
SMOOTHING SPLINES OF APEX PREDATOR MOVEMENT: FUNCTIONAL MODELING STRATEGIES FOR EXPLORING ANIMAL BEHAVIOR AND SOCIAL INTERACTIONS

A PREPRINT

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ABSTRACT

The collection of animal position data via GPS tracking devices has increased in quality and usage in recent years. Animal position and movement, although measured discretely, follows the same principles of kinematic motion, and as such, the process is inherently continuous and differentiable. I demonstrate the functionality and visual elegance of smoothing spline models. I discuss the challenges and benefits of implementing such an approach, and I provide an analysis of movement and social interaction of seven jaguars inhabiting the Taiaamã Ecological Station, Pantanal, Brazil. In the analysis, I derive measures for pairwise distance, cooccurrence and spatiotemporal association between jaguars, borrowing ideas from density estimation and information theory. These measures are feasible as a result of spline model estimation, and they provide a critical tool for a deeper investigation of cooccurrence duration, frequency, and localized spatio-temporal relationships between animals.

Keywords Apex Predators · Animal Telemetry · Smoothing Splines · Functional Data Analysis · Animal Behavior · Animal Interaction

1 Introduction

Technological advancements in remote sensing of animal movement, referred to as animal telemetry, have revolutionized the discipline of movement ecology. Animal movement data provides critical information about ecological processes, and it can be a vital asset to conservation efforts of species and ecosystems. The increased feasibility of tracking and collecting animal movement information has yielded large reservoirs of fine-scale spatio-temporal data, and the challenges of meaningfully modeling animal behavior have resulted in the expansion of holistic machine learning methodology that appropriately considers animal psychology and cognition (1; 2; 3).

The analysis animal telemetry data has a number of challenges. (1) Spatial and temporal density of measurements is subject to extreme variation. Animal behaviors may shift phenologically between migratory and residency states, and even for non-migratory species, this problem can present itself in a smaller scale region as animals shift between resting, foraging, or transit states. Temporal density variation may be caused by loss of connection, malfunctioning, and damage of the device over time. (2) Even with advancements in precision and reliability of animal tracking, the datasets are inherently discrete, and any analysis of such data requires a conscious choice between modeling such processes discretely or attempting to model them continuously. (3) Animal behavior cannot be univariately characterized. Animal movement is characterized by position, rate of change of position, and cooccurrence with other animals, all of which

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may suddenly shift under interactions with an array of environmental factors that alter the allocation of critical resources for survival (2; 3).

Discrete time methods have had steady use in the field (4; 5; 6; 7), but recent literature has provided significant progress in continuous-time modeling (8; 2). Animal movement is explicitly continuous, like any kinematic process, and continuous-time models celebrate and take advantage of this continuity in the modeling process. These models are exceptional and flexible tools for modeling the complexity of animal movement.

However, I emphasize that we should more fully celebrate animal movement as a kinematic process. We must acknowledge that projectile movement in a real space \mathbb{R}^d is smooth, and I propose that we further consider modeling strategies and methodological developments that account for the 1st and 2nd order differentiation of a animal movement processes.

I present a philosophically different approach for analyzing animal telemetry in which the unit of analysis is a curve (or function) as opposed to single site measurements. This approach, widely referred to as functional data analysis (FDA) roots in the assumption that measurements vary over some continuum such as space or time, and that there is an underlying smoothness inherent to the process of interest (9; 10; 11). The assembly of an entire smooth curve of an animal's movement is accomplished using linear combinations basis functions which are the foundation of smoothing spline models. They are widely acclaimed for their ability to model complex and noisy data (9).

Animal movement is a visual spectacle, and the statistical visualization of animal movement is greatly aided using smoothing splines. FDA methods provide a viable and accessible option for examining an estimated complete path and the speed and acceleration (and decelerations) along this path, which are vital in the classification of various types of animal behavior. There have been recent basis function models proposed to model animal movement (1; 12; 13; 14), but there is great need to incorporate a wide array of strategies for an appropriate and application-specific exploration using smoothed spline models.

In this project, I analyze and visualize the movement of seven Jaguars inhabiting the Taiamã Ecological Station, Pantanal, Brazil and the associative and cooccurrence relationships between them. Fine-scale movement of Jaguars in this region has recently been explored using association rule mining algorithms to study their behavior and social interaction. Identifying behavioral changes and social interactions are crucial aspects of species ecology, and this recent work has added to literature of jaguar territory sharing (15). Jaguars are generally solitary and territorial apex predators, but in areas with high primary productivity, the overlap of territory and its effects on mating, cooperation, and competition yield a complex system of interdependent subjects that can directly or passively interact (15; 16; 17).

I construct smoothing spline models to continuously and differentially characterize the movement, resting, and migratory behavior of these 7 jaguars. These smoothing spline models provide exceptional fit, and they provide the means to feasibly measure animal association using a measure of mutual information from the discipline of information theory. Further, I introduce the concept of a *Cooccurrence Potential Plots* which are smooth density functions derived from the distance between pairs of jaguars on the refined and unified grid. The refinement and unification of the time-grid is an inherent and advantageous by-product of spline models.

This application of FDA methods to animal movement showcases the plausibility of studying animal movement with the theoretical backing of the laws of kinematic motion, and most importantly, it the approach provides an increased set of tools to improve the study animal movement in relation to dynamic social and environmental factors.

In this project, it is important to acknowledge that measurement error is not considered as it was not an attributed recorded in the public version of the data product used in this work. FDA methods exists to address measurement error for various disciplines (1; 18; 19), and I leave this important and interesting aspect of animal telemetry to future work.

2 Methods

Fitting smoothed spline models, provides a number of advantages for irregularly and sparsely measured data that is known to vary over some continuum, but it is important to note that some sacrifice of position is made in a model that aims to smooth a function through a series of measurements (9). Since GPS positioning systems have known measurement error (even though measurement error is not reported in this data product), I aim to show that this sacrifice is worth the benefits of this approach, and further that modifications to the model can be instated to adapt and improve this approach.

