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Laura Garland  
*University of Alberta*

Eric Neilson  
*Canadian Forest Service Natural Resources Canada*

Tal Avgar  
*Utah State University*

Erin Bayne  
*University of Alberta*

Stan Boutin  
*University of Alberta*

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1 29 April 2020  
2 Laura Garland  
3 University of Alberta  
4 116 Street and 85 Avenue  
5 Edmonton, AB T6G 2R3  
6 780-492-3111  
7 lgarland@ualberta.ca

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9 **Random Encounter and Staying Time Model Testing with Human Volunteers**

10 LAURA GARLAND<sup>1</sup> *University of Alberta, 116 Street and 85 Avenue, Edmonton, AB T6G 2R3,*  
11 *Canada*

12 ERIC NEILSON, *Canadian Forest Service Natural Resources Canada, 5320-122 Street,*  
13 *Edmonton, AB T6H 3S5, Canada*

14 TAL AVGAR, *Utah State University, Old Main Hill, Logan, UT 84322, USA*

15 ERIN BAYNE, *University of Alberta, 116 Street and 85 Avenue, Edmonton, AB T6G 2R3,*  
16 *Canada*

17 STAN BOUTIN, *University of Alberta, 116 Street and 85 Avenue, Edmonton, AB T6G 2R3,*  
18 *Canada*

19 **ABSTRACT** Ecology and management programs designed to track population trends over time  
20 increasingly are using passive monitoring methods to estimate terrestrial mammal densities.  
21 Researchers use motion-sensing cameras in mammal studies because they are cost-effective and  
22 advances in statistical methods incorporate motion-sensing camera data to estimate mammal  
23 densities. Density estimation involving unmarked individuals, however, remains challenging and  
24 empirical tests of statistical models are relatively rare. We tested the random encounter and  
25 staying time model (REST), a new means of estimating the density of an unmarked population,

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<sup>1</sup> *Email: lgarland@ualberta.ca*

26 using human volunteers and simulated camera surveys. The REST method produced unbiased  
27 estimates of density, regardless of changes in human abundance, movement rates, home range  
28 sizes, or simulated camera effort. These advances in statistical methods when applied to motion-  
29 sensing camera data provide innovative avenues of large-mammal monitoring that have the  
30 potential to be applied to a broad spectrum of conservation and management studies, provided  
31 assumptions for the REST method are rigorously tested and met.

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

34 Abundance and density are fundamental ecological parameters that are difficult to measure  
35 because individuals move in and out of sample plots, and not all individuals present at sample  
36 units are detected (Royle and Nichols 2003). Heterogeneity in individual movement and  
37 presence at sample units necessitates estimating and correcting for the probability of detection.  
38 Count data from repeated surveys of sampling units fundamentally inform abundance estimates  
39 corrected for detection. Capture-mark-recapture (CMR) uses the marked individual as the sample  
40 unit with the pattern of captures over time assisting with abundance estimates (Seber 1982). In  
41 these cases, the model allows heterogeneity of capture probability among individuals (Pollock  
42 1982).

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

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

55           Researchers now commonly use motion-sensitive cameras to estimate habitat use,  
56 distribution, abundance, and density for unmarked wildlife populations (Burton et al. 2015).  
57 Minimal human intervention, reduced cost, and simplified logistics make camera surveys  
58 attractive for high profile species of conservation concern or in conditions that prevent direct  
59 observation or capture of individuals. Photos that identify individuals are useful in standard  
60 CMR methods, but photos of species that do not allow for individual identification can also be  
61 used to calculate abundance estimates using SECR models (Royle and Nichols 2003, Royle  
62 2004) and density (Chandler and Royle 2013, Ramsey et al. 2015).

