

Treed Gaussian processes for animal movement modeling

by

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Abstract

Wildlife telemetry data are widely collected and can be used to answer a diverse range of questions relevant to wildlife ecology and management. While multiple animal movement models exist, current methods face challenges in modeling the nonstationarity of animal movement. Additionally, model implementation often poses barriers to practitioner use. To address these issues, I demonstrated a Bayesian machine learning modeling framework for telemetry data. This framework incorporates Bayesian statistics' ability to quantify uncertainty and estimate comparable movement descriptors, while machine learning enables near automation of modeling. Specifically, my developed framework utilizes treed Gaussian processes (TGPs), a recently developed machine learning model that is well suited to the intrinsic nonstationarity of telemetry data. To ensure accessibility to practitioners, I utilized an existing R package to implement TGP modeling and outlined in detail the nearly automated use of the package within the movement modeling framework. I used telemetry data from a declining grassland bird, the lesser prairie-chicken (*Tympanuchus pallidicinctus*), as a case study to demonstrate the ease and applicability of this framework. I obtained model-based estimates of trajectories to compare individual and population estimates for movement descriptors such as distance traveled and residence time and compared these estimates across grazing management treatments. To maintain broad useability, I outlined all steps necessary for practitioners to specify relevant movement descriptors and apply TGP modeling and trajectory comparison to their own telemetry datasets. As well as modeling the nonstationarity present in animal telemetry data, the combined benefits of this framework increase accessibility and applicability of animal movement modeling, allowing practitioners to model trajectories and estimate comparable movement descriptors to answer applied management questions.

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Introduction

Telemetry studies are conducted throughout wildlife ecology to investigate interactions of individuals with their environments. Telemetry data consist of multiple locations of a tagged animal recorded over time, and these data are now extremely prevalent and accessible across taxa. Technological advancements, such as the use and improvement of Global Positioning System (GPS) satellite transmitters, enable researchers to record locations at finer temporal scales with greater spatial certainty. While telemetry data recorded by such tools hold information for researchers to explore a wide range of topics (e.g., space use, resource selection, and barrier identification), modeling animal movements and achieving useful inference from telemetry data remains challenging due to the complexities of these data. Available models pose additional barriers to use due to the advanced statistical modeling required for their implementation. Because telemetry studies hold the potential to answer a multitude of management and research questions, it is important to improve methods for extracting information from telemetry data. Advancements in Bayesian modeling and machine learning techniques provide promising possibilities for modeling animal movement while lowering practical barriers to application and inference.

Telemetry data are typically comprised of recorded locations at discrete time points at a predetermined time interval (e.g., every 30 minutes, hourly, etc.) with varying intervals of missing location data between recordings. To predict an animal's location between these data points, researchers can estimate the likely trajectory of the animal's movement (Scharf et al., 2017). Using the estimated trajectories, researchers then derive descriptive statistics to summarize movement characteristics such as distance travelled, speed, and directionality. This summarization of trajectories can be used to answer countless ecological questions, such as

comparing how translocated individuals select habitats (e.g., Picardi et al., 2022) or the distance at which anthropogenic infrastructure affects animals' behaviors (e.g., Londe et al., 2022). Using statistical models to estimate trajectories then summarizing trajectories to answer research questions is a widely used inferential framework and can be visualized in Figure 1.

The first step of the inferential framework is to estimate the animal's movement trajectory. There are multiple movement models available to accomplish this, each with their own benefits. The simplest, and still frequently utilized, approach to estimating a movement trajectory is to draw straight lines connecting recorded telemetry points (e.g., Tanner et al., 2021). Although this method continues to be implemented and useful in wildlife ecology, several statistical movement models have been developed beyond this approximation. These more complex approaches fit a statistical model to recorded telemetry points, allowing for model-based prediction of the animal's location at any time point, thus estimating a continuous-time movement trajectory. Many of these models utilize a Bayesian formulation, which strengthens inference by providing quantified uncertainty on the estimated trajectory (Buderman et al., 2016; Hooten et al., 2016; Hooten & Johnson 2017).

Most continuous-time animal movement models are parametric and mechanistic. These models build on a mechanistic understanding of animal movement and result in parameter estimates describing the estimated trajectory (e.g., Hanks et al., 2011). While these parameters can be interpreted to describe movement, they may not always target the desired inference. This is particularly true when the model is used to guide wildlife management or answer specific scientific questions. In such cases, the goal of modeling a trajectory is to estimate statistics that can be interpreted for specific applied purposes. Because these desired statistics will not always

align with the specified parameters of the mechanistic model, the inferential framework suggests that prediction of a trajectory, not model parameters, should be the focus of modeling.

In addition to the possible misalignment of parameters and inferential goals, parametric models can be time consuming to construct and are often specific to one study (Wijeyakulasuriya et al., 2020). This limits applicability of such models for answering real-world and often time-sensitive management questions. Alternatively, we present a phenomenological machine learning approach to modeling animal movement, as was recommended by Wijeyakulasuriya et al. (2020). Accurate prediction of unknown locations is required to reconstruct, and thus draw inference from, animal movement trajectories (Figure 1 step 1). Machine learning offers this accuracy, coupled with speed and ease of implementation (Wijeyakulasuriya et al., 2020). While applying a machine learning model, we utilize Bayesian methods to quantify uncertainty of trajectory estimates. Both machine learning and Bayesian methods are common in wildlife ecology, though Bayesian machine learning remains underutilized, especially in practical applications (Tuia et al., 2022). We implemented a novel application of treed Gaussian process (TGP) models, a recently developed Bayesian machine learning technique, to animal movement modeling (Gramacy, 2005). Applying this phenomenological machine learning model to movement data does not require the practitioner to construct or customize their own model, a task that may require advanced training in mathematics and statistics and can be preventative to practitioners (Hooten & Hefley, 2019). The automation and interpretability provided by a phenomenological machine learning model can greatly increase accessibility of movement modeling.

As well as facilitating model formulation and inference, our Bayesian machine learning model addresses a modeling issue intrinsic to telemetry data. Regardless of their formulation,

continuous-time animal movement models must account for the high variability of animal movement. It is intuitive that animals change their behavior, and therefore movement, at distinct times and often abruptly. Data produced by such a nonstationary process lack a consistent statistical pattern across time, and present challenges to most modeling approaches. McClintock et al. (2014) recognized the need for models to account for abrupt transitions of animal movement, and current research explores different methods to handle the temporal heterogeneity of animal movement, such as a basis function approach or temporal warping (Buderman et al., 2016; Hanks et al., 2011; Harris & Blackwell, 2013; Hooten & Johnson 2017). However, these mechanistic approaches can be complex and require study-specific formulation, and thus are often preventative to implementation by practitioners.

We propose that the nonstationary nature of animal movement can be modeled by TGP. Treed partitioning has an intuitive, yet previously unutilized, application to animal movement (Hanks et al., 2011). Animals move in different ways for distinct periods of time, breaks that naturally suggest a divide and conquer modeling apparatus. Treed Gaussian process modeling allows each of these movement patterns to have different parameterizations, fitting the model more precisely while also accounting for nonstationarity. Treed Gaussian process models have strong predictive power and have been shown to increase the already highly accurate prediction of Gaussian process models; this aligns with our goal of predicting trajectories from telemetry data (Gramacy & Lee 2008; Gramacy, 2020). The machine learning basis underlying TGP offers an accurate, efficient, and easily implemented model for nonstationary and large telemetry data, while TGP's Bayesian formulation allows uncertainty measures to be propagated throughout computations. In addition to the benefits provided by the modeling capabilities of TGP, Gramacy (2007) developed a user-friendly and efficient R package for TGP modeling.

The `tgp` package implements Bayesian modeling of TGPs via Markov chain Monte Carlo (MCMC) integration, which is beneficial to practitioners familiar with MCMC algorithms.

We leverage the accessibility of the `tgp` package in R to apply Bayesian machine learning models to animal movement while simultaneously providing a novel and improved method for modeling the nonstationarity of animal telemetry data. We outline the statistical background for Bayesian continuous-time animal movement models, machine learning, Gaussian processes, treed Gaussian processes, and estimating comparable statistics from these modeled trajectories. Additionally, we demonstrate how our framework performs population inference by estimating statistics describing groups of trajectories. While covering these topics, we maintain accessibility of TGP modeling to non-statisticians. Appendix A provides a guide to the statistical basis for TGP movement models for interested readers, but it is not required for use of the `tgp` R package. To demonstrate the novel application of TGPs to telemetry data, we use a case study of lesser prairie-chicken (*Tympanuchus pallidicinctus*) GPS telemetry data. To facilitate use by practitioners on their own datasets, a guide to implementation of TGP movement modeling in R is provided in the accompanying code tutorial. This paper and its supporting information aim to both improve applicability and accessibility of Bayesian continuous-time animal movement modeling, while simultaneously addressing practical modeling challenges posed by telemetry data.

Methods

Inferential framework

The general paradigm of statistical inference within wildlife ecology is to specify a model, fit it to collected data, and obtain estimates (with uncertainty quantification) of model parameters.

These parameters are then interpreted for the system of interest. Though this paradigm may be applied to inference from telemetry data, we instead follow the framework outlined in Figure 1. Telemetry data are collected and used to estimate the parameters of the movement model, but these parameters are not used for inference. Instead, the fitted model is used for prediction of the complete trajectory traversed by the animal and relevant inference is then derived from the estimated movement trajectory. This general imputation of trajectories between recorded telemetry points was formalized by Scharf et al. (2017).

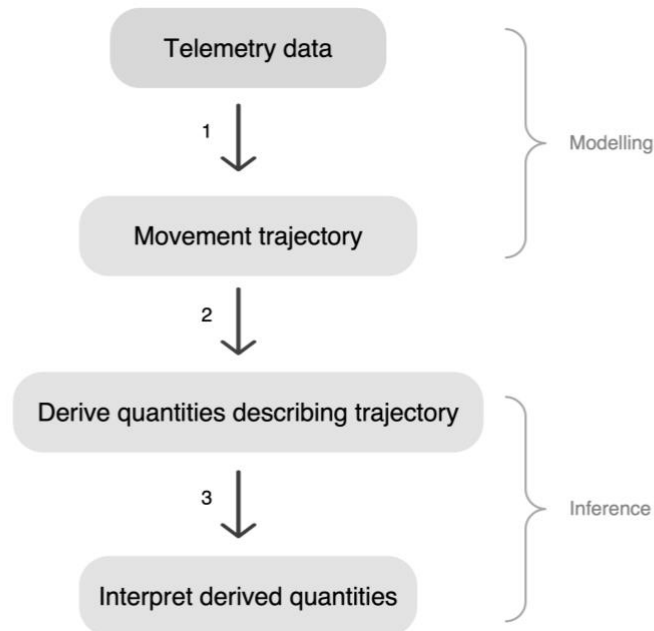


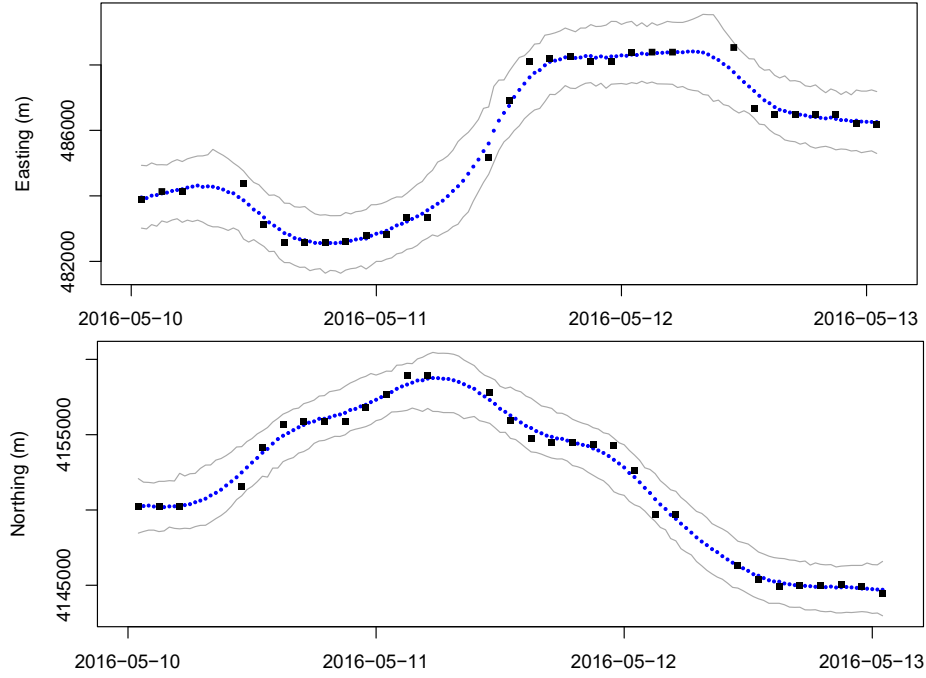
Figure 1. Summary of existing animal movement analysis framework. Step 1 fits a model to telemetry data and uses it to predict locations across the study period, thus estimating a movement trajectory. This may be as simple as connecting points with a straight line, or as complex as obtaining a Bayesian posterior predictive distribution. Step 2 makes inference about movement by estimating statistics describing the trajectory (e.g., average meters per hour). In step 3, researchers and managers interpret these values to evaluate hypotheses and guide management.