2.1 Fitting Smoothed Spline Models to Jaguar Movement

For a collection of raw hourly recordings of a single jaguar's position, denoted by $Y_{lat} = [\vec{y}_{lat\ 1} \dots \vec{y}_{lat\ n}]$ and $Y_{lon} = [\vec{y}_{lon\ 1} \dots \vec{y}_{lon\ n}]$, I estimate $\hat{x}_{lat}(t) = \sum_{k=1}^K c_{lat\ k} \phi_k(t)$ and $\hat{x}_{lon}(t) = \sum_{k=1}^K c_{lon\ k} \phi_k(t)$ subject to a roughness penalty on the second derivative of the basis expansion $\Phi = [\phi_1(t) \dots \phi_K(t)]$ where c_k are the coefficients of the terms of the basis expansion denoted by ϕ_k , which in this project is constructed using a B-spline basis expansion (9; 20). Both latitude and longitudinal movement can be individually expressed as an unconstrained minimization defined by

$$\vec{c} \min \|\vec{y} - \Phi \vec{c}\|^2 + \lambda c^T R c \quad \text{for } \lambda \geq 0, \quad (1)$$

where $R_{jk} = \sum_{l=1}^M \phi_j''(\tilde{t}_l) \phi_k''(\tilde{t}_l) h$ for $h = \tilde{t}_l - \tilde{t}_{l-1}$ (9).

We select an appropriate value for λ coordinates using the optimal lambda for a single site determined by the generalized cross-validation criteria, $GCV = \frac{MSE(\lambda)}{(1 - \frac{df_\lambda}{M})}$. For jaguar movement, I have fitted the spline models with low or negligible roughness penalization, since the precision of movement is of high priority. The roughness of the movement can also be restricted by latitude and longitude separately which may be of interest if we seek to model movement with substantial differences in between latitudinal and longitudinal behavior (such as long distance ungulate or bird migration), but for this work the roughness is penalized equally for both dimensions. The resulting smoothed jaguar movement curves have the form

$$\hat{x}_{lat} = \Phi(\Phi^T \Phi + \lambda_{lon} R)^{-1} \Phi^T \vec{y} = S_{lat} \vec{y}_{lat}. \quad (2)$$

$$\hat{x}_{lon} = \Phi(\Phi^T \Phi + \lambda_{lon} R)^{-1} \Phi^T \vec{y} = S_{lon} \vec{y}_{lon}. \quad (3)$$

The jaguars 2-dimensional movement is then characterized by coordinates on the path $(\hat{x}_{lon}(t), \hat{x}_{lat}(t))$.

In order to meaningfully estimate jaguar position across highly disparate densities of raw time recordings, careful placement of knots is advised. Let (t_1, \dots, t_n) be independently and identically distributed time samples from an unknown distribution f_h . We estimate the density of sampled times for a given jaguar using kernel density estimation defined by $\hat{f}_h(t) = \frac{1}{nh} \sum_{i=1}^n K(\frac{t-t_i}{h})$, where K is gaussian kernel function and h is a smoothing bandwidth parameter where higher values of h yield a smooth estimate of the density (21). Let $k = \hat{f}_h(t^*)$ be selected as a threshold where t_i with $\hat{f}_h(t_i) > k$ are defined as high density times, the collection $\{t_i | \hat{f}_h(t_i) > k\} = (\tau_1, \dots, \tau_m)$ where $\tau_1 < \dots < \tau_m$. This selection of knots is carefully placed to avoid over fitting regions of the time domains that are barren or extremely sparse. This is desirable for periods where GPS tracking devices are out-of-operation for an extended period, but it is still desirable to fit regions with dense recordings with high precision.

Continuous-time estimation of distance and speed has been developed for standard continuous time models (22). In the next two sections, I outline a derivation of speed and distance measures for animal movement in the FDA paradigm.

2.2 Differentiation of the Smoothed Position Functions and Derivation of Rest Period Density Functions

Differentiation of the smoothed position paths is then conveniently estimated using the same collection of coefficients, \vec{c}_{lat} and \vec{c}_{lon} , and the derivation functions are defined by

$$\hat{x}'_{lat}(t) = \sum_{k=1}^K c_{lat\ k} \phi'_k(t), \quad \hat{x}'_{lon}(t) = \sum_{k=1}^K c_{lon\ k} \phi'_k(t) \quad (4)$$

where $\phi'_k(t)$ is the derivative of the basis expansion (9).

The estimated speed of jaguar position can then be defined by $\hat{x}'(t) = \sqrt{(\hat{x}'_{lat}(t))^2 + (\hat{x}'_{lon}(t))^2}$. Behavioral states of animal movement are generally characterized by different speed of movement. As an example a resting state should be characterized by lower estimated speeds while migratory, foraging, and other transitory states are characterized by faster speeds. For this project, I used a speed of 0.25 meters/second as a cutoff between resting and transit states. Clearly, a literal resting state should have a derivative value of zero, so in this application resting state has a looser interpretation that characterized by stationary and exceptionally small changes in position. Similar to before, I subset "resting state"

times and derive a kernel density function for the distribution of resting times, $\hat{f}_h(t) = \frac{1}{nh} \sum_{i=1}^n K(\frac{t-t_i}{h})$, where K is gaussian kernel function and h is a smoothing bandwidth parameter where t_1, \dots, t_n are restricted from to the set $\{t_i | \hat{x}'(t) < 1\}$.

2.3 Pairwise Jaguars Distance Functions and Derivation of Cooccurrence Potential Plots

For any pairs of jaguars, J_1 and J_2 with geographic position monitored on the domain $[a, b]$ and $[c, d]$, respectively, with $a < c < b < d$, a distance measure can be defined between pairwise estimations of position on the refined regular time grid t_1, \dots, t_p where $c = t_1$ and $b = t_p$. This regular time grid is subsetting from the refined global time grid used to smooth jaguar position which in our application has been smoothed to provide an estimate of position every 60 minutes. Although not finer than the raw grid, this grid resolution was chosen since already provides extensive interpolation of missing hours, and the smoothed spline model are smaller in size. The choice of time grid is arbitrary in the FDA paradigm, and it can be readily refined to a desired resolution. As an example, the smoothed spline models implemented in this project could be refined to provide 1 minute estimations, and they would still follow the same smoothed path defined on the selected resolution. There may be clear advantages to estimating movement on this resolution, but this is a question that will be left to future work.

, and the approach used in this project is similar

2.4 Mutual Information of Jaguar Movement

Mutual information is a measure of mutual dependence between two random variables, or more simply, the amount of information gained about one variable by observing the other (23). Let (X, Y) be a pair of random variables with values spanning the space $(\mathcal{X} \times \mathcal{Y})$. The mutual information between two jointly continuous random variables X and Y is defined by

$$I(X; Y) = \int_{\mathcal{Y}} \int_{\mathcal{X}} p_{(X,Y)}(x, y) \log \frac{p_{(X,Y)}(x, y)}{p_X(x)p_Y(y)} dx dy \quad (5)$$

where $p_{(X,Y)}$ is the joint probability density function of X and Y , and p_X and p_Y are the respective marginal density functions. It is clear that if X and Y are independent then information gained from observing one of the random variables does not provide information about the other, and recall that for independent random variables, $p_{(X,Y)}(x, y) = p_X(x)p_Y(y)$, which implies from Equation (4) that $I(X; Y) = 0$ (23).

