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Software note

Revisitation analysis uncovers spatio-temporal patterns in animal movement data

Chloe Bracis, Keith L. Bildstein and Thomas Mueller

C. Bracis (http://orcid.org/0000-0003-4058-7638) (chloe.bracis@gmail.com) and T. Mueller, Senckenberg Biodiversity and Climate Research Centre (BiK-F) and Dept of Biological Sciences, Goethe Univ. Frankfurt, Frankfurt (Main), Germany. – K. L. Bildstein, Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA, USA.

Ecography
41: 1–11, 2018
doi: 10.1111/ecog.03618

Subject Editor: Thiago Rangel
Editor-in-Chief:
Jens-Christian Svenning
Accepted 3 February 2018

Animals regularly return to locations such as foraging patches, nests, dens, watering holes, or movement corridors, and these revisited locations are often sites of ecological significance. Analyzing the temporal and spatial pattern of revisitation can lead to important insights into the life history and ecology of populations. We introduce the R package ‘recurse’ to calculate revisitations to locations in the movement trajectory or other locations for one or multiple individuals. The package also calculates metrics such as residence time and time between visits. It can be used to quantitatively identify frequently used sites (e.g. dens, nests, foraging locations), to examine patterns of revisitation and link them with covariates such as habitat features or climatic data, and to address conservation questions of interest about specific locations. We present an example application with movement trajectory data from a turkey vulture *Cathartes aura* during the breeding season and demonstrate analyzing recursions, specific locations, seasonal and daily temporal patterns, and visit timing. The ‘recurse’ package should be of interest both to ecologists looking to analyze their movement data and to conservationists needing site-specific information for management and conservation actions.

Keywords: recursion, movement trajectory, revisit

Introduction

Animal movement data have been collected at an explosive rate as both the cost and size of satellite tracking tags has decreased (Kays et al. 2015). One benefit of individual tracking data is the ability to analyze an individual’s revisits, or returns to specific areas. Revisited locations are usually sites of ecological significance in the life history of animals, and their analyses can lead to important insight regarding the life history and ecology of populations. The revisited site could be regularly used resources, such as foraging areas or watering holes. For example, gorilla’s *Gorilla gorilla beringei* return interval to foraging patches was related to food abundance and quality (Watts 1998). Similarly, elk *Cervus elaphus* returned most frequently to high productivity patches

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and tended to exhibit directed movements there (Seidel and Boyce 2015). Forest elephants *Elephas maximus borneensis* spending more time at a foraging site were likely to revisit it at longer intervals (English et al. 2014). African savannah elephants *Loxodonta africana* likely use spatial memory to revisit watering holes, as evidenced by their directed movement paths and likelihood of selecting the closest watering hole whether revisiting the same watering hole or switching (Polansky et al. 2015). Revisitations can also be to places used for other purposes like roosts, nests, and dens. The scale of revisitation can be both short-term such as daily movements within a season or year, as well on a larger scale as animals return to or move sites across years (e.g. bat roost site fidelity (Lewis 1995), seabird nest fidelity (Coulson 2016)).

Animals could return to regenerating patches based on spatial memory (Boyer and Walsh 2010) or through selection of preferred habitats using perceptual cues (Van Moorter et al. 2013). The recursion dynamics also relate to optimal foraging theory (Charnov 1976), as applied to regenerating resources. For example, optimal foraging theory has been used to show that regeneration rate affects trapline foraging dynamics (Ollason 1987), to reveal the optimal direction a forager should select (Pyke 1978, Zimmerman 1979), and to indicate a preferred foraging strategy (Cole et al. 1982). Also, residence time is one measure used to evaluate the predictions of optimal foraging theory models (McNair 1982, Stephens and Krebs 1986, WallisDeVries et al. 1999, Nonacs 2001). In addition, there has been recent interest in extending principles of optimal foraging theory to foraging over larger spatiotemporal scales to large herbivores known to track temporally-varying but spatially-persistent resources (Owen-Smith et al. 2010).

Despite the widespread nature of recursions across taxa, spatial scale, and life-history stage, within the realm of movement ecology, recursions have still received relatively little attention, and separate lines of investigation exist in different areas of research, such as traplining, foraging behavior, and predator–prey interactions (Berger-Tal and Bar-David 2015). This may be because easy-to-use, common methods for ecologists to study recursions are rare. In particular, an R package that identifies revisitations along a movement trajectory and provides metrics on the visits, such as time, duration, and intervisit interval, does not exist to our knowledge. Previous work has provided complementary approaches, but most have focused on different aspects of revisitations or were not directly based on the locations of the trajectory. For example, the 'adehabitatLT' package (Calenge 2006) calculates residence time (Barraquand and Benhamou 2008), a point-based method that provides a measure of the intensity of space use across trajectory locations. This method, however, does not differentiate between a single long visit and numerous shorter visits and, indeed, very frequent but brief visits would be easy to miss. Other methods focus on the spatial distribution of revisits, either with a fixed grid or constructed tessellation. One approach is to count revisitations by computing when the trajectory forms a circle using a grid of arbitrary size (Bar-David et al. 2009); however, to our knowledge this method is not available in an R package. Alternatively, the 'adehabitatHR' package (Calenge 2006) can compute the utilization distribution (UD) via movement-based kernel density estimation that can be partitioned into a recursion distribution (i.e. the number of visits) and an intensity distribution (i.e. the mean residence time per visit) (Benhamou and Riotte-Lambert 2012). Finally, T-LoCoH (time local convex hull, available in the 'tlocoh' package) is another UD approach which constructs polygons around trajectory points with neighbors defined spatially or additionally temporally, and then calculates time use metrics such as time spent or revisitations to these polygons (Lyons et al. 2013). All of these methods are excellent for examining the spatial pattern of revisitation, but less so for point- or visit-based analyses or for the temporal patterns of revisitations. At another level of abstraction from the spatial pattern of revisitations, the 'ctmm' package can calculate periodograms to examine periodic patterns in space use from movement trajectories (Péron et al. 2016). Here the focus is on the timescales rather than the locations of periodicity. Determinism has been proposed to measure recurrent behavior such as trapline foraging, but the analysis focuses on the sequence of visits to pre-specified locations (i.e. individual flowers) (Ayers et al. 2015) (R code provided in Supplementary material).

