly discriminated for all tested time-
336 steps, although discrimination was a bit lower for the shortest time-step, of
337 30 seconds (Table 1). Using Model 2, inferred behaviours were similar for
338 all time-steps for the two travelling trajectories and the second stationary
339 trajectory (Figure 4). Stationary trajectory 1 showed a higher proportion of
340 resting behaviour for the four longest time-steps (120 to 300 seconds) (Figure
341 4); for the two shortest time-steps, some movements were associated with
342 moving behaviour, or else were not discriminated (Figure 5). Similarly, the
343 stationary phase at the end of the bi-type 1 trajectory was more associated
344 with moving behaviour (or else not discriminated) for the two shortest time-
345 steps (Figure 5). Concerning the bi-type 2 trajectory, a higher proportion
346 of resting behaviour was inferred for the four longest time-steps (Figure 4),
347 due to the increased number of locations in the stationary phase at the end
348 of the trajectory (Figure 5).

349 *Simulated data analysis.* For the three longest time-steps (180, 240 and 360
350 seconds), the models (Model 1 and Model 2) failed to converge and dis-
351 criminate between behaviours. For raw data, 99% of the inferred behaviours
352 matched the simulated ones (RMSE of 0.01) (Appendix D Table D1). For the
353 three shortest tested time-steps (30, 60 and 120 seconds), RMSE increased
354 with time-step. For the two shortest time-steps (30 and 60 seconds), RMSE
355 was lower on Model 2 than on Model 1. Part of the trajectory, with true and
356 inferred behaviours for the three shortest tested time-steps (30, 60 and 120
357 seconds), is shown in Appendix D, Figure D1.

358 3.2. Behaviour discrimination with the state-space model

359 3.2.1. Interest of the two additional variables

360 For stationary trajectories ("S"), U_1 was lower than for travelling trajec-
361 tories ("T"), and showed average values for bi-type trajectories ("B") (Figure
362 2 (a)). This was due to the higher rate of star-shaped trajectories when the
363 individual was stationary: in star-shaped trajectories, distance covered was
364 shorter on interpolated than raw data, due to the triangulation artefact.
365 U_2 was lower for travelling than stationary trajectories and intermediate for
366 bi-type trajectories (Figure 2 (b)). The differences shown by U_1 and U_2 be-
367 tween the different types of trajectory provide information for discriminating
368 "resting" versus "moving" behaviour related to "stationary" and "travelling"
369 trajectory types, respectively. Behaviours were slightly better discriminated
370 (*i.e.*, were in most cases inferred as being either resting or moving), with the
371 addition of U_1 and U_2 (Table 1).

372 Finally, we fitted the model on all the 731 available trajectories, except for
373 those comprising fewer than 5 locations. At first, neither of the two models
374 (Model 1 and Model 2) was able to converge. We therefore added a third
375 behaviour in the models. This third behaviour was an intermediate between
376 the resting and moving behaviours, with mean turning angle close to that
377 of the resting behaviour, and mean speed between the mean speeds of the
378 other two behaviours. With the third behaviour, Model 2 converged whereas
379 Model 1 still failed to converge.

380 3.2.2. Fit between inferred behaviours and observed trajectories

381 Overall, with Model 2, inferred behaviours were consistent with observed
382 trajectories: moving behaviours were mostly inferred in travelling trajecto-

383 ries, and resting behaviours in stationary trajectories (Figure 4). For the
 384 bi-type 2 trajectory, the travelling (starting) and stationary (ending) phases
 385 mostly corresponded to moving and resting behaviours, respectively, as ex-
 386 pected. Some movements in stationary phases were, however, associated with
 387 moving behaviour, or with resting behaviour with low certainty, for the two
 388 shortest time-steps. Increasing time-step increased mean duration for each
 389 behaviour (Table 2), and also increased the difference in duration between
 390 the behaviours: the longer the time-step, the longer the resting duration,
 391 compared to the moving duration.

392 4. Discussion

393 4.1. Influence of time-step on behaviour discrimination and computation 394 time

395 A wide range of durations between two consecutive locations (*i.e.*, time-
 396 steps) are used in animal movement studies: for example from 60 seconds
 397 (eels, (Bassett and Montgomery 2011)) to several minutes (caribou, 15 min-
 398 utes (Andersen et al. 2017)), one hour (sea lions, (Breed et al. 2012)), or
 399 several hours (turtles, 6 hours (Bailey et al. 2008), wolves, 12 hours (Franke et al. 2006)).
 400 Time-steps should be adapted to the species, its travel mode and the question
 401 being addressed. For resident fish moving in small areas, time-steps shorter
 402 than several minutes are necessary to explore the different behaviours. We
 403 observed progressive but not major differences between variables (*i.e.*, the
 404 movement variables mean speed and turning angles (Appendix A, Figure
 405 A2 (a) and (b)) and the additional variables U_1 and U_2) used to evalu-
 406 ate the tested interpolation time-steps. As of the second tested time-step

(60 seconds), behaviours were better discriminated. However, with time-steps longer than 120 seconds, interpolation generated trajectories that were very remote from the raw data, considerably degrading location information. This can cause problems: for instance, when the individual often switches behaviour or when spatial data such as environmental parameters are to be included in the analysis. Likewise, the differences in mean duration per behaviour according to time-step showed that switching phases may be overlooked if a long time-step is used and, consequently, information on species ecology can be lost due to unreliable interpolation. Furthermore, model fit to the data (speed and turning angles; data not shown) was better for the two shortest time-steps. This is supported by the analysis of simulated data, which gave satisfactory behaviour predictions for the two shortest time-steps (30 and 60 seconds), poorer prediction for 120 seconds, and no discrimination between behaviours for the three longest time-steps (180, 240, and 360 seconds).

Overall, computation time (Appendix B, Table B2) was reasonable. There were no large differences between the time-steps from 60 to 240 seconds. However, computation time was almost twice as long for the shortest (30 seconds) as for the longest (300 seconds) time-step. For simulated data, computation time was almost 12-fold longer for raw data (3 seconds) than for the shortest time-step (30 seconds) and 2.5-fold longer for the 30-second than the 60-second time-step (Appendix D, Table D2). Such a difference can be critical when analysing all trajectories of all individuals together, even though data generated by interpolation made the model inference feasible, in terms of computation time, for all tested time-steps.

4.2. Model results and behaviour discrimination

The results concerning the movement descriptors (*i.e.*, speed and turning angle distributions) in resting behaviour should be regarded with caution. Most artefactual trajectories that are "star-shaped" are stationary phases which mainly include resting behaviour. Nevertheless, interpolation with all tested time-steps reduced that artefact, enabling discrimination between moving and resting behaviours. The high estimated transition probabilities $q_{R \rightarrow R}$ and $q_{M \rightarrow M}$ (above 0.80) imply that behaviours presented long duration, and are clearly influenced by our choices of "exemplary" trajectories displaying contrasted movement phases.

In order to check whether behaviours were adequately discriminated according to the tested time-steps, the selected trajectories had to be composed of phases that clearly represent the two main behaviours. As a consequence, some other patterns of movement were firstly discarded. When all trajectories were included (even excluding those with fewer than 5 locations), the simple model with two behaviours did not converge, partly due to the presence of these other movement patterns. In addition, we assumed a constant transition matrix, which is too simplistic since fish behaviour is influenced by environmental factors. This might also prevent the model from converging. Further validation with all data is needed, but a simple model tested on a set of sample trajectories is still useful to determine the pre-processing to be performed on the data.

Additional variables. Focusing on the 16 selected trajectories, including the two variables U_1 and U_2 in the model improved discrimination of behaviours. The simulated data analysis showed that including the additional variables

reduced prediction error for the two shortest time-steps (30 and 60 seconds). Thus, it appears highly profitable to combine these kinds of variable, calculated from raw data, with a short time-step to compensate the deficit in behaviour discrimination. Furthermore, using all trajectories (except for those with fewer than 5 locations) confirmed the benefit of including the additional variables U_1 and U_2 for a given interpolation time-step (here, 60 seconds). Other additional variables could have been considered such as specific indicators related to the known behaviours of the studied species.

4.3. *Implications of the interpolation and trajectory cutting processes for behaviour discrimination*

Tools from earlier studies of state-space models (*e.g.*, (Johnson et al. 2008, Jonsen et al. 2003, Vermard et al. 2010)) attempted to deal with irregular time-steps, location errors or the reconstruction of entire trajectories. Such tools could have been appropriate to process the present data, but the prime issue was computing time, and increasing the time-step solved this while also dealing with most of the numerous small gaps in location. Combined with the use of the two additional variables U_1 and U_2 , the proposed processing reduced computing time, dealt with irregularly time-spaced locations and preserved the information provided by the initial 3-second- time-step of the raw data. For the present study, several smaller unconnected trajectories provided enough information, and we did not seek to determine individual locations and behaviours when the signal had been lost for a long period of time (several hours). To achieve convergence with the 3-behaviour model, the shortest trajectories (fewers than 5 points) were deleted from the dataset. This necessity might be due to a bias in estimating transition probabilities

482 for these very short trajectories. An initial behaviour (namely z_{init} , see Ap-
 483 pendix C, Model code) was mandatory to initiate the Markov chain of be-
 484 haviours across time: z_{init} was derived from a categorical [distribution](#) with
 485 the 3 equal probabilities. When short trajectories are numerous, the esti-
 486 mated transition probability from the initial behaviour to the first behaviour
 487 of the trajectory has a major weight, although it is only an "artefact" of the
 488 modelling procedure.

489 As short trajectories may bias the estimation of transition probabilities, a
 490 more suitable dataset would favour long trajectories (*i.e.*, with the maximum
 491 number of points). For this, two possibilities emerged. Firstly, long time-
 492 steps could be used, so that the raw dataset is less divided: trajectories are
 493 longer in time, and also likely made up of numerous points. However, tra-
 494 jectories shorter in time than twice the chosen time-step were deleted due to
 495 interpolation, because at least two movements are needed to calculate speed
 496 and turning angle. These trajectories would be preserved with a smaller
 497 time-step. Secondly, a short time-step could be preferred, in which case tra-
 498 jectories are denser in points, but the cutting process of the raw data to
 499 obtain trajectories excludes more points than with a long time-step, because
 500 the s threshold is lower.

501 The cutting process and the chosen s threshold are thus appear key points
 502 in data pre-processing. The present cutting method has two main disad-
 503 vantages. [Firstly, the different time-steps were difficult to compare, as the](#)
 504 [number of locations differed between the tested time-steps.](#) Secondly, with a
 505 small threshold, trajectories are liable to be small, which could lead to over-
 506 looking some switches in behaviour. One solution could be to use a higher

threshold, chosen on the basis of the histogram of trajectory durations, combined with a small time-step. But this solution would lead to interpolating data on time ranges for which no observed locations are available, which is not desirable. An auto-correlogram of covered distances in the raw data could also give indications on where to cut the raw data to obtain trajectories. Missing locations could also be considered as missing data, instead of interpolating them. In the present case, this was not possible because using a Wrapped Cauchy distribution for turning angles within JAGS required using observed turning angles as input rather than observed variable (see Annex C Model code and BUGS trick in (Morales et al. 2004), Supplementary Information).

4.4. *Outline*

The present study developed a generic method of data pre-processing to handle trajectories at fine time scales and infer behaviours based on telemetry data, which could be transposed to other datasets. Data pre-processing is an essential step in trajectory analysis, although rarely highlighted. Increasing time-steps allowed efficient discrimination between behaviours, with locations regularly spaced in time and a smaller amount of data to process. At the same time, the additional variables computed from the raw data compensated for the loss of information in interpolated trajectories resulting from the increased time-step. The time-step should be adapted according to the ecology and habitat preference of the studied species. The raw data cutting process should be explored to optimise trajectory length while preserving small time-steps and correspondence between trajectories and raw data. We demonstrated the possibility of discriminating behaviours for the whole

dataset of a given individual, using a state-space model. This opens up interesting perspectives. Individual variation in movement or behavioural parameters could be quantified using the trajectories of several individuals, by hierarchical modelling (Jonsen 2016) using a 3-behaviour state-space model including additional variables computed from the raw data. The reduction in computation time is then particularly valuable when all trajectories of several individuals are included. Datasets for several individuals of various species have more sources of variability. Hierarchical modelling is then necessary to deal with individual and species variability. Environmental variability requires explicit modelling of the link between environmental variables, such as hydraulic or thermal parameters, and the transition matrix. **Considering that i) behavioural state and habitat selection are linked, and ii) movement and trajectory changes are behavioural state proxy, movement analysis is a way of investigating dynamical selection of habitat (short term, below several minutes) in a highly contrasted and variable (below the hour) environment. Therefore,** dynamically favourable habitats (according to dynamic hydraulic conditions) should be mapped, providing quantitative information to evaluate the impact of events such as thermal discharge or dam functioning.

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556 6. Figures titles and captions

557 6.1. Figure 1

558 *Title.* Six trajectories and raw data superimposed, for all the tested time-
559 steps.

560 *Caption.* Gray triangles are the raw data and black dots are the interpolated
561 locations (linked by black lines) for each time-step (*i.e.*, the trajectories).
562 These trajectories were chosen because they are characteristic of a stationary
563 behaviour (Stationary 1 and 2), of an active travelling behaviour (Travelling
564 1 and 2), or of an alternation between these two behaviours (Bi-type 1 and
565 2).

566 6.2. Figure 2

567 *Title.* Distributions of the additional variables U_1 (a) and U_2 (b), for all the
568 tested time-steps.

569 *Caption.* U_1 is the ratio between covered distances according to interpolated
570 data and covered distances according to raw data. U_2 is the variance of
571 turning angles of raw data within the interpolation time-step.

572 6.3. Figure 3

573 *Title.* Posterior distributions of the parameters, for all the tested time-steps,
574 from Model 2.

575 6.4. Figure 4

576 *Title.* Percentages of each inferred behaviour for six trajectories, for all the
577 tested time-steps (computed from Model 2).

578 *Caption.* Resting and Moving correspond to locations where resting and
579 moving behaviour respectively was inferred with probability > 0.8 (*i.e.*, for
580 80% of the MCMC iterations the estimated behaviour was resting/moving).
581 Hesitating corresponds to locations where behaviours were inferred with
582 probability < 0.8 .

583 6.5. Figure 5

584 *Title.* Six trajectories with inferred behaviour, for all the tested time-steps
585 (computed from Model 2).

586 *Caption.* These trajectories were chosen because they are characteristic of a
587 stationary behaviour (Stationary 1 and 2), of an active travelling behaviour
588 (Travelling 1 and 2), or of an alternation between these two behaviours (Bi-
589 type 1 and 2).

590 7. Appendix A: Figures

591 7.1. Figure A1

592 *Title.* Example of a star-shaped trajectory.

593 7.2. Figure A2 (a) and (b)

594 *Title.* Distributions of movement variables (speed and turning angles), for
595 all the tested time-steps.

596 7.3. Figure A3

597 *Title.* The 16 selected trajectories with inferred behaviour (red: moving,
598 blue: resting), for the 60-second time-step (computed from Model 2).

