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

A PREPRINT

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ABSTRACT

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

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

13 **1 Introduction**

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

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

*Use footnote for providing further information about author (webpage, alternative address)—*not* for acknowledging funding agencies.

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

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

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

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

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

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

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

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

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

69 2 Methods

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

76 2.1 Fitting Smoothed Spline Models to Jaguar Movement

77 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
 78 $Y_{lon} = [\vec{y}_{lon\ 1} \dots \vec{y}_{lon\ n}]$, 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
 79 roughness penalty on the second derivative of the basis expansion $\Phi = [\phi_1(t) \dots \phi_K(t)]$ where c_k are the coefficients
 80 of the terms of the basis expansion denoted by ϕ_k , which in this project is constructed using a B-spline basis
 81 expansion (9; 20). Both latitude and longitudinal movement can be individually expressed as an unconstrained
 82 minimization defined by

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

83 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).

84 We select an appropriate value for λ coordinates using the optimal lambda for a single site determined by the generalized
 85 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
 86 roughness penalization, since the precision of movement is of high priority. The roughness of the movement can also be
 87 restricted by latitude and longitude separately which may be of interest if we seek to model movement with substantial
 88 differences in between latitudinal and longitudinal behavior (such as long distance ungulate or bird migration), but for
 89 this work the roughness is penalized equally for both dimensions. The resulting smoothed jaguar movement curves
 90 have the form

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

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

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

92 In order to meaningfully estimate jaguar position across highly disparate densities of raw time recordings, careful
 93 placement of knots is advised. Let (t_1, \dots, t_n) be independently and identically distributed time samples from an
 94 unknown distribution f_h . We estimate the density of sampled times for a given jaguar using kernel density estimation
 95 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
 96 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
 97 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 $\tau_1 < \dots < \tau_m$.
 98 This selection of knots is carefully placed to avoid over fitting regions of the time domains that are barren or extremely
 99 sparse. This is desirable for periods where GPS tracking devices are out-of-operation for an extended period, but it
 100 is still desirable to fit regions with dense recordings with high precision.

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

103 2.2 Differentiation of the Smoothed Position Functions and Derivation of Rest Period Density Functions

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

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

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

107 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
 108 animal movement are generally characterized by different speed of movement. As an example a resting state should be
 109 characterized by lower estimated speeds while migratory, foraging, and other transitory states are characterized by faster
 110 speeds. For this project, I used a speed of 0.25 meters/second as a cutoff between resting and transit states. Clearly, a
 111 literal resting state should have a derivative value of zero, so in this application resting state has a looser interpretation
 112 that characterized by stationary and exceptionally small changes in position. Similar to before, I subset "resting state"

113 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
 114 is gaussian kernel function and h is a smoothing bandwidth parameter where t_1, \dots, t_n are restricted from to the set
 115 $\{t_i | \hat{x}'(t) < 1\}$.

116 2.3 Pairwise Jaguars Distance Functions and Derivation of Cooccurrence Potential Plots

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

127 , and the approach used in this project is similar

128 2.4 Mutual Information of Jaguar Movement

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

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

133 where $p_{(X,Y)}$ is the joint probability density function of X and Y , and p_X and p_Y are the respective marginal
 134 density functions. It is clear that if X and Y are independent then information gained from observing one of the
 135 random variables does not provide information about the other, and recall that for independent random variables,
 136 $p_{(X,Y)}(x, y) = p_X(x)p_Y(y)$, which implies from Equation (4) that $I(X; Y) = 0$ (23).

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

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

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

143 Ultimately, the advantage of this approach is to construct a bivariate measure of mutual information, and finally to
 144 generate of mutual information function with respect to time. For two bivariate random vectors $X = (X_{lat}, X_{lon})$ and
 145 $Y = (Y_{lat}, Y_{lon})$, I define joint local mutual information by

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

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

151 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
 152 application the values of t are limited to the defined resolution of the spline model.

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

157 2.5 Data: Taiama Ecological Station Jaguar Movement Data

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

165 The selection of jaguars examined in this project on the condition that they shared an overlapping monitoring period
 166 with at least one jaguar from the monitoring period with the highest activity monitoring period from December 2014 to
 167 the summer of 2015. The final and more detailed investigation of social interactions is performed for Jaguars 12, 13, 18,
 168 41, and 81.