There is no currently available easy-to-use method to calculate the revisits to particular locations for a movement trajectory that is broadly applicable to data collected at a variety of temporal scales that may include gaps. We introduce the R package 'recurse', which calculates revisitations to the locations in the movement trajectory itself or other arbitrary locations for an individual or across multiple individuals. Further, in addition to the number of revisitations, additional metrics such as time spent and time between visits are also calculated and directly provided as output. The output then allows easy visit-level analysis with the data. The package integrates with the 'move' package, accepting 'Move' and 'MoveStack' objects as input, making working with Movebank (movebank.org) data straightforward. One possible application of our point-based method when applied to the movement trajectory itself is to identify quantitatively areas of frequent use that may correspond to burrows, dens, nests, roost sites, or the like. It also can be used to examine patterns of revisitation across the movement trajectory and correlate them with other covariates such as habitat features or climatic data. The ability to specify locations can be used to restrict the analysis to already identified sites, to cross-reference known ecological features such as watering holes, or to address conservation questions of interest about specific locations.

Methods

Calculating revisits

The method works by taking a circle of a user-specified radius and moving it along the trajectory (or set of other specified locations). At each point, the number of trajectory segments entering and exiting the circle is counted to determine the number of revisitations (Fig. 1). Therefore, each movement trajectory location has one visit for the piece of the trajectory centered on it plus additional visits that could occur before or after (note that this is not necessarily true for other specified locations which could have zero visits). Summing the total time spent during all the visits provides the residence time (Barraquand and Benhamou 2008). Additionally, the time spent for each visit and the time between visits is also calculated. It is possible to set a threshold, so brief excursions outside the circle do not count as new visits but part of the previous visit. Finally, the analysis can be run for a single individual or across multiple individuals. The functions in the package are summarized in Table 1.

Consider a series of locations, $y_1,y_2,y_3,\ldots,y_n$, and a movement trajectory, $x_1,x_2,x_3,\ldots,x_m$, collected at times $t_1,t_2,t_3,\ldots,t_m$. In the simplest case, each location y_i would be the same as the movement trajectory location x_i. Revisitations are then counted within a radius r for location y_i analogous to the residence time calculation (Barraquand and Benhamou 2008, Benhamou and Riotte-Lambert 2012). For location y_i, a circle of radius r is drawn around it, and trajectory locations $x_1,x_2,x_3,\ldots,x_m$ are determined to be inside or outside the circle. Then each segment entering and exiting the radius is determined in order to sum up the number of revisits (Fig. 1A). Short excursions can be ignored by setting a threshold parameter (default zero) so visits where the time between them is less than the threshold are combined into a single visit. This can be helpful when the animal is wandering briefly outside the radius (e.g. area-restricted search), without needing to increase the radius to an unacceptably large value for most of the analysis. In the case when there are multiple individual trajectories, the process is repeated for each individual trajectory, so that the number of revisits for each location is the total across all individuals.

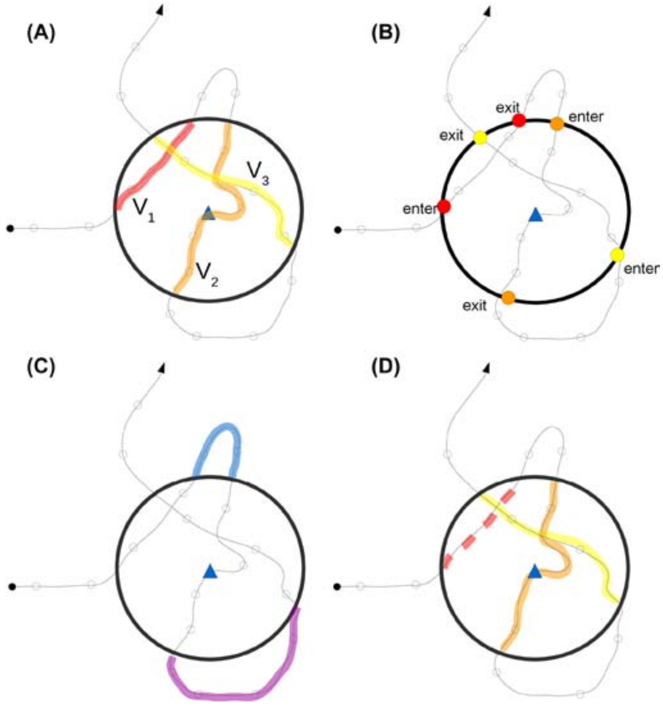

Figure 1. Revisitations are calculated for a movement trajectory shown by the line and observed locations by open circles. The current focal point is marked by a triangle with the circle showing the radius around that point. (A) Three visits, (red), (orange), and (yellow) are counted inside the circle demarcating the radius. (B) The entrance and exit times for each visit are calculated by linear interpolation between the trajectory locations inside and outside the radius and do not necessarily lie on the actual trajectory. The sum of the time spent inside the circle for all visits is the residence time. (C) The time since the last visit is calculated for the second (blue) and third (purple) visits. (D) Trajectory segments that may cross the circle but with no observations within the circle (dashed line) will not be counted, which could occur due to gaps as illustrated here or not sampling the data finely enough.