Continuous-time movement models

An animal's true trajectory exists in continuous time, but telemetry data are often recorded at discrete points in time. For many species, current technology limits GPS transmitters to record locations at interspersed intervals (e.g., every two hours). In addition, data losses, limited battery strength, and transmitter failures can increase these intervals and make them irregular.

Estimating the continuous trajectory of movement of an animal from these discrete and irregularly spaced data points is the first step to answering applicable research questions. The continuous trajectory allows for inference about many attributes of animal movement, such as how long the animal spent in a place, when it interacted with a feature, or what behavior it may have exhibited (McClintock et al., 2014). The simplest way to obtain an estimate of this continuous trajectory is to draw the straight-line Euclidian minimum distance between recorded points (Scharf et al., 2017). Expanding beyond this simplest approach, continuous-time animal movement models have been developed that model an animal's coordinate location as a function of time (Harris and Blackwell 2013). The model is fit using telemetry data: X values (e.g., GPS transmitter recorded longitude or easting) and Y values (e.g., GPS transmitter recorded latitude or northing) and their corresponding times (Appendix A). This can be achieved by fitting a time series for X values and fitting a separate time series for Y values and recombining them in two-dimensional space (Figure 2). Once fit, the model can estimate the animal's X-Y location at times when there is not a telemetry data point. These predicted values produce an approximately continuous trajectory of the estimated X-Y locations that the animal travelled.

a)



b)

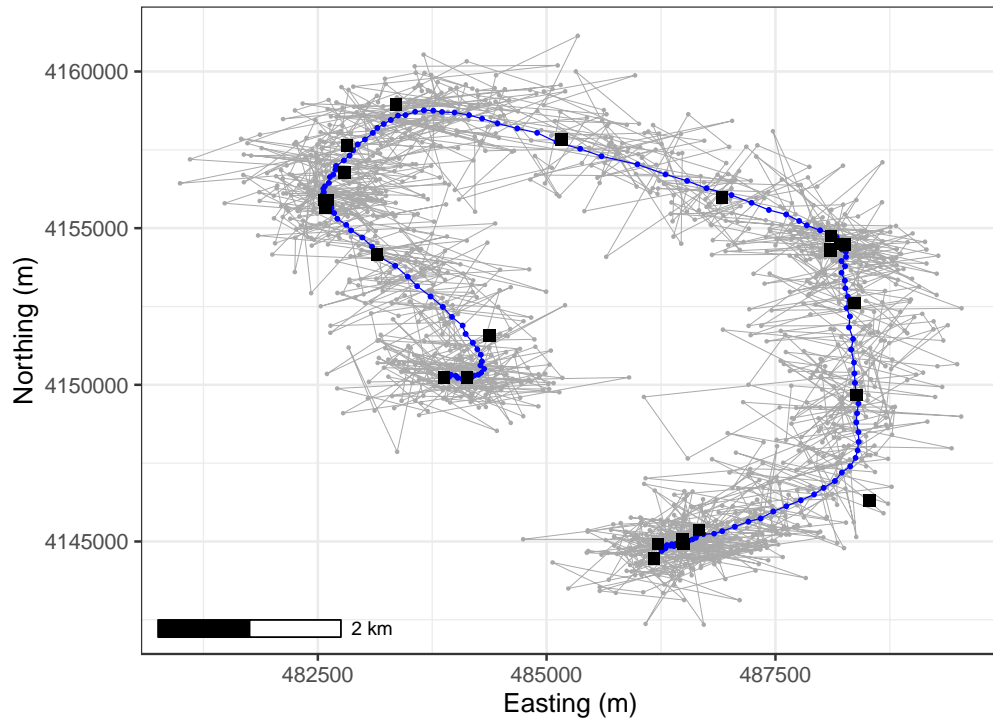


Figure 2. Locations of one lesser prairie-chicken in both one (**a**, **b**) and two (**c**) dimensional space over three days. Black squares represent recorded GPS data points and blue circles represent the mean (expected value) of 1000 MCMC samples from the posterior distribution of predicted location at $\Delta t = 0.5$ hours: (**a**) and (**b**) include 95% credible intervals from the full MCMC sample and (**b**) includes 10 sampled trajectories in gray to visually represent the full MCMC sample.

Bayesian continuous-time movement models

Using Bayesian models to estimate continuous-time animal movement trajectories allows for quantification of the statistical uncertainty surrounding location estimates. Because of this benefit, Bayesian animal movement models have been developed and applied to estimate animal movement trajectories from telemetry data (Buderman et al., 2016; Hooten et al., 2016; Hooten & Johnson, 2017). As opposed to obtaining point estimates for parameters and associated location estimates of the trajectory, Bayesian movement models produce distributions of parameters and location estimates, thus providing quantification of uncertainty surrounding trajectory estimation. This maintenance of statistical uncertainty measures throughout estimates is necessary for statistical comparison and inference.

Predicting trajectories

In wildlife ecology, statistical inference is generally performed through interpretation of model parameters. However, parameters associated with animal movement models often do not have an intuitive or straightforward interpretation and can instead be treated as a means to estimate an animal's location at a given time. The purpose of such a model then becomes most accurately predicting the unrecorded locations between telemetry data points, thus estimating the animal's continuous trajectory.

In the Bayesian formulation, these unrecorded locations are estimated by the posterior predictive distribution. By taking posterior predictive samples at small time intervals in the desired time frame, we can produce a distribution of expected trajectories at any desired resolution (e.g., predicted locations every hour, minute, second, etc.). For example, one may generate 1000 samples from the posterior predictive distribution of true location at a time point and use these samples to estimate the true location. Doing this at multiple (e.g., hourly) time

points will estimate the predicted trajectory, thus capturing the uncertainty of the trajectory estimate (Figure 2b).

The temporal resolution at which predictions are made is referenced as Δt . Selection of Δt depends on the temporal scale of data being analyzed, and scale of desired inference. An appropriately small Δt in relation to the time of inference (e.g., $\Delta t = 1$ hour and inference is over months) allows for approximation to a continuous movement trajectory (Buderman et al., 2016; Hanks et al., 2011). These predicted, approximately continuous, trajectories allow for statistical inference on an animal's movement.

Machine learning

Because prediction of trajectories, and not parameter interpretation, is our initial goal in modeling telemetry data, we recognize that machine learning is a powerful tool for this task. In the broadest sense, machine learning encompasses all methods wherein a computer uses inputted data to make predictions (Tuia et al., 2022). Modern computational power allows this prediction to go beyond familiar linear regression to far more complicated relationships between inputs and response. Machine learning methods are often unparalleled in predictive accuracy, yet their application to animal movement modeling has gone underutilized, despite the fact that many animal movement models are used only for prediction (Wijeyakulasuriya et al., 2020).

We utilize Gaussian processes (GPs), a method of Bayesian supervised machine learning, to model animal trajectories. A GP defines a distribution over the infinite number of functions that could fit the given data, creating a flexible and nonlinear regression between data points. Gaussian processes are nonparametric and focus on accurate prediction of unknown values (e.g., an animal's location at any time point). Importantly for spatiotemporal data, GP modeling inherently accounts for autocorrelation of input data within the model's covariance structure.

Because of this, GPs are often used for modeling continuous spatial data (Gramacy, 2020). A Gaussian assumption of animal movement is common throughout the literature and can be conceptualized as using a flexible “wire” to estimate the animal’s next location, with strong influence (autocorrelation) from the previous locations (Hooten & Johnson, 2017). The flexibility of these models increases the accuracy of regression predictions beyond that of a standard linear model, and their Bayesian nature provides quantified uncertainty for predictions (Gramacy & Lee, 2008).

Treed Gaussian processes

Gaussian processes are stationary across time and fit a smooth function globally. This means they assume the same parameterization throughout the data, and all data points affect model prediction and variance in all portions of the time series. Because of this assumption, stationary GPs do not perform well with large datasets or highly varied data (Gramacy & Lee, 2008). Animal movement data, even those describing a single trajectory, are usually large and highly varied. Animals do not behave as a consistent function; rather they perform variable behaviors at different periods of time. For example, a foraging behavior will have a different movement parameterization than a traveling behavior. Likewise, a resting behavior will have lower variability in position than a moving behavior. This lack of a consistent pattern and parameterization over space or time within data is termed nonstationarity.

When fitting a movement model to telemetry data, models must account for potential nonstationarity. If distinct animal movement states are modeled using a stationary process, uncertainty will be inflated unnecessarily and movements of an animal at separate periods of time will inaccurately affect trajectory predictions (Gramacy, 2020). Different methods, such as temporal warping, have been used to model the heterogeneity in telemetry data across smoothed

functions (Hooten & Johnson 2017; Hooten et al. 2018). However, we recognize that animals do not always behave in smooth transitions of movement or behavior (e.g., sleeping to foraging, foraging to predator escape). Including treed partitioning within the movement model offers an alternative to these smooth functions; partitions intuitively capture differing movement patterns and preserve the sometimes abrupt transitions between them.

Treed Gaussian process models were developed by Gramacy (2005) by pairing stationary GPs and Bayesian treed partition models. In this Bayesian machine learning model, data are used to simultaneously partition the domain (time) into distinct regions and fit independent stationary GPs within those regions (e.g., at the nodes of the tree). This allows for fitting of a single treed model across the entire range of telemetry data. The TGP model retains the benefits of the GP model, while also allowing for uncertainty estimates to better reflect the nonstationarity of the underlying process. Computational efficiency is also increased from a stationary model, because far smaller amounts of data are being fit to a GP at once (Gramacy & Lee, 2008).

It is intuitive to model different animal movement patterns separately to prevent disparate behaviors from overly influencing predicted locations; for example, diurnal foraging movement should not affect the estimated variance of an animal's nocturnal rest. The regression tree framework of TGP reflects this separation within the model. In addition to fitting GPs at the nodes of the tree, inclusion of limiting linear models in Gramacy and Lee's (2008) TGP development helps to capture periods of animal rest or consistent movement. The TGP simply fits a linear model, as opposed to a GP, at the end of a partition when appropriate (e.g., when the animal is motionless), increasing simplicity and efficiency of the model.

TGP implementation

Because TGPs are used across a diverse range of applications, a well-developed R package exists for user-friendly implementation of TGPs (Gramacy, 2007). Though this package was developed for general application and is utilized by a number of fields, we offer its first application to animal movement modeling. Our demonstrated use of the `tg` package allows for streamlined fitting of TGP models to animal telemetry data, and practitioners are not required to perform excessive manipulation of their data or write their own MCMC sampling algorithm. We outline steps for implementing the `tg` package (version 2.4) in R to obtain inference from GPS telemetry data for individual animals (see accompanying code tutorial for detailed steps and R code). Preprocessing of GPS data is not required, though removal of data points arising from clear GPS errors is expected prior to running `tg` (see Appendix B for more details). Beyond these errors, there is no need to “thin” or remove any data points, nor must data fit a required frequency.

