The Journal of Wildlife Management 84(6):1179–1184; 2020; DOI: 10.1002/jwmg.21879

Research Article

Random Encounter and Staying Time Model Testing with Human Volunteers

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ABSTRACT Ecology and management programs designed to track population trends over time increasingly are using passive monitoring methods to estimate terrestrial mammal densities. Researchers use motion-sensing cameras in mammal studies because they are cost-effective and advances in statistical methods incorporate motion-sensing camera data to estimate mammal densities. Density estimation involving unmarked individuals, however, remains challenging and empirical tests of statistical models are relatively rare. We tested the random encounter and staying time model (REST), a new means of estimating the density of an unmarked population, using human volunteers and simulated camera surveys. The REST method produced unbiased estimates of density, regardless of changes in human abundance, movement rates, home range sizes, or simulated camera effort. These advances in statistical methods when applied to motion-sensing camera data provide innovative avenues of large-mammal monitoring that have the potential to be applied to a broad spectrum of conservation and management studies, provided assumptions for the REST method are rigorously tested and met.

KEY WORDS density, human volunteers, mammals, motion-sensing camera, random encounter and staying time method, REST.

Abundance and density are fundamental ecological parameters that are difficult to measure because individuals move in and out of sample plots, and not all individuals present at sample units are detected (Royle and Nichols 2003). Heterogeneity in individual movement and presence at sample units necessitates estimating and correcting for the probability of detection. Count data from repeated surveys of sampling units fundamentally inform abundance estimates corrected for detection. Capture-mark-recapture (CMR) uses the marked individual as the sample unit with the pattern of captures over time assisting with abundance estimates (Seber 1982). In these cases, the model allows heterogeneity of capture probability among individuals (Pollock 1982).

Ambiguity in the area over which researchers estimate abundance can make translating abundance into density (i.e., number/unit area) less than straightforward. Individuals living on the boundary of the study area substantially affect density estimates (Efford 2004). Spatially explicit capture recapture (SECR) models use the spatial pattern in the recaptures of individuals to estimate probable locations of home range centers within a study area to address this issue (Efford 2004, Royle et al. 2013).

Received: 26 October 2019; Accepted: 24 April 2020

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Chandler and Royle (2013) built on the SECR model to consider sampling site locations and their associated count statistics to estimate density without the need for marking individuals. This model infers the number and locations of home range centers from the spatial autocorrelation of the count data. Surveyors must space sampling sites so an individual can encounter multiple traps, in contrast with the assumption of site independence assumed with previous models.

Researchers now commonly use motion-sensitive cameras to estimate habitat use, distribution, abundance, and density for unmarked wildlife populations (Burton et al. 2015). Minimal human intervention, reduced cost, and simplified logistics make camera surveys attractive for high profile species of conservation concern or in conditions that prevent direct observation or capture of individuals. Photos that identify individuals are useful in standard CMR methods, but photos of species that do not allow for individual identification can also be used to calculate abundance estimates using SECR models (Royle and Nichols 2003, Royle 2004) and density (Chandler and Royle 2013, Ramsey et al. 2015).

By assuming individuals encounter point detectors randomly, Rowcliffe et al. (2008) developed the random encounter model (REM). The REM uses independent estimates of travel speed (obtained through observation), time active each day, group size, and the area of the detection zone of each camera to relate photos/time to density (Rowcliffe et al. 2008). The model assumes that samples from each camera are independent and uses count data (photos/unit time) for estimations but bases estimation on individual movement rather than inferred spatial point process. The model depends on accurately estimating movement speed, time active, and group size, necessitating considerable additional effort that may not be possible for many species. Rowcliffe et al. (2016) present suggestions on feasible approaches.

Nakashima et al. (2018) modified Rowcliffe's original method to measure the staying time of an individual within the detection area of remote cameras. They referred to this model as the random encounter and staying time (REST) method. The REST model assumes that researchers place cameras randomly relative to individual movement within the study area. With this assumption, the residence time of an individual at any given detector is a function of the duration of time the detector is deployed and the proportion of the study area it samples. Under the assumption of random movement, residence time scales linearly with the number of individuals, thereby allowing an estimate of density without the need to estimate rate of movement, home range size, or individual identity. The model also does not require closure of the study area in the sense that individuals do not leave or enter the area, but only that immigration, emigration, births, and mortality are balanced during the study period.