Along with the number of revisitations for each location, several other metrics are also calculated. The residence time (Barraquand and Benhamou 2008) is the total time spent within the radius across all visits, and in the case of multiple trajectories, this is the total time spent across all individuals. For each visit, the visit duration is calculated, as well as the entrance time and exit time of the trajectory crossing the circle defined by the radius (Fig. 1B). This calculation uses linear interpolation between the trajectory locations just inside and just outside the circle. For visits after the first visit (per individual), the time between that visit and the previous visit is also calculated (Fig. 1C).

Several considerations are important with respect to the data used and the radius chosen. The data can be supplied as either a data frame or as a 'Move' or 'MoveStack' object from the 'move' package, a convenient choice when working with Movebank (movebank.org) data. The data are assumed to be in temporal sequence. While the method is robust to some gaps or irregular sampling in the data, regular data are preferable. If the gaps are random, then the results should be broadly similar, though fewer recursions will be detected (Fig. 1D). That said, the method is susceptible to any bias in the data collection. For example, if positional fixes are less likely to be taken in denser forest, the number of revisits to such areas will also be biased downwards. Another important consideration is the projection used for the data. Since segments are counted passing through circles drawn around points, an equal area projection would ensure similar size comparisons. In general, a geographic projection (i.e. latitude and longitude) is not appropriate because the length of a degree of longitude varies latitudinally. Also, when comparing several radii, note that the area encompassed by the circle is proportional to the square of the radius, so using several linearly spaced radii will not correspond to linearly increasing areas.

It is critical to consider the scale of the ecological question when selecting the radius. That is, one might use a fairly small radius to detect nests or dens but a larger radius based on the average patch size to examine foraging behavior. The data available also limit reasonable radius values at both extremes.

Table 1. The main functions in the 'recurse' package.

Function	Description
getRecursions	Calculates recursion information for the specified radius from the trajectory (Move, MoveStack, or data frame) for **every location** in the trajectory and returns a 'recurse' object.
getRecursionsAtLocations	Calculates recursion information for the specified radius from the trajectory (Move, MoveStack, or data frame) for **specified locations** and returns a 'recurse' object.
calculateIntervalResidenceTime	When passed a 'recurse' object, calculates the residence time during user-specified intervals in the radius around each location.
plot	When passed a 'recurse' object and the trajectory data, plots location data colored by number of recursions.
drawCircle	Convenience function to add a circle of specified radius to a plot.

The radius should be larger than the measurement error in the trajectory locations. Otherwise a stationary animal could appear to move in and out of the radius due to measurement error, which would then be erroneously counted as revisits. The time scale of the data can also constrain the radius, in that the radius should not be greatly smaller than the length of most steps. It is preferable that the number of revisits and visit duration are calculated based on several trajectory points inside the radius rather than a single point. The linear interpolation of entrance and exit times will be more accurate when there are more points inside the radius and when data is finer scale. Note that this only needs to be true, however, for the behavior of interest. A smaller radius can still be appropriate for examining nesting or foraging behavior even if the step lengths during searching or predator evasion, for example, are much larger. If the behavior of interest is brief, such as visits to a watering hole, it is important that the data also be finely sampled. Finally, care should also be taken not to make the radius too large as well, which can lead to many overlapping circles. One can use a criterion such as limiting the radius to no larger than a quarter of the net displacement to avoid this (Barraquand and Benhamou 2008), and something smaller would be more appropriate for most questions.

Although it is preferable to allow the ecological question to determine the radius, this may not always be possible, or one may be calculating recursions as part of data exploration. For example, the ecological question may involve the revisitations of foraging patches, but patch size may be unknown. In this case, the best course of action is to consider a range of reasonably-sized radii and compare across them. In general, increasing the radius will increase the mean revisitations. However, revisitations can decline once the radius is extremely large and encompassing most of the study region, making it difficult to exit and re-enter the circle. Another radius-based method, the first-passage time, also increases with increasing radius, and maximizing the variance in the log of the first-passage time across radii is suggested as a measure to determine the scale of the search pattern in area-restricted search (Fauchald and Tveraa 2003). This approach also applies to recursion analysis. The log transformation is also useful in this case to avoid unduly weighting very highly visited areas. Assume a patchy landscape with some areas visited more than others. When the radius is smaller than the spatial scale of the patch, increasing the radius will increase the variance in revisits, as more visits to highly visited areas are included, but revisits to other areas do not change as dramatically. Once the radius increases beyond the scale of the fragments, then highly visited as well as less visited areas are both likely to slowly continue accumulating noise, thus decreasing the variance or slowing its increase.

Example application

Data

We provide an example of applying the 'recurse' package with data from an adult female turkey vulture *Cathartes aura*, Leo (id 65545), that migrates seasonally between summer breeding grounds in Saskatchewan, Canada and wintering grounds in Venezuela (Supplementary material Appendix 1 Fig. A1; Dodge et al. 2014). Leo was an adult (> three years old) when captured at her nesting site in an abandoned farm-site near Leoville, Saskatchewan. In this analysis, we focused on the summer breeding season only, from approximately May through September, in the years 2008–2011 by limiting the data geographically (west of –106°W and north of 53°N). Although Leo bred successfully in 2007, her breeding success was not measured in the years covered by this analysis. The data are hourly with some gaps (about 5% of intervals, with half of those being only one missing location and only a few gaps of several days). The complete R code is available in the supplementary online material.