The TGP model is fit to easting and northing (or latitude and longitude) telemetry data separately. Bayesian TGP models with jumps to the limiting linear model are fit to these data using the `btgpllm` function in the `tg` package. These fitted models are then used to make predictions within the desired time frame. The times of predictions will depend on the practitioner selected Δt . For the sequence of Δt across the time period of inference, the `tg` `predict` function is used to take samples from the posterior predictive distribution of the location at each Δt time point. These samples provide all information necessary for inference by approximating the posterior predictive distribution of the trajectories at Δt scale. Minimal tuning is required of practitioners, but selection of MCMC sampling parameters (burn in, total samples,

and thinning) is necessary (see Appendix B and the accompanying code tutorial for more details).

Derived quantities

Once the trajectory for an individual animal has been estimated, statistics describing the trajectory can be used for inference and comparison (Figure 1). Examples of statistics that summarize movement include distance travelled, turn angle, and amount of time spent in a geographic area. These values are directly computed from a deterministic function of the model output (i.e., from the predicted trajectory), and in the Bayesian formulation such values are referred to as derived quantities. Bayesian derived quantities are treated as random variables and have their own posterior distribution and corresponding summary statistics (e.g., means and estimates of uncertainty such as credible intervals; Hobbs & Hooten, 2015). These uncertainty estimates are vital to statistically comparing and drawing inference from trajectories.

Some common derived quantities of interest, and their computations, are provided in Table 1. This is not an exhaustive list, but our outlined procedure follows for any deterministic function of the random variables (locations) and fixed variables (covariates). In addition to those listed in Table 1, investigators can easily perform transformations of derived quantities, which remain derived quantities. For example, $\cos(\text{turn angle})$ and $\text{displacement} * (\text{time of day})^2$ have been computed for ecological reasons (Londe et al., 2022). Because any deterministic function can be used to compute a derived quantity from the predicted trajectory, the possibilities are infinite and the desired movement descriptor must be carefully defined to address the specific research question.

Table 1. Four common base derived quantities and formulas for their computation. Formulas are based on $\mathbf{s}_t^{(k)}$, the k^{th} MCMC sample of the animal's location at time t . Examples are provided of possible extensions and applications of the base derived quantity, as well as example uses in the literature. Examples are non-exhaustive, and many more applications exist.

Base	MCMC formula	Extensions	Applications	Examples
Velocity	$v_t^{(k)} = \sqrt{(s_{t_1}^{(k)} - s_{(t+1)_1}^{(k)})^2 + (s_{t_2}^{(k)} - s_{(t+1)_2}^{(k)})^2}$	<ul style="list-style-type: none"> Distance traveled Average distance travelled over a period Max speed over a period Average max speed over a period Max distance traveled Net displacement 	<ul style="list-style-type: none"> Migration patterns Habitat quality Avoidance Behavior classification 	<ul style="list-style-type: none"> Tanner et al., 2021 Buderman et al., 2018 Hanks et al., 2011
Turn angle	$a_t^{(k)} = \arccos\left(\frac{(d_1^{(k)})^2 + (d_2^{(k)})^2 + (d_3^{(k)})^2}{2 \cdot d_1^{(k)} \cdot d_2^{(k)}}\right)$ $d_1^{(k)} = \sqrt{(s_{t_1}^{(k)} - s_{(t-1)_1}^{(k)})^2 + (s_{t_2}^{(k)} - s_{(t-1)_2}^{(k)})^2}$ $d_2^{(k)} = \sqrt{(s_{t_1}^{(k)} - s_{(t+1)_1}^{(k)})^2 + (s_{t_2}^{(k)} - s_{(t+1)_2}^{(k)})^2}$ $d_3^{(k)} = \sqrt{(s_{(t-1)_1}^{(k)} - s_{(t+1)_1}^{(k)})^2 + (s_{(t-1)_2}^{(k)} - s_{(t+1)_2}^{(k)})^2}$	<ul style="list-style-type: none"> Average turn angle within period Tortuosity Period or area where average turn angle crosses threshold 	<ul style="list-style-type: none"> Avoidance Behavior classification 	<ul style="list-style-type: none"> Londe et al., 2022 Picardi et al., 2021 Postlethwaite et al., 2013
Residence time	$r_t^{(k)} = \begin{cases} 1 & \text{if } \mathbf{s}_t^{(k)} \in A \\ 0 & \text{if } \mathbf{s}_t^{(k)} \notin A \end{cases}$ <p>where A is the area of interest</p> $r^{(k)} = \sum_{t=1}^T r_t^{(k)}$	<ul style="list-style-type: none"> Proportion of time in habitat type 	<ul style="list-style-type: none"> Habitat and resource selection Home range determination 	<ul style="list-style-type: none"> Brown et al., 2017 Pozdnyakov et al., 2014 Buderman et al., 2018
Point of contact	<p>$\mathbf{s}_t^{(k)}$ such that:</p> $\mathbf{s}_t^{(k)} = \mathbf{p}$ <p>where \mathbf{p} is the point of interest</p>	<ul style="list-style-type: none"> Probability of contact 	<ul style="list-style-type: none"> Road crossings Encountering conspecifics Human wildlife conflict Disease spread 	<ul style="list-style-type: none"> Long et al., 2021 Eriksen et al., 2009 Dodge et al., 2021

Derived quantity estimation

The full posterior distribution of a derived quantity may be difficult to obtain directly, but it can be approximated by sampling from the posterior distribution of the derived quantity (Appendix A; Hobbs & Hooten, 2015). This step continues from our previously established MCMC sampling from the posterior distribution of the animal's trajectory. After obtaining samples from the trajectory's distribution using the predict function in the `tgp` package, sampling from the posterior distribution of the derived quantity is as simple as implementing the deterministic function across the trajectory samples. Because the derived quantity is a function of the trajectory random variable, the equivariance property of MCMC ensures that the derived quantity is also a random variable, and the transformed MCMC sample is a sample from the distribution of that derived quantity (Hobbs & Hooten, 2015).

In this MCMC framework, we iterate through the K samples of predicted trajectories, transforming each k^{th} sample from the posterior predictive distribution into a sample from the chosen derived quantity. This applies to any derived quantity formula (Table 1). We demonstrate the MCMC approximation for the example derived quantity of displacement at each Δt . From the K samples of predicted trajectories at Δt resolution, we individually transform each k sampled trajectory into a sequence of the derived quantity at Δt resolution. For this example, this is as simple as computing the distance between two points:

$$d_t^{(k)} = \sqrt{(s_{t_1}^{(k)} - s_{(t+1)_1}^{(k)})^2 + (s_{t_2}^{(k)} - s_{(t+1)_2}^{(k)})^2}.$$

Performing the derived quantity calculation (in this case, the distance formula) at the Δt interval and across all K samples produces K samples of derived quantities at Δt resolution. Detailed code for a displacement example is provided in the accompanying tutorial. Formulas for

sampling other derived quantities are in Table 1. Appendix A provides additional information on applying the Monte Carlo approximation to the underlying continuous-time model.

Transforming temporal scale

The output of the derived quantity computation is samples of the derived quantity at every Δt interval for the entire time period. For example, this could be 744 hourly displacements over a month across 1000 samples. This distribution of temporally fine-scale derived quantities will likely have no interpretation for the application of interest and must be transformed to a useable scale. The flexibility of our presented modeling framework is that averages of the desired derived quantity can be easily computed at any scale greater than the initially set Δt .

Though it may be tempting to reduce the large, fine-scale derived quantity distribution into summary statistics and transform these, it is necessary to transform the entire distribution to preserve its properties (e.g., uncertainty measures). To continue with the displacement example, we can transform the distribution of 744 hourly displacements into a distribution of average daily distance travelled in that month. First, we sum within days within each trajectory sample to obtain 1000 samples each with 31 daily totals. The 31 daily total displacements are then averaged within each of the 1000 trajectory samples. This transformation maps a distribution of displacements at a fine Δt to a distribution (in this case 1000 samples) of a single value. The distribution of this desired value (average daily distance travelled in the month) can be summarized for interpretation using statistics such as its mean and 95% credible interval. This example is shown visually in Appendix C. Code for performing derived quantity transformations is detailed in the accompanying tutorial.

Population level inference

Population-level inference is made by aggregating individual-level derived quantities, and thus is itself a derived quantity (Buderman et al., 2016). Instead of being a function of one random variable (one trajectory), estimates of population-level statistics are a function of multiple random variables (multiple trajectories). The necessary equivariance property of the population-level derived quantity will hold when MCMC samples are aligned properly (see Hobbs & Hooten 2015: Chapter 8.3; Appendix B). This fits within our outlined MCMC framework for sampling from the posterior distribution of the movement trajectories and their resulting derived quantities. To continue with the previous example, we first obtain N individual distributions of average daily distance travelled in the month for N different animals. These N distributions are aggregated into a single distribution of average daily distance travelled in the month, for the population of N individuals. In the MCMC framework, this aggregation is accomplished by averaging across all individuals within each of the K samples (Hobbs & Hooten, 2015). Code for this sampling is provided in the accompanying tutorial. A visualization of this example is provided in Appendix C.

Case study: lesser prairie-chicken movement under differing land use

We used telemetry data collected from lesser prairie-chickens (*Tympanuchus pallidicinctus*) to demonstrate the utility, ease, and direct management applications of applying TGP to modeling and analyzing animal movement data. Researchers collected GPS telemetry data to assess lesser prairie-chicken movements and test for habitat selection by this species of conservation concern. Between 2013 and 2018, researchers fitted female lesser prairie-chickens with transmitters that recorded GPS locations every two hours, between 0500 and 2300 CST (Gulick, 2019; Lautenbach et al., 2021; Verheijen et al., 2021). We used data from the Red Hills region of

south-central Kansas, USA, for our case study. This study area included spatial data on ecologically relevant land use, classified into rotationally grazed, patch-burn grazed, or unclassified ranchland (see Gulick, 2019 for additional information).

From this case study, we present two illustrations of benefits of applying the TGP model. First, we demonstrate the unique ability of TGP modeling to handle extreme or unusual animal movements. We identified one such movement in 2014, when bird 135489 travelled at least 14.2 km in the two hours between GPS recordings. We modeled and examined movement trajectories for this individual using both TGPs and stationary GPs.

Our second illustration demonstrates application of the TGP model and example inference using the 2016 nesting season (2016-04-15 through 2016-06-15). For the 11 individual birds within this sub-dataset that survived the whole season, we fitted individual movement models and sampled from posterior distributions of each animal's trajectory and four derived quantities of that trajectory: average hourly displacements, average daily distance travelled, percent of time spent in each grazing treatment, and average hourly displacements within each grazing treatment. We then computed the aggregated population-level derived quantity of population average hourly displacement within each grazing treatment.