To measure dependence or strength of association between pairs of jaguar movements, it is clear that a global measure of mutual information is insufficient to measure correlation between jaguars since their relationships may be dynamic and shifting. I propose the use of the localized mutual information measure $I_{\mathcal{L}}$. Other localized mutual information measures have been derived for various applications (24; 25; 26). In this work, I define $I_{\mathcal{L}}$ by

$$I_{\mathcal{L}}(X; Y) = \int_{\mathcal{Y}_{\mathcal{L}}} \int_{\mathcal{X}_{\mathcal{L}}} p_{(X_{\mathcal{L}}, Y_{\mathcal{L}})}(x, y) \log \frac{p_{(X_{\mathcal{L}}, Y_{\mathcal{L}})}(x, y)}{p_{X_{\mathcal{L}}}(x)p_{Y_{\mathcal{L}}}(y)} dx dy \quad (6)$$

where $\mathcal{X}_{\mathcal{L}}$ and $\mathcal{Y}_{\mathcal{L}}$ are restrictions of the random variable to the domain defined by the set $\mathcal{L} = \{t_i | t \in [t_i - \lambda, t_i + \lambda]\}$. The parameter λ defines the bandwidth or radius over which local mutual information is measured.

Ultimately, the advantage of this approach is to construct a bivariate measure of mutual information, and finally to generate of mutual information function with respect to time. For two bivariate random vectors $X = (X_{lat}, X_{lon})$ and $Y = (Y_{lat}, Y_{lon})$, I define joint local mutual information by

$$I_{\mathcal{L}}(X, Y | \lambda) = \sqrt{I_{\mathcal{L}}(X_{lat}; Y_{lon})^2 + I_{\mathcal{L}}(X_{lon}; Y_{lat})^2}. \quad (7)$$

Clearly, various weighting schemes for combining local mutual information for latitude and longitude could be derived. (Also, since the measure of mutual information is measured from the center of a interval, it may be advantageous to weight the contribution of realizations of a random variable in the mutual information computation based on their proximity to the center of the interval although this is not explored here.) Finally, I define the joint local mutual information function with respect to time by

$$\mathcal{I}(t; \lambda) = I_{\mathcal{L}_j}(X, Y | \lambda). \quad (8)$$

Table 1: Monitoring statistics of Jaguars from the Taiaamã Ecological Station

Jaguar Local ID	Frequency	Monitoring Period
12	2681	12/5/14 to 4/18/15
13	5040	12/7/14 to 8/24/15
18	2314	11/29/14 to 4/13/15
22	4709	9/11/14 to 5/21/15
41	4952	12/5/14 to 8/17/15
81	10988	10/15/13 to 5/29/15
88	1296	10/9/13 to 4/20/14

where $j = 1, \dots, \dim(\vec{t})$ and \vec{t} is the vector of times from the refined time grid. It is important to note that in application the values of t are limited to the defined resolution of the spline model.

This derived result can be used to monitor periods of time where high an low correlation between a pair of jaguars is observed, and it provides a tool for monitoring if periodicity in the strength of their relationships exists. An example we might look for would be strength of relationships in movement between a male-female pair of jaguars during and between potential mating periods.

2.5 Data: Taiama Ecological Station Jaguar Movement Data

I add to the the previous investigation of movement and social interaction of a collection of jaguars in the Taiaamã Ecological Station, Pantanal, Brazil. The animals were fitted with GPS-satellite collars (Lotek Wireless, Inc.) and monitored for periods of 60 to 591 days (27). The authors of the study have made it public and freely available at DOI: 10.1002/ecy.2379 and also at Dryad Digital Repository (<https://doi.org/10.5061/dryad.2dh0223>). In this project, I utilized data from the full monitoring periods on 7 jaguars from this region, and Table1 presents the number of recordings and the length of the monitoring period. The finest temporal resolution of the data is on hourly intervals, however there are frequent gaps in recordings where missing measurements may be present for 2 hours to several days.

The selection of jaguars examined in this project on the condition that they shared an overlapping monitoring period with at least one jaguar from the monitoring period with the highest activity monitoring period from December 2014 to the summer of 2015. The final and more detailed investigation of social interactions is performed for Jaguars 12, 13, 18, 41, and 81.

For all visualization used in this work, I numerically transform to time in days from the earliest available date 10/9/13 for Jaguar 88. As such $t = 0$ is the first day recorded for Jaguar 88, and the final day on this scale is $t = 591$ when the final measurement on Jaguar 13 is recorded, 08/24/15. This is particularly useful for monitoring periodicity and duration of events, since it is difficult to quickly understand the number of days or weeks between two dates.

3 Results

The primary challenge in mapping and analyzing relationships between Jaguars at the Taiama Ecological Station is the staggered time windows that each Jaguar is monitored coupled with the inconsistent temporal resolution of GPS readings. To reach our final selection of 7 jaguars, we removed two jaguars with less the 100 GPS recordings and two jaguars (Jaguar 91 and 92) that were monitored many months after the remaining jaguars (Jaguar 116 and 117). There are 3 females (Jaguars 12, 41, and 88) and 4 males (Jaguars 13, 18, 22, 81). I visualize the remaining 7 jaguars in Figure 1. Across the three plots provided, we can develop a short narrative of a few major movement characteristics. Within their respective time domains, most of the 7 jaguars have consistent stable fluctuations in position within their territories (with some clear overlap in territories). However, Jaguar 81 (male, age=4yrs) with the longest monitoring window, makes a significant territorial transition from residing in the same region as Jaguar 88 (female, age=5yrs) to the territory of Jaguar 12 (female, age=4yrs). There appears to be a period of interaction between Jaguar 12 and Jaguar 81, and then Jaguar 12 makes a temporary but significant migration south for approximately 3 months before returning to the same region again as Jaguar 81. There are other male-female interactions that not as easily discernible, and more investigation is clearly required.