Turkey vultures are highly migratory New World vultures in the avian family Cathartidae. One of the smallest of all vultures, the species is an obligate scavenging bird of prey (Bildstein 2006). Vultures are extraordinarily adept soaring birds, scavenging both small and large carcasses, as a well as human refuse, and readily adapt to human-modified landscapes. Individual turkey vultures search for carrion both visually and olfactorally while engaged in low-cost soaring flight at both low to high altitudes (Mallon et al. 2016). In summertime turkey vultures breeding in central Canada feed principally on dead livestock and road-killed mammals and other dead wildlife across breeding home ranges of 47 to 953 km^2 (Houston et al. 2011).

Analysis

We were interested in examining frequently used locations (e.g. nest or roost sites) during the breeding season and therefore selected a relatively small radius. Constraints on the radius size were the accuracy of the GPS tags used in the study (± 18 m) and hourly sampling rate (median step length 29 m), leading us to select a radius of 50 m. In the initial exploratory analysis, one can see that most sites had few visits, but there was a very long tail of highly visited sites (Supplementary material Appendix 1 Fig. A2). Looking at the revisits geographically, the more frequently visited sites appear to be located near roads (Fig. 2). Additionally, turkey vultures in the region use abandoned farm houses near roads as nesting sites and also use roads to locate road kills, making distance to road a potentially interesting environmental covariate. We obtained road data for Saskatchewan (National Road Network dataset from <www.geobase.ca>) and used the 'gDistance' method in the 'rgeos' package (Bivand and Rundel 2017) to calculate the shortest distance from each location in Leo's trajectory to the nearest road. Almost half of locations were less that 250 m from a road and nearly 90% were less than 1 km away, with distances reaching up to 3.3 km. The highly visited sites (i.e. over 75 visits or the upper 35% of revisited trajectory locations) were all less than 500 m from a road, though there were sites with up to 45 revisits about 1.5 km from any road (Fig. 3).

These highly visited sites appear to be clumped in five areas (Fig. 2). Based on this, we performed a cluster analysis of the (*x, y*) position of the trajectory locations with 75 or more visits. Note that none of these five sites are the nest at which Leo was tagged (and bred successfully) in 2007, so they are more likely to be roost sites. We used the 'fanny' method in the 'cluster' package (Maechler et al. 2017), specifying five clusters (Supplementary material Appendix 1 Fig. A3). Next we conducted an analysis only examining revisits to those five highly visited sites. This demonstrates specifying locations for analysis rather than using the entire movement trajectory. Here we used a cluster analysis of the most frequently visited locations from the preliminary examination of revisits in the movement trajectory. However, locations also could come from external sources, such as coordinates for watering holes, areas of conservation concern, etc. We also chose to use the year for the id (while normally the id identifies which individual is which), thus treating each year as a separate individual using the multi-individual functionality. This facilitated comparisons among years. Additionally, years were disjoint due to the intervening migration to the wintering grounds, so it made more sense to consider years separately rather than treat a

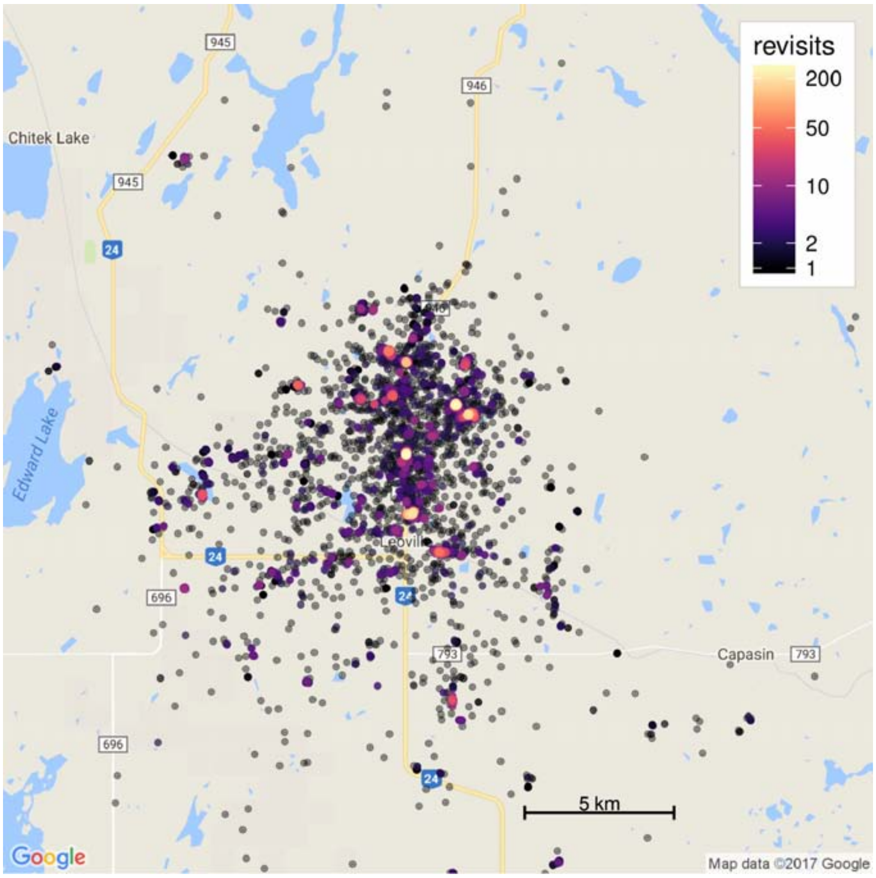

Figure 2. Movement data for the turkey vulture 'Leo' during its summer residence in the breeding habitat near Leoville, Saskatchewan, Canada. The number of revisitations to a location is shown on a logarithmic scale from black (low) to yellow (high), with several areas of concentrated visits apparent.

