Putting Distance Back Into Area-Restricted Search: A New Method to Describe Behavior States from Tracking Data

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Abstract

As high-resolution biologging technology becomes more readily accessible, there is a growing demand for methods of animal movement analysis. Previous studies have focused on evaluating area-restricted search (ARS) behavior within tracking data through time-dependent metrics, which can give erroneously high values for non-ARS behaviors. Furthermore, there have not been general, objective methods for classifying animal behaviors from tracking data. This study aims to improve current methods for evaluating ARS by introducing a metric based on distance rather than time. In addition, we develop a method for differentiating between major behavior states (foraging, resting, and transit behaviors), and discuss its use at various scales.

Introduction

It is well established that resources in marine ecosystems are distributed in a patchy, hierarchical manner (Fauchald, 1999). An extensive field of research is dedicated to describing how marine predators move and behave within this dynamic marine system to meet their physiological and reproductive demands (McArthur and Pianka, 1966). A primary focus of these studies has been to describe the foraging ecology of animals, which requires the ability to actively differentiate behavior states form the geometry of animal tracking data. Over time, examinations of marine predator habitat associations have reduced in scale as both tracking technology has become more highly resolved. Furthermore, the miniaturization and accessibility of track technology has caused a recent increase in the amount of animal tracking data. Yet, an objective, effective, and rapid method of animal behavior classification based on animal tracking data is still lacking. In this study, we develop, test, and evaluate an animal movement analysis method that proves effective at differentiating between major behavior classes (foraging, rest, travel) at various scales.

Foraging behavior, at multiple scales, is typically discerned from tracking data using area-restricted search (ARS), which was initially described as where the predator spends more time in the vicinity of recent captures before continuing a search (Kareiva and O'dell, 1987). ARS is characterized by low speeds with frequent turning, and results in patterns at multiple scales as the predator turns from wider-range explorations to focused, smaller-range searches. The assumption that marine predator foraging is characterized by ARS allows for analysis of foraging behavior through tracking data, since information on search effort will be captured in the geometry of the track. There are several geometric methods for quantifying search effort as a function of ARS from tracking data, including First-Passage Time (FPT), residence time, grid methods, and fractal methods (Fauchald and Tverra, 2003; Barraquand and Benhamou, 2008; Milne, 1997).

FPT analysis determines the scale at which ARS occurs and assesses ARS activity along a trajectory. The FPT of a point on the track is defined as the amount of time it takes for an animal to pass through a circle centered around that point (Fauchald and Tverra, 2003). By comparison, while the residence time method does not provide an estimate of the scale for trajectory analysis, it similarly quantifies the spatial distribution of search time along a trajectory. First, a radius R is manually chosen. For each point on the trajectory, the residence time value is defined to be the time spent inside of a circle of radius R centered at the point, including temporally close re-entries into the circle (Barraquand and Benhamou, 2008). Therefore, residence time gives comparable values to those derived from FPT, but accounts for backtracking within the trajectory. Other methods divide the area of study into a grid, and calculate the time spent within each grid element. It is important to note that all of these methods are time-based calculations of movement data. Yet another alternative is to describe animal behavior by calculating a fractal dimension for the trajectory, but these methods have been criticized for assuming scalability of results (Turchin, 1996).

Despite these advances in calculating ARS, the ability to differentiate between behavior states with similar temporal patterns is limited. Behavior classification is a critical component to the analysis of movement data because the animals are not constantly engaged in various levels of ARS, but rather also exhibit travel and rest behaviors, as well as other non-ARS foraging methods, such as ambush tactics. Rest periods can be caused by physiological needs and diurnal cycles of activity, as well as extrinsic factors that impede energetically efficient movement, such as low wind speeds for a large seabird. Like ARS, rest and ambush behavior states incur increased time spent in concentrated areas, causing previous time-based analysis methods to incorrectly assign high values to track locations where ARS did not occur. Previous studies have attempted to account for these regions of falsely high values by manually removing non-ARS points using criteria of speed and path tortuosity, but this is time-consuming and may be somewhat subjective (Torres et al, 2013). Ideally, a metric of foraging effort should assign high values to regions characterized by the geometry of ARS activity, and low values elsewhere.