599 **8. Appendix B: Table of model parameters**

600 **9. Appendix C: JAGS code for Model 2**

601 **10. Appendix D: Simulated data analysis**

602 *10.1. Tables 1 and 2, Appendix D*

603 *10.2. Figure D1*

604 *Title.* Portion of the simulated trajectory with true (triangles) and predicted
605 (circles) behaviours for the three shortest tested time-steps (30, 60 and 120
606 seconds, from top to bottom), with Model 1 (left side) and Model 2 (right
607 side). Red stands for moving behaviour, and blue for resting.

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806 tions. *Methods in Ecology and Evolution*, (February):1–14, 2019.

807 [Woillez et al. 2016] M. Woillez, R. Fablet, T.-T. Ngo, M. Lalire, P. Lazure,
808 and H. de Pontual. A HMM-based model to geolocate pelagic fish from
809 high-resolution individual temperature and depth histories: European
810 sea bass as a case study. *Ecological Modelling*, 321:10–22, 2016.

Table 1: Percentage of locations where moving or resting behaviour was inferred with probability > 0.8 .

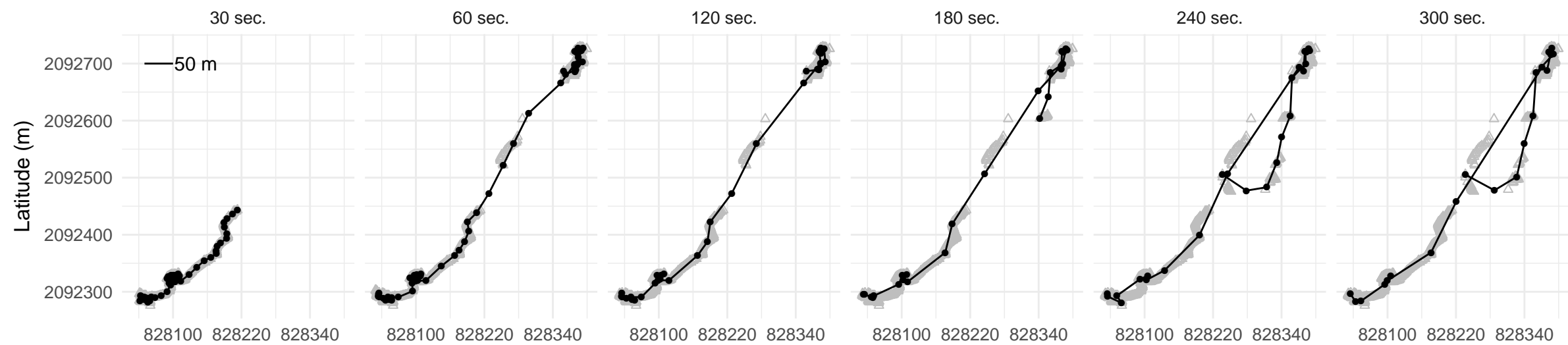
Time-step (sec.)	Model 1, without U_1 and U_2 (%)	Model 2, with U_1 and U_2 (%)
30	83	91
60	92	94
120	96	98
180	92	99
240	92	99
300	91	99

Table 2: Mean duration (minutes) in resting or moving behaviour according to the tested time-steps (computed from Model 2).

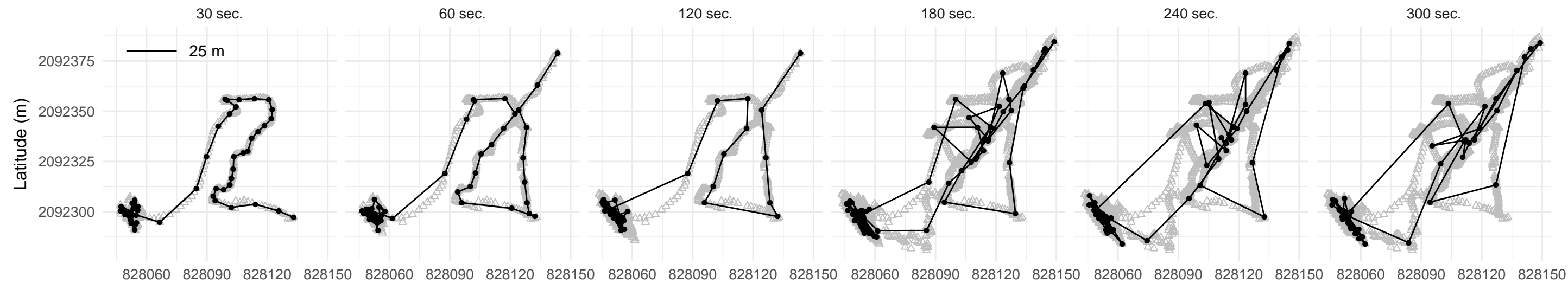
Time-step (sec.)	Resting	Moving
30	4.1 [3.2, 5.5]	3.7 [2.9, 4.9]
60	21 [14, 33]	12 [8.8, 18]
120	65 [43, 106]	15 [11, 22]
180	118 [74, 208]	24 [17, 36]
240	229 [125, 499]	38 [25, 61]
300	234 [129, 486]	45 [30, 73]

The mean duration (median and 95% credibility interval) in resting, or moving, behaviour was computed as the expected value (*i.e.*, the number of independent trials to get the first success) from the geometric distribution of probability equal to $1 - q_{R \rightarrow R}$, or $1 - q_{M \rightarrow M}$, multiplied by the time-step.