169 For all visualization used in this work, I numerically transform to time in days from the earliest available date 10/9/13
 170 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
 171 the final measurement on Jaguar 13 is recorded, 08/24/15. This is particularly useful for monitoring periodicity and
 172 duration of events, since it is difficult to quickly understand the number of days or weeks between two dates.

173 3 Results

174 The primary challenge in mapping and analyzing relationships between Jaguars at the Taiama Ecological Station is
 175 the staggered time windows that each Jaguar is monitored coupled with the inconsistent temporal resolution of GPS
 176 readings. To reach our final selection of 7 jaguars, we removed two jaguars with less the 100 GPS recordings and two
 177 jaguars (Jaguar 91 and 92) that were monitored many months after the remaining jaguars (Jaguar 116 and 117). There
 178 are 3 females (Jaguars 12, 41, and 88) and 4 males (Jaguars 13, 18, 22, 81). I visualize the remaining 7 jaguars in
 179 Figure 1. Across the three plots provided, we can develop a short narrative of a few major movement characteristics.
 180 Within their respective time domains, most of the 7 jaguars have consistent stable fluctuations in position within their
 181 territories (with some clear overlap in territories). However, Jaguar 81 (male, age=4yrs) with the longest monitoring
 182 window, makes a significant territorial transition from residing in the same region as Jaguar 88 (female, age=5yrs) to
 183 the territory of Jaguar 12 (female, age=4yrs). There appears to be a period of interaction between Jaguar 12 and Jaguar
 184 81, and then Jaguar 12 makes a temporary but significant migration south for approximately 3 months before returning
 185 to the same region again as Jaguar 81. There are other male-female interactions that not as easily discernible, and more
 186 investigation is clearly required.

187 In Figure 2, I present a detailed visualization of the smoothing of Jaguar 12's residential to migratory transition. As a
 188 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
 189 line. This is an acknowledged sacrifice of information, in exchange for a number of benefits, primarily the refinement
 190 of the time resolution and consistency to a uniform time grid shared by all jaguars. In Figure 3, I present the smoothed