In Figure 2, I present a detailed visualization of the smoothing of Jaguar 12's residential to migratory transition. As a can be seen visually, the fit of this spline model is exceptional and only a small selection of points are not well fit to the line. This is an acknowledged sacrifice of information, in exchange for a number of benefits, primarily the refinement of the time resolution and consistency to a uniform time grid shared by all jaguars. In Figure 3, I present the smoothed

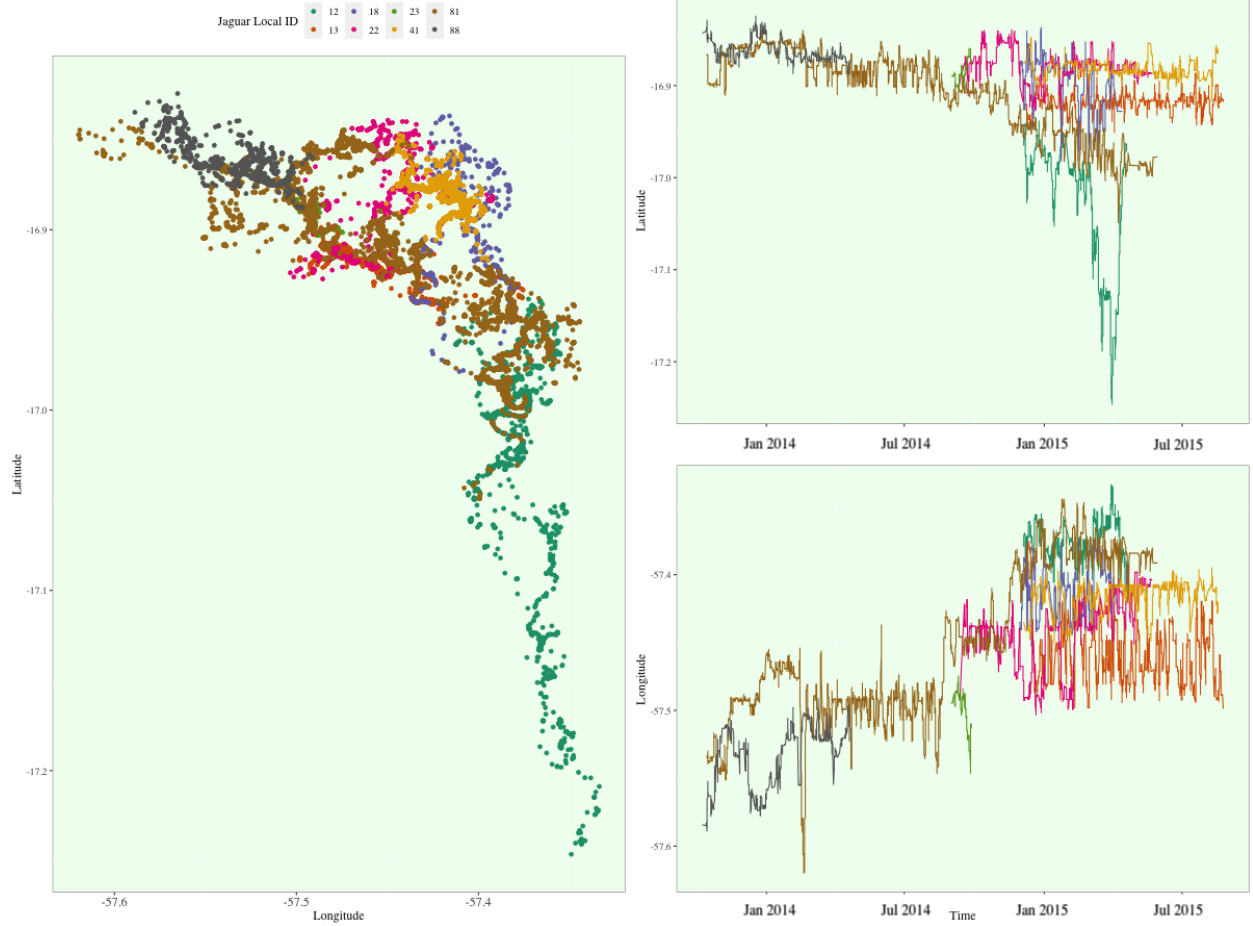


Figure 1: Visualization of Jaguar Movement in the Taiaimã Ecological Station. (Right) The spatial distribution of GPS recordings is plotted and colored by Jaguar ID. (Left) The temporal change in each Jaguar’s latitudinal and longitudinal position (28; 29). A terrain map of this region is provided in Figure8

Figure 2: Smoothing Spline Model for Jaguar 12 (female, age=4). (Left) The raw latitude-by-longitude position and spline model estimations are overlaid. (Right) The raw and smoothed components (latitude and longitude) are plotted with respect to time in days where $t = 0$ identifies the beginning of the study period in this region.

spline models for the remaining seven jaguars. Not every path is a perfectly refined, but Jaguars 13, 18, 22, and 81 have exceptionally well fit models. The remaining jaguars have some points that the spline models did not fit as well under the general temporal density distribution procedure for knot placement documented in the methods section. There are some cases where it appears that the spline model “overshot” the path when an animal changed direction suddenly, or where there were a couple outlier points that the algorithm did not prioritize fitting. We will use these models as is, since the deviations from the raw movement path are still limited, and most of movement profiles from these jaguars are well captured. All smoothing spline models have been smoothed to estimate behavior on a 1 hour resolution.

In Figures 4 and 5, I present the first derivative functions of the each jaguar’s movement, as well as, the density of rest periods. Rest periods are defined (with some level of arbitration that is worthy of discussion) as times when the estimated speed of a given jaguar is less than 0.25 meters per second. Any times where this condition is satisfied are depicted as below the orange line. My working definition of a jaguar rest period is inherently a binary classification of movement, and the times that satisfy this condition are subsetting to derive rest-period densities. I emphasize the substantial shift in the rest-period density structure of Jaguar 12. Jaguar 12 in the first half of her tracked time domain has higher rest period density, meaning that she is estimated to have more rest periods or periods of slower movement. In the latter half, her rest period density drastically drops to below a third of previous levels. No other jaguars show this trends as drastically; Jaguar 81 has a drop in rest period density during the a migratory period prior to entering the