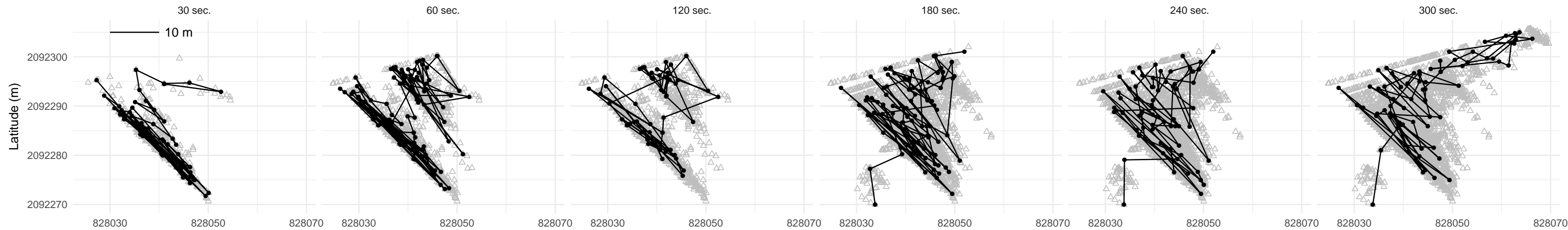
Bi-type 1



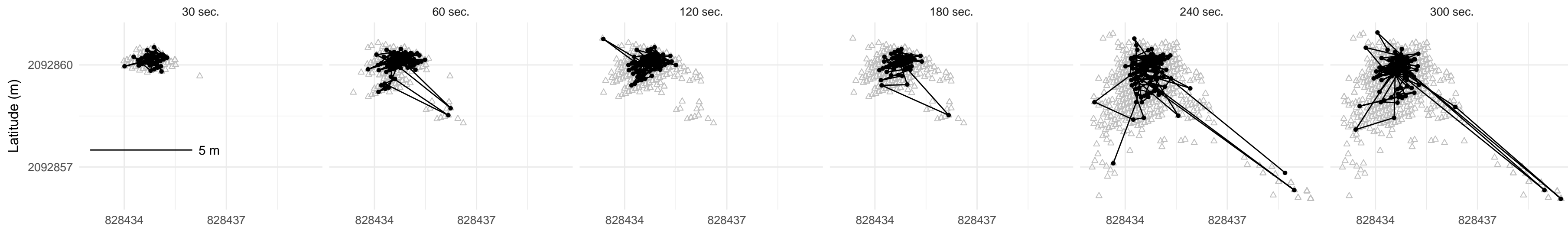
Bi-type 2



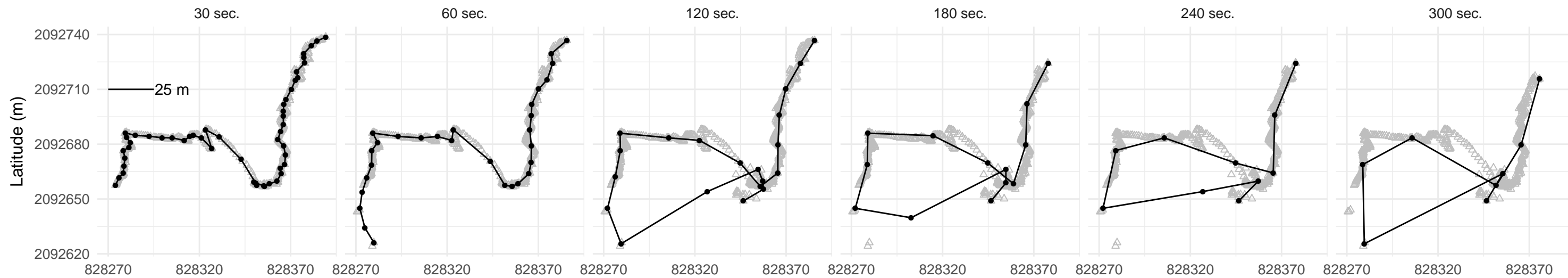
Stationary 1



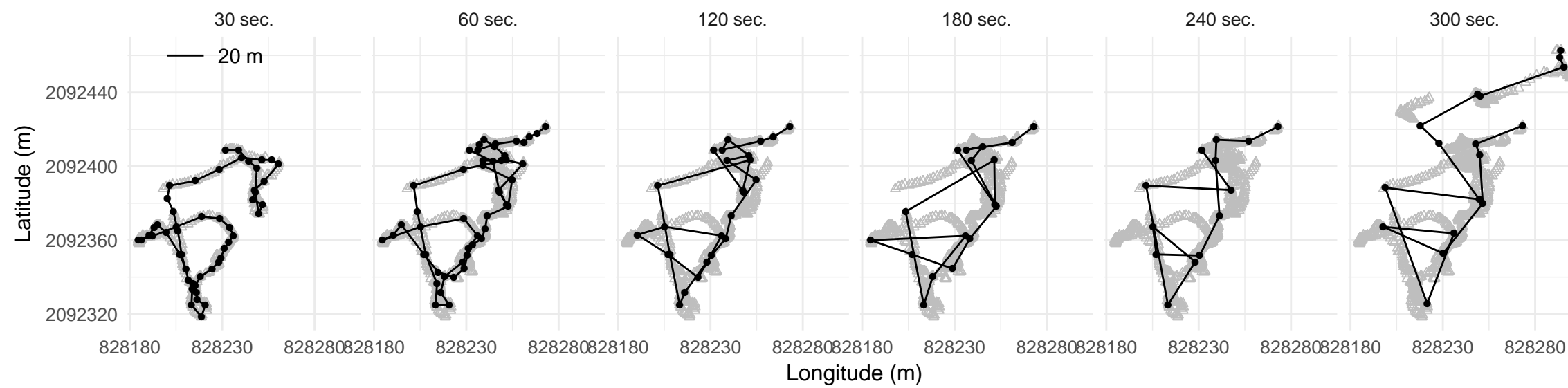
Stationary 2

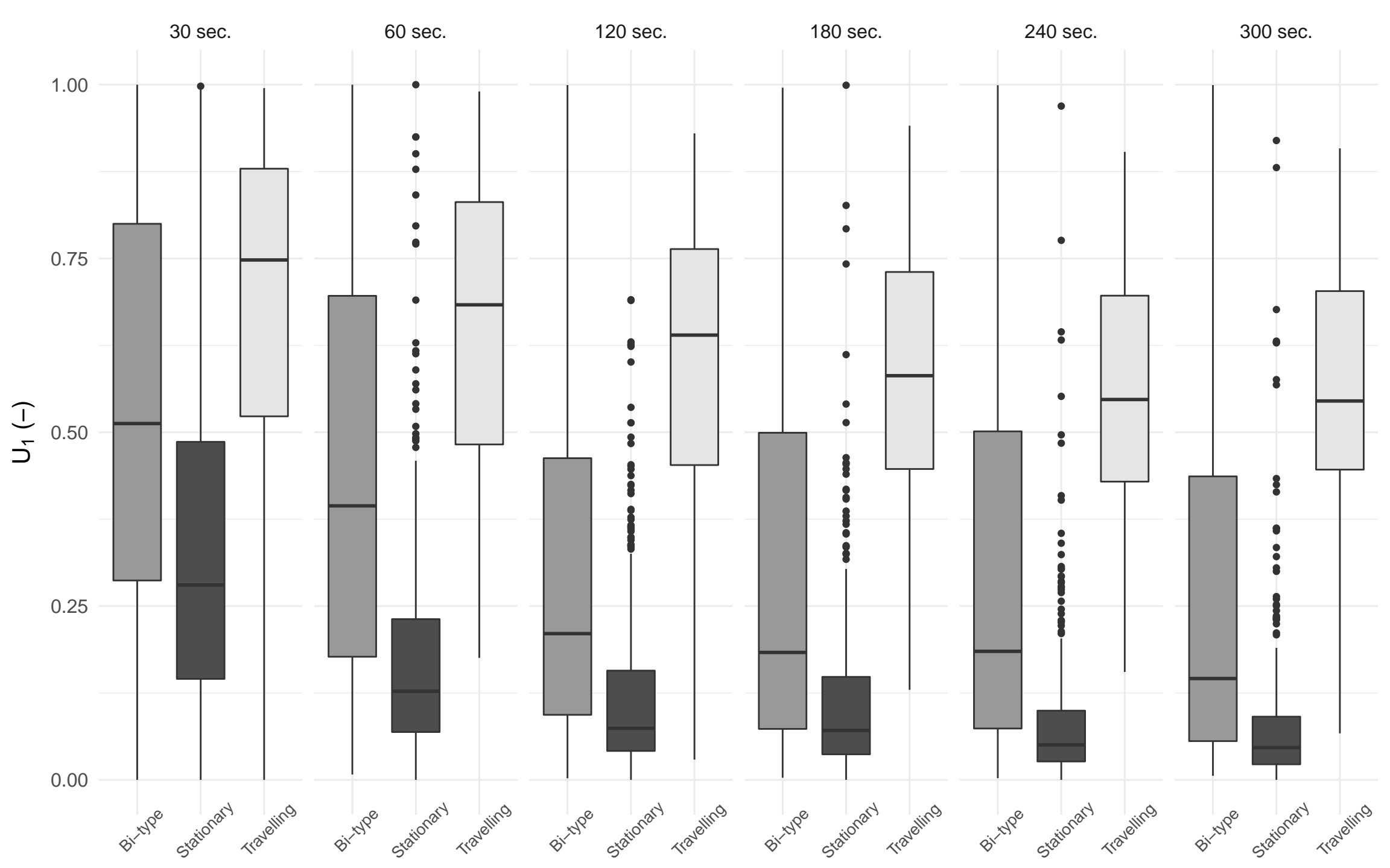


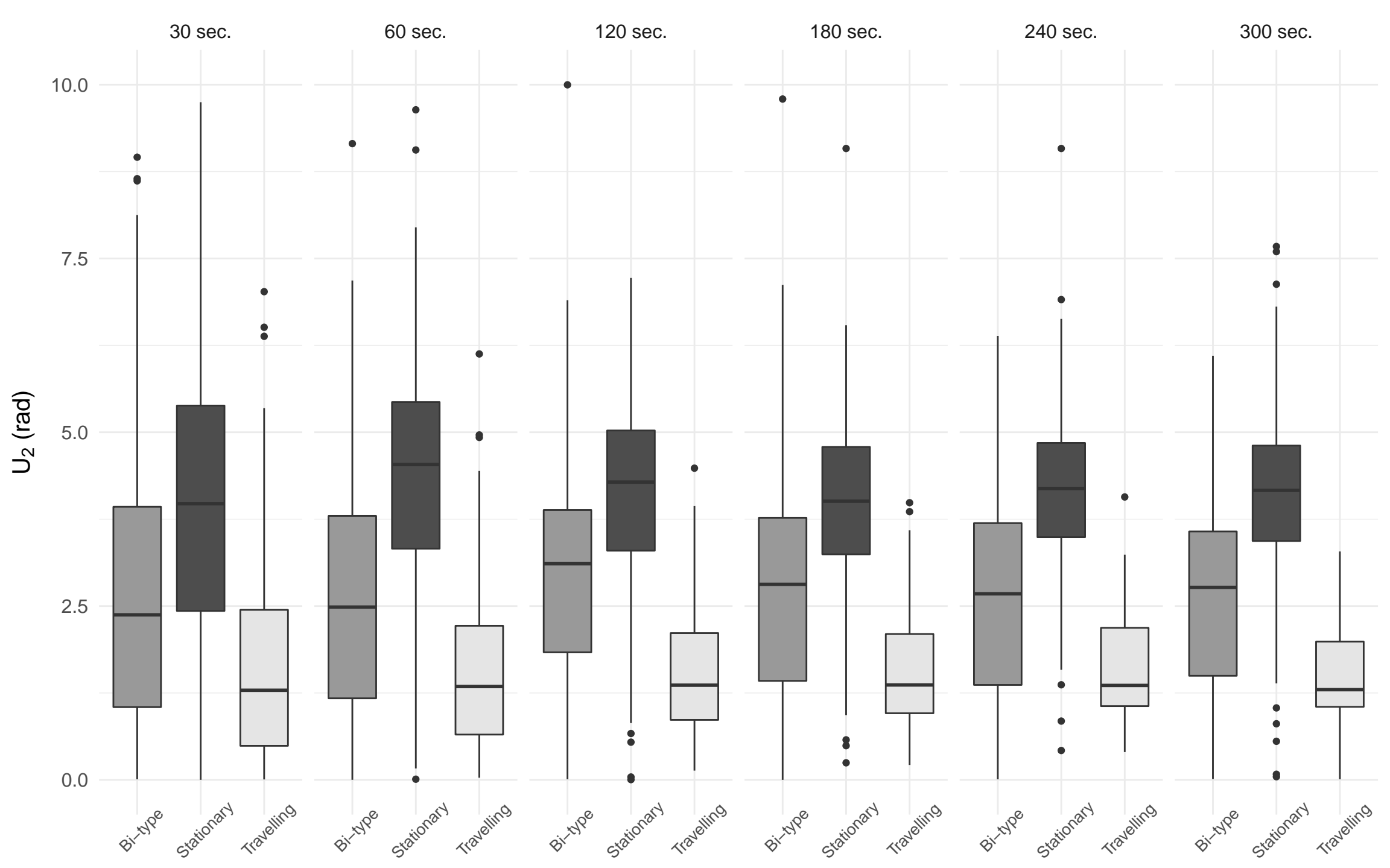
Travelling 1

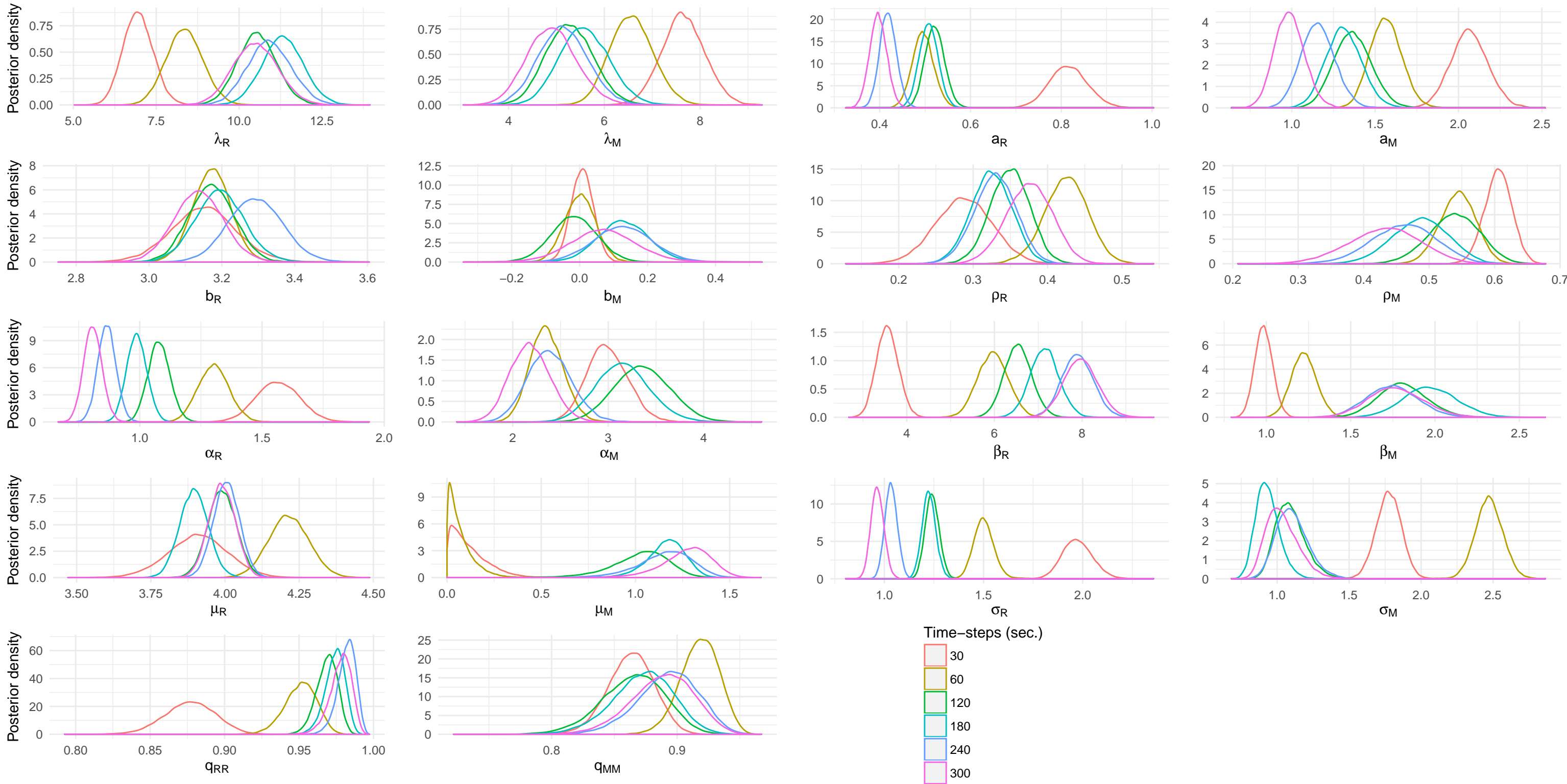


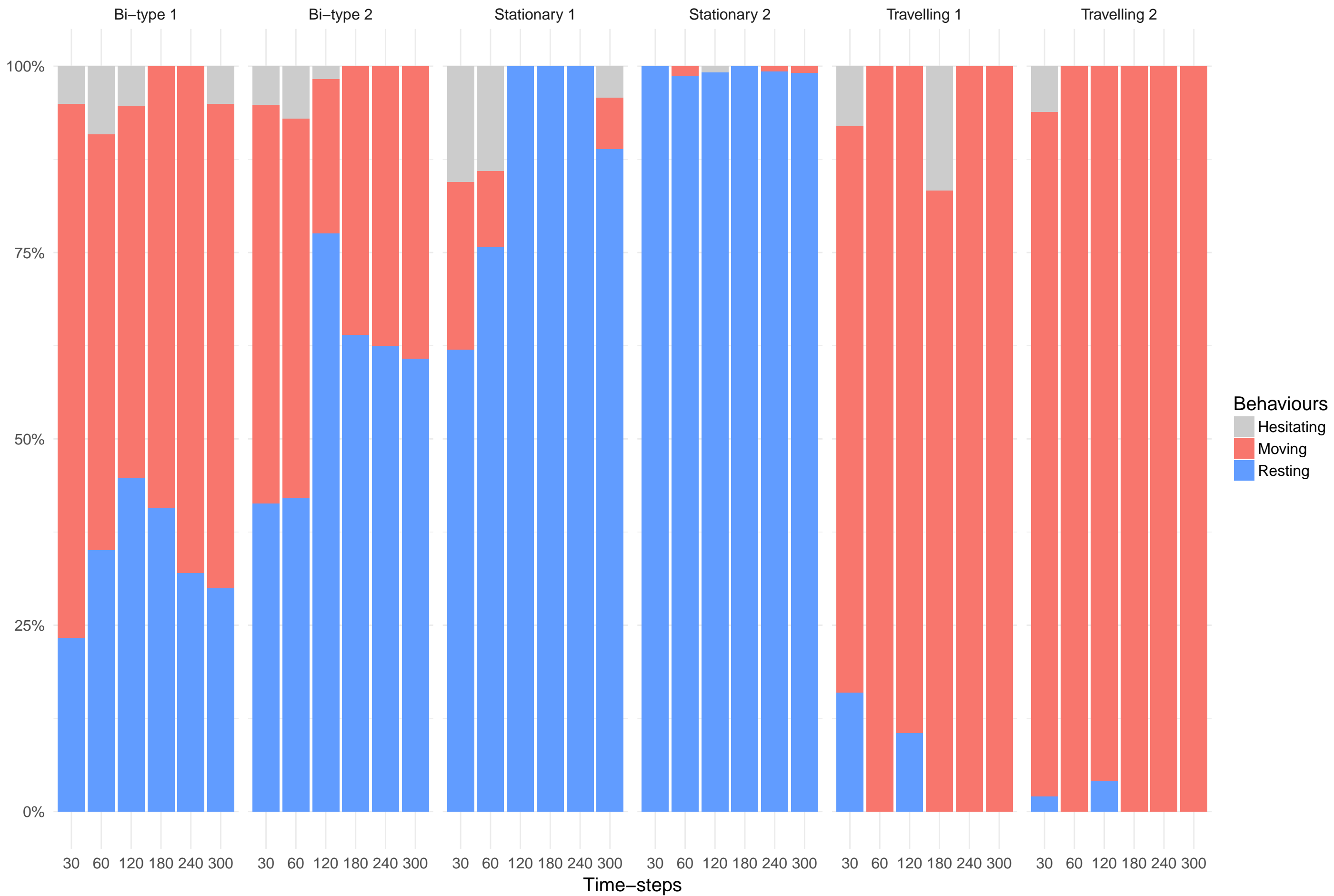
Travelling 2