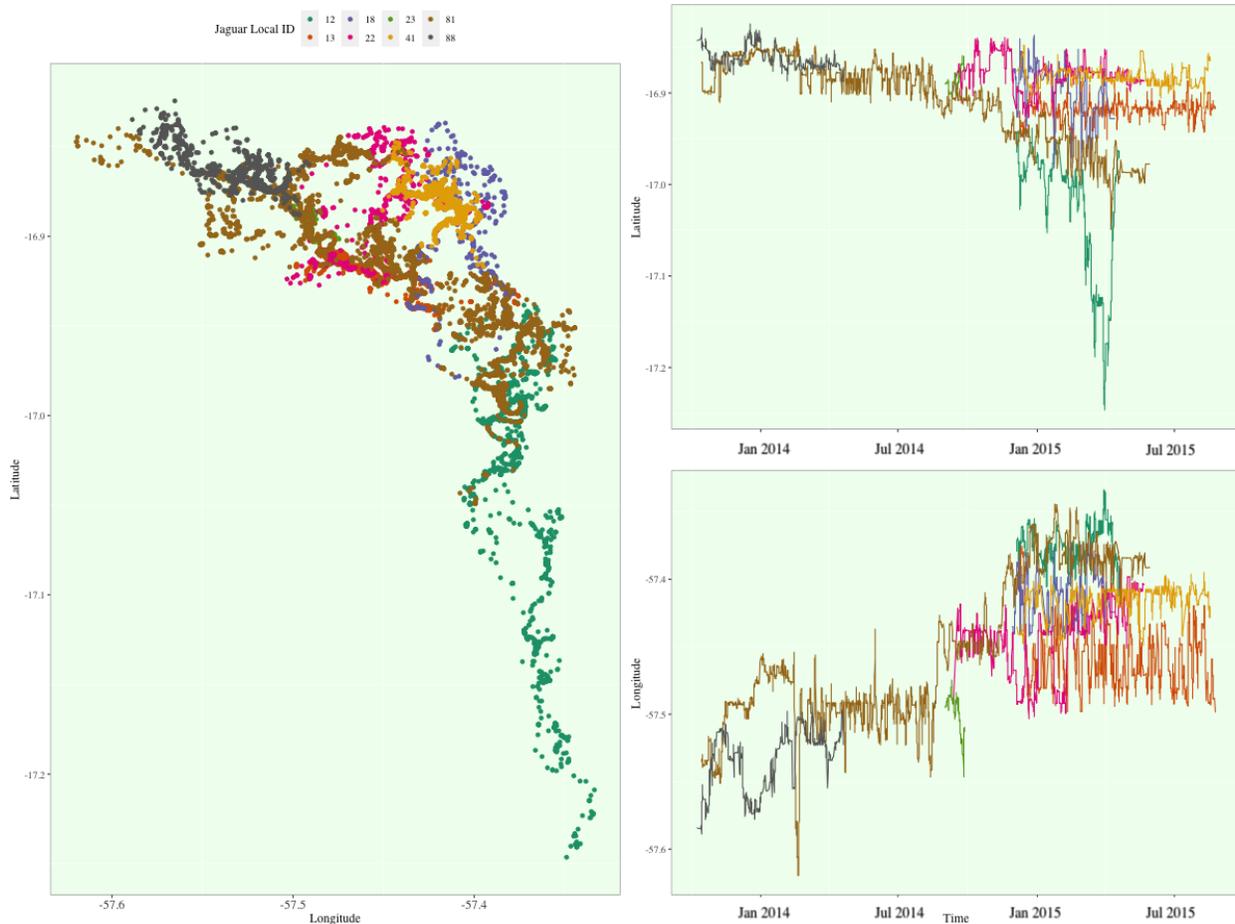


Figure 1: Visualization of Jaguar Movement in the Taiamã Ecological Station. (Right) The spatial distribution of GPS recordings is plotted and colored by Jaguar ID. (Left) The temporal change in each Jaguar’s latitudinal and longitudinal position (28; 29). A terrain map of this region is provided in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