For both illustrations, we followed the outlined methods to fit tgp models to easting and northing Universal Transverse Mercator (UTM) data for each bird. In the first illustration, we fit a GP model to the bird's location data as well. We used these models to sample from the posterior predictive distributions for locations at $\Delta t = 1$ hour across the study period. We used the base tgp MCMC settings for fitting models and a MCMC sample size of 1000 (burn in of 2,000, total MCMC iterations of 12,000, and thinned by 10) for the posterior predictive distribution of movement trajectories. Due to listing of lesser prairie-chickens under the United States

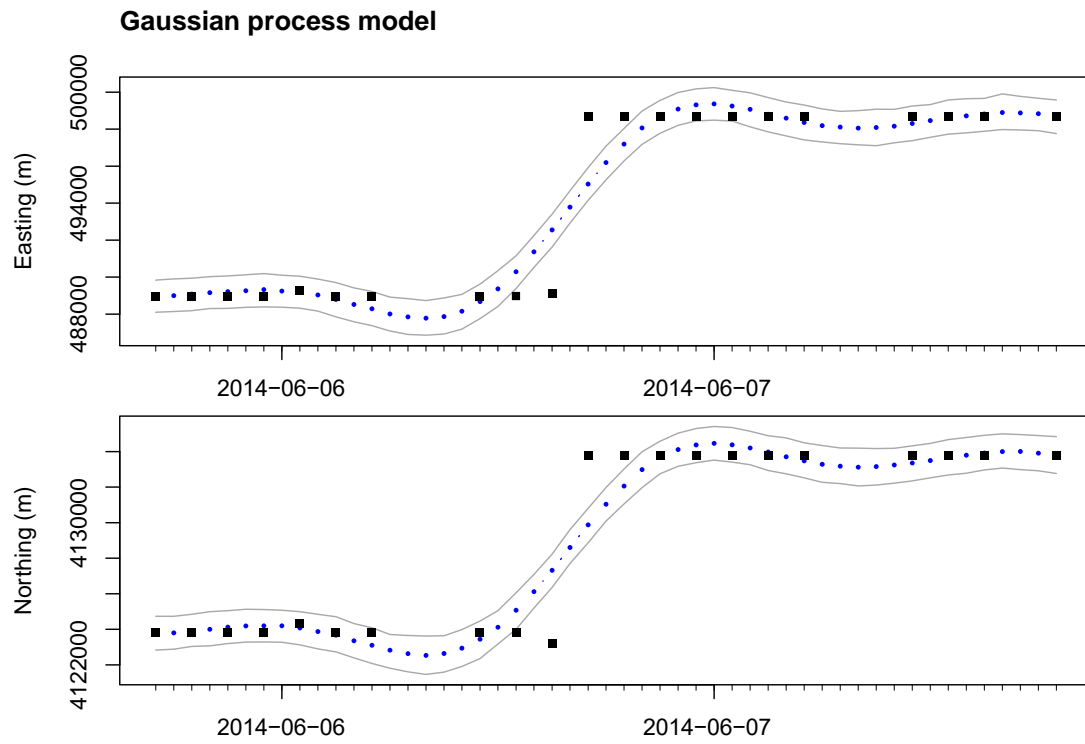
Endangered Species Act, data and code for the case study analyses may be provided with reasonable request.

Results

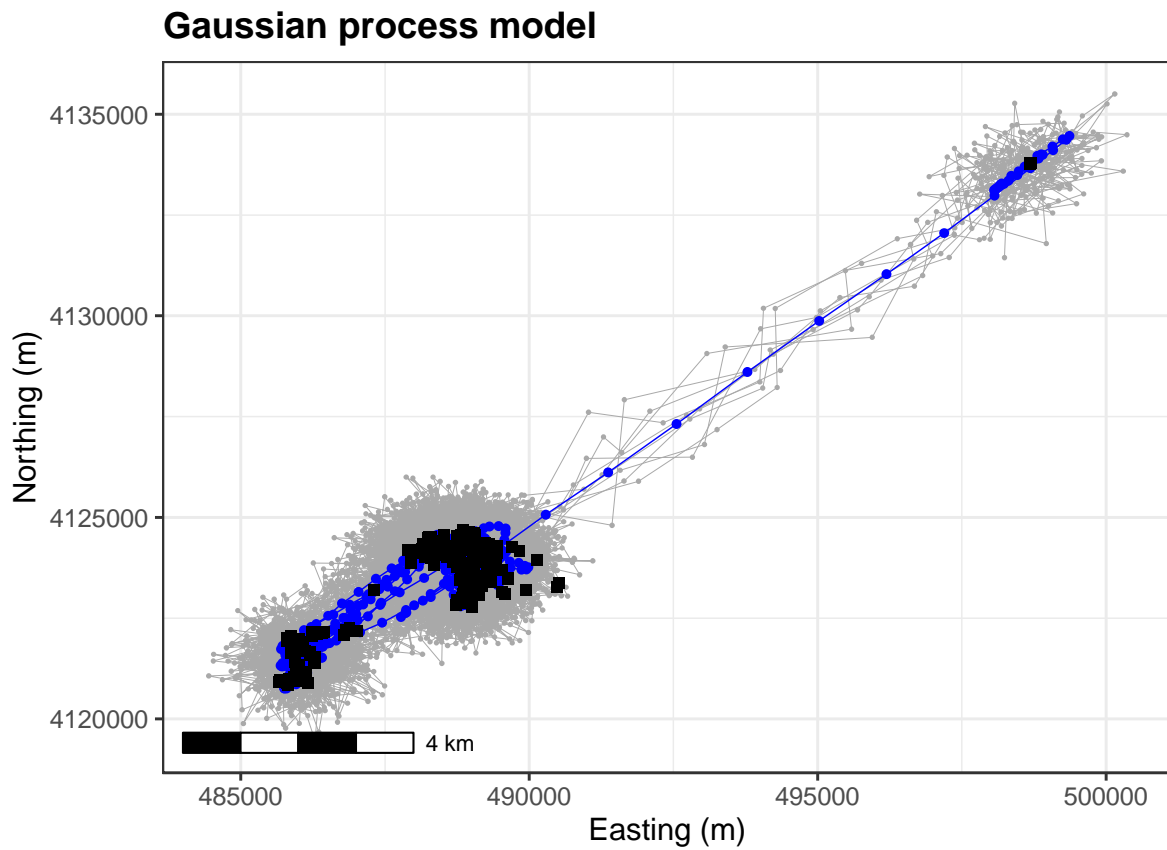
Illustration 1

We fit TGP and GP models to the example bird and obtained 1000 MCMC samples each from the models' respective posterior distributions of trajectories. We compared the treed and non-treed trajectory distributions in both one and two dimensions (Figures 3a, b). The treed model more closely follows the data during the extreme movement, while the non-treed Gaussian process smooths over the notable movement present in the data. In attempting to fit two drastically different movement patterns with one continuous function, the smoothed model loses the underlying movement pattern provided by the data and fails to detect the notable movement of 14 km in two hours (Figure 3a). Additionally, the GP results in increased variance and lack of fit within those two sections (visible in the wider 95% credible intervals of the GP model, Figure 3). Treed partitioning gracefully handles these modeling challenges with a more precise fit to the data (Figure 3), demonstrating the superior ability of TGPs for modeling real animal movements that fail to behave in a mechanistically predictable manner.

a)

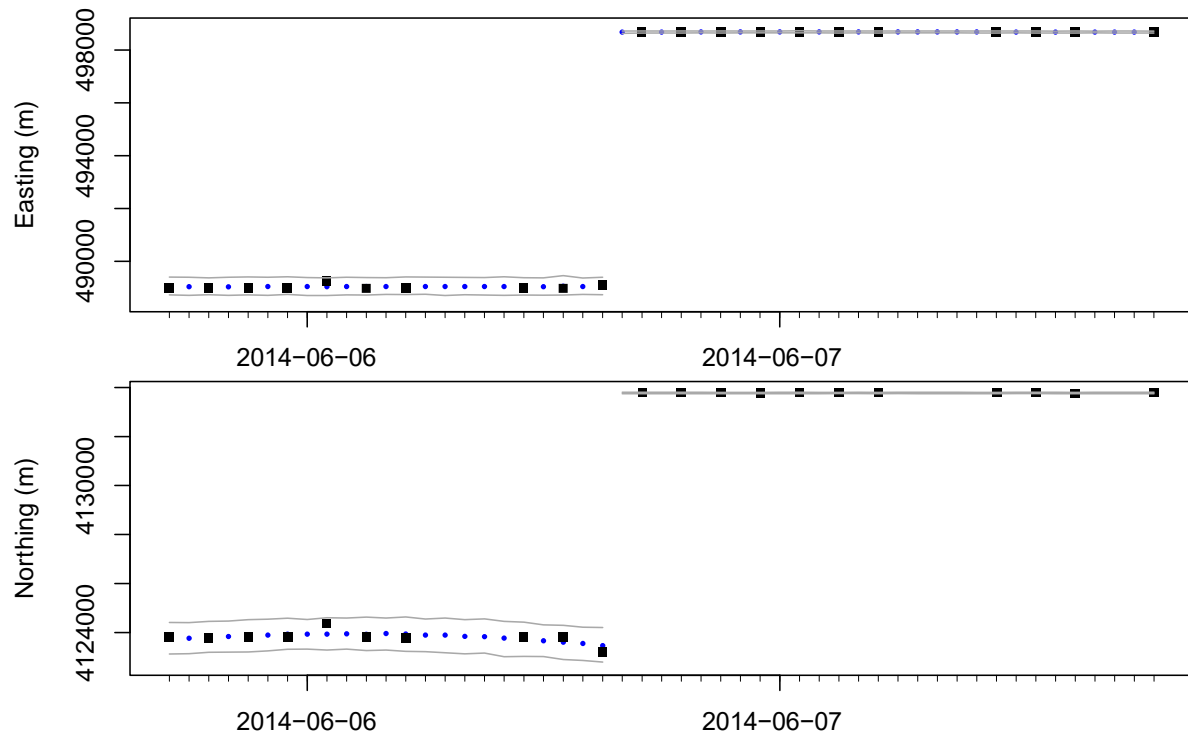


b)



c)

Treed Gaussian process model



d)

Treed Gaussian process model

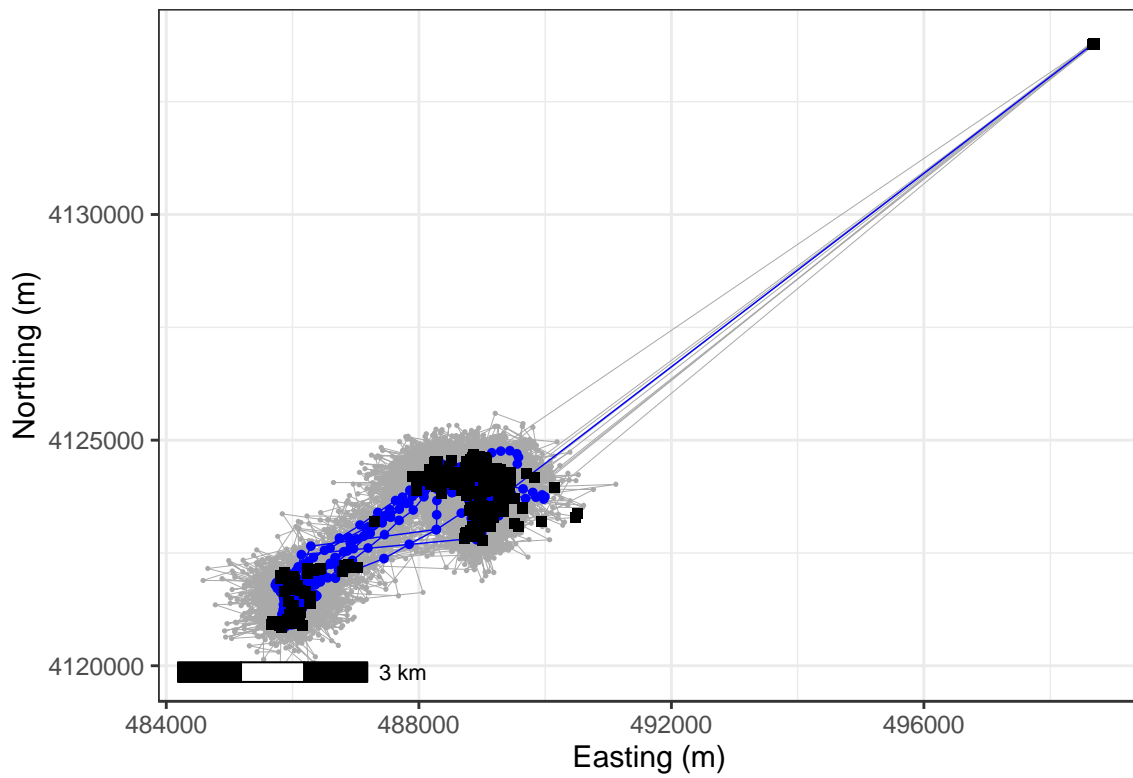


Figure 3. Results for the extreme movement case study illustration in one (**a, c**) and two (**b, d**) dimensions. Results from both stationary Gaussian process modeling (**a, b**) and treed Gaussian process modeling (**c, d**) are presented. Black squares represent recorded GPS data points and blue circles represent the mean (expected value) of 1000 MCMC samples from the posterior distribution of predicted location at $\Delta t = 0.5$ hours. (**a**) and (**c**) include 95% credible intervals from the full MCMC samples. (**b**) and (**d**) include 10 sampled trajectories in gray to visually represent the full MCMC sample. (**a**) and (**c**) show data across two days while (**b**) and (**d**) show data across two months.