The time-dependence of FPT, residence time, and grid methods is problematic, as it introduces a temporal component to otherwise spatially determined behavioral patterns. In this paper, we develop (1) a robust metric for evaluating ARS which is based on distance rather than time, and therefore less likely to be influenced by alternate activities, and (2) a quantitative and objective method of differentiating between several behavioral states. After introducing these methods, we use them to analyze fine-scale GPS tracking data for a breeding seabird population, which allows for verification of their performance over a collection of tracks at different sampling rates. Additionally, we test the calculations at a variety of radii to determine the optimal scale of analysis, and state a general method for estimating this scale for a given track.

Specifically, we use fine-scale GPS tracking data of grey-headed albatrosses (*Diomedea chrysostoma*) breeding at Campbell Island, in the New Zealand sub-Antarctic region. The breeding season of grey-headed albatrosses lasts through the austral summer, from October to May. Adults lay eggs in late September to early October, and incubate these eggs until they hatch n mid-December (Moor and Moffat 1990). The chicks are reared for a period of about 150 days at Campbell Island, from December to May. A previous large-scale tracking study demonstrates that grey-headed albatrosses are oceanic (deep water) foragers (Waugh, 2000), and commute about 600-800 km southeast of Campbell Island to their foraging grounds. During the breeding season, albatrosses are central-place foragers, and are therefore limited in the distance and time they may spend at seas before returning to the nest to switch incubation shifts or feed a demanding chick. Tracking studies of grey-headed albatrosses from other colonies has shown strong diurnal activity patterns and no sex-specific differences in foraging patterns.

Materials and methods

During the austral summers (Oct. – Dec.) of 2011, 2012, and 2013, grey-headed albatrosses breeding at Campbell Island were tagged with igotU GPS archival tags, set to record a position and time approximately every ten minutes. There were 2 tracks collected in 2011, 23 tracks in 2012, and 29 tracks in 2013 (for a total of 54). Of these, 52 were usable for analysis. The stage of chick development (incubation or chick rearing) was also recorded, with a total of 31 incubation tracks and 21 chick-rearing tracks. Each bird is identified by a band ID, and most birds are sexed based on morphological measurements taken on tag deployment (Table 1).

We first computed residence values for all trajectory points with both the residence distance and time methods. To calculate residence distance, a circle of a given radius (*R*) is constructed around every point on a trajectory. The distance traveled between consecutive points within the circle is calculated (in km). If the circle was exited and re-entered with no more than the threshold distance value (*Th*) traveled outside, the new stretches of the track inside the circle are also included in the residence value of the point. This exiting and re-entry can occur multiple times, and the contribution of distance traveled will continue to be added to the total residence distance as long as the consecutive distance traveled outside of the circle is below the given threshold value.

Similarly, the residence time of every point along a trajectory was calculated by finding the time spent in a consecutive part of the track within a circle of given radius around that point (in minutes), following the methods of Barraquand and Benhamou (2008). Time segments spent within the circle after re-entries were added to the residence time as long as they were within the given threshold distance from a previous stretch of time within the circle.

Note that the definitions of both residence time and distance assign a value of zero to points that are more than a “radius” away from all other points. As a result, this definition is scale-dependent; the distribution of residence values will change with different choices of radii. Hence, we tested various radii values (1 km, 2.5 km, 5 km, 10 km, and 20 km) to determine the best scale of analysis for our track data, and derive a possible method for the objective determination of appropriate radius value for tracking data collected at different spatial and temporal scales.

We assessed the relationship of residence time and residence distance with respect to the time of day and wind magnitude, factors that are known to affect the flight behavior of albatrosses. Daytime was defined to be 4:30 am to 9 pm, local time.