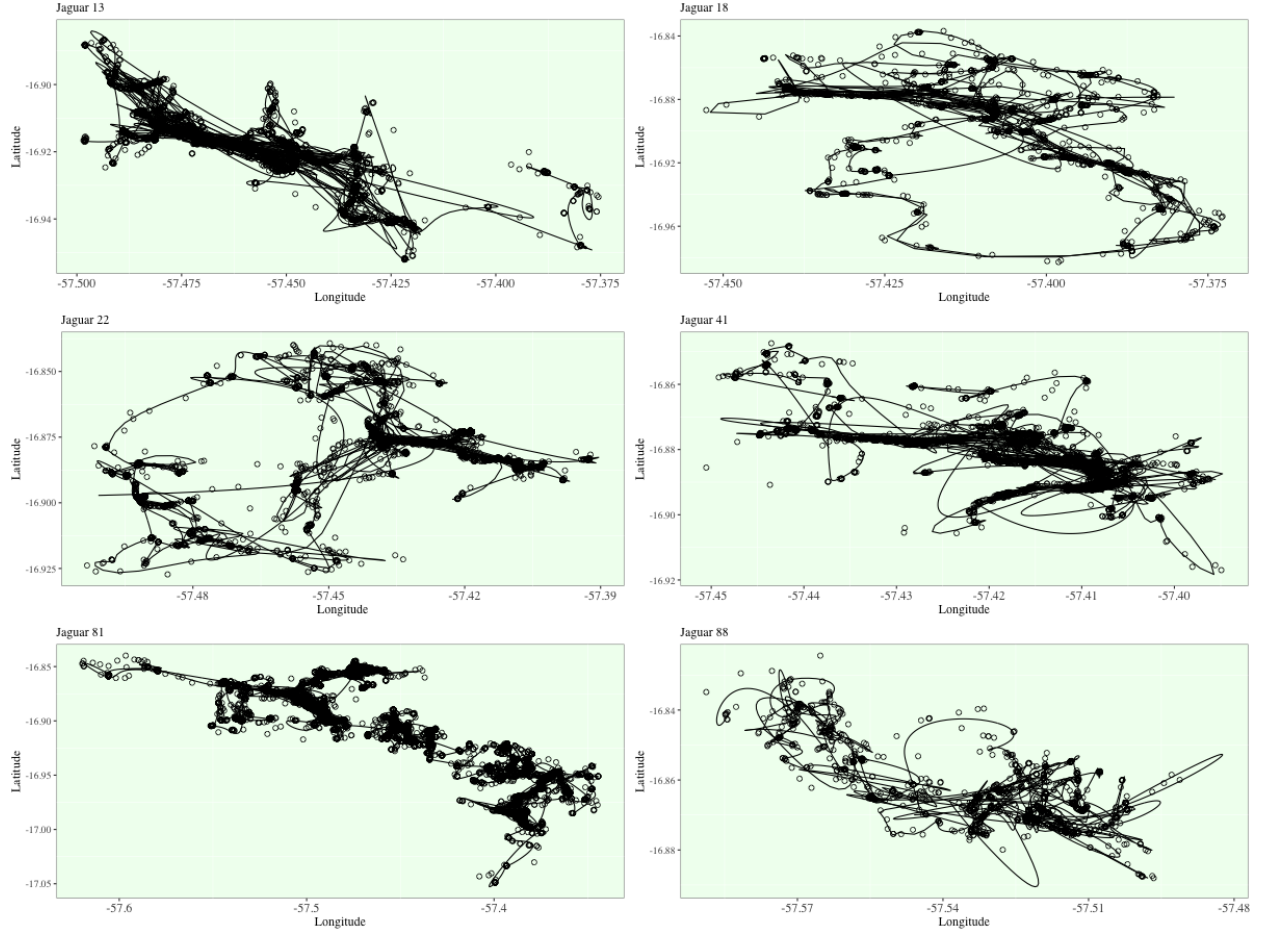


Figure 3: Smoothing Spline Model for Jaguars 13,18,22,41,81, and 88. For brevity, the decomposition of the spline models to latitude and longitude is not shown.

initial territory of Jaguar 12. In all of the remaining density plots, however, there is an apparent cyclic nature to rest period density that is approximately weekly to bi-weekly for most jaguars.

In Figure 6, I present the pair-wise distance relationships between several jaguar pairs, and their respective cooccurrence potential measures (30). The four selected pairs, are chosen deliberately as many jaguars had zero or near zero cooccurrence potential. The male-female pairs are Jaguar 12 and 81 and Jaguar 18 and 41, and the male-male pairs are Jaguar 18 and 81 and Jaguar 13 and 81. The cooccurrence potential was defined to have a threshold of 1800m, meaning that times where a pair of jaguars are estimated to be within this threshold have a high probability of (either passive or direct) cooccurrence. This choice of threshold is chosen with the intent to only capture time periods where a high probability of interaction is possible.

In the distance function plots, which are all identically scaled on the vertical axis, we note the significant differences in distance functions across all chosen pairs. For Jaguar 12 and 81, there is a first encounter with the highest cooccurrence potential, and then there is an extended period of zero cooccurrence potential. Following this hiatus, there is an extended period of regularly occurring bursts of high cooccurrence potential, which is then followed by the long migration of Jaguar 12 away from Jaguar 18. At the end of their shared time domain Jaguar 12 returns and there is a short period of moderate cooccurrence potential that is evidence of some final return to territory sharing before we lose sight of their movement.

The other male-female pair (Jaguars 18 and 41) on the other hand, has regular intervals of high cooccurrence, but we note that in a similar seasonal time window (at approximately time=72000 minutes) Jaguar 41 distances herself from Jaguar 18, but at a much lower magnitude than Jaguar 12.