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

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

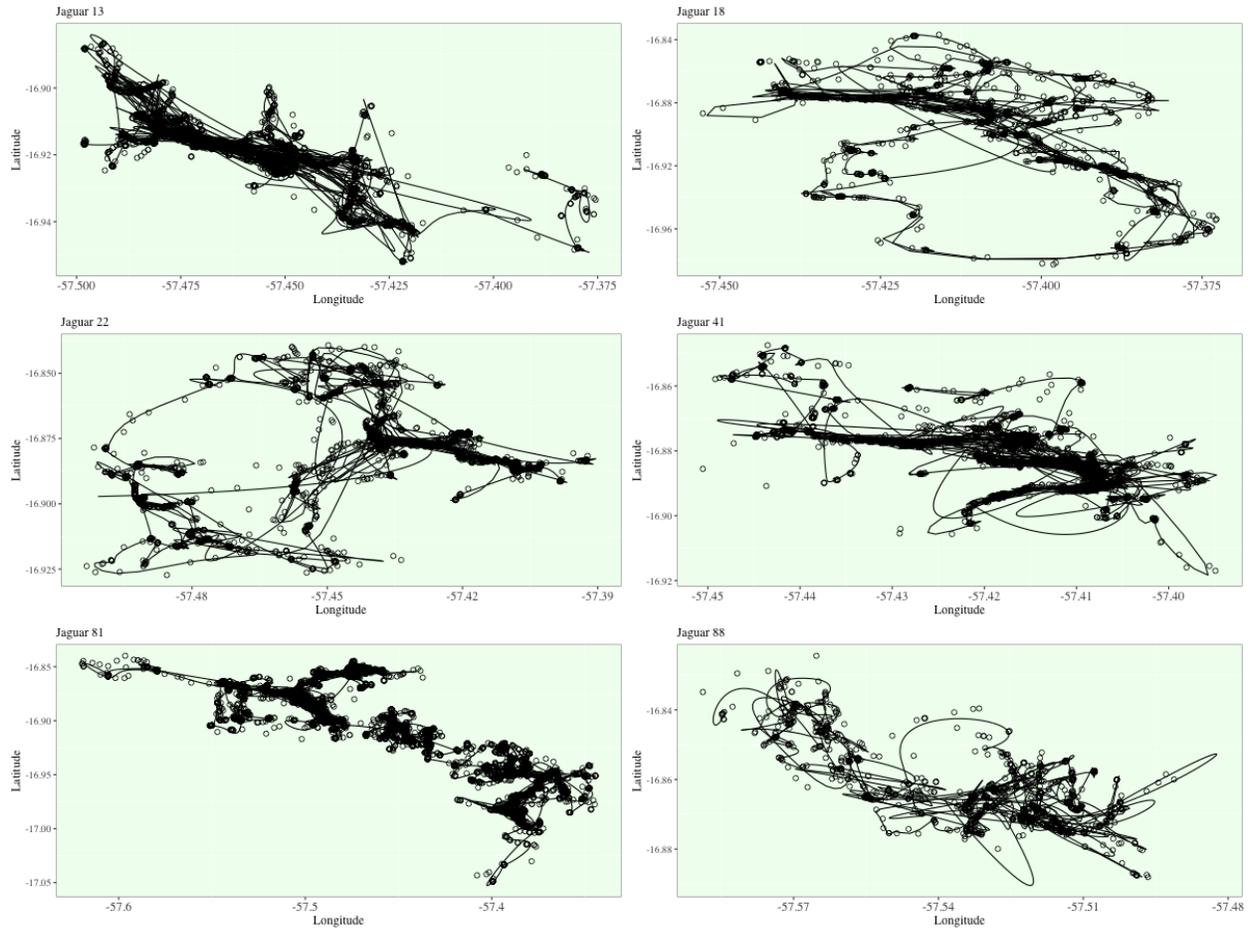


Figure 3: Smoothing Spline Model for Jaguars 13,18,22,41,81, and 88. For brevity, the decomposition of the spline models to latitude and longitude is not shown.

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

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

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

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

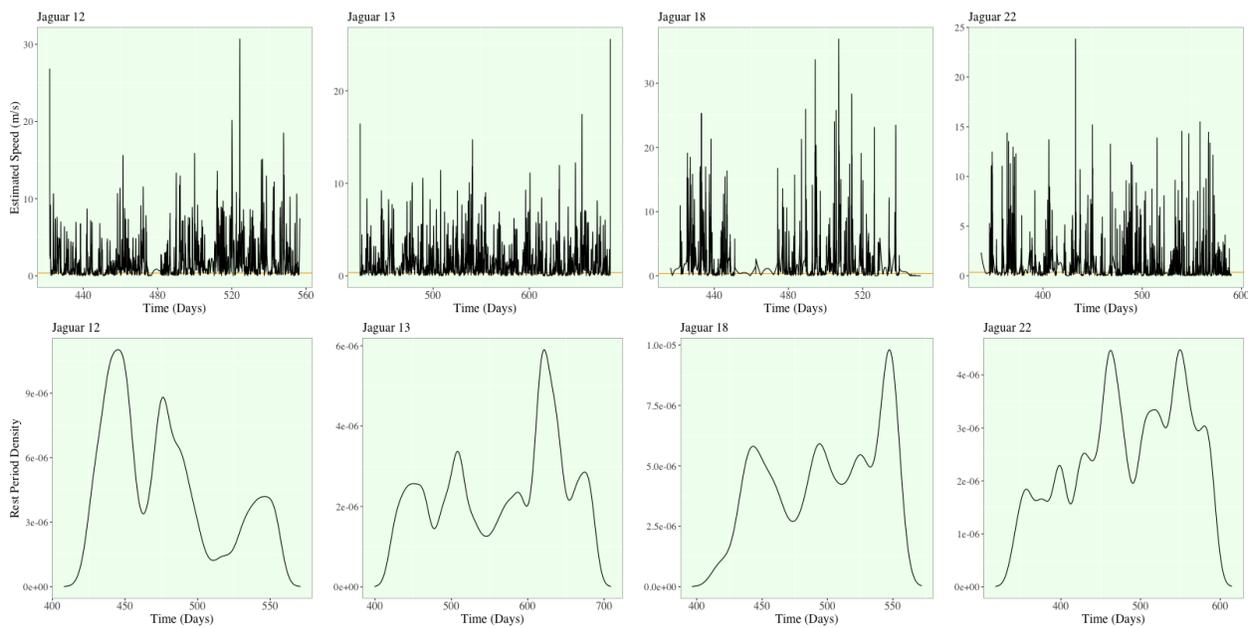


Figure 4: Spline model estimation of speed and rest period density for Jaguars 12,13,18,22. (Upper) A horizontal orange line is plotted at a speed of 0.25 m/s. (Lower) All hours in the spline model that are estimated to have speeds lower than this line are subsetting as a new vector to compute the density 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.