Once both residence time and distance were calculated for all trajectories, we assessed regions of similarity and divergence between the two metrics. Both metrics were normalized by dividing the residence values by the maximum residence value for the individual bird. Then, we defined the residuals to be the difference of residence distance and residence time at each point, with the hypothesis that variation in residuals is representative of variation in behavior. Specifically, we hypothesized that positive residuals correspond to ARS behavior, negative residuals correspond to non-ARS behavior, and residuals equal to 0 correspond to transit. To visually assess this hypothesis, we color-coded randomly chosen tracks by the sign of the residuals. Then, we made a reduced ARS dataset containing the points defined to be ARS behavior by the residual method, and evaluated the response of this dataset to time of day and wind magnitude.

All data manipulation was done in R, with residence time and distance computed in C, called through R. The code for both metrics will be freely available for public use.

Results

The distribution of grey-headed albatross GPS tracks illustrates a concentration of foraging effort in a sub-Antarctic region between 165E and 170W degrees longitude, and 52S to 62S degrees latitude (Figure 1).

For each track, we calculated residence time and distance with a set radius of 2.5 km and a threshold distance of 1.25 km. The distribution of residence time is monotonously decreasing and very left-skewed, with a median of 18.2 minutes and a mean of 67 minutes. In contrast, the distribution of residence distance is bimodal, with a median of 3.21 km and a mean of 3.22 km (Figure 2).

Overall, residence time and distance demonstrated similar responses to track geometry (Figure 3). Residence time exhibited very high values at night, multiple times larger than its average daytime values. In contrast, residence distance resulted in flat “plateaus” at night, but these segments were close in magnitude to the mean residence distance values (Figure 4).

For a radius of 2.5 km, the average value of normalized residence time was 0.161, and the average value of normalized residence distance was 0.171. Hence, on average, the residuals were -0.01, and therefore close to zero. The residuals show a characteristic division between most daytime and nighttime values: they show smooth, negative dips at night and scattered, positive values during the day (Figure 5). Across all of the tracks, about 45% of points had positive residuals, 31% had residuals equal to zero, and 24% had negative residuals.

The residual analysis was run with varying values of circle radii, and the resulting racks, color-coded by residuals, were compared to determine the optimal scale of analysis (Figures 6-8).

Discussion

To date, most metrics for foraging activity have been based on time. Consequently, a fault of these metrics is an erroneously high response to time-consuming but non-ARS activity such as drift. The residence distance method developed in this paper is able to counter this fault. Figure 4 shows the residence values obtained from both residence time and distance over a single track. Overall, the two metrics agree, though residence time has much higher peaks for drift segments, while residence distances plateaus. Additionally, residence distance results in more evenly distributed values, instead of the very left-skewed residence time distribution, which may make it a more informational metric for statistical analysis (Figure 2).

Furthermore, apart from using residence distance as a metric for ARS activity, the residuals (the difference in normalized values of residence time and distance), are also ecologically interesting. Grey-headed albatrosses exhibit several visually recognizable behaviors through GPS tracking data, including: transit to, from, and throughout the foraging region in between foraging bouts; rest or drift segments, especially at night; ARS, especially during the day. When grouped by sign, the residuals shown in Figure 5 have a high visual correspondence with these different behaviors. Specifically, positive residuals indicate ARS, negative residuals indicate drift or non-ARS, and residuals with a value of zero indicate transit. In other words, the comparison of residence distance and residence time allows for objective classification of behavioral states. In contrast, previous studies have been unsuccessful in automatically classifying regions corresponding to different behaviors, and would isolate foraging points through manual extraction relying on somewhat subjective evaluations of speed, tortuosity, or other variables. Our method aims at creating a more objective alternative that incorporates those variables into one metric. In addition, this method provides information on transiting and drifting/non-ARS behaviors, which may be of interest in future analysis. The residual method is general, and can be applied to a variety of animal tracking data across different habitats and taxa.