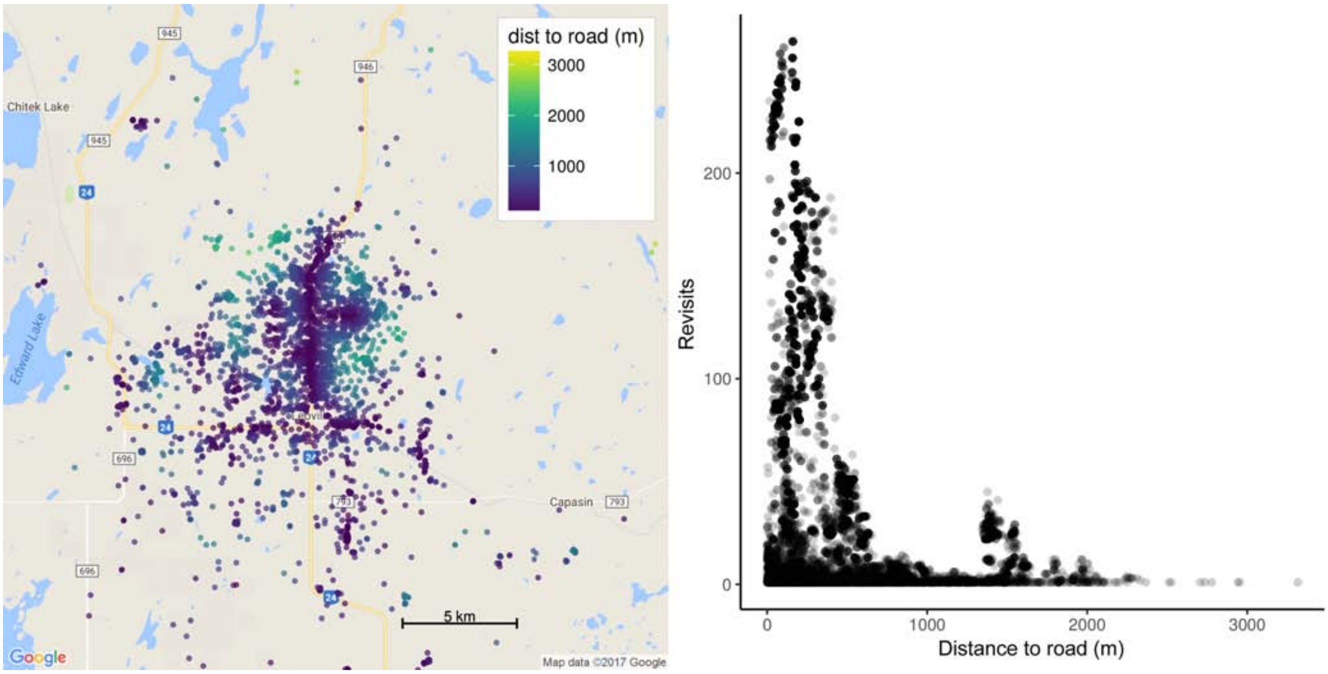

Figure 3. Distance from roads for the turkey vulture 'Leo' during its summer residence in the breeding habitat near Leoville, Saskatchewan, Canada (left), and the number of revisits to a location based on its distance from a road (right).

revisit a year later as part of the previous year. We again used a radius of 50 m.

The temporal pattern of visits to these frequently visited sites (sites 1–5, Supplementary material Appendix 1 Fig. A3) varied both within and between years (Fig. 4). In most years, one or two sites were used predominately to the near exclusion of other sites, though in 2010 all sites (with the possible exception of site 2) received some use, though in different periods of the summer. Site 1 was primarily used in 2008 and 2011, but the temporal pattern differed, with visits declining throughout the summer in 2008 but more evenly spread in 2011. Sites 2 and 3 were predominately used in a single year, 2009 and 2010 respectively. Site 5 was unique in receiving absolutely no use in 2008 (the first year of data), the most use in the later part of the 2009 breeding season, and declining use in subsequent years.

Next we examined how the visit entrance time predicted the visit duration (Fig. 5). The visits naturally partitioned into two main clusters, with short visits commencing throughout the daytime hours and peaking at midday and longer visits starting in the afternoon to evening. Interestingly, for the overnight visits, there was a linear decline in visit duration with arrival time, corresponding to a morning departure. The longer visits are generally early in the season for sites 1–3, but throughout the entire breeding season for sites 4–5 (Supplementary material Appendix 1 Fig. A4). For a potential nesting site, the seasonal pattern of longer visits followed by shorter visits could represent first incubation and brooding bouts and then feeding visits to larger nestlings. However, the longer visits were nearly universally overnight visits, and this would not support sites 1–3 being nesting sites, as incubation and brooding would also need to occur during daytime hours.