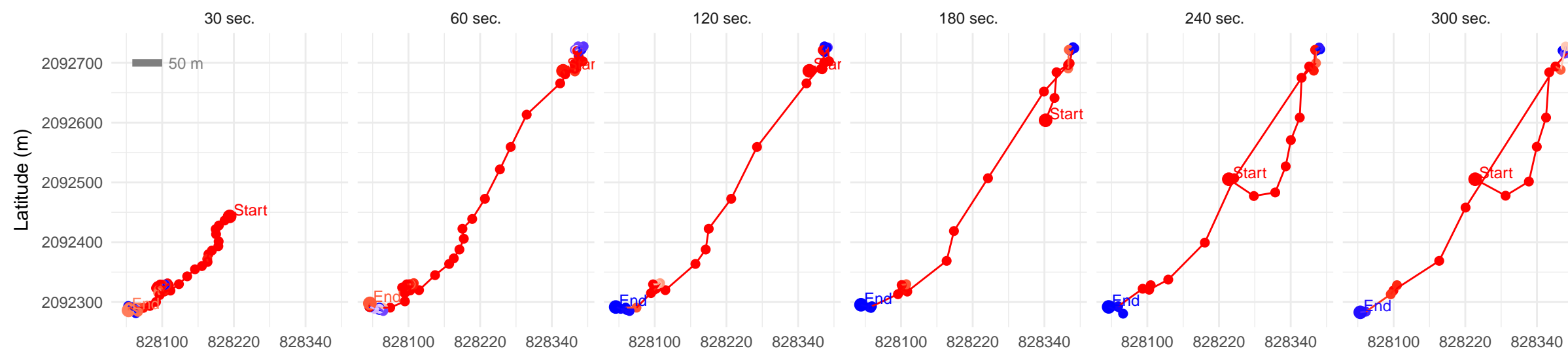




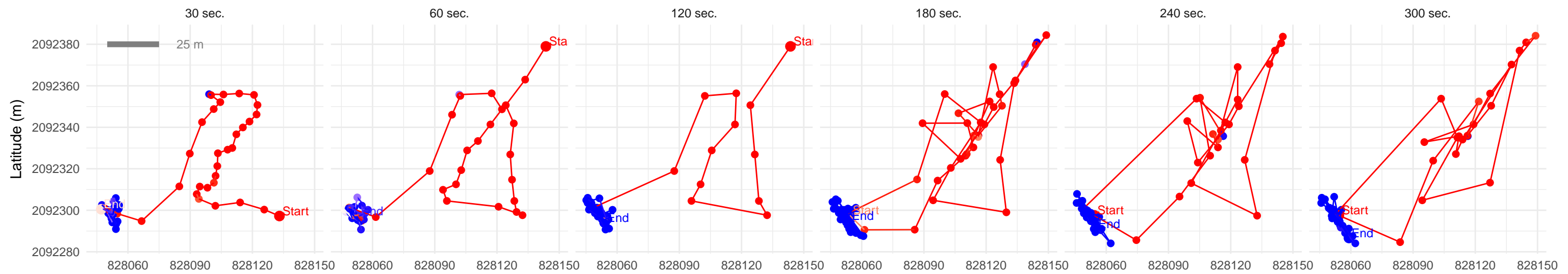




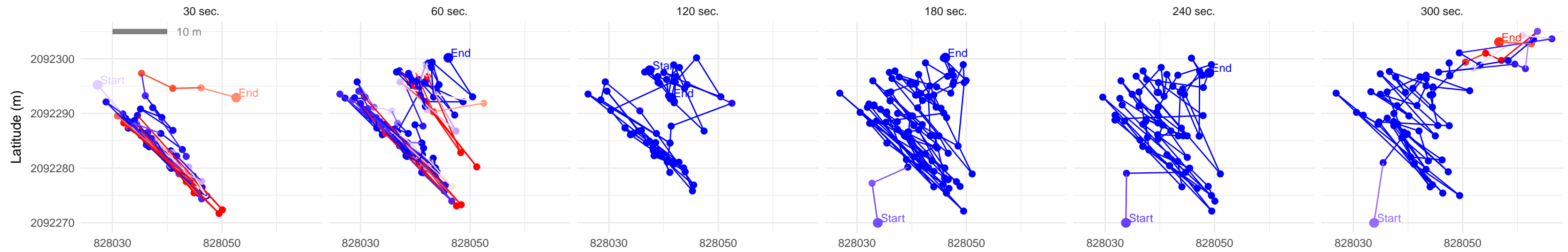
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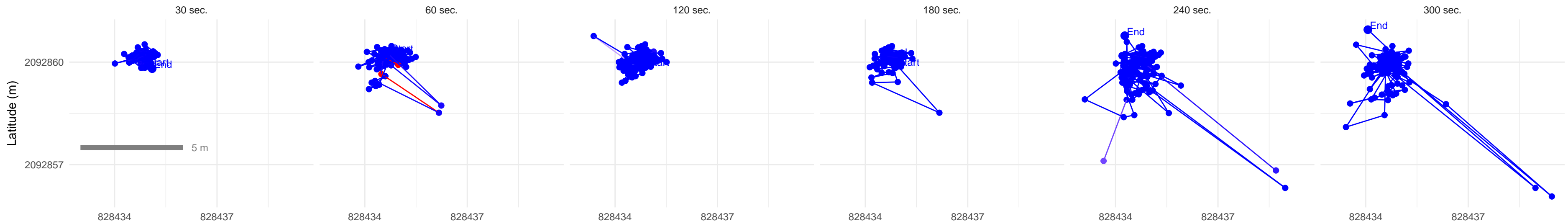
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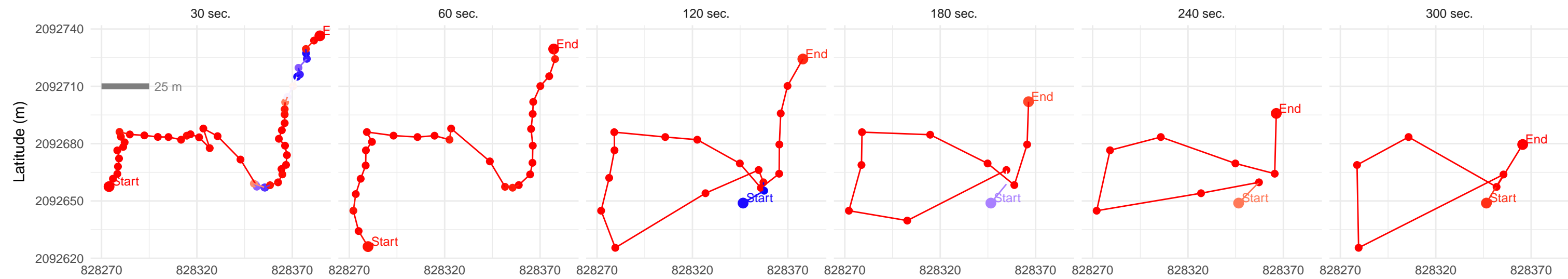
Stationary 1



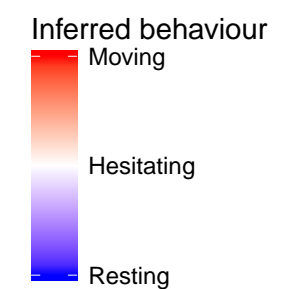
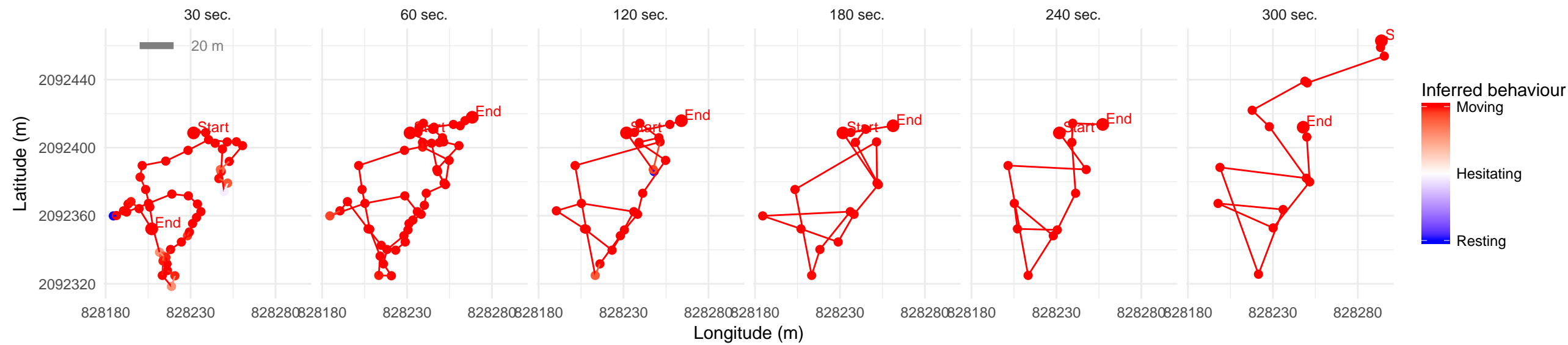
Stationary 2