As with many other foraging metrics, residence distance is scale-dependent; the analysis relies on the choice of a radius. For evaluating residence, this choice will depend on the scale of interest: radii on the order of hundreds of kilometers may reveal macro-scale patterns in behavior, while radii on the scale of tens of kilometers may show meso-scale interactions between birds and the environment. Finally, radii of kilometers or below are relevant for fine-scale analysis. Unlike First-Passage Time, the residence time metric does not provide a method for choosing a scale of analysis. For this project, we experimented with multiple scales to understand the change in both residence values and behavior classification by residuals (Figures 6-8). We found that the change in the scale of analysis was very visible through the distribution of transit points: small radii resulted in a large number of transit points, while choices of larges radii classified these points into either ARS or drift. This is reasonable, as "transit" points are determined by points with residuals equal to zero, which usually result at locations where both residence time and residence distance are zero. This occurs when only the central point falls inside of the set circle. In other words, if the radius is less than the shortest distance between a track point and all of its neighbors, that point will be classified as a "transit" point. Therefore, to choose a scale which most accurately separates the ARS, transit, and non-ARS behaviors, we can focus on accurate classification of transit points, as these draw the dividing line between ARS and non-ARS behavior. Assuming a constant temporal sampling rate within a track, the average distance between transit points should be approximately equal to the average flight speed in transit multiplied by the sampling rate. Therefore, our radius of choice should be approximately half of this value. Further research is needed to validate this choice of scale through analysis of tracking data from other species with a variety of transit speeds and sampling rates.

The residual method provides information on behavior states across the time of day. It is known that GHAL are diurnal foragers, and they are not believed to exhibit ARS at night. This is supported by the residual method, which contrasts scattered daytime ARS with very consistent nocturnal drifting behavior. There have been multiple studies examining the daytime and nighttime behaviors of seabirds, and investigating the large amount of time spent on the water at night. For instance, a study of GPS tracking data of four albatross species at the South Georgia Island proposed a series of hypotheses for this phenomenon: the birds may be taking time for rest or digestion; the conditions may be less suitable for flight due to weaker winds; it may be difficult to navigate in the dark; it may be difficult to find prey in the dark; the birds may be preying on bioluminescent organisms which undergo vertical migration at night (Phalan et al, 2007).

This introduces several interesting points. First, foraging behavior may be influenced by wind magnitude, which may be a factor in determining diurnal drift segments. Additionally, drift segments may be related to foraging behaviors other than ARS, such as the "sit-and-wait" behaviors (Phalan et al, 2007). Albatrosses feed primarily on cephalopods. During the day, these prey species are several meters underneath the surface. However, multiple species are believed to migrate to the surface at night, when there is less of a threat from visually-cued predators (Croxall and Prince, 1994). As a result, albatrosses may partake in foraging behaviors that are not evaluated through metrics such as residence time or distance, and which are very difficult to distinguish by use of only GPS tracking data. Therefore, it is important to note that residence distance and the residual method provide information on foraging through area-restricted search, but may not be informative with regards to other strategies for prey consumption.

Further studies may use other datasets with different taxa and scales to compare the responses of residence time and distance to statistical modeling, and evaluate the efficiency of the residual method in reducing the dataset to points marked as foraging. In addition, it would be interesting to determine environmental parameters that may impose limitations on foraging behavior – such as wind magnitude or visibility -- and identify variables responsible for daytime drift segments.