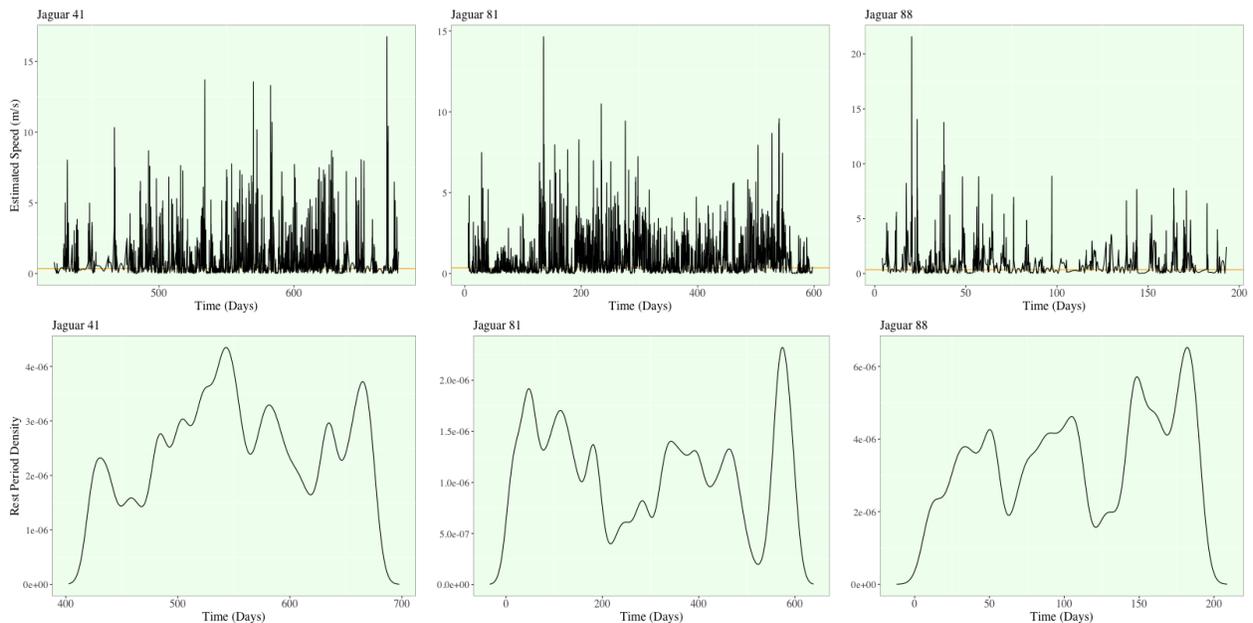


Figure 5: Spline model estimation of speed and rest period density for Jaguars 41,81,88. Refer to the caption of 4 for the interpretation.

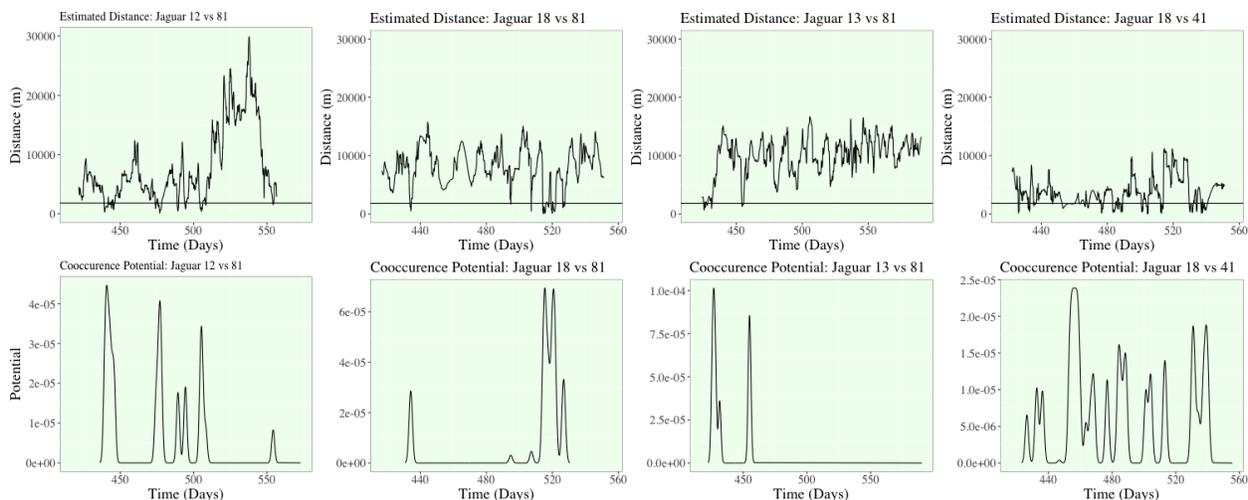


Figure 6: (Upper) Distance plots for Jaguars 12-81, 18-81, 13-81, and 18-41. Distance is derived from pairs of smoothed spline models. A horizontal line at Distance=1800m is placed to mark the defined threshold of cooccurrence. (Lower) All times that distance between a pairs of jaguars are subsetted 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.