The REST model calculates population density as a function of the residency time the target species spends in front of a camera. The equation, modified from Nakashima et al. (2018) to account for potentially different sampling durations and areas between cameras, is:

$$\hat{\rho} = \frac{\sum_{i=1}^{n} t_i}{\sum_{i=1}^{n} T_i \times \mathrm{a}_i}, \quad (1)$$

where $\hat{\rho}$ is the estimated density, n is the number of cameras, t_i is the staying time of an individual at the ith camera, T_i is the time the ith camera was active, and a_i is the area sampled by the ith camera (its 100% detection zone; s in Nakashima et al. 2018).

If a camera records multiple individuals at the same time, the model estimates residency time independently for each individual. Importantly, calculating the cumulative residence time (t in the above equation) does not require identifying distinct residency bouts, eliminating the need to define a camera detection; one can simply sum the time individuals spend in front of each camera. This method is applicable to territorial and non-territorial species, provided researchers distribute cameras randomly in relation to animal space-use patterns (i.e., no baiting or placing cameras only in areas with preferred habitat characteristics).

The REST model assumes that cameras sample habitat proportional to their availability. The precision and accuracy of estimates to movement within the territory or home range relies on the assumption of equal probability of a home range existing within the study area (i.e., homogeneity of the point-pattern describing the distribution of home ranges). Additionally, detectability within the detection zone of the cameras must be perfect ($p = 1$). This method also assumes the detection device does not modify individual movement.

Nakashima et al. (2018) tested the REST model using computer simulations and field surveys of duiker populations (red forest duiker [*Cephalophus natalensis*] and blue duiker [*Philantomba monticola*]) in Moukalaba-Doudou National Park, Gabon. The REST model provided unbiased estimates of abundance for nearly all simulated populations representing paired and solitary movement, continuous movement, and movement with resting. The REST estimates from camera surveys of actual duiker populations were similar to estimates made via line transect surveys. Nakashima et al. (2018) provided strong evidence for the robustness of the REST method in computer simulations, but they did not know the true densities of the duiker populations they tested.

We sought to test the REST method using known densities of human volunteers, which provided us with proof of concept. Human volunteers were advantageous because they allowed for more realistic movement paths than computer simulations. Our objective was to determine if movement rate, home range size, and density affected bias and precision of the estimates produced by REST. We equipped human volunteers with global positioning system (GPS) devices and gave them precise movement rules such that home range size and movement rate were varied.

STUDY AREA

Our test took place at the Louise McKinney Riverfront Park in Edmonton, Alberta, Canada (53°N 113°W) on 16 and 23 September 2017. The entire park is approximately 4.0 ha in size and the weather on both days was clear and sunny (~15°C). The study area was approximately 1.5 ha in size, and consisted of flat, open, grassy areas, walking paths, and a pavilion, all of which were accessible to the volunteers.

METHODS

The Research Ethics Office at the University of Alberta granted approval for using human volunteers in our test (application number pro00075181). We employed 12 volunteers as proxies for non-territorial, unmarked terrestrial mammals. We assigned volunteers to use first the entire park and then half the park as their home range. We designated home range boundaries with flags. We gave each volunteer either a GPSMap64 or a GPSMap78 unit (Garmin, Olathe, KS, USA), both of which are accurate within 5–10 m to track their movements every second for the duration of each scenario.

We conducted 6 scenarios, each scenario being a different combination of movement rates and home range sizes. Each scenario lasted 16 minutes and included 3 movement patterns (jogging for 10 minutes and resting for 6 minutes, walking for 10 minutes and resting for 6 minutes, and walking for 16 minutes continuously) performed within 2 home range sizes (0.75 ha and 1.50 ha). We instructed

Table 1. Movement rates of the human volunteers and home range sizes (ha) available in each scenario on 16 and 23 September 2017 at the Louise McKinney Riverfront Park, Edmonton, Alberta, Canada, where the cell area (m^2) refers to the approximate cell size per scenario. We recorded the duration of each scenario in seconds (s), and included the number of points tracked per second (point freq).