Acknowledgements

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Figures

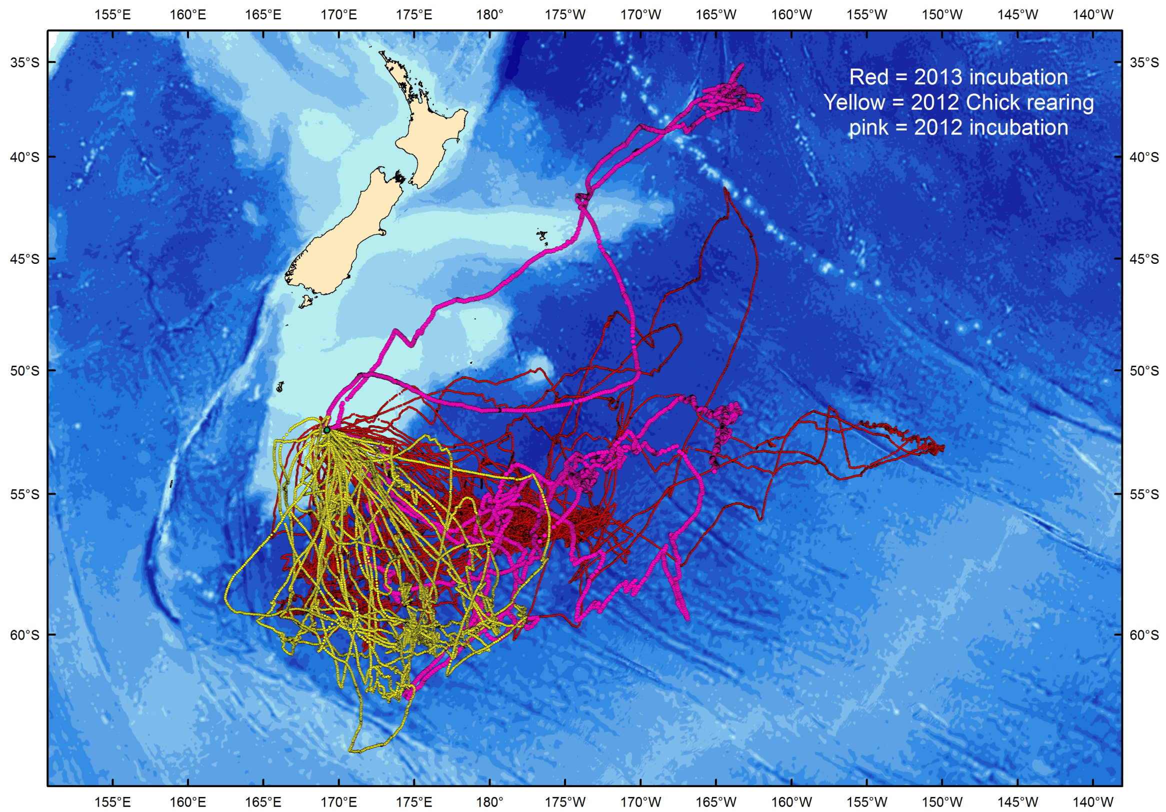

Figure 1: Spatial distribution of tracks collected in 2012 and 2013, colored by year and stage of chick development.

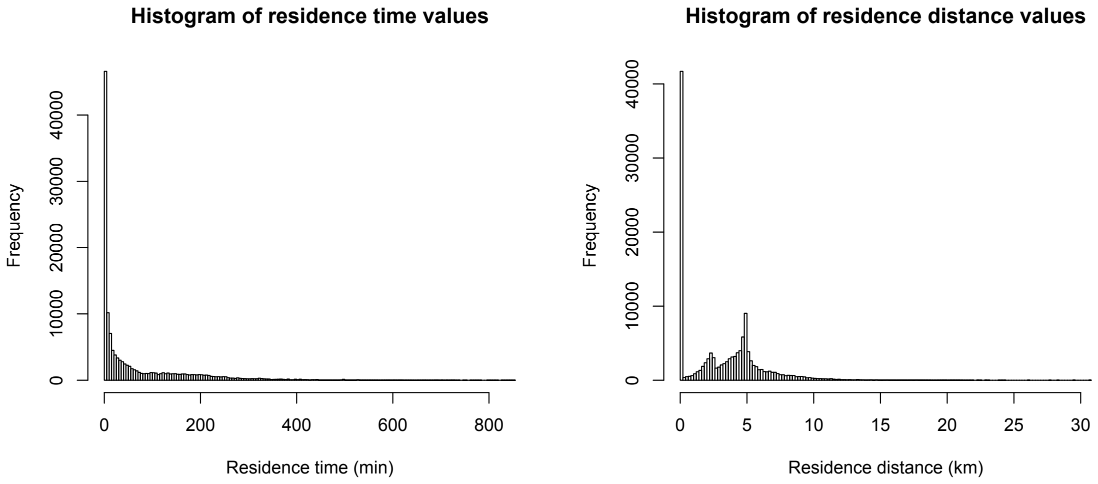

Figure 2: Histograms of residence time and distance values for a radius of 2.5 km and threshold distance of 1.25 km.