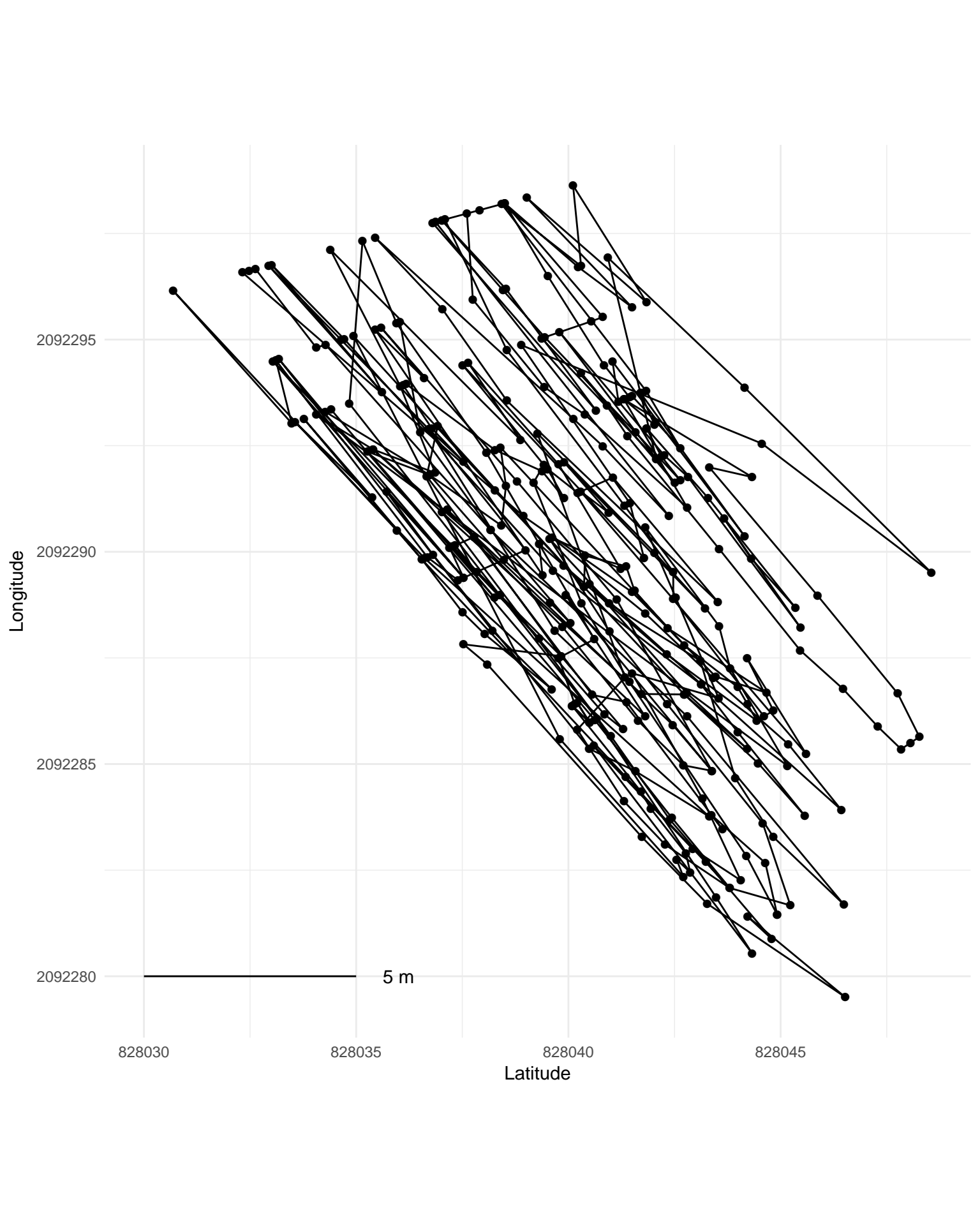


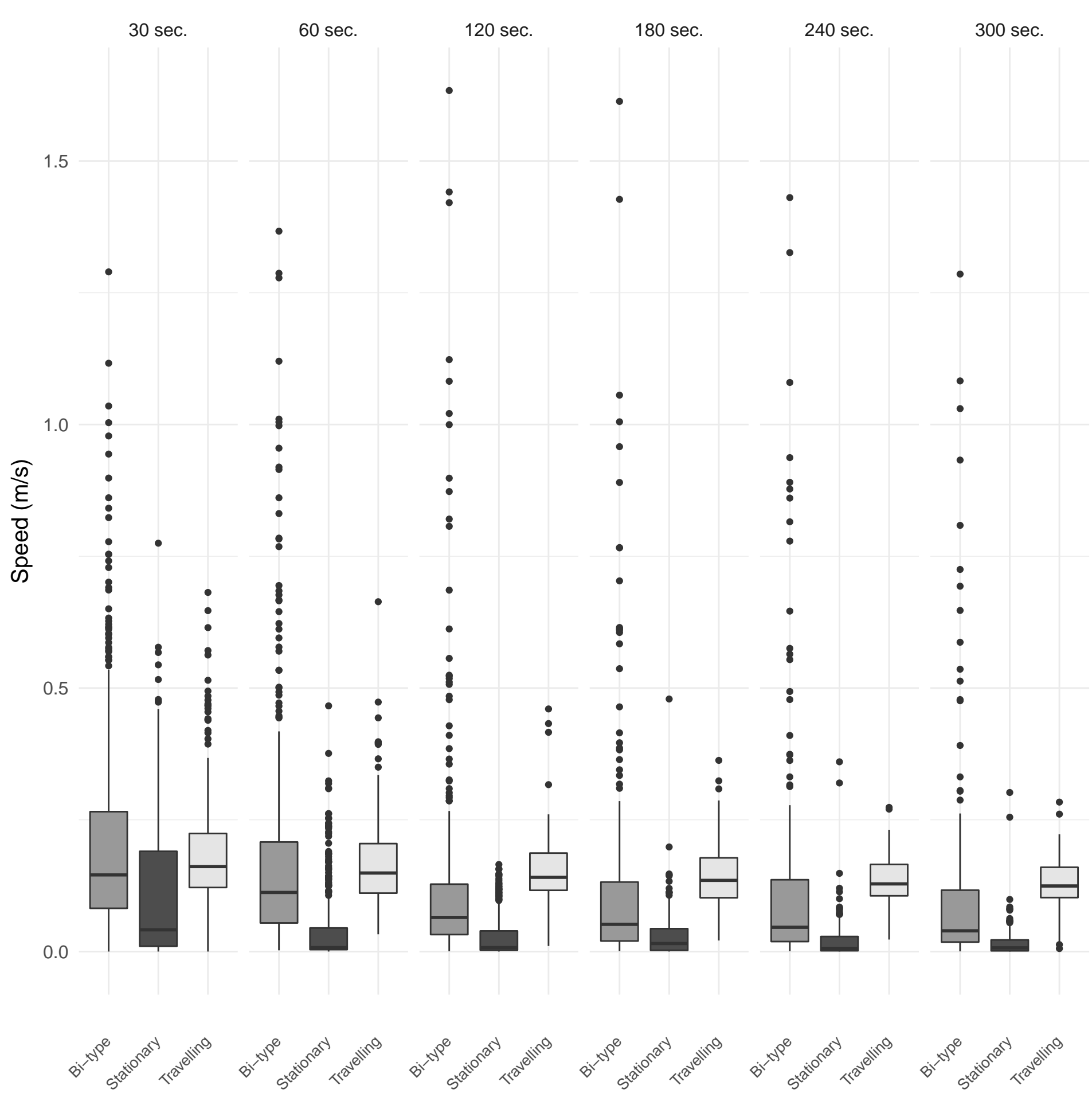
Travelling 1

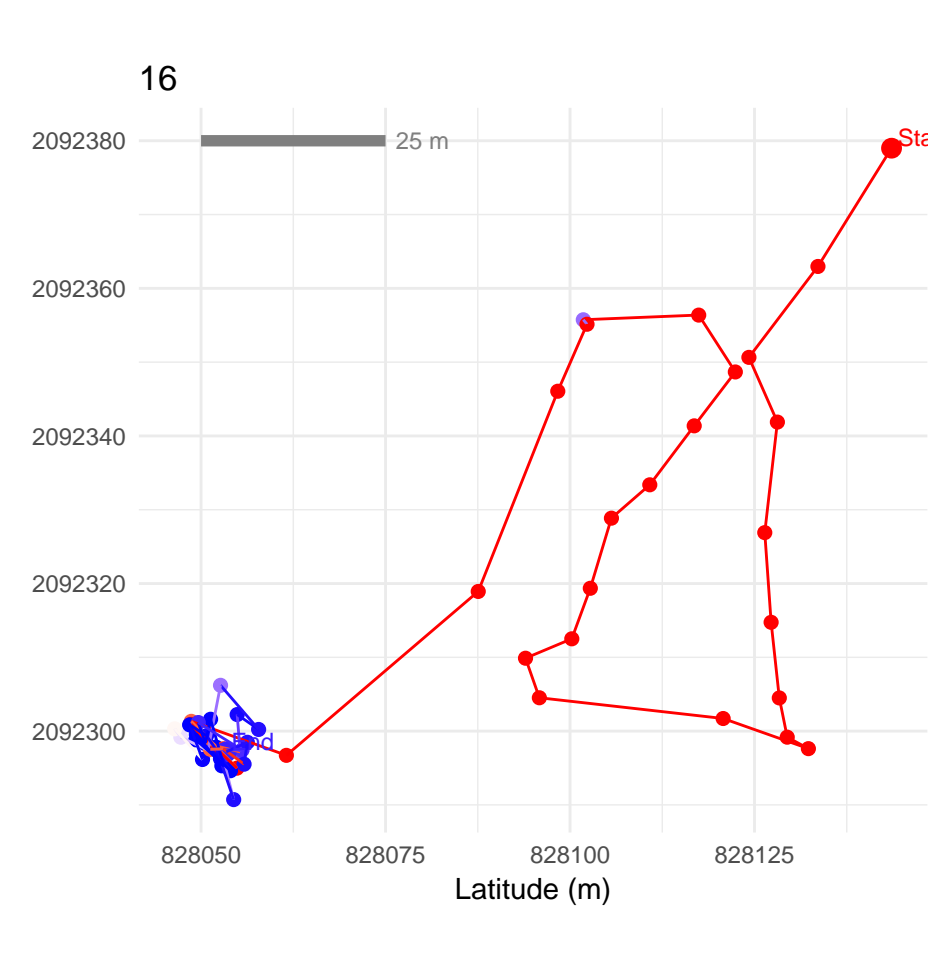
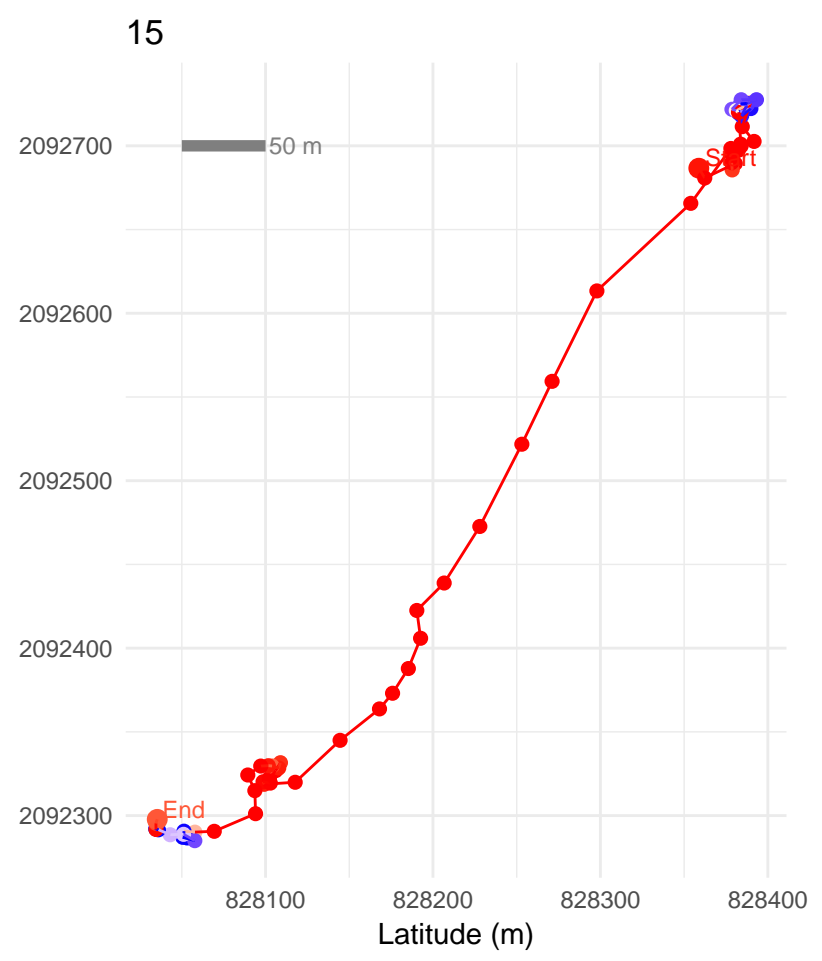
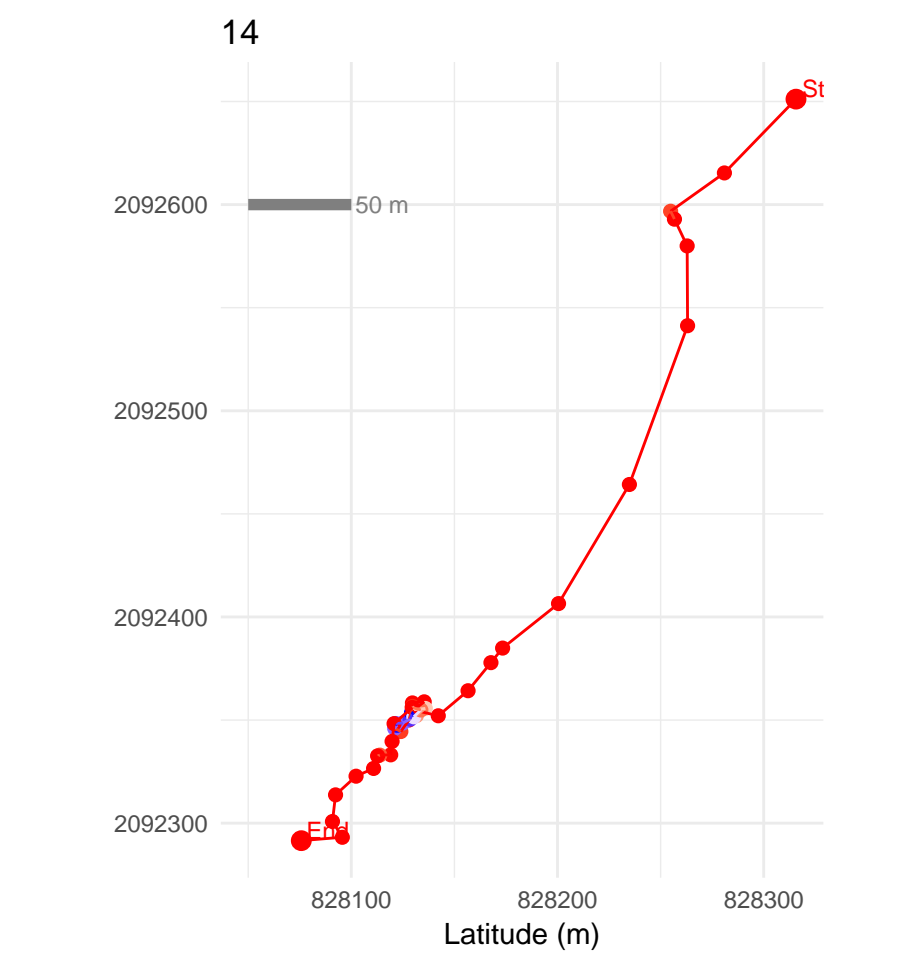
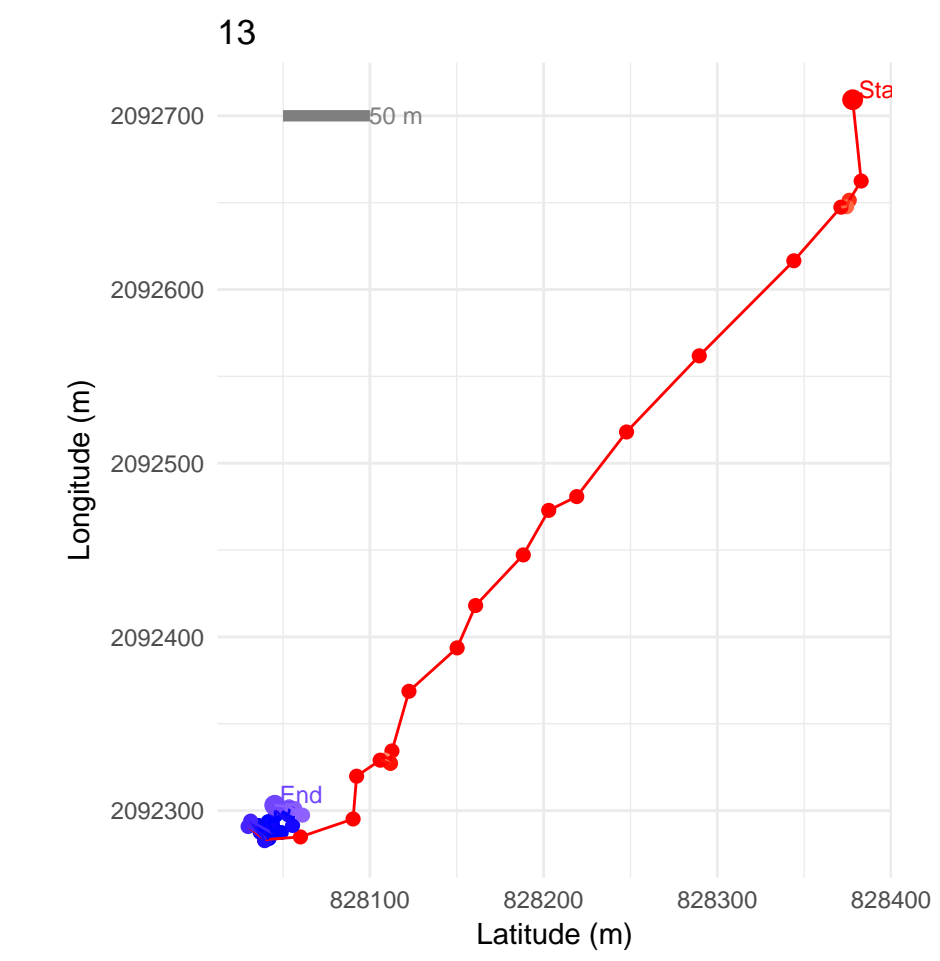