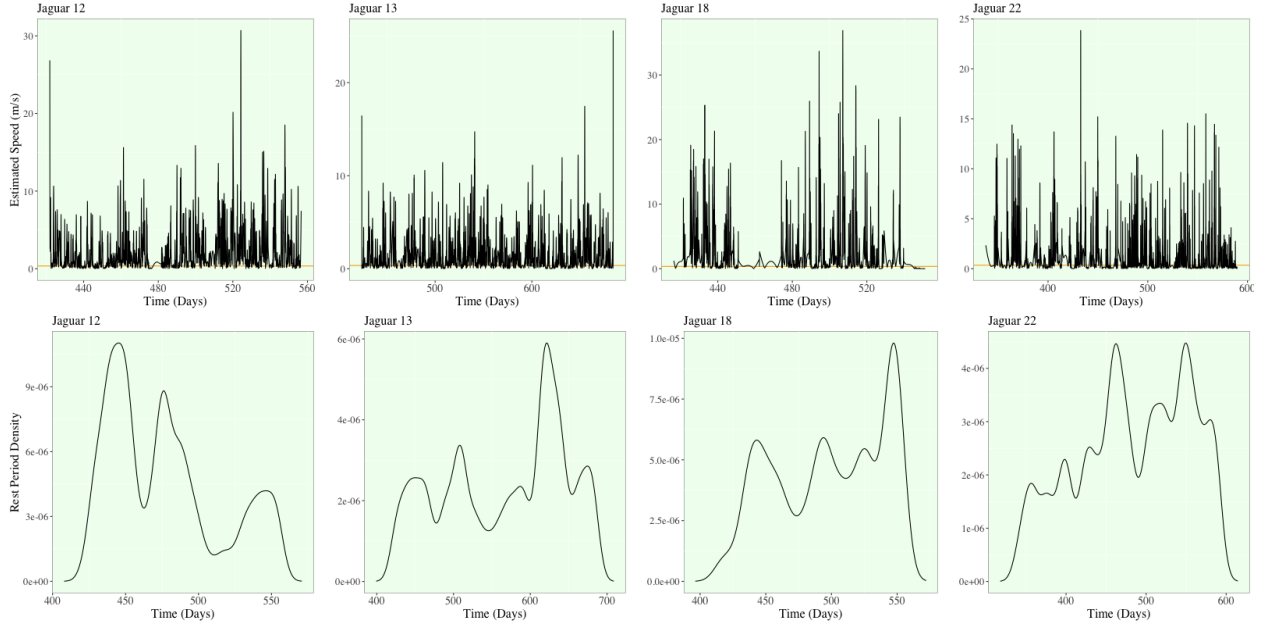


Figure 4: Spline model estimation of speed and rest period density for Jaguars 12,13,18,22. (Upper) A horizontal orange line is plotted at a speed of 0.25 m/s. (Lower) All hours in the spline model that are estimated to have speeds lower than this line are subsetting as a new vector to compute the density of rest periods. The selected bandwidth for estimation varies by jaguar and they range from approximately 4 to 12 days. As a result, a detected shift in the density of rest periods over time would indicate a shift to lower or higher density of rest periods occurring in a 4 to 12 day window.

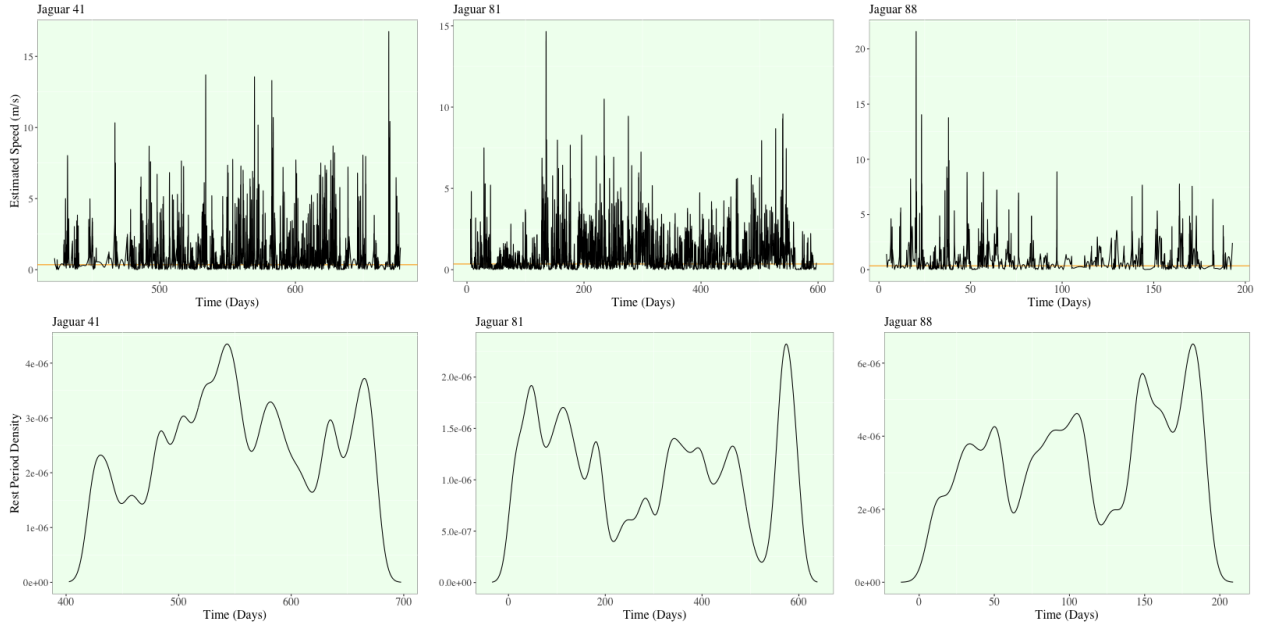


Figure 5: Spline model estimation of speed and rest period density for Jaguars 41,81,88. Refer to the caption of 4 for the interpretation.

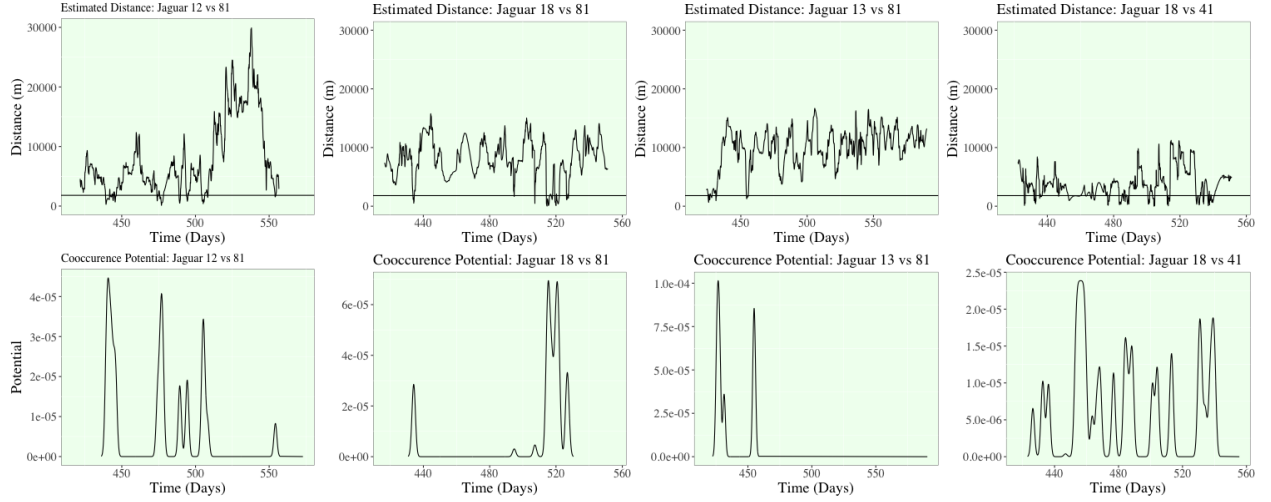


Figure 6: (Upper) Distance plots for Jaguars 12-81, 18-81, 13-81, and 18-41. Distance is derived from pairs of smoothed spline models. A horizontal line at Distance=1800m is placed to mark the defined threshold of cooccurrence. (Lower) All times that distance between a pairs of jaguars are subsetting to derive the density of times where jaguars fall within this threshold. The spacing and duration of close proximity is accentuated and this measure of cooccurrence provides easy access to measures of duration and frequency of cooccurrence or gaps in cooccurrence.

For the male-male pairs, Jaguar 13 and 81 only have high cooccurrence for a small time-window while Jaguar 81 is still migrating to new territory. Jaguar 18 and Jaguar 81's relationship is particularly interesting as there is an early period of high cooccurrence, and then, during the period of high cooccurrence between Jaguar 12 and 81, there is a hiatus in their cooccurrence. High cooccurrence between these two males is then resumed once Jaguar 12 leaves the territory and they move within short distances of each other for an extended period which ends before the return of Jaguar 12.