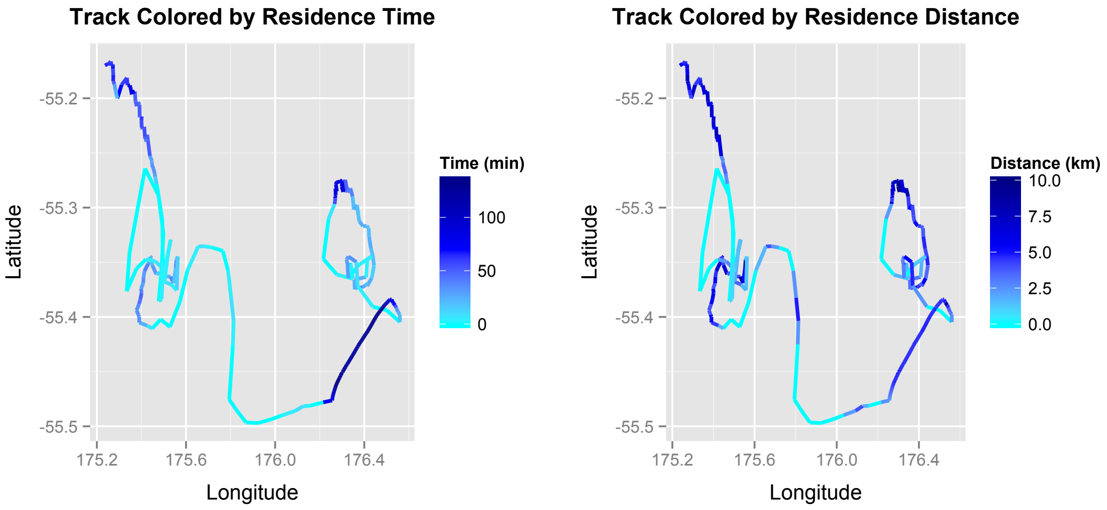

Figure 3: Spatial representation of a subsection of one track, colored by the corresponding values of residence time (left) and residence distance (right).

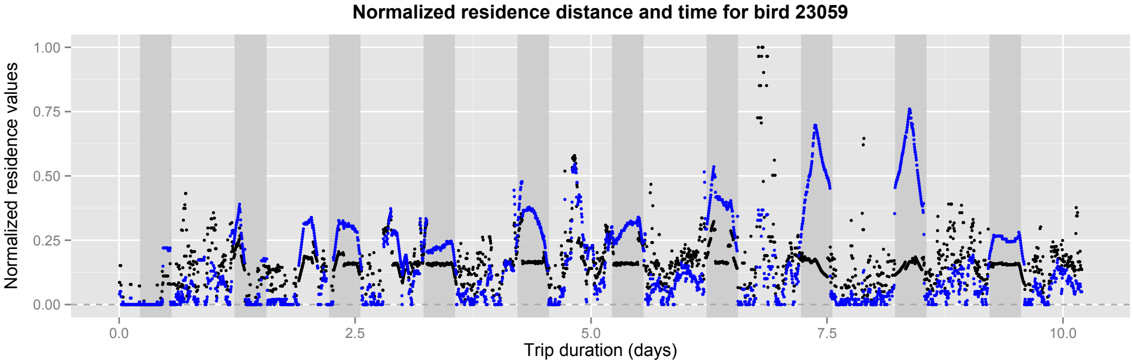

Figure 4: Normalized residence time (in blue) and distance (in black) of one track, plotted against the trip duration.