Taking a location- and visit-based approach to recursion analysis allowed us to examine residence time in more detail. For example, seasonal and inter-annual patterns could be of interest (e.g. Fig. 4) as well as patterns within a day. Turkey vultures typically rely on thermals and updrafts, especially during long-distance flight such as migration (Mandel et al. 2008). Overall, this precludes nighttime flight, although the species has also been observed using anthropogenic thermals in the early evening hours (Mandel and Bildstein 2007). Most visits began and ended during the daytime hours (entrance time: day = 480, night = 142; exit time: day = 500, night = 122), although about 20% began or ended at night. We further analyzed the time of day of occupancy at the five frequently used sites by rounding the entrance and exit times to the nearest hour (as the data was collected hourly) and counting hours of occupancy (Fig. 6). Note that this is therefore an approximate rather than precise total time spent, but appropriate for relative comparisons. There is a clear distinction between sites 1–3, where the sites were approximately equally likely to be used at all hours of the day (though a slight nocturnal preference with sites 1 and 3) and sites 4 and 5 which have a strong diurnal pattern with predominately nighttime occupancy, complementing the distinction seen with the visit duration analysis (Fig. 5) and suggesting that sites 4 and 5 are overnight roosting locations. While this usage pattern is compatible with sites 1–3 being nest sites, they could also be both day- and night-time roost sites.

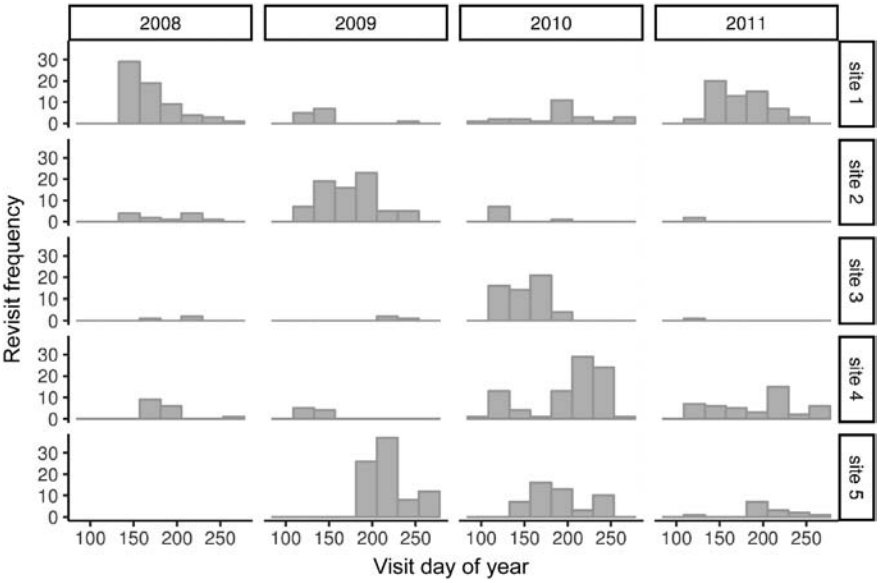

Figure 4. Temporal pattern of visitation of the most frequently used locations (rows, sites 1–5) across years (columns) throughout the breeding season on a weekly basis.

The inverse of residency time, or time spent between visits, can be of particular interest for behavioral patterns that may occur regularly but not of long duration, for which residence time is not a good measure, such as visits to watering holes, short duration feeding visits to nests, or other important but briefly used resources. Unlike methods for examining periodicity (Péron et al. 2016), with our recursion analysis, the time scale of revisitation need not be regular. The recency of the last visit can be compared with other metrics such as visit duration (Fig. 7). For the sites predominately used at night (4–5), there was no relationship between the visit duration and recency of last visit, meaning visits lasted as long when there had been a visit the same day or not for several days. For the other sites (1–3), on the other hand, visits tended to be shorter if there had not been a visit for two days compared to more recent visits. This complements the occupancy time of day analysis (Fig. 6), showing that time spent at night-time roost sites is not predicated on the recency of last visit. For potential nest sites, one explanation for short visits after an absence is short feeding visits to the chicks after time away from the nest (Houston et al. 2011). Although field observations indicate that Leo bred successfully in 2007 and 2014 at the same nest site, her breeding success was not measured in the intervening years that cover this study. It is possible that she bred successfully or attempted to breed successfully at the same abandoned farm house in the period of the data used here. In that scenario, annual differences described in this paper do not reflect inter-annual differences in her breeding behavior. All five of the most routinely revisited sites (Supplementary material Appendix 1 Fig. A3) were in remnant patches of boreal forest 14 to 22 km from the capture nest site, and thus could represent day- and night-time roost sites (Fig. 6, sites 1–3) or mainly night-time roosts (Fig. 6, sites 4–5). Turkey vultures often roost communally, even when breeding (Kirk and Mossman 1998), and other turkey vultures nesting in the area sometimes roosted as far as 38 km from their nests (Houston et al. 2011). We believe that roosting at such distances from their nests most likely results

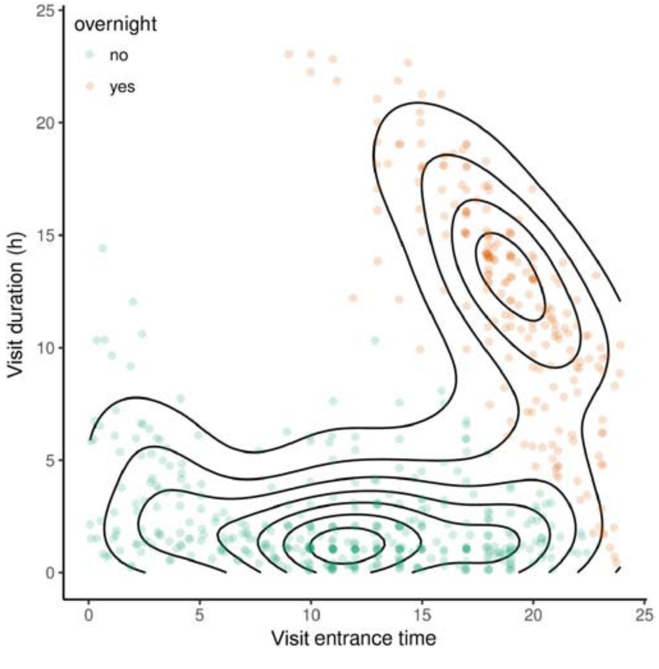

Figure 5. Patterns of visit duration vary with the hour of day the visit commenced. The two clusters correspond to whether the visit was overnight (arrival the day before departure) or not, with short visits throughout daytime arrival hours and peaking midday and overnight, longer visits commencing in the afternoon to evening with a declining duration with arrival hour corresponding to a morning departure.