Illustration 2

For the complete application of the TGP inferential framework in illustration two, we fit TGP models to the 11 individual birds and obtained 11 sets of MCMC samples of 1000 trajectories each. We used these 11 individual sets of trajectory samples to derive quantities that statistically describe differences in movements observed in the individual lesser prairie-chickens (Figure 4). First, we obtained 1000 samples from the posterior distribution of hourly displacements across the study period for each bird. We then transformed these into 1000 samples of average hourly displacement across the whole season for each bird (Figure 5a). To represent this at a different temporal scale, we transformed hourly displacements to daily total distance travelled for each bird (Figure 5b). The 95% Bayesian credible intervals demonstrate clear statistical differences within these two derived quantities across individual birds.

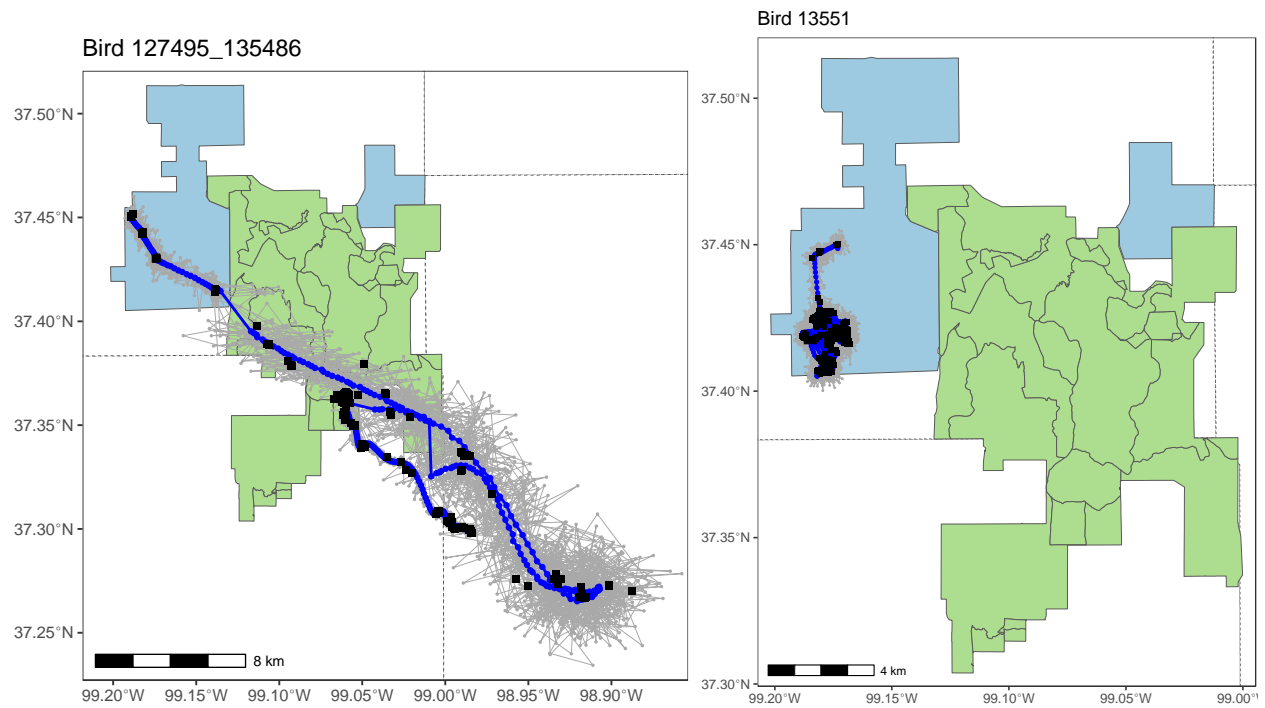
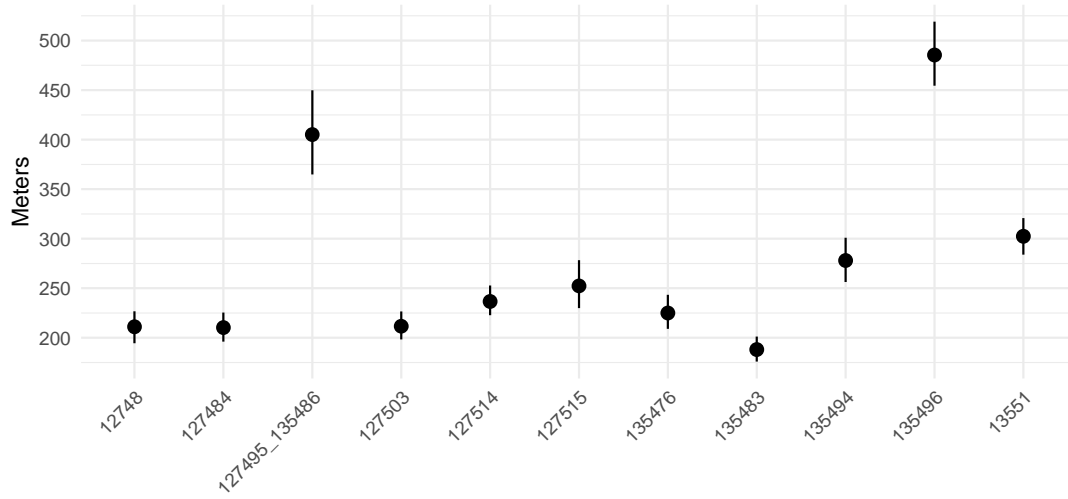


Figure 4. Locations of two lesser prairie-chickens across the 2016 nesting season (two months) in relation to two cattle grazing systems in the Red Hills of Kansas, USA. Rotationally grazed land is shown in blue, and patch-burn grazed land is shown in green. Black squares represent recorded GPS data points and blue circles represent the mean (expected value) of 1000 MCMC samples from the posterior distribution of predicted location at $\Delta t = 1$ hour. Ten sample trajectories from the full MCMC sample are represented in gray.

a)



b)

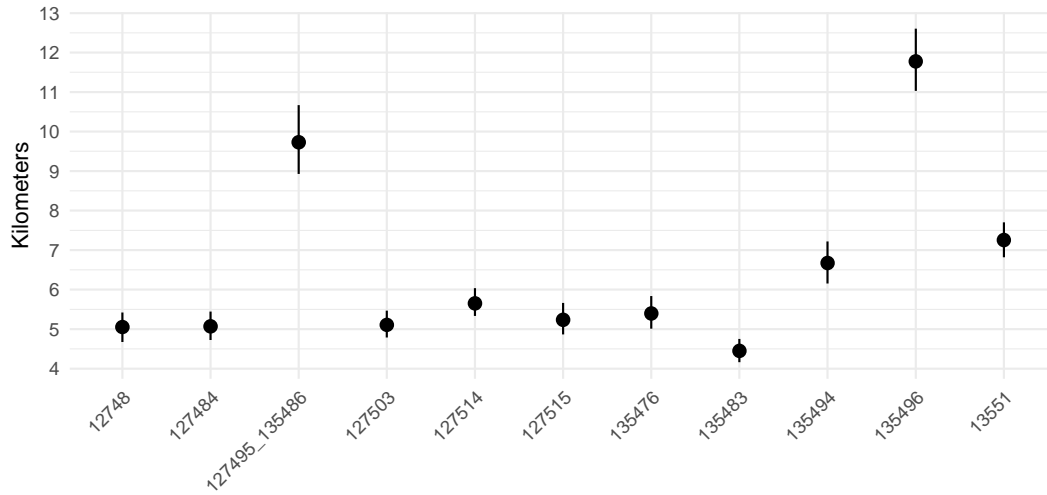


Figure 5. Individual summaries for average hourly displacement (**a**) and average daily distance traveled (**b**) across the 2016 nesting season for the 11 case study female lesser prairie-chickens, labeled by bird ID. For each individual bird, points represent the mean value of 1000 MCMC samples from the posterior distribution of the derived quantity, and error bars show 95% credible intervals. Values are the average across the season of the total distance travelled in each hour or each day, at $\Delta t = 1$ hour.

At each Δt point in the sample of 1000 trajectories, we classified the location of each bird as within one of the three mutually exclusive grazing treatments. By working within the MCMC framework, we obtained point estimates of percent of time spent in each treatment for each bird, as well as associated 95% Bayesian credible intervals (Figure 6a). Continuing with these classified samples, we sampled hourly displacements within each of the three grazing treatments

(i.e., the hourly displacement when the sampled trajectory is in that treatment). We transformed these sampled displacements to average hourly displacements within each grazing treatment (Figure 6b). The associated 95% Bayesian credible intervals show that six birds have statistically significant within-bird differences in average hourly displacements between different grazing treatments. Population-level aggregation resulted in distributions (MCMC sample sizes of 1000) of average hourly displacement within each grazing treatment, averaged across the 11 birds (Figure 7). Though point estimates for these estimates differ (mean = 0.39, 0.53, and 0.48 km/hr for patch-burn, other, and rotational respectively), 95% Bayesian credible intervals show overlap and a lack of statistically significant differences. These results are a demonstration for a sub-dataset of two months and are not reflective of the results for the entire dataset.

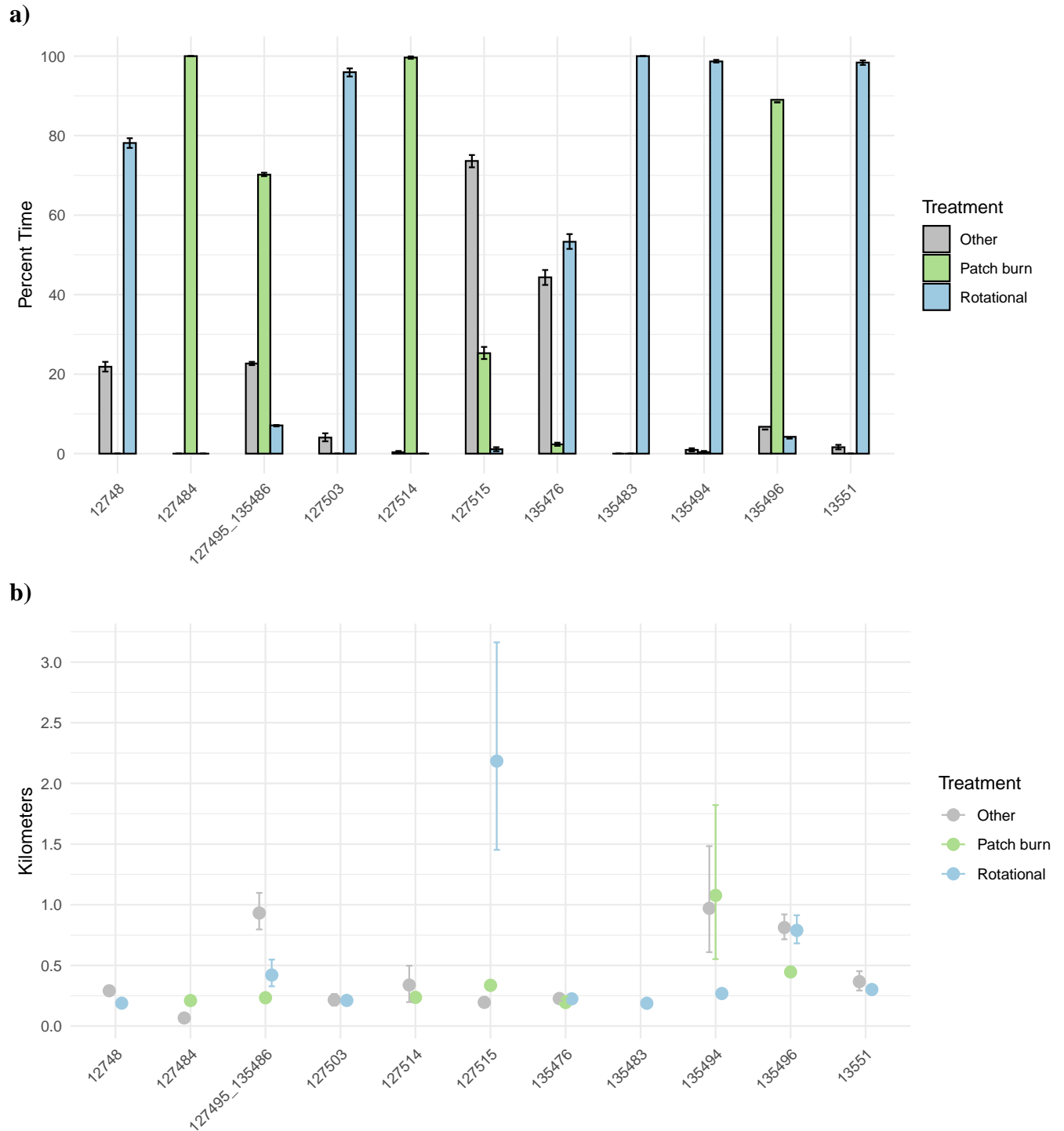


Figure 6. Treatment-based derived quantities for the 11 individual female lesser prairie-chickens in the 2016 nesting season case study, labeled by bird ID. Percent time spent by the individual bird in each grazing treatment (**a**) and average hourly displacement by the individual bird while within each grazing treatment (**b**). Point estimates represent the mean of the 1000 MCMC samples from the posterior distribution of the derived quantity, and error bars represent the 95% credible intervals.