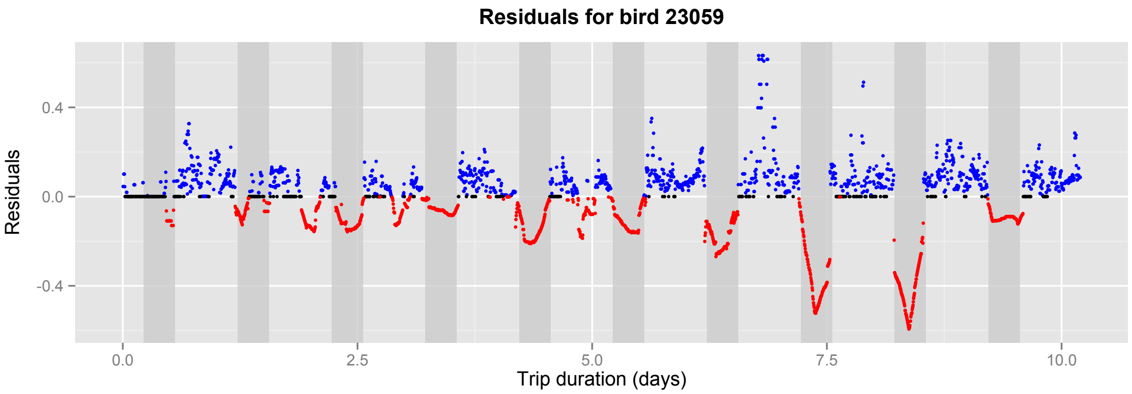

Figure 5: Residuals (difference between normalized residence distance and normalized residence time) for one track, color-coded by sign.

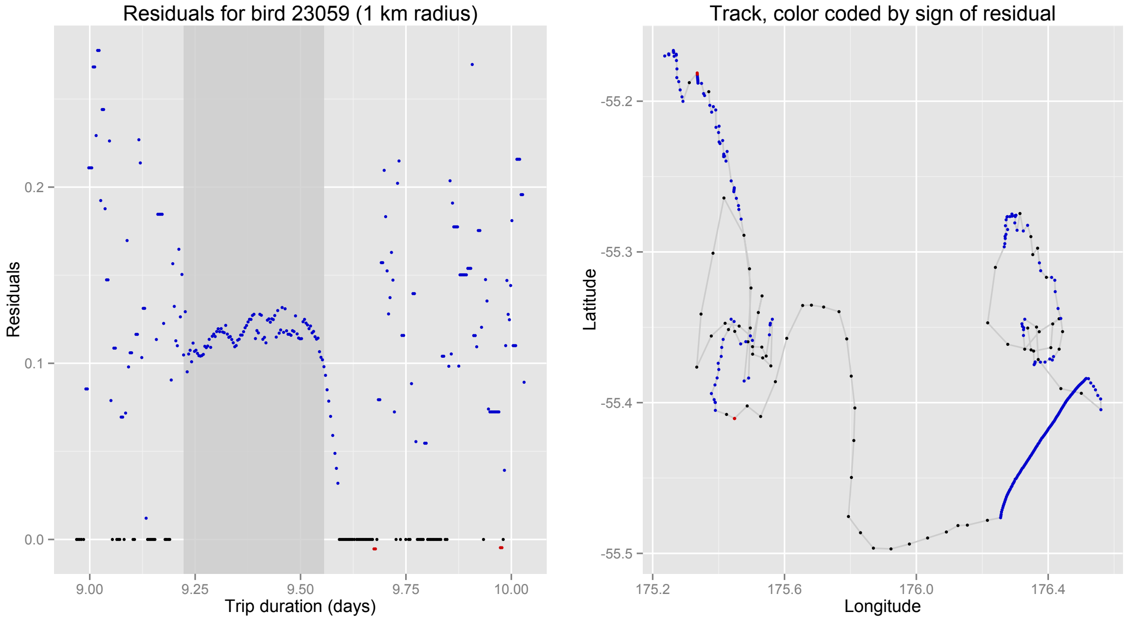

Figure 6: Residuals, color-coded by sign, as a function of trip duration (left), and corresponding color-coded track (right) for a 1 km radius.