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

231 I present the localized mutual information profiles for the same four pairs jaguars in Figure 7 using a bandwidth of
 232 $\lambda = 48$ hours. This bandwidth identifies that the measure of localized mutual information is computed for a 4 day
 233 period centered on a given time. For Jaguar 12 and 81, there is a cyclical spike in the strength of association (i.e. local
 234 mutual information) immediately prior to and during most of the periods of high cooccurrence potential. The times of
 235 strongest association in movement occur during the second and longest period of high cooccurrence from approximately
 236 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,
 237 although regularly experiencing period of high cooccurrence, do not show a similar associative trends. Their movement
 238 has the strongest association early in the study period and then it gradually decline in the following weeks.

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

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

248 4 Discussion:

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

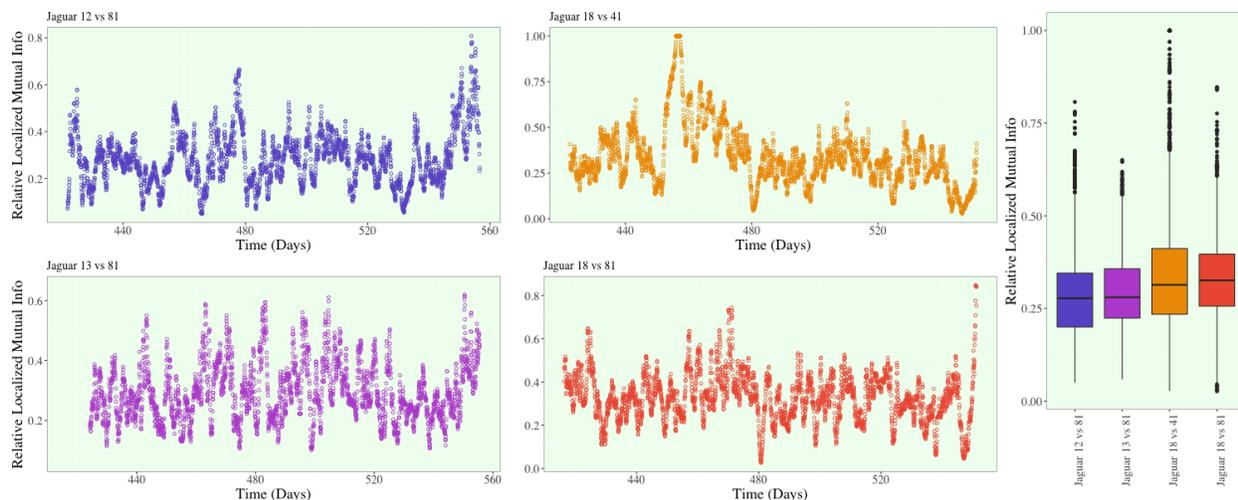


Figure 7: Localized mutual information plots. (Left) The localized mutual information with a bandwidth of $\lambda = 48$ hours for each time point in the refined time grid is plotted by each pair of Jaguars. The y-axis is scaled by the maximum localized mutual information at each time point and as a 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.

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

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

271 The nomadic behavior of Jaguar 81, which is recorded at a fine-scale for almost two years, provides particular insights
 272 regarding male-male relationships between established and nomadic male interactions. Jaguar 13 and 81 only seem to
 273 interact for a brief time in passing, and Jaguar 81 continues to move past Jaguar 13's territory. However, Jaguar 18 and
 274 81 show evidence of coexisting in a similar region with distinct shifts in behavior. *Jaguar 18 and 81 have the strong*
 275 *associations in movement in the presence of a local female*. Jaguar 18 keeps at a farther distance from Jaguar 81 once
 276 high cooccurrence between Jaguar 12 and 81 begin, and Jaguar 18 is not shown to near Jaguar 81 until Jaguar 12 has
 277 initiated a prompt departure from the region.