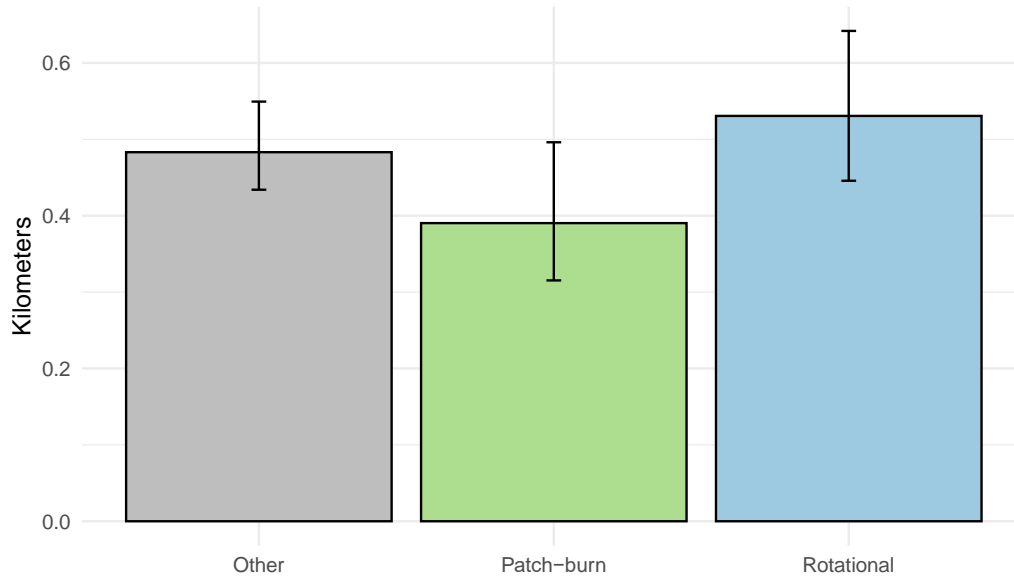


Figure 7. Population-level average hourly displacements for the 11 female lesser prairie-chickens within the 2016 nesting season, separated by grazing treatment. Point estimates represent means of the aggregated posterior distributions for each treatment, and error bars represent 95% Bayesian credible intervals.

Discussion

The distinct partitions of TGP models reflect how animals change their movement in abrupt ways (e.g., flushing, ambushing prey, reacting to a conspecific). The ability to model these extreme movements and rare events is valuable to wildlife ecologists as unusual movements such as traveling to a water source during a drought, evading a predator, or sheltering during extreme weather may be a determining factor of survival for an individual. Incorporating these movements into a model could greatly benefit understanding of a species' resource requirements. While our work focused on the ability of TGPs to predict the underlying movement trajectory, the partitioning capabilities of TGPs hold promise for data-driven classification of movement (Broderick & Gramacy, 2011). Identifying likely behavior states from telemetry data is valuable to practitioners, and movement models focused on classifying behaviors are common in the

literature (Edelhoff et al., 2016; Wang, 2019). Harnessing the classification power of TGP to study behavior states is a natural direction for future research.

In addition to modeling the intrinsic nonstationarity of animal telemetry data, use of machine learning within the TGP model increases the ease and automation of animal movement modeling. Utilizing a prespecified, phenomenological machine learning model shifts focus from model development and parameter interpretation to prediction and derived quantity estimation, which machine learning excels at (Gramacy, 2020). The existence of an established R package for TGP implementation greatly increases the accessibility of this modeling, as use of R is commonplace for wildlife ecologists. Our short code tutorial facilitates application of TGPs to telemetry data using R. Aside from removal of clear telemetry errors, there is no required preprocessing or discarding of data, and the core modeling component is only a few lines of code. This allows practitioners to estimate movement descriptors and answer applied questions from their telemetry data without extensive programming or experience with MCMC algorithms. Fitting TGP models within the `tgpr` package is relatively fast (within the order of minutes or hours, depending on study period), and additional optional modifications to achieve faster speeds are described in the accompanying code tutorial. Because TGPs are used across multiple fields, increases in computational speed made elsewhere can benefit wildlife movement modeling (Gramacy, 2020).

The machine learning approach of TGP modeling allows for accurate prediction and accessible implementation, while the Bayesian formulation of the TGP model allows for application to research questions. The five derived quantities estimated in our case study compress complex individual and population movement trajectories into statistically comparable values and demonstrate the flexibility of our framework to both inclusion of covariates and

different scales of analysis. This flexibility allows for creativity in developing derived quantities that suit the research question of interest. Utilizing different derived values to describe movement is common in both Bayesian and frequentist inference and there is a wide body of work on this topic and its applications (Table 1). Our modeling framework provides trajectories that directly and easily estimate a distribution for any derived quantity of interest, and thus is an ideal starting point for continued development and applications of quantitative descriptors of animal movement.

Derived quantities that describe multiple trajectories (e.g., multiple individuals within a population) are worth emphasizing because of their value to practitioners. Population-level inference fits within our framework of estimating derived quantities, allowing for estimation of a descriptor of multiple animals' movements after modeling the individual trajectories.

Additionally, population-level modeling, as opposed to population-level inference, is a possible avenue for future research and could be pursued by applying the TGP model to a full population model using either hierarchical modeling and the Lunn method (Hooten et al., 2016), or by using the intrinsic treed partitioning of TGPs (discussed in Appendix B). While population-level movement modeling is an area of developing research (e.g., Hanks et al., 2011), our current model is able to perform population-level inference by fitting individual movement models then estimating derived quantities at the population-level. Our framework's ability to statistically compare movements of populations of individuals across treatments holds great potential for wildlife management and ecology applications.

Understanding how animals move within their environments is key to data-driven wildlife management. Though researchers have access to large amounts of telemetry data, current modeling methods can fall short statistically or be preventatively difficult to implement. By

applying Bayesian machine learning through TGP modeling, we have improved the first step in using telemetry data: modeling an animal's trajectory. Treed Gaussian processes both utilize a novel method for modeling the nonstationary structure of telemetry data and simultaneously free researchers from the burden of developing custom movement models to estimate trajectories. From TGP-estimated trajectories, our framework allows researchers to estimate statistically comparable descriptors of individual or group movement. Use of TGP modeling within our inferential framework facilitates a shift in animal movement modeling from focusing on model construction and interpretation to focusing instead on the inference that can be made from easy to implement Bayesian machine learning movement models.

References

- Broderick, T., & Gramacy, R. B. (2011). Classification and categorical inputs with treed Gaussian process models. *Journal of Classification*, 28(2), 244-270. <https://doi.org/10.1007/s00357-011-9083-y>
- Brown, L. M., Fuda, R. K., Schtickzelle, N., Coffman, H., Jost, A., Kazberouk, A., Kemper, E., Sass, E., & Crone, E. E. (2017). Using animal movement behavior to categorize land cover and predict consequences for connectivity and patch residence times. *Landscape Ecology*, 32(8), 1657-1670. <https://doi.org/10.1007/s10980-017-0533-8>
- Buderman, F. E., Hooten, M. B., Ivan, J. S., & Shenk, T. M. (2016). A functional model for characterizing long-distance movement behavior. *Methods in Ecology and Evolution*, 7(3), 264-273. <https://doi.org/10.1111/2041-210X.12465>
- Buderman, F. E., Hooten, M. B., Ivan, J. S., & Shenk, T. M. (2018). Large-scale movement behavior in a reintroduced predator population. *Ecography*, 41(1), 126-139. <https://doi.org/10.1111/ecog.03030>
- Dodge, S., Su, R., Johnson, J., Simcharoen, A., Goulias, K., Smith, J. L., & Ahearn, S. C. (2021). ORTEGA: An object-oriented time-geographic analytical approach to trace space-time contact patterns in movement data. *Computers, Environment and Urban Systems*, 88, 101630. <https://doi.org/10.1016/j.compenvurbsys.2021.101630>
- Edelhoff, H., Signer, J., & Balkenhol, N. (2016). Path segmentation for beginners: an overview of current methods for detecting changes in animal movement patterns. *Movement Ecology*, 4(1), 1-21. <https://doi.org/10.1186/S50462-016-0086-5>
- Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., Milner, J. M., Liberg, O., Linnell, J., Pedersen, H., Sand, H., Solberg, E., & Storaas, T. (2009). Encounter frequencies between GPS-collared wolves (*Canis lupus*) and moose (*Alces alces*) in a Scandinavian wolf territory. *Ecological Research*, 24(3), 547-557. <https://doi.org/10.1007/s11284-008-0525-x>
- Gramacy, R. B. (2005). Bayesian treed Gaussian process models. [Doctoral dissertation, University of California, Santa Cruz].
- Gramacy, R. B. (2007). tgp: an R package for Bayesian nonstationary, semiparametric nonlinear regression and design by treed Gaussian process models. *Journal of Statistical Software*, 19, 1-46. <https://doi.org/10.18637/jss.v019.i09>
- Gramacy, R. B., & Lee, H. K. H. (2008). Bayesian treed Gaussian process models with an application to computer modeling. *Journal of the American Statistical Association*, 103(483), 1119-1130. <https://doi.org/10.1198/016214508000000689>
- Gramacy, R. B., & Taddy, M. (2010). Categorical Inputs, Sensitivity Analysis, Optimization and Importance Tempering with tgp Version 2, an R Package for Treed Gaussian Process

- Models. *Journal of Statistical Software*, 33(6), 1–48.
<https://doi.org/10.18637/jss.v033.i06>
- Gramacy, R. B. (2020). *Surrogates: Gaussian process modeling, design, and optimization for the applied sciences*. Chapman and Hall/CRC. <https://doi.org/10.1201/9780367815493>
- Guenther, J., & Lee, H. K. (2020). An Improved Treed Gaussian Process. *Applied Mathematics*, 11(07), 613. <https://doi.org/10.4236/am.2020.117042>
- Gulick, C. K. (2019). Effects of working grassland management on lesser prairie-chicken resource selection within home ranges and during dispersal events [Master's thesis, Kansas State University].
- Hanks, E. M., Hooten, M. B., & Alldredge, M. W. (2015). Continuous-time discrete-space models for animal movement. *The Annals of Applied Statistics*, 9(1), 145-165.
<https://doi.org/10.1214/14-AOAS803>
- Hanks, E. M., Hooten, M. B., Johnson, D. S., & Sterling, J. T. (2011). Velocity-based movement modeling for individual and population level inference. *PLoS One*, 6(8), e22795.
<https://doi.org/10.1371/journal.pone.0022795>
- Harris, K. J., & Blackwell, P. G. (2013). Flexible continuous-time modeling for heterogeneous animal movement. *Ecological Modeling*, 255, 29-37.
<https://doi.org/10.1016/j.ecolmodel.2013.01.020>
- Hefley, T. J., Broms, K. M., Brost, B. M., Buderman, F. E., Kay, S. L., Scharf, H. R., Tipton, J. R., Williams, P. J., & Hooten, M. B. (2017). The basis function approach for modeling autocorrelation in ecological data. *Ecology*, 98(3), 632-646.
<https://doi.org/10.1002/ecy.1674>
- Hooten, M. B., & Hefley, T. J. (2019). *Bringing Bayesian models to life*. CRC Press.
<https://doi.org/10.1201/9780429243653>
- Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models*. Princeton University Press.
<https://doi.org/10.23943/princeton/9780691159287.003.0005>
- Hooten, M. B., Buderman, F. E., Brost, B. M., Hanks, E. M., & Ivan, J. S. (2016). Hierarchical animal movement models for population-level inference. *Environmetrics*, 27(6), 322-333.
<https://doi.org/10.1002/env.2402>
- Hooten, M. B., & Johnson, D. S. (2017). Basis function models for animal movement. *Journal of the American Statistical Association*, 112(518), 578-589.
<https://doi.org/10.1080/01621459.2016.1246250>
- Hooten, M. B., Scharf, H. R., Hefley, T. J., Pearse, A. T., & Weegman, M. D. (2018). Animal movement models for migratory individuals and groups. *Methods in Ecology and Evolution*, 9(7), 1692-1705. <https://doi.org/10.1111/2041-210X.13016>