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

72 Nakashima et al. (2018) modified Rowcliffe's original method to measure the staying  
 73 time of an individual within the detection area of remote cameras. They referred to this model as  
 74 the random encounter and staying time (REST) method. The REST model assumes that  
 75 researchers place cameras randomly relative to individual movement within the study area. With  
 76 this assumption, the residence time of an individual at any given detector is a function of the  
 77 duration of time the detector is deployed and the proportion of the study area it samples. Under  
 78 the assumption of random movement, residence time scales linearly with the number of  
 79 individuals, thereby allowing an estimate of density without the need to estimate rate of  
 80 movement, home range size, or individual identity. The model also does not require closure of  
 81 the study area in the sense that individuals do not leave or enter the area, but only that  
 82 immigration, emigration, births, and mortality are balanced during the study period.  
 83 The REST model calculates population density as a function of the residency time the target  
 84 species spends in front of a camera. The equation, modified from Nakashima et al. (2018) to  
 85 account for potentially different sampling durations and areas between cameras, is:

$$86 \quad \hat{\rho} = \frac{\sum_{i=1}^n t_i}{\sum_{i=1}^n T_i \times a_i},$$

87 (1)

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

91 If a camera records multiple individuals at the same time, the model estimates residency  
 92 time independently for each individual. Importantly, calculating the cumulative residence time ( $t$   
 93 in the above equation) does not require identifying distinct residency bouts, eliminating the need

94 to define a camera detection, simply sum the time individuals spend in front of each camera. This  
95 method is applicable to territorial and non-territorial species, provided researchers distribute  
96 cameras randomly in relation to animal space-use patterns (i.e., no baiting or placing cameras  
97 only in areas with preferred habitat characteristics).

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

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

113         We sought to test the REST method using known densities of human volunteers, which  
114 provided us with proof of concept. Human volunteers were advantageous because they allowed  
115 for more realistic movement paths than computer simulations. Our objective was to determine if  
116 movement rate, home range size, and density affected bias and precision of the estimates

117 produced by REST. We equipped human volunteers with global positioning system (GPS)  
118 devices and gave them precise movement rules such that home range size and movement rate  
119 were varied.

## 120 **STUDY AREA**

121 Our test took place at the Louise McKinney Riverfront Park in Edmonton, Alberta, Canada  
122 (53°N 113°W) on 16 and 23 September 2017. The entire park is approximately 4.0 ha in size and  
123 the weather on both days was clear and sunny (~15° C). The study area was approximately 1.5  
124 ha in size, and consisted of flat, open, grassy areas, walking paths, and a pavilion, all of which  
125 were accessible to the volunteers.

## 126 **METHODS**

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

134         We conducted 6 scenarios, each scenario being a different combination of movement  
135 rates and home range sizes. Each scenario lasted 16 minutes and included 3 movement patterns  
136 (jogging for 10 minutes and resting for 6 minutes, walking for 10 minutes and resting for 6  
137 minutes, and walking for 16 minutes continuously) performed within 2 home range sizes (0.75  
138 ha and 1.50 ha). We instructed volunteers to move independently of each other during each test  
139 but we synchronized their movement and rest periods.

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

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

155 We varied human densities to include 2, 6, and 12 people. We varied sampling effort by  
156 varying the number of cells selected randomly as camera deployments. We selected 8, 20, 50, or  
157 100 cells as camera deployment sites, resulting in 1%, 2.5%, 6.25%, and 12.5% coverage of the  
158 study area, respectively. We used 1,000 bootstrap samples with replacement of camera effort in  
159 each scenario of movement speed, human densities, and home range area for 72 different  
160 scenarios in R (R version 3.5.1, [www.r-project.org](http://www.r-project.org), accessed 10 Oct 2018). We estimated the  
161 density of human volunteers across each combination of movement speed, true human density,  
162 and home range area using equation 1. We then multiplied the resulting density by the area to



163 calculate abundance for comparison to the number of volunteers per scenario. We calculated  
164 means and confidence intervals across bootstrapped samples to estimate abundance and quantify  
165 precision (data and r code available online in Supporting Information).

## 166 **RESULTS**

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

173         In scenarios representing human densities of 2 people, we observed the least amount of  
174 error across all movement or home range size. In scenarios with 20 and 50 cameras, as human  
175 abundance in the park increased, precision decreased.