Scenario	Home range (ha)	Movement rate	Duration (s)	Point freq (s)	Cell area (m^2)	Total area (m^2)
1	0.75	Jog 5 min, rest 3 min (2×)	11,424	952	20	16,000
2	0.75	Walk 5 min, rest 3 min (2×)	11,184	932	19	15,200
3	0.75	Walk continuously (16 min)	11,268	939	20	16,000
4	1.50	Jog 5 min, rest 3 min (2×)	11,208	934	20	16,000
5	1.50	Walk 5 min, rest 3 min (2×)	10,752	896	20	16,000
6	1.50	Walk continuously (16 min)	11,244	937	20	16,000

volunteers to move independently of each other during each test, but we synchronized their movement and rest periods.

We tracked the duration of each scenario using a stopwatch and used a whistle to signal when subjects were to change movement rates and end each scenario. Because of variation among volunteers in the time they took to start, stop, and save their individual tracks, each scenario varied slightly from 960 seconds (16 min; Table 1). We merged tracks collected over both days according to scenario in ArcMap version 10.5.1 (Esri, Redlands, CA, USA) and clipped each track to the shortest duration of any given volunteer within scenarios to standardize the number of points per person per scenario (932 ± 19 [SD] seconds). We created polygons consisting of 800 cells around each scenario based on the coordinates of the outermost tracks (Fig. 1). Each cell was approximately 20 m^2. We summed the number of points per cell for each scenario as a proxy of time spent in each cell. If a point fell on the border of 2 adjacent cells, we randomly assigned it to 1 cell.

We assumed the habitat characteristics in the study area were homogenous during this study, and detectability was perfect given that GPS units tracked each volunteer and never failed during the simulations. Volunteers were not attracted to detection devices because we did not actually deploy any cameras.

We varied human densities to include 2, 6, and 12 people. We varied sampling effort by varying the number of cells selected randomly as camera deployments. We selected 8, 20, 50, or 100 cells as camera deployment sites, resulting in 1%, 2.5%, 6.25%, and 12.5% coverage of the study area, respectively. We used 1,000 bootstrap samples with replacement of camera effort in each scenario of movement speed, human densities, and home range area for 72 different scenarios in R (R version 3.5.1, www.r-project.org, accessed 10 Oct 2018). We estimated the density of human volunteers across each combination of movement speed, true human density, and home range area using equation 1. We then multiplied the resulting density by the area to calculate abundance for comparison to the number of volunteers per scenario. We calculated means and confidence intervals across bootstrapped samples to estimate abundance and quantify precision (data and R code available online in Supporting Information).

RESULTS

The REST model provided accurate estimates of human density regardless of movement rate, home range area, camera effort, or number of volunteers (Fig. 2). Precision decreased when our sampling effort was low (i.e., 1% coverage). Neither movement rate nor home range size affected estimator accuracy, although the REST model consistently estimated abundance with lower precision under walking-and-resting and jogging-and-resting scenarios compared to scenarios representing homogenous walking speeds.

In scenarios representing human densities of 2 people, we observed the least amount of error across all movement or home range size. In scenarios with 20 and 50 cameras,

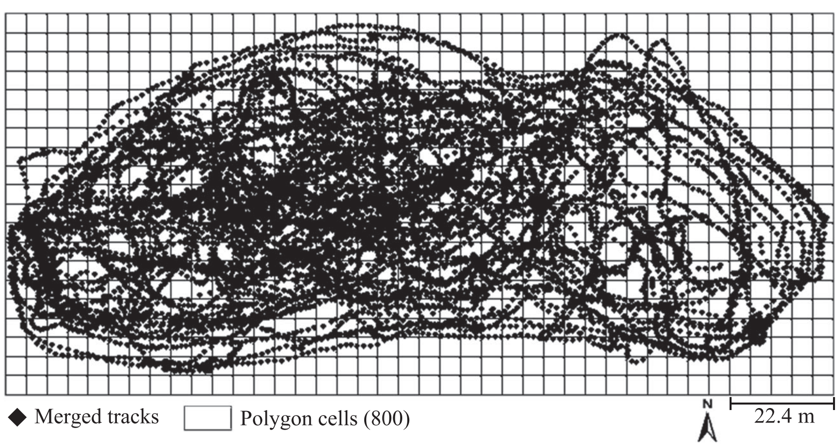

Figure 1. Merged tracks of 12 human volunteers in the 800-cell polygon from scenario 5. In scenario 5, the entire Louise McKinney Riverfront Park, Edmonton, Alberta, Canada, was available to everyone on 16 and 23 September 2017, and the movement rate was walking for 10 minutes and resting (no movement) for 6 minutes.