- Lautenbach, J. D., Haukos, D. A., Lautenbach, J. M., & Hagen, C. A. (2021). Ecological disturbance through patch-burn grazing influences lesser prairie-chicken space use. *The Journal of Wildlife Management*, 85(8), 1699-1710. <https://doi.org/10.1002/jwmg.22118>
- Londe, D. W., Elmore, R. D., Davis, C. A., Hovick, T. J., Fuhlendorf, S. D., & Rutledge, J. (2022). Why did the chicken not cross the road? Anthropogenic development influences the movement of a grassland bird. *Ecological Applications*, 32(3), e2543. <https://doi.org/10.1002/eap.2543>
- Long, J. A., Webb, S. L., Harju, S. M., & Gee, K. L. (2022). Analyzing contacts and behavior from high frequency tracking data using the wildlifeDI R Package. *Geographical Analysis*, 54(3), 648-663. <https://doi.org/10.1111/gean.12303>
- McClintock, B. T., Johnson, D. S., Hooten, M. B., Ver Hoef, J. M., & Morales, J. M. (2014). When to be discrete: the importance of time formulation in understanding animal movement. *Movement Ecology*, 2(1), 1-14. <https://doi.org/10.1186/S50462-014-0021-6>
- Picardi, S., Coates, P., Kolar, J., O'Neil, S., Mathews, S., & Dahlgren, D. (2022). Behavioral state-dependent habitat selection and implications for animal translocations. *Journal of Applied Ecology*, 59(2), 624-635. <https://doi.org/10.1111/1365-2664.14080>
- Postlethwaite, C. M., Brown, P., & Dennis, T. E. (2013). A new multi-scale measure for analysing animal movement data. *Journal of Theoretical Biology*, 317, 175-185. <https://doi.org/10.1016/j.jtbi.2012.10.007>
- Pozdnyakov, V., Meyer, T., Wang, Y. B., & Yan, J. (2014). On modeling animal movements using Brownian motion with measurement error. *Ecology*, 95(2), 247-253. <https://doi.org/10.1890/13-0532.1>
- R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Scharf, H., Hooten, M. B., & Johnson, D. S. (2017). Imputation approaches for animal movement modeling. *Journal of Agricultural, Biological and Environmental Statistics*, 22(3), 335-352. <https://doi.org/10.1007/s13253-017-0294-5>
- Tanner, E. P., Tanner, A. M., Fuhlendorf, S. D., Elmore, R. D., Davis, C. A., & Polo, J. A. (2021). Land enrolled in the Conservation Reserve Program supports roosting ecology of the lesser prairie-chicken. *Global Ecology and Conservation*, 32, e01916. <https://doi.org/10.1016/j.gecco.2021.e01916>
- Tuia, D., Kellenberger, B., Beery, S., Costelloe, B. R., Zuffi, S., Risse, B., Mathis, A., Mathis, M. W., Langevelde, F., Burghardt, T., Kays, R., Klinck, H., Wikelski, M., Couzin, I. D., van Horn, G., Crofoot, M. C., Stewart, C. V., & Berger-Wolf, T. (2022). Perspectives in machine learning for wildlife conservation. *Nature Communications*, 13(1), 792. <https://doi.org/10.1038/S51467-022-27980-y>

- Verheijen, B. H., Plumb, R. T., Gulick, C. K., Hagen, C. A., Robinson, S. G., Sullins, D. S., & Haukos, D. A. (2021). Breeding Season Space Use by Lesser Prairie-Chickens (*Tympanuchus Pallidicinctus*) Varies Among Ecoregions and Breeding Stages. *The American Midland Naturalist*, 185(2), 149-174. <https://doi.org/10.1674/0003-0031-185.2.149>
- Wang, G. (2019). Machine learning for inferring animal behavior from location and movement data. *Ecological Informatics*, 49, 69-76. <https://doi.org/10.1016/j.ecoinf.2018.12.002>
- Wijeyakulasuriya, D. A., Eisenhauer, E. W., Shaby, B. A., & Hanks, E. M. (2020). Machine learning for modeling animal movement. *PloS One*, 15(7), e0235750. <https://doi.org/10.1371/journal.pone.0235750>

Appendix A - Movement model notation and specification

In this appendix, we provide details on the notation and models for the application of treed Gaussian processes to animal movement. This guide is not necessary for applying treed Gaussian processes but provides deeper understanding of the statistical underpinning of our model.

Terms:

$\mathbf{y}_t \equiv (y_{t_1}, y_{t_2})$	One recorded animal location at time t
$\mathbf{Y} \equiv \begin{bmatrix} y_{1_1} & y_{1_2} \\ \vdots & \vdots \\ y_{n_1} & y_{n_2} \end{bmatrix}$	$n \times 2$ matrix of all recorded locations
$\mathbf{s}_t \equiv (s_{t_1}, s_{t_2})$	One true animal location at time t
$\mathbf{S} \equiv \begin{bmatrix} s_{1_1} & s_{1_2} \\ \vdots & \vdots \\ s_{m_1} & s_{m_2} \end{bmatrix}$	$m \times 2$ matrix of true animal locations at temporal resolution of Δt
$f(\mathbf{S})$	Deterministic function of locations

Models:

$\mathbf{Y} \sim [\mathbf{Y} \mathbf{S}, \sigma^2]$	Data model
σ^2	Parameter for data location error
$\mathbf{S} \sim [\mathbf{S} \boldsymbol{\theta}]$	Process model

\mathbf{S} is distributed as a treed Gaussian process with the parameters $\boldsymbol{\theta}$.

Parameter models are pre-specified within the `tgpr` function in program R.

Posterior Distribution for Discrete Approximation of True Trajectory:

$$[\mathbf{S} | \mathbf{Y}] = \int [\mathbf{S} | \boldsymbol{\theta}] [\boldsymbol{\theta} | \mathbf{Y}] d\boldsymbol{\theta}$$

Expected Value of a Derived Quantity of the Trajectory:

$$E(f(\mathbf{S}) | \mathbf{Y}) = \int f(\mathbf{S}) [\mathbf{S} | \boldsymbol{\theta}] [\boldsymbol{\theta} | \mathbf{Y}] d\boldsymbol{\theta}$$

Monte Carlo Approximation of Expected Value of a Derived Quantity:

$$E(f(\mathbf{S}) | \mathbf{Y}) \approx \sum_{k=1}^K \frac{f(\mathbf{S}^{(k)})}{K}$$

The following table outlines the relationships between the underlying theoretical continuous time movement model, the practical computer implemented discrete approximation of the continuous time model (described on the previous page), and the Monte Carlo sampling-based algorithm used to fit this model to our data and estimate derived quantities.

Continuous Time Model	Discrete Approximation	Monte Carlo Approximation
<p>Posterior predictive distribution of continuous stochastic process:</p> $\mathbf{s}(t) \sim [\mathbf{s}(t) \mathbf{Y}]$ <p>\mathbf{s} is defined as the true trajectory, modelled as a treed Gaussian process. $\mathbf{s}(t)$ is a continuous function of continuous time.</p>	<p>Posterior predictive distribution of discretized continuous stochastic process:</p> $\mathbf{S} \sim [\mathbf{S} \mathbf{Y}]$ <p>\mathbf{S} is a discretization of the true continuous trajectory. \mathbf{S} is a finite vector of true locations at each Δt time.</p>	<p>One trajectory sampled from the posterior distribution of the discretized continuous stochastic process:</p> $\mathbf{S}^{(k)} \sim [\mathbf{S} \boldsymbol{\theta}^{(k)}]$ <p>To obtain a sample of size K from the posterior predictive distribution of $[\mathbf{S} \mathbf{Y}]$:</p> <ol style="list-style-type: none"> 1. Take a draw of $\boldsymbol{\theta}^{(k)}$ from $[\boldsymbol{\theta} \mathbf{Y}]$ 2. Take a draw of $\mathbf{S}^{(k)}$ from $[\mathbf{S} \boldsymbol{\theta}^{(k)}]$ 3. Repeat K times
<p><u>Apply derived quantity function</u></p> $f(\mathbf{s}(t))$ <p>Ex. instantaneous velocity:</p> $\mathbf{v}(t) \sim \mathbf{s}'(t)$ <p><i>Result: distribution of function providing velocity across continuous time</i></p>	<p><u>Apply derived quantity function</u></p> $f(\mathbf{S})$ <p>Ex. average velocity across interval $(t, t+1)$:</p> $\mathbf{v}_t = \frac{\sqrt{(s_{t_1} - s_{(t+1)_1})^2 + (s_{t_2} - s_{(t+1)_2})^2}}{2}$ <p><i>Result: distribution of $m-1$ dimension vectors \mathbf{V} of average velocities at each time t</i></p>	<p><u>Apply derived quantity function</u></p> $f(\mathbf{S}^{(k)})$ <p>Ex. average velocity across interval $(t, t+1)$:</p> $\mathbf{v}_t^{(k)} = \frac{\sqrt{(s_{t_1}^{(k)} - s_{(t+1)_1}^{(k)})^2 + (s_{t_2}^{(k)} - s_{(t+1)_2}^{(k)})^2}}{2}$ <p><i>Result: K samples of $m-1$ dimension vectors $\mathbf{V}^{(k)}$ of average velocities at each time t</i></p>
<p><u>Transform derived quantity</u></p> $g(f(\mathbf{s}(t)))$ <p>Ex. average daily distance travelled over a period of a days:</p> $\sim \frac{1}{a} \int_0^T \mathbf{v}(t) dt$ <p><i>Result: distribution of a scalar value</i></p>	<p><u>Transform derived quantity</u></p> $g(f(\mathbf{S}))$ <p>Ex. average daily distance travelled over a period of a days:</p> $\sim \frac{1}{a} \sum_{t=1}^m \mathbf{v}_t$ <p><i>Result: distribution of a scalar value</i></p>	<p><u>Transform derived quantity</u></p> $g(f(\mathbf{S}^{(k)}))$ <p>Ex. average daily distance travelled over a period of a days:</p> $\approx \frac{1}{a} \sum_{t=1}^m \mathbf{v}_t^{(k)}$ <p><i>Result: sample of size K of a scalar value</i></p>

Appendix B - Additional information

Outliers and unusual movements

For telemetry data, we classify outliers (locations unexpectedly far from their temporal neighbors) into two types: location error outliers and process model outliers. Location error outliers arise from mechanical (or even data processing) errors and provide an unexpected location that is unrelated to where the animal actually was (beyond our expectations of telemetry device error). These outliers are common and familiar to practitioners working with telemetry data. They can be removed from datasets by setting a cut-off value for location or distance moved, based on knowledge of study site and species behavior. These are removed before application of the TGP framework.

Process model outliers occur when the telemetry device is performing within its expected accuracy, but the animal has moved in some unusual way outside the pattern of the rest of the telemetry data. These outliers fall within the cutoffs that remove location error outliers, but still pose a challenge to modelling. They are considered outliers because they stand alone without a clear pattern. However, these points only appear as outliers because of the temporal fineness with which the data were collected. Remember that the model is seeking to express the true continuous time path that underlies the discrete data points: there are no outliers in this true path. For example, a single data point that appears as a huge jump at a two-hour data scale could be easily explained and modeled if data were recorded at the minute scale.