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

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

## 184 **DISCUSSION**

185 The REST method accurately estimated human densities regardless of movement rate, home  
186 range size, and camera coverage in these scenarios. Increased density resulted in decreased  
187 precision because of the increased variability of staying times across cameras. Although  
188 movement rate and home range size did not affect estimator error, estimators were least precise  
189 in scenarios involving resting. Increased precision when volunteers were moving at slower paces  
190 continuously as opposed to moving and resting supports the theory that homogenous movements  
191 rates result in more precise estimates. Nakashima et al. (2018) noted that the REST method may  
192 be less precise for species that have long periods of inactivity because cameras rarely capture the  
193 target animal resting. Our human scenarios partially accounted for this potential bias by  
194 incorporating resting, in which volunteers did not move from their locations for approximately  
195 38% of the survey period during 2 of the scenarios. Despite this lack of movement, the REST  
196 method was still able to estimate density in those scenarios; however, the estimates were less  
197 precise than other movement rates. Further testing of the effects of species with long periods of  
198 inactivity may be warranted. We deviated from Nakashima et al. (2018) by using boot-strapping  
199 rather than likelihood-based quantification of uncertainty. As such, we demonstrate the potential  
200 for unbiased estimation of staying time even where it does not necessarily follow a parametric  
201 distribution.

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

208 Environmental variation or attributes of the study species may influence detectability.  
209 Dense vegetation and inclement weather can decrease the effective detection areas of cameras,  
210 leading to overestimation of population density. Surveyors commonly clear vegetation blocking  
211 the camera view or deploy cameras in relatively open sites (Rowcliffe et al. 2011, Rovero et al.  
212 2013, Villette et al. 2016). Additionally, researchers must account for the variation in the  
213 detection area of cameras between daytime and nighttime, with nighttime detection areas being  
214 more limited. Regardless of where cameras are placed, researchers need to measure the effective  
215 detection area of each camera in the field to accurately measure population densities (Nakashima  
216 et al. 2018).

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

## 221 **MANAGEMENT IMPLICATIONS**

222 Obtaining unbiased density estimates of unmarked terrestrial mammal populations continues to  
223 be a problem in wildlife management. Our evaluation of the REST method using human  
224 volunteers indicates the robustness of the method to variation in movement rate, home range  
225 size, and number of individuals estimated. Based on the results of the park scenarios, we suggest  
226 that future tests or applications of the REST method have >1% coverage of the study area to  
227 increase the precision of estimates. This method offers a cost-effective, unbiased means to  
228 estimate animal densities from motion-sensitive camera data without the use of marked  
229 individuals or estimates of home range sizes. The application of the REST method to motion-

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230 sensing camera studies may have the potential to improve monitoring efforts for several species,  
231 provided assumptions are met.

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282 *Associate Editor: Quresh Latif.*

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284 **Figure Captions and Tables**

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

289 Figure 2. Bootstrapped mean estimates and 95% confidence intervals of human densities  
290 including 2, 6, and 12 people with motion-sensitive camera effort of 8, 20, 50, and 100 cameras  
291 across all 6 scenarios of movement rate and home range size in the Louise McKinney Riverfront  
292 Park, Edmonton, Alberta, Canada on 16 and 23 September 2017. Small (purple) and large  
293 (orange) in the legend refer to the home range size available to the volunteers, either 0.75 ha or  
294 1.5 ha, respectively. JogRest, Walk, and WalkRest refer to the movement rates in each scenario  
295 and are differentiated by triangles, circles, and squares, respectively.

296

297 Table 1. Movement rates of the human volunteers and home range sizes (ha) available in each  
 298 scenario on 16 and 23 September 2017 at the Louise McKinney Riverfront Park, Edmonton,  
 299 Alberta, Canada, where the cell area (m<sup>2</sup>) refers to the approximate cell size per scenario. We  
 300 recorded the duration of each scenario in seconds (s), and included the number of points tracked  
 301 per second (point freq).  
 302

Scenario	Home range (ha)	Movement rate	Duration (s)	Point freq (s)	Cell area (m <sup>2</sup> )	Total area (m <sup>2</sup> )
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



303 **Summary for online Table of Contents**

304 The random encounter and staying time (REST) method produced unbiased estimates of density,  
305 regardless of home range size and movement rate of human volunteers. Although our tests  
306 suggest the REST method may be a viable means of unmarked mammal density estimation,  
307 further testing of the REST method may be warranted to account for species with varying body  
308 sizes and periods of non-movement.

309

310

311