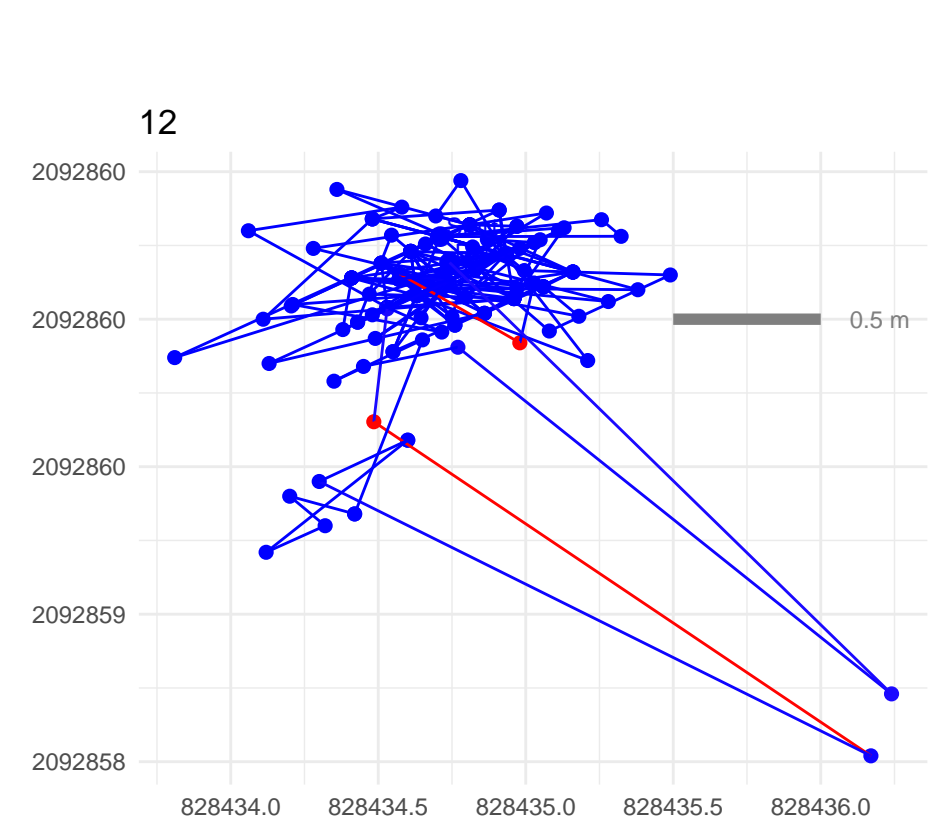
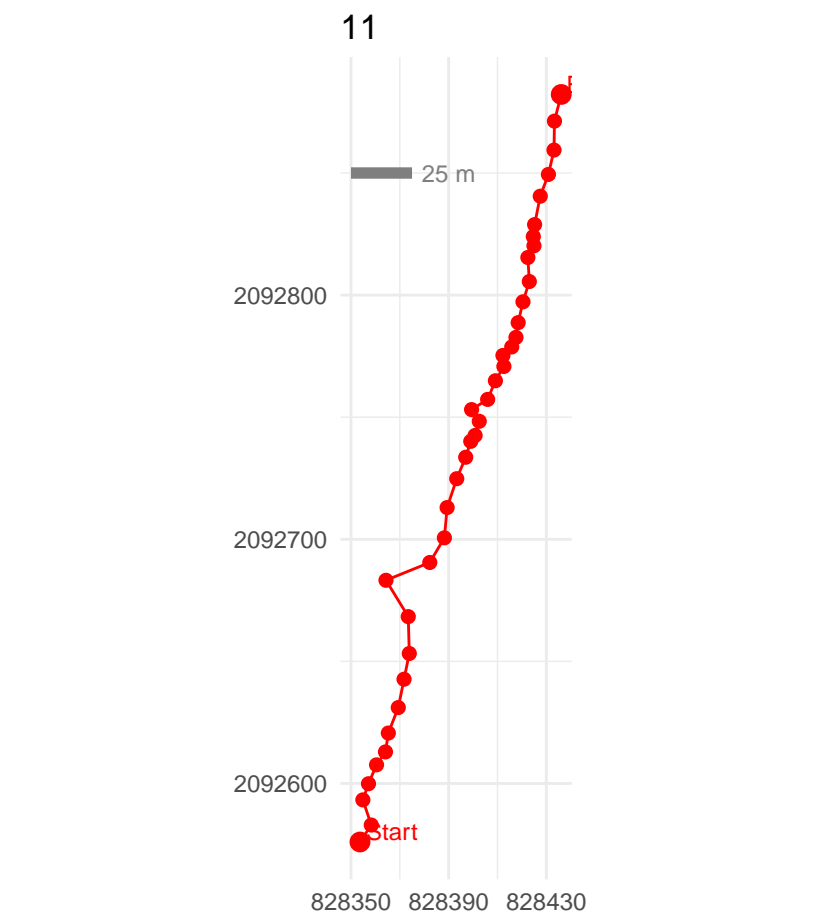
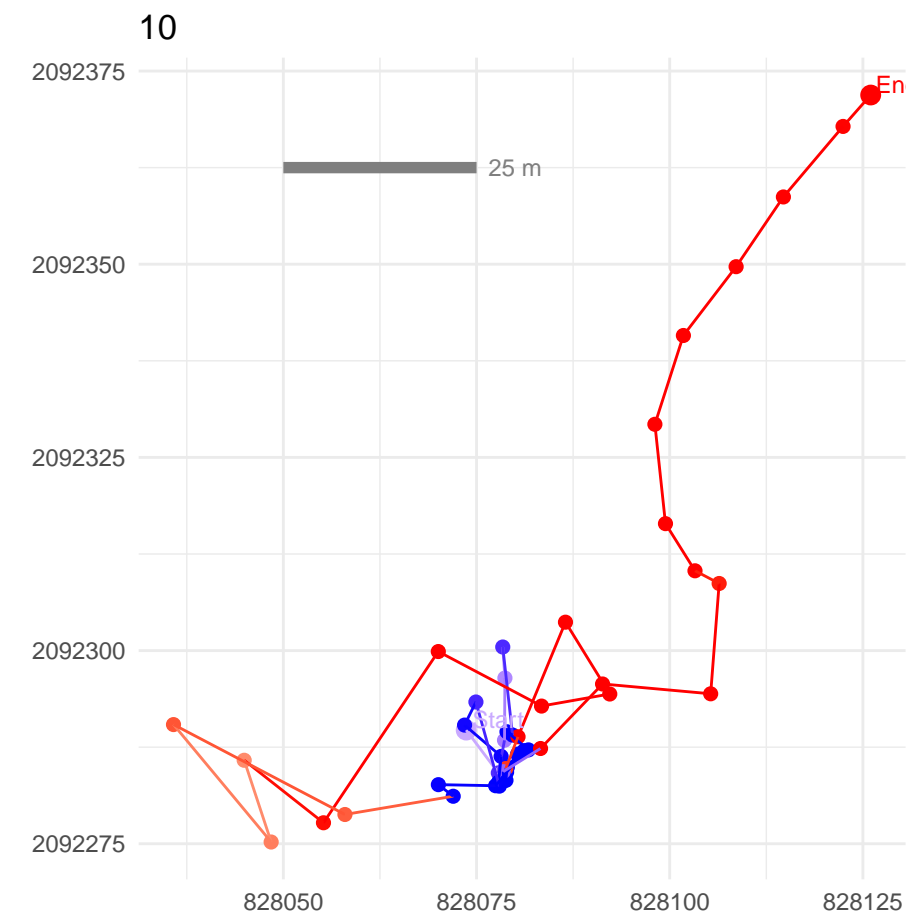
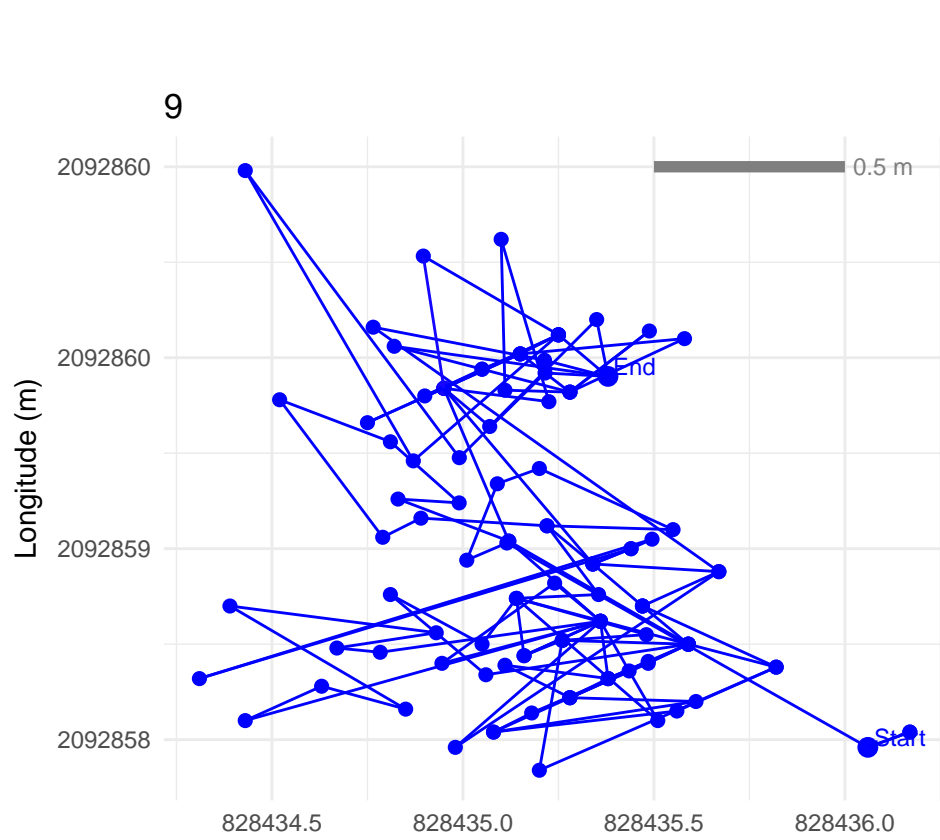
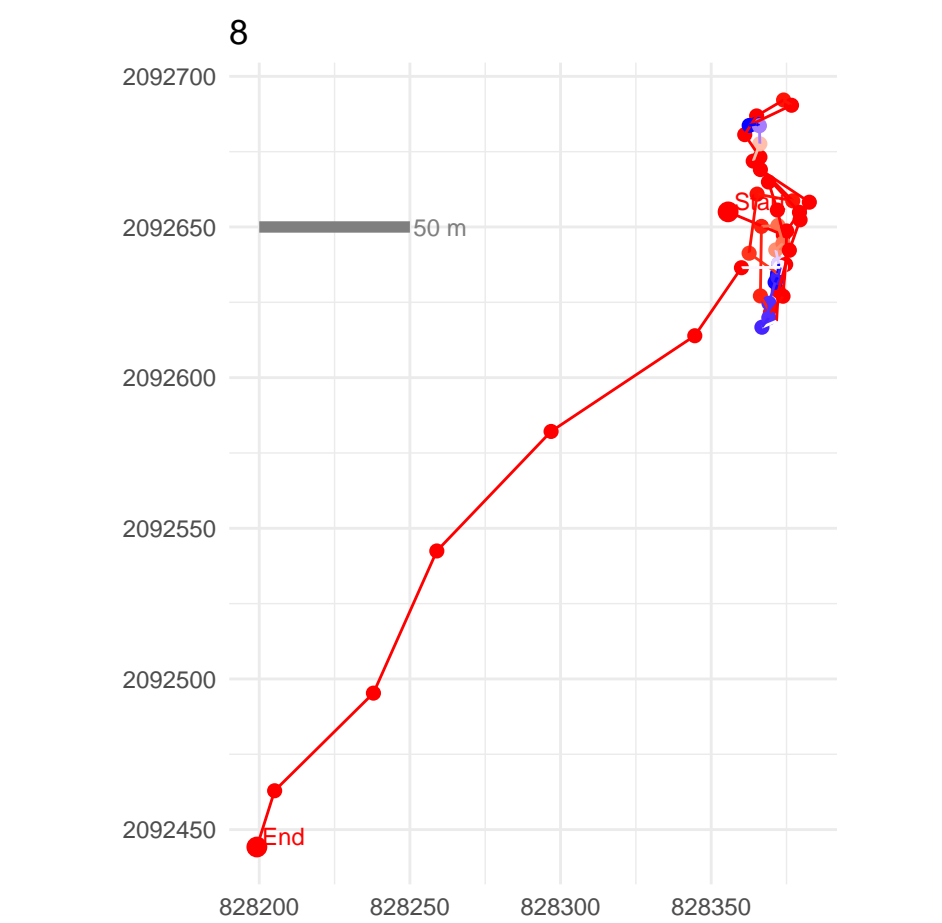
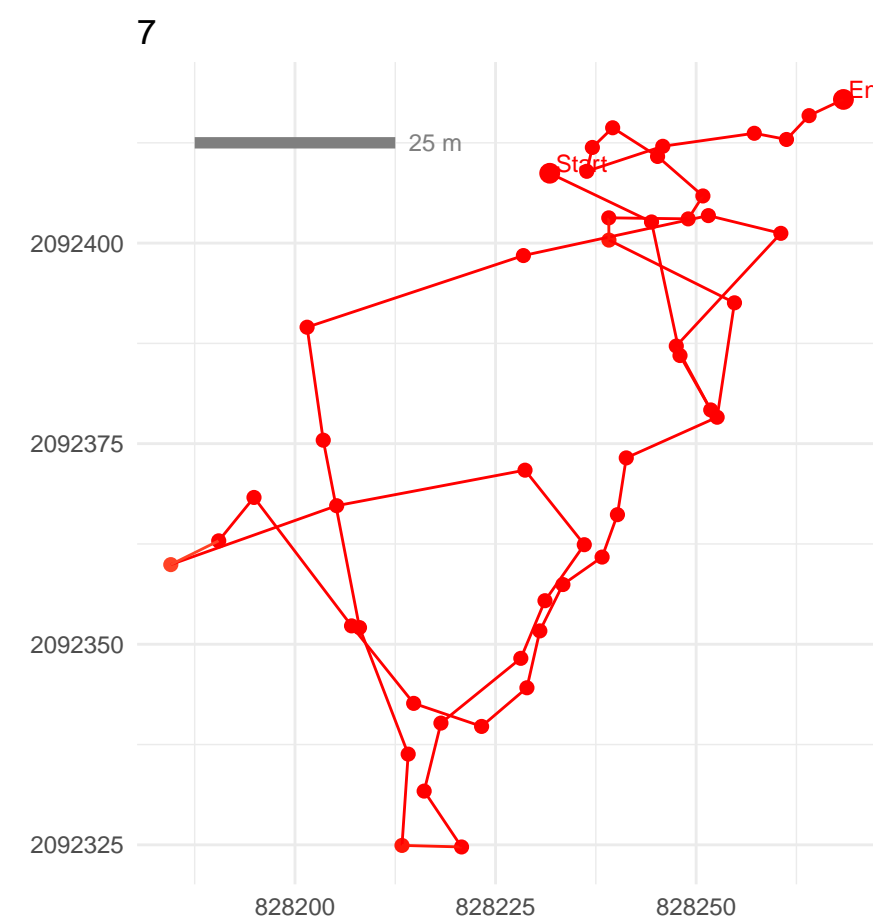