It is important to recognize that the unusual movements present in process model outliers are likely very important ecologically, as is emphasized in the discussion. TGPs are able to detect these unusual movements when there are enough datapoints available (when the frequency of data collection is sufficiently smaller than the duration of the unusual movement). Figure 3 is

an example of TGP successfully capturing an unusual movement, that was missed (treated as an outlier) by a non-treed model. However, all models, including TGP, are unable to model movements that occur at a finer temporal scale than the data is recorded at. This is why our model is not performing perfectly between the recorded datapoints at times 1262 and 1264 in Figure 3. In such a case there is not enough information present in the data, and the ideal would be to collect more data while this extreme movement is occurring.

While treed Gaussian processes perform very well at capturing extreme movement patterns that are present in the data, no modelling technique can compensate for a lack of data, and future work could investigate the scale at which data must be collected in order to detect a movement of interest. Knowledge of data requirements specific to the TGP model and the species and behavior of interest could be incorporated into adaptive sampling designs and this is an area for future research.

Telemetry device error

Incorporating and modelling telemetry device (e.g., GPS) error is common within animal movement models (e.g., Buderman et al., 2016). However, device error is not what wildlife practitioners are ultimately interested in. They instead wish to separate signal (actual movements of the animal) from noise (device error). As telemetry technology continues to improve, and errors become small enough to be relatively unimportant (e.g. ± 18 m accuracy), we believe too much focus on modelling device error detracts from more pressing scientific questions.

Treed Gaussian processes, like all models, do estimate noise in the data. In a Gaussian process, the nugget hyperparameter captures the discontinuity between the predicted and recorded location (Gramacy, 2020). While this may be interpreted quite literally as an estimate of

device error, we would not use it as such. The model's estimate of the nugget incorporates *all* the “noisiness” in the data, most notably that created by process model outliers discussed in the previous section. This means we expect the nugget estimated from the data to be higher than the actual device error in most cases of animal movement data.

Again, this overestimation of noise is not a problem with the model, but one of not enough data. If the data is being interpreted by the model as noisy, it is because there are not enough datapoints to produce a clear signal. The model then interprets the process model outliers as noise, and inflates the nugget estimate and prediction variance. If there are enough data points, for example in Figure 3, the model can distinguish those unusual locations as signal instead of noise and model them as a separate node on the tree.

Selection of MCMC sampling parameters

Within the *tgp* package, both fitting the model to the data and using the model to predict locations (the *predict* function) utilize Markov chain Monte Carlo (MCMC) sampling. MCMC methods are used to sample from the targeted posterior distribution, and there is a tradeoff between MCMC sample size (computation time and costs) and accuracy. For full understanding of MCMC sampling and its tuning, we recommend knowledge of Bayesian statistics at the level of Hobbs and Hooten (2015). MCMC methods do require some evaluation by the practitioner and possible tuning of hyperparameters, however MCMC methods are now common in wildlife biology, and familiar to many practitioners.

In the *tgp* package, three MCMC hyperparameters are required to take a sample from the posterior, denoted by BTE and representing “burn in,” “total,” and “every.” For example, `BTE = c(1000, 5000, 2)` will remove the first 1000 samples as burn in, and thin by 2, resulting in an

MCMC sample of size 2000. The `btgpllm` function for fitting the model (estimating model parameters) has default BTE settings of (2000, 7000, 2) and these do not need to be edited by the practitioner.

Sampling from the posterior predictive distribution of predicted locations, using the `predict` function, does require practitioner setting of the BTE hyperparameters. We recommend that practitioners tune this based on their data and knowledge of MCMC methods. Code for this is provided in the accompanying tutorial. If tuning this value is infeasible, we recommend a MCMC sample size of 1000 using $\text{BTE} = (2000, 12000, 10)$, however we have not tested this on multiple datasets. Practitioners may also avoid this tuning by choosing very large MCMC sample sizes at the cost of long run times.

Delta t choice

The Δt interval allows approximation of a continuous process by a finite number of discrete points. Including the uncertainty added by this Δt approximation in the total model uncertainty is an area for future research. A Δt approximation for continuous time modelling is used elsewhere in the animal movement modelling literature, and all require the user to select a Δt value (e.g. Buderman et al., 2016; Hanks et al., 2011). Smaller versus larger Δt presents a tradeoff between accuracy and precision of the resulting estimates, and time of computation. Optimization of this tradeoff is also an area for future research.

For the purposes of our targeted practitioners, users can simply select a reasonable Δt (such as one hour to make inference on monthly derived quantities), fit the model and determine if computation times are reasonable for their needs, and adjust accordingly. The Δt tuning parameter is simple to adjust within our framework. The value of precision versus computation

time will depend on the research project and must be assessed by the user. The flexibility of our method allows users to set a very fine Δt at areas of interest (for example, an area of a potential road crossing) and a larger Δt at areas of less management interest. However, comparing derived quantities computed using different Δt values can present a problem as the selected Δt will affect the resulting derived quantity estimate. If comparing results across studies or models, we recommend setting equal Δt values.

Population-level modelling and model splits

The treed aspect of the TGP modelling framework is conducive to the concept of a complete or full model that models and includes all information in the dataset. This full model would simultaneously model information from both X and Y directions, and information from all individuals in the dataset. Splits in the treed partitioning would then separate sub-models pertaining to individuals, or groups of individuals, that travel together. This is a possible basis for population level modelling using the TGP framework. If we instead model individual animals separately, we are assuming they move independently. This may be functionally true for some species and individuals, but not others.

With current computation capacities, fitting the full model to all aspects of the dataset would be computationally preventative for many datasets and practitioners. In our framework, we chose to separate individuals and lose the possible information gained from modelling multiple individuals' movements simultaneously. This allowed our first TGP applications to be computationally tractable and accessible.

When fitting separate models to different data, we assume independence of those processes and accept any loss of information from possible lack of independence between those

processes. Deciding where to split data and models is therefore a balance between computational simplicity and possible loss of information. In addition to modelling individuals separately, we chose to model X and Y directions separately, making the simplifying assumption that movement in one direction is independent of movement in the other. Practically, by assuming X-directional and Y-directional movements are independent, we can cut our model fitting time in half by fitting separate btgpllm models to X data and Y data, allowing for parallelization.

Modelling can be further split based on research questions and ecological knowledge of the system and animals. If an animal has data that spans a long time period, for example years, the researcher may wish to divide data into known life history seasons for the species under the assumption that the animal behaves and moves differently in these seasons. This will greatly speed up computation. However, like with individuals, the full model would model all the seasons together and allow the treed partitioning to make seasonal divisions. In this latter case, the seasonal divisions are made based on the data, as opposed to life history cutoff dates. For example, a researcher may use a nesting season start date from the literature of June 15th to divide the data and fit a model for the nesting season, but in a full model the treed Gaussian process may find that the bird doesn't begin nesting characteristic movements until June 19th, and thus the full model makes a treed split there.

Splitting at time periods also assumes independence of an individual animal's movements at different periods. Though an animal's movements are not truly independent at different times of its life as they still come from the same individual, this may be a valuable simplifying assumption for practical modelling purposes and reduce computation costs. Splitting within time periods will also increase ease if research questions are already framed within the scale of these time periods. Generally, model splitting decisions will be up to the practitioner's discretion and

depend on the amount of data, computational constraints, research questions, and the known life history and patterns of the species.

Tree breaks and discontinuities:

Treed Gaussian processes have been recognized for their ability to model discontinuities in data, and this strength applies directly to the abrupt changes present in animal movement data (Gramacy & Lee, 2008). We recognize that physical movement is not in reality discontinuous. In using TGP we break from the mechanistic models most frequently used to model telemetry data based on the physical laws of movement and instead present a phenomenological model focused on predictive accuracy and increased model fitting abilities.

Figure 3 demonstrates the ability of TGPs to model abrupt transitions in patterns of movement and location. Our recorded GPS data show that the lesser prairie-chicken in Figure 3 traveled over 14 km in the two-hour interval between recordings at hours 1262 and 1264, a movement that the Gaussian process model fails to capture. In the TGP model, this extreme change is treated as a “break” in the model: a shift to a different node of the treed partitioning. Having such a break implies discontinuous movement, going against natural instincts of continuous time movement: as Δt approaches zero, a bird cannot actually travel 14 km between consecutive time points (e.g., infinite velocity of a bird).

However, we continue with our phenomenological (TGP) approach to modelling and argue that the model is performing as we would hope to meet our predictive and inferential goals. Though this discontinuous movement may be viewed as a mechanistic failing, mechanistic accuracy is not our goal. Our phenomenological model is performing prediction as desired for that individual’s extreme movement. If we step back from modelling, it is clear that the GPS data

we have are incapable of accurately telling us where the bird was at time 1263 during such an extreme and unprecedented movement behavior. Thus, the phenomenological model makes predictions in either of the two data clumps at time 1263. Our model does not provide information that was not present in the data, but it does estimate what we need to obtain our derived quantities and appropriate uncertainty.

The future of animal movement analysis

As telemetry data continues to improve and device error continues to decrease, our data itself will approach the true trajectory. This will decrease the importance of the modelling steps in Figure 1, while increasing the importance of the inference steps. Our proposed TGP modelling framework is a statistical stand-in until the future time when we have data on the complete animal trajectory. However, even when TGPs are replaced by improved machine learning models, and eventually replaced by near-continuous animal telemetry data, the inferential framework outlined in Figure 1 will still hold. Utilizing machine learning to nearly automate the process of estimating continuous trajectories from discrete telemetry data allows animal movement modelling to follow technology's progression towards continuous telemetry data.

Appendix C - Example applied trajectory transformations

This appendix walks through an example of estimating average daily total distance traveled across one month, starting from a sample of outputted trajectories. It continues with a demonstration of population level inference. Tables of example values are provided, similar to how they would appear in R (see accompanying tutorial for full R code).

Period = 1 month

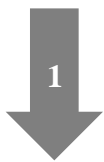
$\Delta t = 1$ hour

MCMC sample size = 1000

MCMC sample of \mathbf{S} :

Units = UTM

\mathbf{t} - hour	\mathbf{X}_1	\mathbf{Y}_1	\mathbf{X}_2	\mathbf{Y}_2	...	\mathbf{X}_{1000}	\mathbf{Y}_{1000}
0	483382.5	4144834	483213.4	4145334		483420.9	4144674
1	482812.7	4145860	483149.9	4145201		483121.6	4145108
...							
744	500295.2	4128498	500221.0	4128543		500278.8	4128570

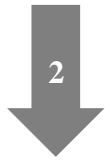


Use distance formula to compute displacement (hourly velocity) between each Δt set of points

MCMC sample of \mathbf{V}_t :

Units = meters/ Δt = meters/hour

\mathbf{t} - hour	\mathbf{V}_1	\mathbf{V}_2	...	\mathbf{V}_{1000}
1	1173.41451	148.16156		527.19819
2	791.75742	168.24507		52.77138
...				
744	63.811221	61.99200		180.248800



Sum within each column's day

MCMC sample of daily total distance traveled:

Units = meters/day

t - day	D₁	D₂	...	D₁₀₀₀
24 – day 1	9884.867	7074.448		6867.132
48 – day 2	9365.736	9002.061		7493.807
...				
744 – day 31	1969.755	2986.166		2441.949



Take column averages

MCMC sample of average daily distance traveled in that month:

Units = meters/day

	D₁	D₂	...	D₁₀₀₀
Whole season	10143.601	9038.150		9691.998

Extension to Population:

Population level inference on average daily distance traveled across a *population* of n animals:

Compute the above vector (dimension = 1×1000) for each of the n birds.

Row bind these vectors into a table of dimension = $n \times 1000$

Take column averages – this ensures MCMC samples are aligned. See Hobbs and Hooten (2015) chapter 8.3 for more details on aligning derived quantities.

This results in a 1×1000 vector of samples from the posterior distribution of population average daily distance traveled.