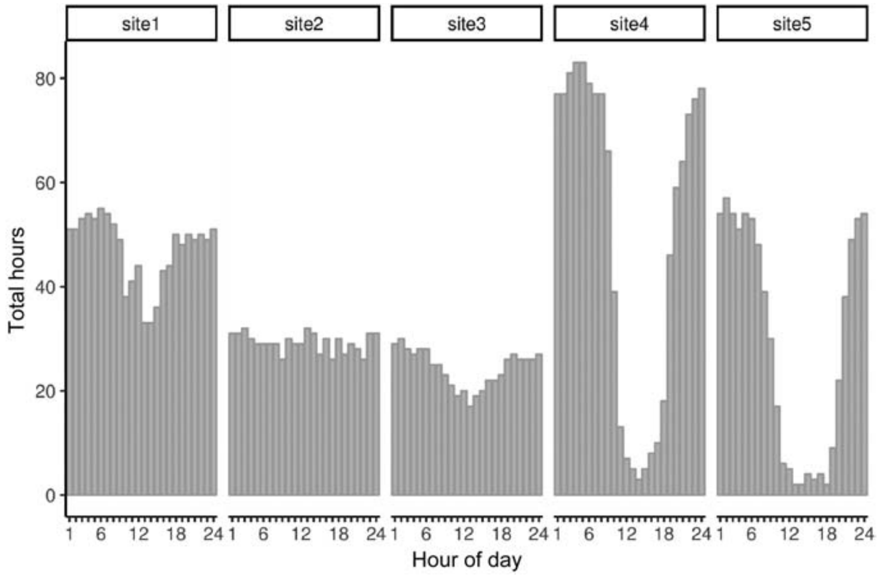

Figure 6. Time spent at the five most frequently used sites varies by hour of day. Sites 1–3 tended to be used at all times of day or night with slightly higher nighttime usage at sites 1 and 3. Sites 4–5 were predominately used at night with very little daytime usage, especially in the middle of the day.

from the fact that birds in this region typically nest in abandon farm sites surrounded by treeless farmed areas that are not necessarily close to appropriate forested roosting areas, or that roosting close to the nest is not a critical factor in nest protection for the species.

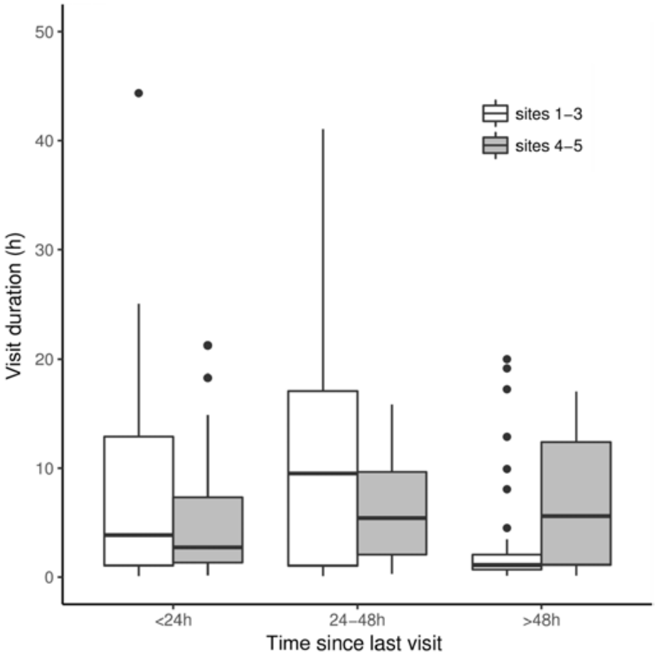

Figure 7. Visit duration shows no clear pattern with the time since the most recent visit. However, there may be a difference between sites 1–3 (white), used throughout the day and night, and sites 4–5 (gray), primarily used at night (Fig. 6) after an absence. There may be a tendency with the former towards very short visits when the last visit was over two days ago.

Discussion

Example application

We used the ‘recurse’ package to identify locations revisited by an adult female turkey vulture in this study, and, in particular, to identify five sites which were used very frequently, most likely as roosting sites. With a subsequent analysis focused on these sites, we were able to see the temporal patterns of visitation, both seasonally and among years, something we believe not possible with other tools. From that analysis, we saw that different sites were important in different years, and that there were interesting patterns of use throughout the breeding season. For example, the number of sites predominately used in a year varied from one to two or more, and multiple sites tended to be used at different but overlapping times in a single year. We were also able to partition the pattern of visit duration and visit entrance time into shorter-duration non-overnight visits and longer duration overnight visits with a departure around dawn. This ability to do a visit-level analysis beyond the spatial pattern of revisits is a feature of this method. Similarly, examining occupancy by hour of day showed distinct patterns among sites for the times the bird was present, enabled by the tracking of individual visits. Finally, another unique feature of the package is the calculation of time between visits, which can complement a periodicity analysis (Péron et al. 2016). The time since the last visit was generally not predictive of visit duration, except that visits after an absence of several days tended to be short for those sites used at all hours of the day (versus mainly at night).