I present the localized mutual information profiles for the same four pairs jaguars in Figure 7 using a bandwidth of $\lambda = 48$ hours. This bandwidth identifies that the measure of localized mutual information is computed for a 4 day period centered on a given time. For Jaguar 12 and 81, there is a cyclical spike in the strength of association (i.e. local mutual information) immediately prior to and during most of the periods of high cooccurrence potential. The times of strongest association in movement occur during the second and longest period of high cooccurrence from approximately Day 475 to Day 510, and when Jaguar 12 returns at the end of the study period. On the other hand, Jaguars 18 and 41, although regularly experiencing period of high cooccurrence, do not show a similar associative trends. Their movement has the strongest association early in the study period and then it gradually declines in the following weeks.

For the male-male pairs of jaguars, there are repeated periods of high mutual association that do not show clear trends with cooccurrence potential. For Jaguar 13 and 18, there is a drop in the strength of association in their movement in the final weeks of the study and this is when these two jaguars are consistently the furthest apart.

Interestingly, Jaguar 18 and 81 have the strongest association in their movement at almost an identical time (Day 475) to the peak in association between Jaguar 12 and 81. These two associations are characterized by a distancing (decreasing cooccurrence potential) between the male pairs of jaguars, and increasing cooccurrence potential between the female-male pair. Following Day 475, Jaguar 18 and 81 have a steep decline in the association implying that their movements show minimal evidence of being coordinated. The comparison of localized mutual information plots for Jaguar's 12, 18, and 81, provides a clear characterization of interaction a local male-male-female triad of jaguars.

4 Discussion:

The apparent complexity of jaguar movement and interaction in the Taiamã Ecological Station is driven by the high density of jaguars (15; 16). Monitoring the complex fine-scale movement of multiple animal with shifts in territorial and social nature differs from previous examinations of animal movement using smoothing spline models (1; 12; 13; 14). This work provides a preliminary strategies for monitoring movement, behavior, social interactions, and the strength of association between animal movement, all of which are best explored on a refined and unified time grid smoothed using spline models.

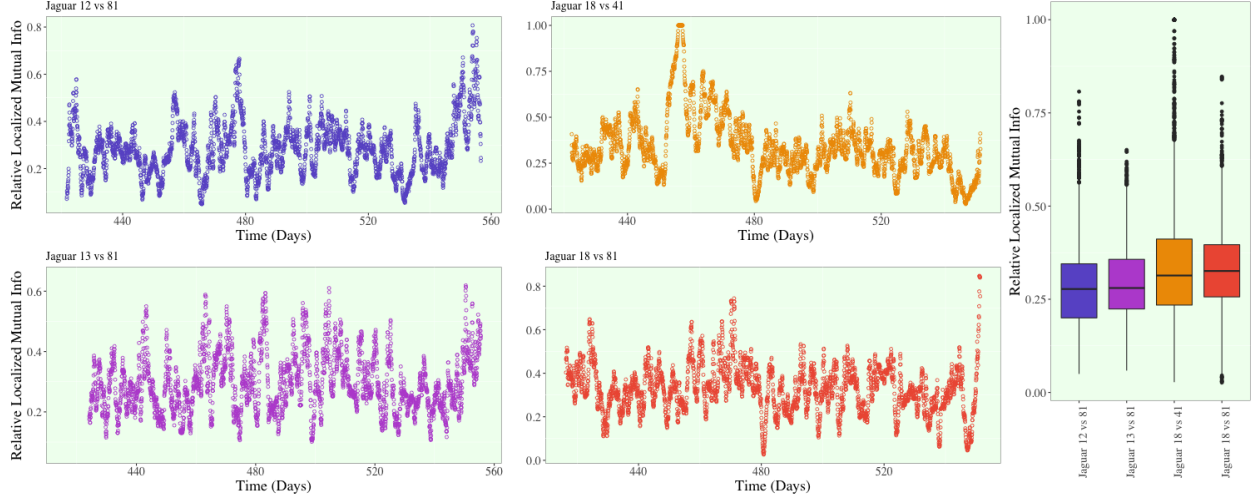


Figure 7: Localized mutual information plots. (Left) The localized mutual information with a bandwidth of $\lambda = 48$ hours for each time point in the refined time grid is plotted by each pair of Jaguars. The y-axis is scaled by the maximum localized mutual information at each time point and as a result the range of the y-axis is from 0.00 to 1.00. As a result, the scaled localized mutual information can be handle similarly to a measure of correlation, where 0.00 denotes no correlation between the movements and 1.00 defines a perfect unity in movement. (Right) The overall spread of localized mutual information measures across the time grid is summarized using boxplots.

Jaguar social interaction, although primarily characterized by direct (or close-proximity) interactions, is not the only form of social interaction that exists and should be detectable. Like many apex predators, territorial marking, is a common form of passive communication. Jaguars may deliberately avoid or follow these routes which should be characterized by higher associations between animals. Young male have a tendency to be nomadic and older jaguars tend to have established territory with minimal overlap (where overlap is typically shared with females in the region). Female jaguars behavior is also generally characterized by a temporary associations with a male, and then they avoid male interactions when caring for cubs(17; 32; 33; 34; 35).

All of these characteristics of jaguar movement and interaction are detectable in this analysis. Jaguar 12 (female; age = 4) and Jaguar 81 are detected to have strong but temporary associations which *increase in frequency* as time progresses, and then there is a rapid distancing between the pair and the association in their movement drops for over two months. The ability to detect an increase in frequency in high cooccurrence is visually inconclusive without the use of cooccurrence potential plots. Finally, their association and cooccurrence potential increase at the end of the study as she returns to her baseline territory at the beginning of the study. Jaguar 12's resting behavior also shows distinct shifts from the period of high cooccurrence potential with Jaguar 81 to the farthest point in her migration south. It is suspect that Jaguar 12's sudden drop in rest period densities suggests a shift between mating and cub rearing movement behaviors where she is depended on to make successful hunts to provide for her young.

The nomadic behavior of Jaguar 81, which is recorded at a fine-scale for almost two years, provides particular insights regarding male-male relationships between established and nomadic male interactions. Jaguar 13 and 81 only seem to interact for a brief time in passing, and Jaguar 81 continues to move past Jaguar 13's territory. However, Jaguar 18 and 81 show evidence of coexisting in a similar region with distinct shifts in behavior. *Jaguar 18 and 81 have the strong associations in movement in the presence of a local female.* Jaguar 18 keeps at a farther distance from Jaguar 81 once high cooccurrence between Jaguar 12 and 81 begin, and Jaguar 18 is not shown to near Jaguar 81 until Jaguar 12 has initiated a prompt departure from the region.