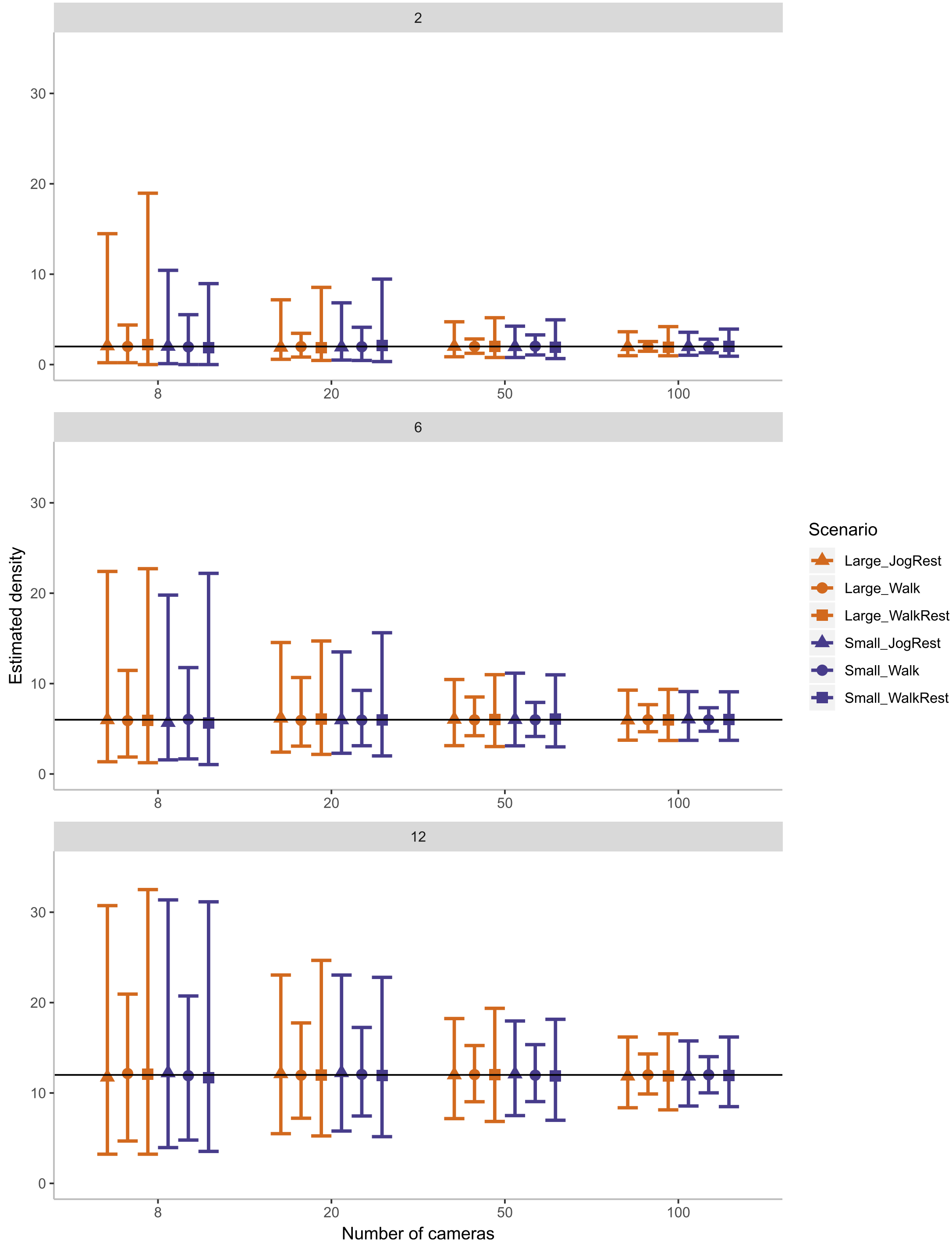

Figure 2. Bootstrapped mean estimates and 95% confidence intervals of human densities including 2, 6, and 12 people with motion-sensitive camera effort of 8, 20, 50, and 100 cameras across all 6 scenarios of movement rate and home range size in the Louise McKinney Riverfront Park, Edmonton, Alberta, Canada on 16 and 23 September 2017. Small (purple) and large (orange) in the legend refer to the home range size available to the volunteers, either 0.75 ha or 1.5 ha, respectively. JogRest, Walk, and WalkRest refer to the movement rates in each scenario and are differentiated by triangles, circles, and squares, respectively.

as human abundance in the park increased, precision decreased.