Analyses beyond the example application

Here we have provided an example of the types of analyses possible using the 'recurse' package, though it is by no means complete. This analysis focused on a single individual, but the package also supports analyzing multiple individuals, either independently or jointly to uncover locations revisited across the population. In the context of turkey vultures in this study, expanding the analysis to multiple individuals could be used to examine questions such as differences within and among breeding pairs within and across years, differences between breeding versus wintering sites, and how habitat differences may affect revisitations in different part of their extensive range.

We demonstrated examining an environmental covariate with the distance to roads. Further possibilities include comparing covariates such as food availability at locations with high or low numbers of revisits. With methods that focus on mapping the spatial pattern of recursions (Benhamou and Riotte-Lambert 2012, Lyons et al. 2013), this is also possible using a single measure, such as an average vegetation index. With our location-specific and visit-level approach, one could associate a temporally coincident measure of food quality (e.g. satellite-based such as NDVI or field-based such as fruit count on trees) with each visit and then examine the temporal pattern of visits correlated with the food quality. In this way, recursive movements could be applied to investigate the phenology of green up, i.e. the 'green wave' (Bischof et al. 2012). This same idea could be applied to other biotic or abiotic factors available as a time series, such as predation risk, temperature, or precipitation. One could also combine recursion analysis with behavioral segmentation (Gurarie et al. 2016), in order to examine questions about site usage or return frequency in different behavioral states, such as foraging versus searching.

One interesting application of the time between visits is in a trapline foraging context to gauge the revisitation interval. Periodicity analysis (Péron et al. 2016) can be useful for determining the timescales of periodic patterns in space use for the trajectory as a whole. The time between revisits could then be used to further analyze revisits to determine how the intervisit interval varies among and within particular locations. That is, do various foraging locations have similar intervisit intervals (perhaps related to plant characteristics) and are intervisit intervals consistent for a given location (perhaps related to seasonality). The spatial scale of analysis could also move from using a plant-sized radius to consider revisits to specific plants on a circuit within a patch to a patch-sized radius to consider revisits to patches/circuits. The revisits plus a clustering process like we demonstrated could also be used to automate the process of transforming movement data into tagged locations needed for a sequence-level analysis (Ayers et al. 2015).

With the package, it is possible to perform an analysis based not only on trajectory locations (though this may be the most common use case) but also on pre-defined locations. We demonstrated this here with the five frequently visited sites determined via cluster analysis, but this is also possible with independently derived locations. These could be sites of ecological interest or conservation concern. Thus the package could be useful for answering questions related to disturbance that may be site-based. For example, in our analysis of occupancy time of day (Fig. 6), one could conclude that potentially disturbing daytime activities may be a problem at some sites but not others.

Conservation implications

As part of the push for more evidence-based conservation, one challenge in conservation is the need to collect better site-specific information both to prioritize areas for conservation and inform management actions (Theobald et al. 2000, Sutherland et al. 2004). The 'recurse' package can aid in quantifying and ranking the importance of locations based on revisits. For example, the nursery-role hypothesis states that certain habitats (e.g. seagrass beds or wetland areas) are important juvenile habitat and thus key for recruitment to adult populations, and it is important to use criteria such as movements between juvenile and adult habitats and adult recruitment to identify such habitats, as well as measure biotic and abiotic factors that contribute to variation in site quality in habitats (Beck et al. 2001). Evidence suggests that habitat quality and area are particularly important compared to the spatial structure or matrix (non-breeding habitat) quality for population viability (Hodgson et al. 2011). Novel information, such as predation risk, has been suggested for consideration during conservation planning (Ward et al. 2012). The 'recurse' package helps not only to identify important sites spatially but can also link them to environmental covariates. By measuring repeat usage, managers can quantify a site's importance on another dimension than residence time. It is also possible to quantify the temporal dynamics of a site's usage to potentially identify critical times of day or year.

Movement data has been used both to identify movement corridors connecting foraging areas or suitable habitat, e.g. elephants (Douglas-Hamilton et al. 2005), lynx (Squires et al. 2013), and ungulates (Sawyer et al. 2009), and to asses landscape connectivity (Richard and Armstrong 2010). The 'recurse' package provides another possible window into movement data where some more visited sites, especially across a population, could be important for connectivity. Locations along the trajectory that are used with intermediate frequency may be those traveled relatively often to get to and from sites with particularly intensive usage and may thus be useful to identify corridors. Looking across a population could differentiate frequently visited foraging sites by individuals from those used by multiple individuals and that are therefore key to connecting important resources even if the time spent there is minimal.

To cite 'recurse' or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for 'version 0':

Bracis, C., Bildstein, K. L. and Mueller, T. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. – Ecography 41: 000–000 (ver. 0).

Data accessibility

The data for the turkey vulture 'Leo' are available from MoveBank < http://dx.doi.org/10.5441/001/1.46ft1k05 >. An R script with the example analysis and a .csv file with the distances for each location to roads are available in the Supplementary material.

Acknowledgements – Dejid Nandintsetseg and AniMove course participants provided helpful discussion of this work. We thank two anonymous reviewers for comments that improved the manuscript.
Funding – CB was partially funded by the Goethe International Post-Doc Programme (GO-IN; 291776), funded under the 7th Framework Marie Curie Actions of the European Commission. CB and TM were partially funded by the Robert Bosch Foundation.

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Supplementary material (Appendix ECOG-03618 at < www.ecography.org/appendix/ecog-03618 >). Appendix 1.