Smooth spline modeling of jaguar movement, as demonstrated in this study, is not without some caveats that should demand further attention in future work. As mentioned earlier, smoothing of paths requires some sacrifice of the exactness of position, and some particular movements are more difficult to catch than others. For animal telemetry, spline models are subject to over- and under-fitting challenges which can be observed in 3. Some paths are clearly more variable than the smoothed model suggests, and depending on the density of time measurements in some region, the model may tend to overshoot or undershoot a sharp change in direction. As in recent developments in standard continuous time models, there are opportunities to improve the fit of the model by accounting for geographic features/barriers, social encounters, atmospheric conditions etc (36). Random walk schematics have shown great potential improving the modeling of animal movement, and these methods should be adapted to the FDA paradigm.

In this analysis, there is no accounting of measurement error, which is a significant element of most animal telemetry data. The data used in this provide did not publicly provide measurement error to pair with GPS point estimates of position. As mentioned previously, some recent work has provided possible methods for accounting for measurement error in spline models, and these should be adaptable to many applications in animal movement.

The use of information theory in animal telemetry is sparse, but this work demonstrates the value of adapting measures of entropy and mutual information to animal telemetry. The derived measure of localized mutual information, verifies that although the distance between jaguars has a tendency to yield higher associations in their movement, this is not uniformly true and there are strong associative movements between male-male and male female pairs that can occur far beyond the cooccurrence potential threshold that I have defined in this work.

In overview, the approach used in this work effectively handles the challenges of spatial and temporal density, modeling continuity and differentiability of spatial movement, and multivariate characterization of animal behavior. To elaborate on the latter, the spline models that I construct in this work retain information about animal position and rate of change of position while refining the movement uniformly with other animals which ultimately allows for a unique and visual-friendly characterization of shifts in interaction and social behavior.

I commend past work in the study and modeling of animal telemetry, social interaction monitoring, and I encourage further work in modeling of these complex processes and relationships.

5 Data Accessibility:

Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. (27)

The authors of the study own the data set and made it public and freely available at DOI: 10.1002/ecy.2379 and also at Dryad Digital Repository (<https://doi.org/10.5061/dryad.2dh0223>).

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7 Appendix

7.1 Figure A1: Terrain Map of the Taiaimã Ecological Station

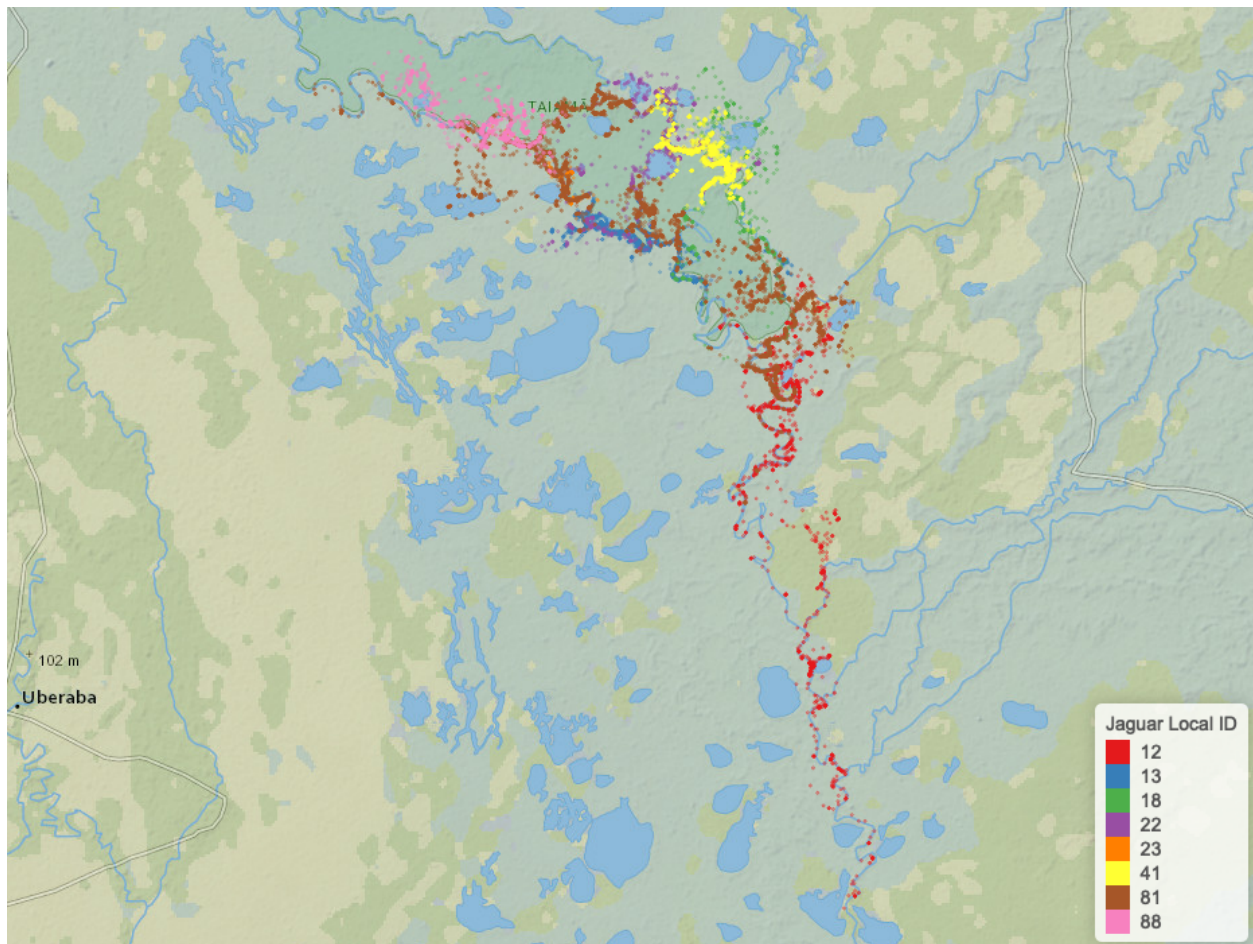


Figure 8: Terrain image base layer of jaguar spatial distribution in the Taiaimã Ecological Station. It is important to note the movement around waterways. A well fit smoothed spline model should generally avoid fitting paths directly through natural barriers that restrict jaguar movement in areas with a generous density of measurements in an area, but future work should be done to ensure that a fitted spline model avoids drawing an unrealistic path in areas that have sparse data.