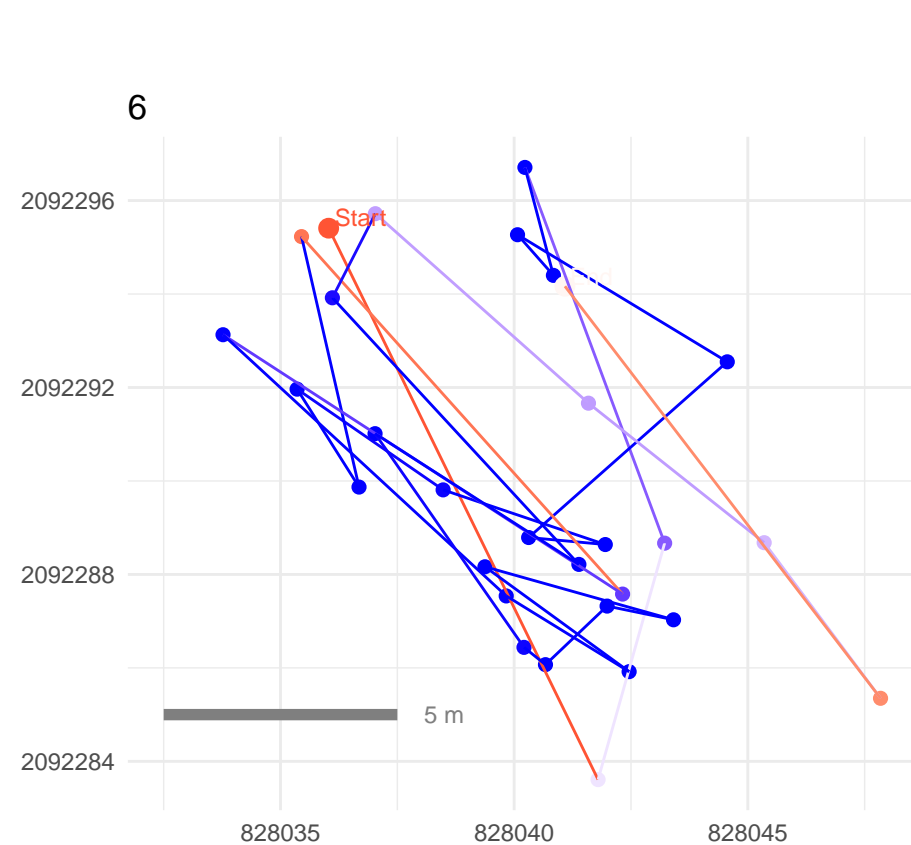
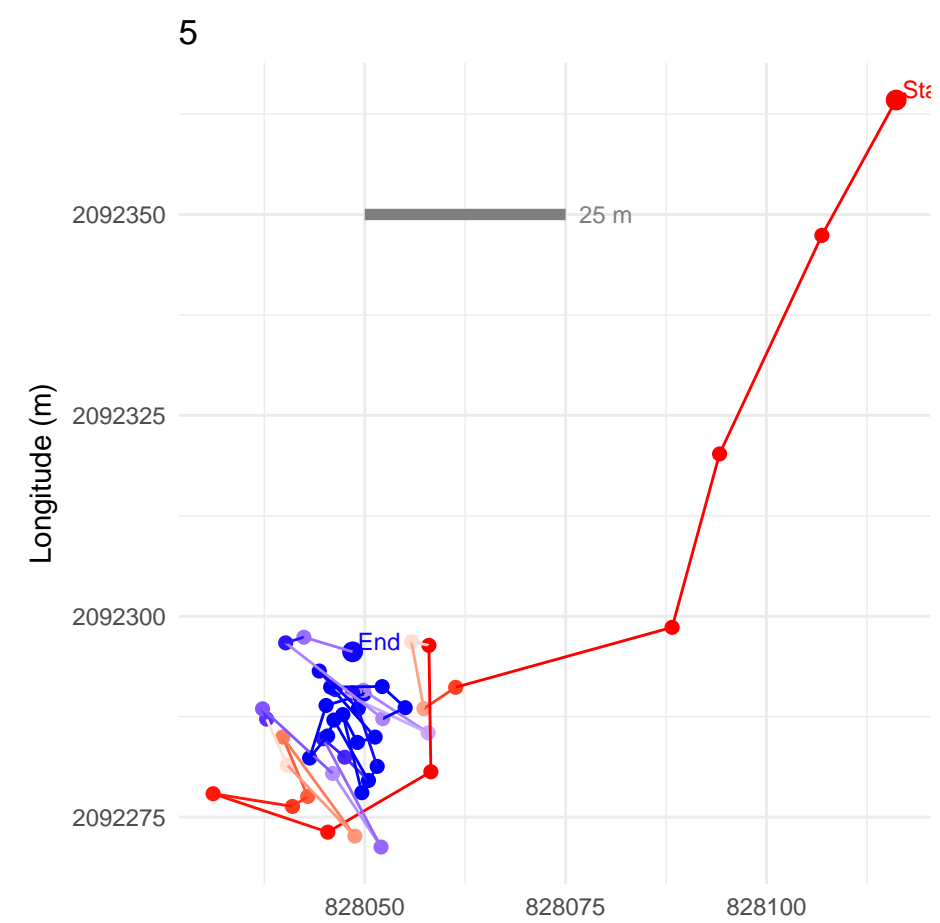
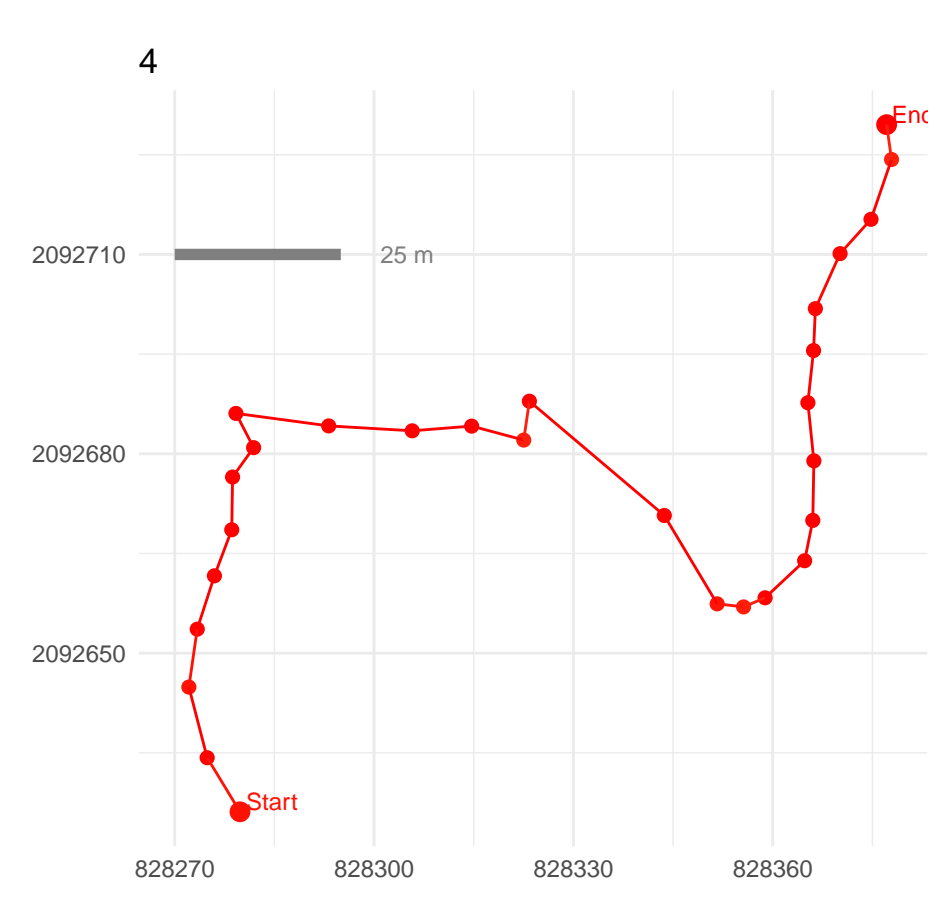
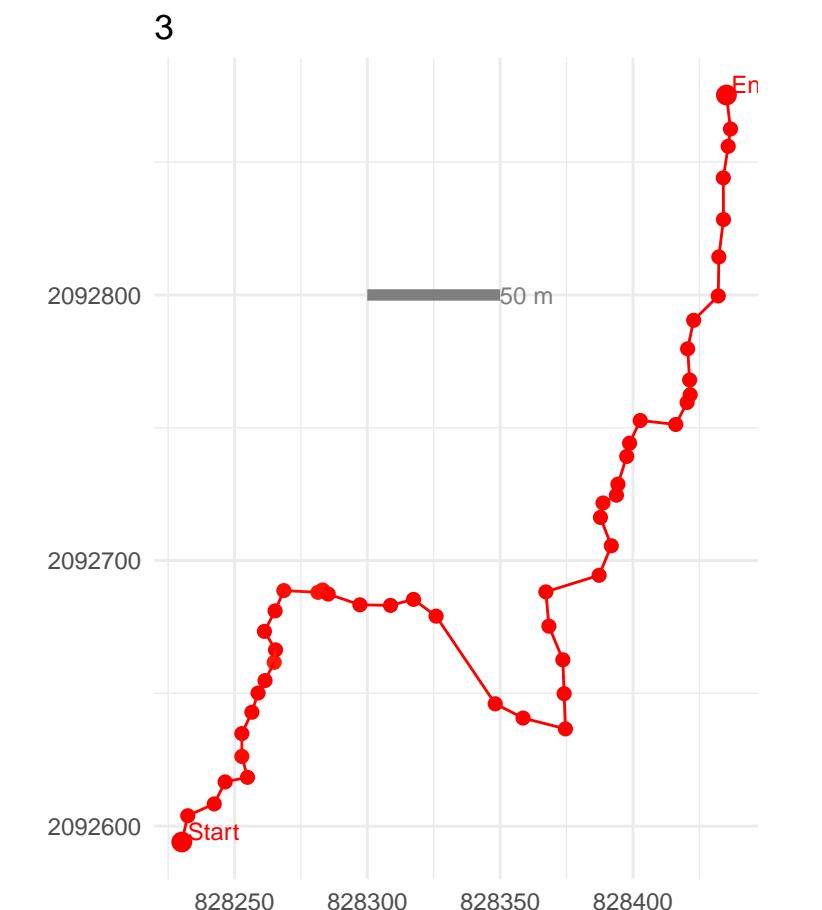
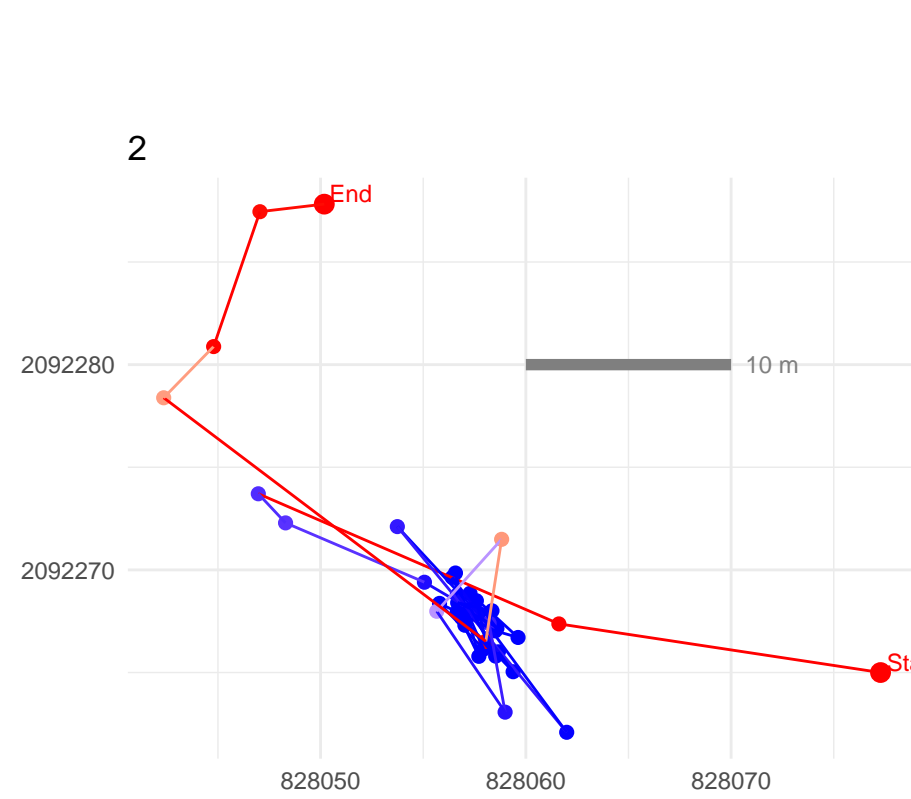
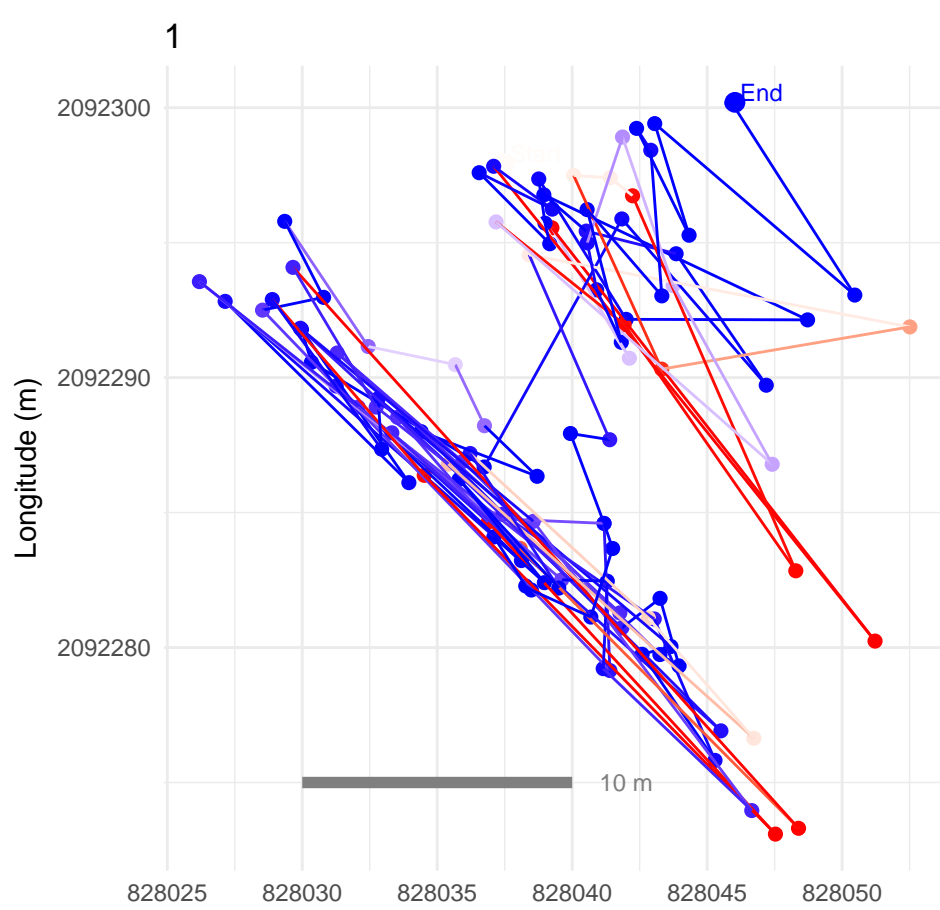