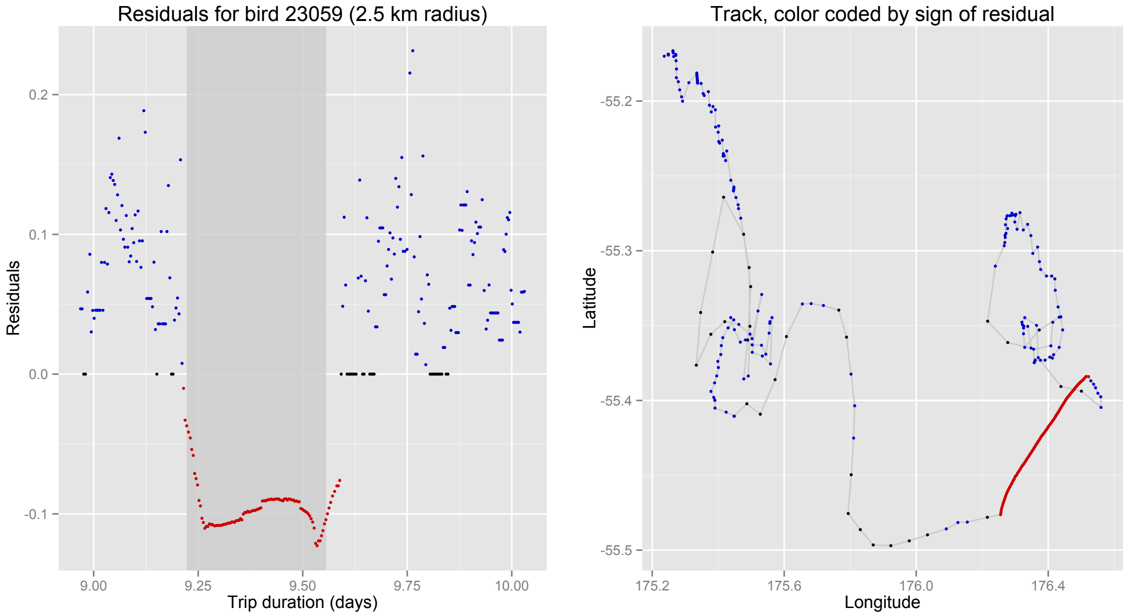

Figure 7: Residuals, color-coded by sign, as a function of trip duration (left), and corresponding color-coded track (right) for a 2.5 km radius.

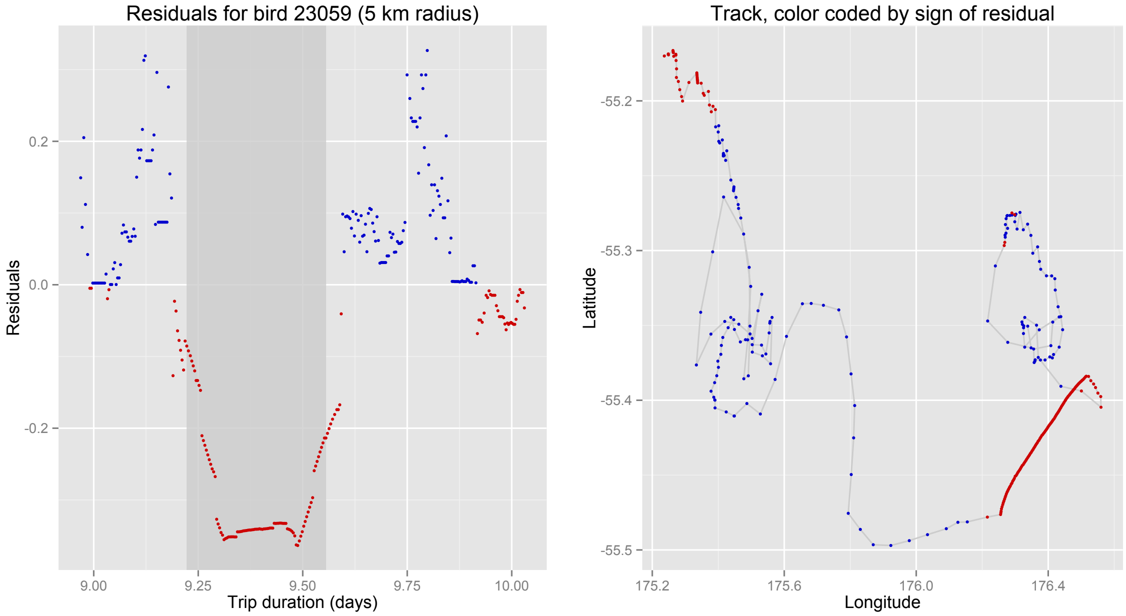

Figure 8: Residuals, color-coded by sign, as a function of trip duration (left), and corresponding color-coded track (right) for a 5 km radius.