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

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

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

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

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

303 **5 Data Accessibility:**

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

305 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
306 Dryad Digital Repository (<https://doi.org/10.5061/dryad.2dh0223>).

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390 7 Appendix

391 7.1 Figure A1: Terrain Map of the Taiamã Ecological Station

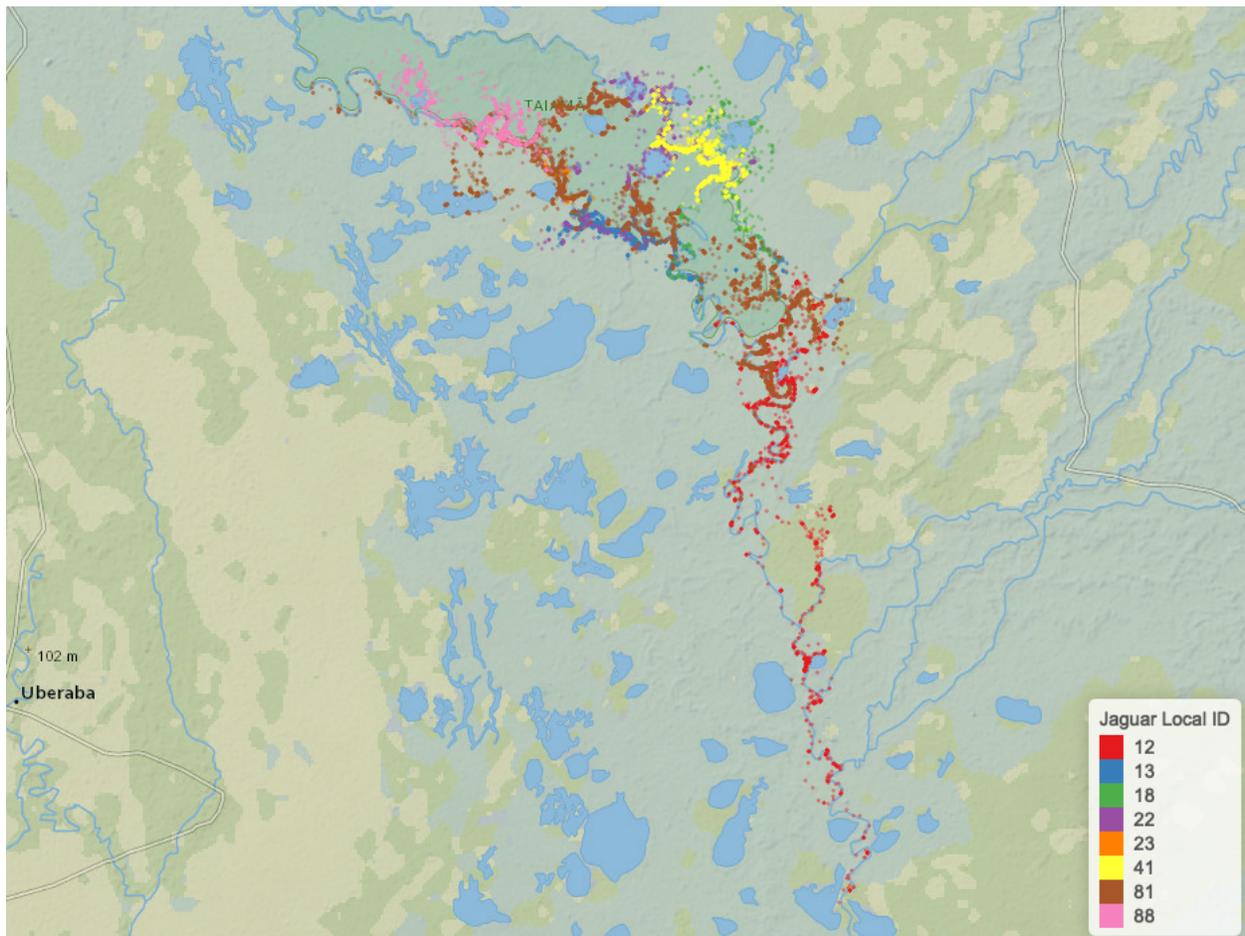


Figure 8: Terrain image base layer of jaguar spatial distribution in the Taiamã Ecological Station. It is important to note the movement around waterways. A well fit smoothed spline model should generally avoid fitting paths directly through natural barriers that restrict jaguar movement in areas with 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.