Across all home range sizes and movement rates, the REST method accurately estimated human densities. We found no effect of home range size on estimator accuracy or precision. Estimators provided the greatest precision under continuous-walking scenarios across all levels of camera effort, human density, and home range size. The introduction of heterogeneity in movement rate did not affect estimator accuracy but did reduce precision.

Not surprisingly, estimator precision increased with camera effort. With 100 camera cells, confidence intervals were, on average, an order of magnitude smaller than in scenarios with 8 camera cells (Fig. 2).

DISCUSSION

The REST method accurately estimated human densities regardless of movement rate, home range size, and camera coverage in these scenarios. Increased density resulted in decreased precision because of the increased variability of staying times across cameras. Although movement rate and home range size did not affect estimator error, estimators were least precise in scenarios involving resting. Increased precision when volunteers were moving at slower paces continuously as opposed to moving and resting supports the theory that homogenous movements rates result in more precise estimates. Nakashima et al. (2018) noted that the REST method may be less precise for species that have long periods of inactivity because cameras rarely capture the target animal resting. Our human scenarios partially accounted for this potential bias by incorporating resting, in which volunteers did not move from their locations for approximately 38% of the survey period during 2 of the scenarios. Despite this lack of movement, the REST method was still able to estimate density in those scenarios; however, the estimates were less precise than other movement rates. Further testing of the effects of species with long periods of inactivity may be warranted. We deviated from Nakashima et al. (2018) by using boot-strapping rather than likelihood-based quantification of uncertainty. As such, we demonstrate the potential for unbiased estimation of staying time even where it does not necessarily follow a parametric distribution.

Nakashima et al. (2018) also suggested that cameras have sensitive sensor settings, no delay period between photos, or alternatively, take video recordings, and that the effective detection area be tested *in situ* according to methods proposed by Rowcliffe et al. (2011). We excluded potential effects of delayed camera capture rates and imperfect detectability by having each volunteer tracked every second. Camera capture rates and imperfect detectability, however, could present challenges in field settings when researchers use real cameras.

Environmental variation or attributes of the study species may influence detectability. Dense vegetation and inclement weather can decrease the effective detection areas of cameras, leading to overestimation of population density. Surveyors commonly clear vegetation blocking the camera view or deploy cameras in relatively open sites (Rowcliffe et al. 2011, Rovero et al. 2013, Villette et al. 2016). Additionally, researchers must account for the variation in the detection area of cameras between daytime and nighttime, with nighttime detection areas being more limited. Regardless of where cameras are placed, researchers need to measure the effective detection area of each camera in the field to accurately measure population densities (Nakashima et al. 2018).

Smaller species may be less detectable, resulting in lower capture rates and potentially causing underestimation, despite being present in the detection area (Tobler et al. 2008, Anile and Devillard 2016, Nakashima et al. 2018). Evaluation of the REST model across multiple species would complement our study for targeting its application.

MANAGEMENT IMPLICATIONS

Obtaining unbiased density estimates of unmarked terrestrial mammal populations continues to be a problem in wildlife management. Our evaluation of the REST method using human volunteers indicates the robustness of the method to variation in movement rate, home range size, and number of individuals estimated. Based on the results of the park scenarios, we suggest that future tests or applications of the REST method have >1% coverage of the study area to increase the precision of estimates. This method offers a cost-effective, unbiased means to estimate animal densities from motion-sensitive camera data without the use of marked individuals or estimates of home range sizes. The application of the REST method to motion-sensing camera studies may have the potential to improve monitoring efforts for several species, provided assumptions are met.

ACKNOWLEDGMENTS

We thank the University of Alberta Research Ethics Office for allowing us to complete this study, in addition to the 12 volunteers who participated in the park scenarios. We also thank E. K. for helpful comments and feedback on an earlier draft of this manuscript. Finally, we thank the University of Alberta and Natural Sciences and Engineering Research Council of Canada (NSERC) CREATE-EI scholarships for their financial support during this study.

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Associate Editor: Quresh Latif.

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