Travelling 2

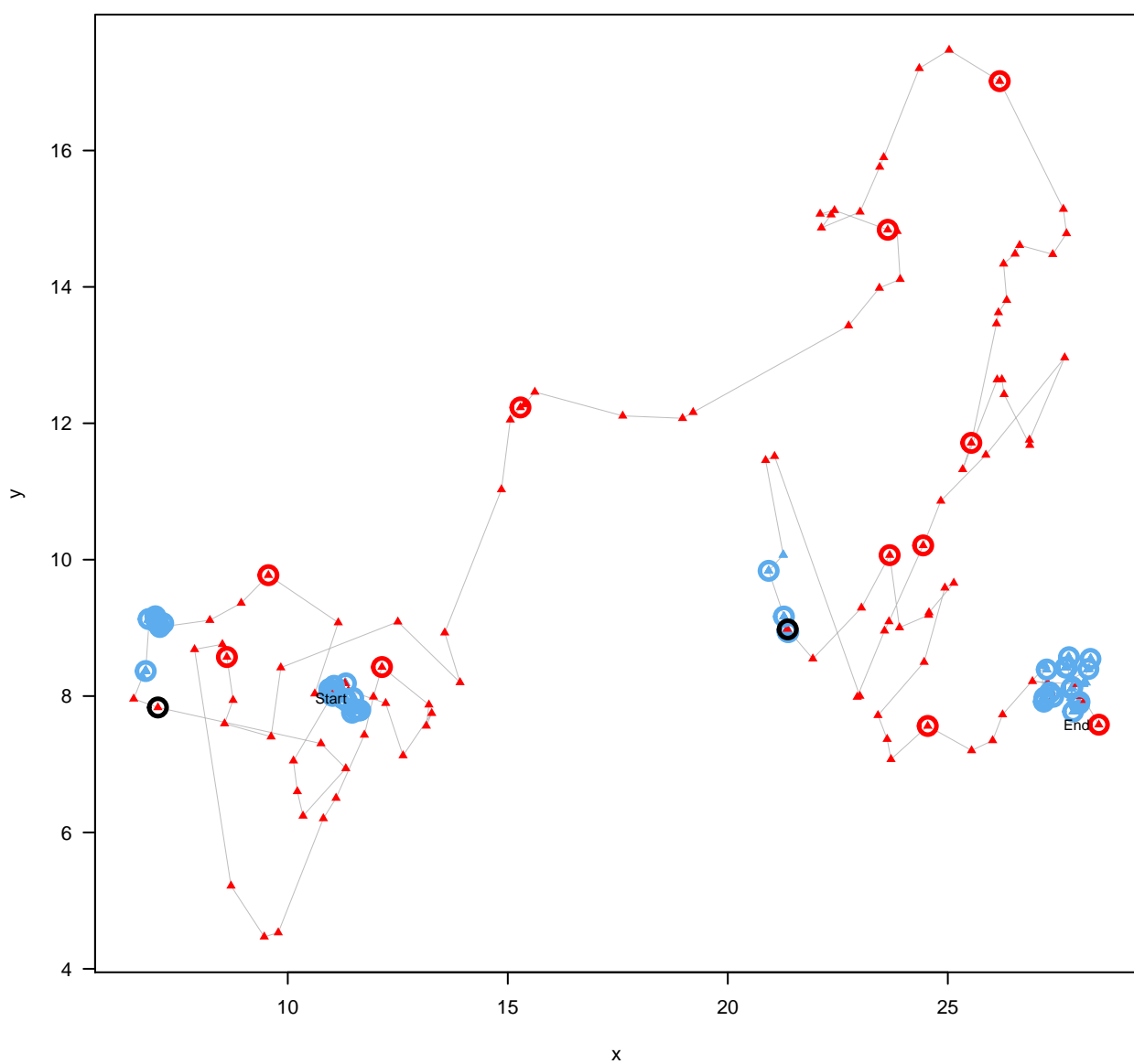




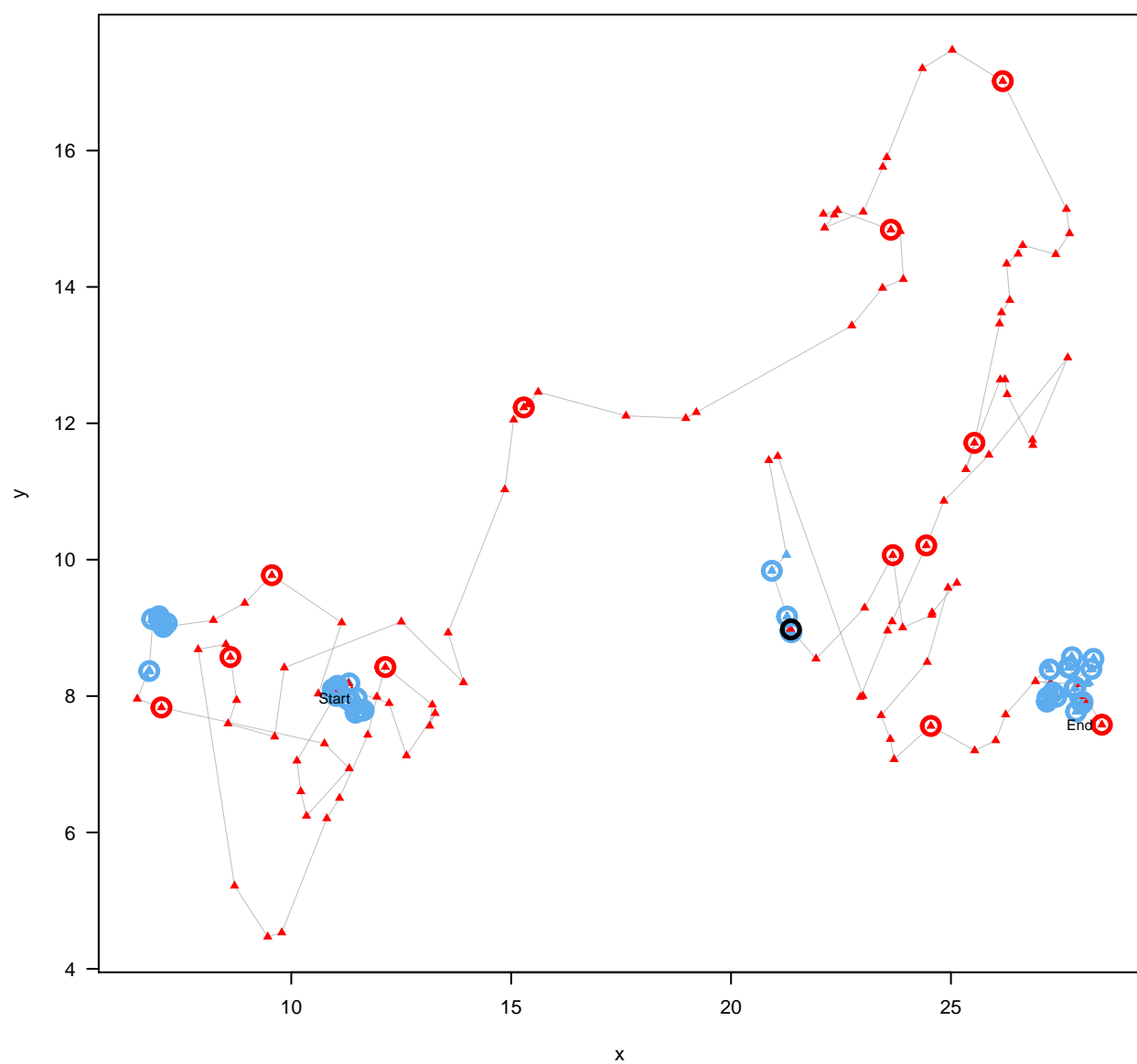




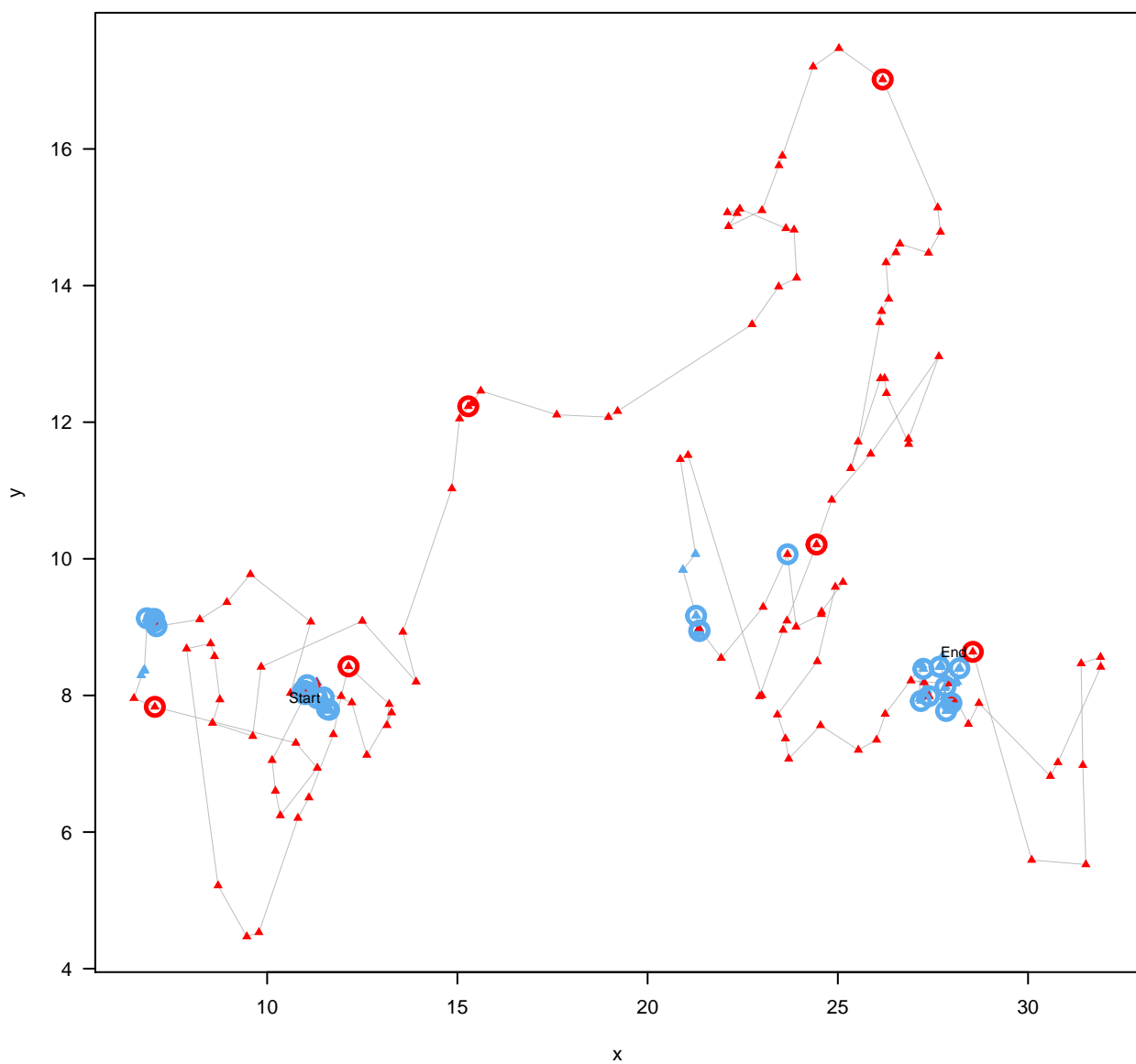
time-step=30s, without U1 and U2



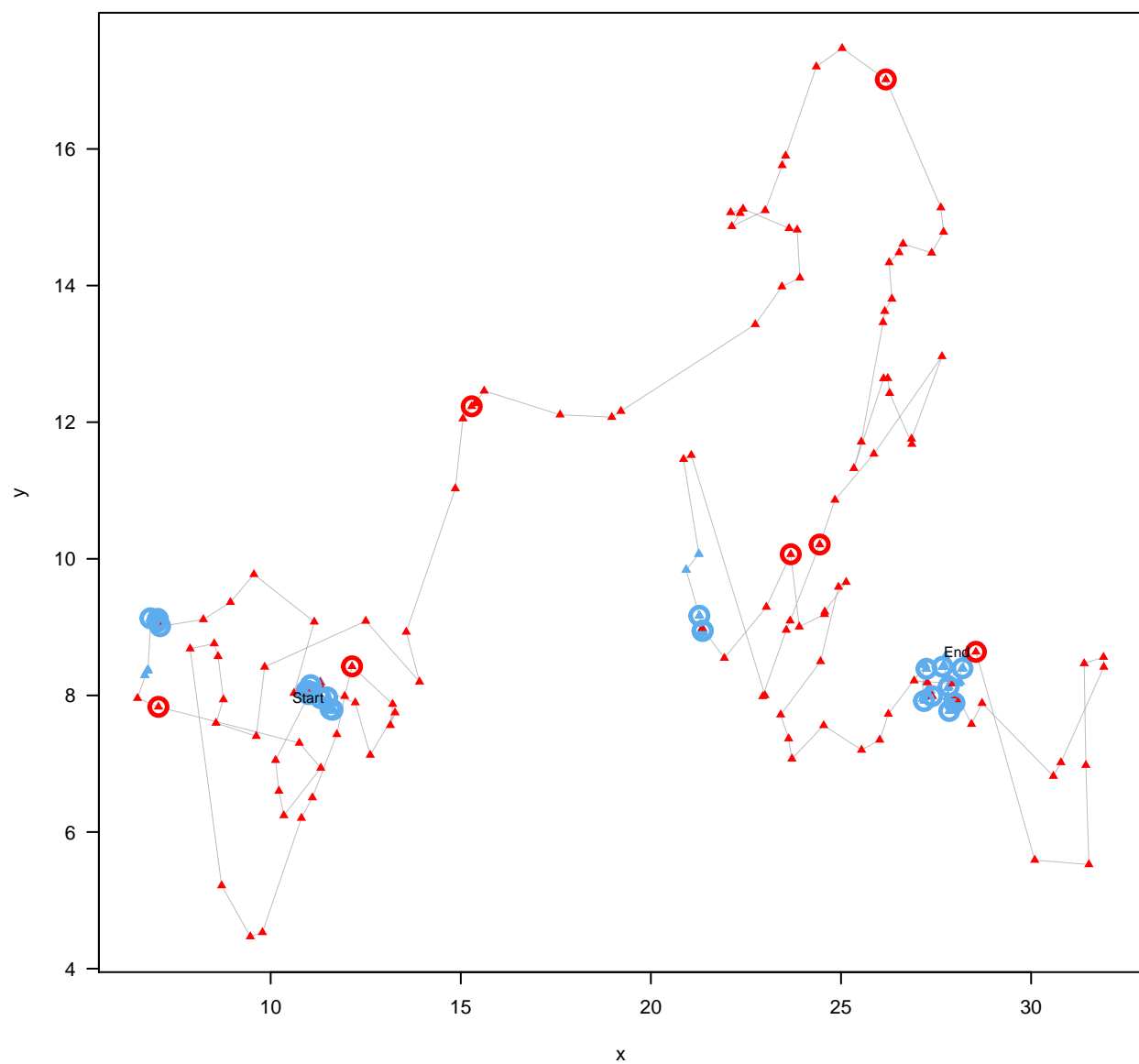
time-step=30s, with U1 and U2



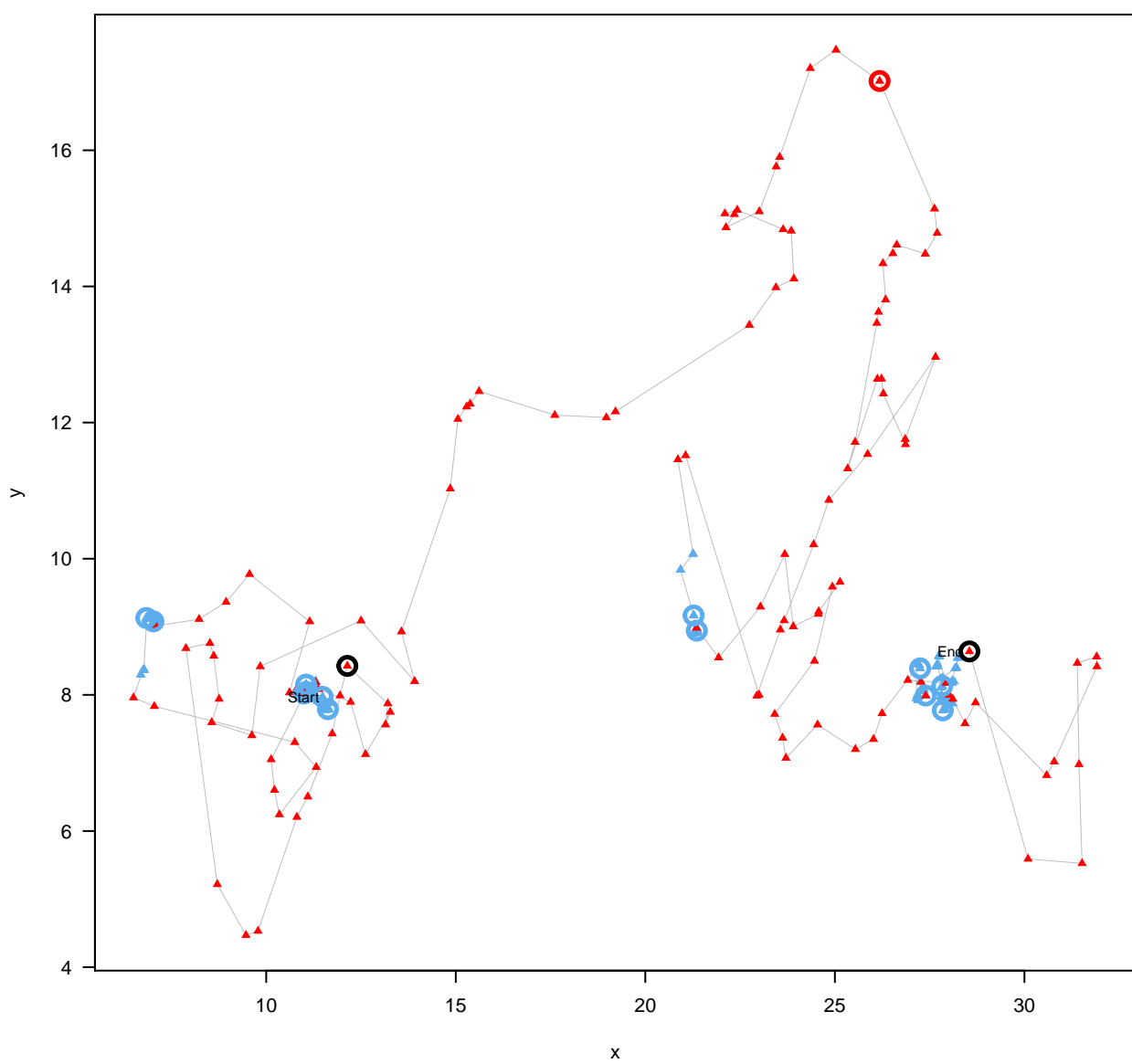
time-step=60s, without U1 and U2



time-step=60s, with U1 and U2



time-step=120s, without U1 and U2



time-step=120s, with U1 and U2

