



### Challenges and opportunities in population monitoring of cheetahs

Journal:	<i>Population Ecology</i>
Manuscript ID	POEC-2019-0051.R2
Wiley - Manuscript type:	Original Article
Date Submitted by the Author:	26-Feb-2020
Complete List of Authors:	Linden, Daniel W.; NOAA Fisheries Service, Green, David; Michigan State University, Department of Integrative Biology Chelysheva, Elena; Mara-Meru Cheetah Project Mandela, Salim; Mara-Meru Cheetah Project Dloniak, Stephanie; Michigan State University, Department of Integrative Biology
Manuscript Category:	1.010: Applied ecology < 1: Field of ecology, 1.100: Population ecology < 1: Field of ecology, 2.040: Distribution and abundance < 2: Topic, 2.080: Spatial distribution < 2: Topic, 2.180: Statistical method < 2: Topic
Manuscript Keywords:	cheetah, Mara-Serengeti ecosystem, population monitoring, non-invasive sampling, spatial capture-recapture
Abstract:	<p>Population monitoring is key to wildlife conservation and management but is challenging at the spatial and temporal extents necessary for understanding changes. Non-invasive survey methods and spatial capture-recapture (SCR) models have revolutionized wildlife monitoring by providing the means to acquire data at large scales and the framework to generate spatially-explicit predictions, respectively.</p> <p>Despite opportunities for improved monitoring, challenges can remain in the study design and model fitting phases of an SCR approach. Here, we used a search-encounter design with multi-session SCR models to collect spatially-indexed photographs and estimate changes in density of cheetahs between 2005 and 2013–2016 in the Masai Mara National Reserve (MMNR) in Kenya. Our SCR models of cheetah encounters suggested little change in cheetah density from 2005 to 2013–2016, with some evidence that density fluctuated annually in the MMNR. The sampling period length (5 vs. 10 months) and timing (early, late, full year) over which spatial encounters were modeled did not alter inferences about density when sample sizes were adequate (&gt;20 spatially distinct encounters). Our average density estimate of ~1.2 cheetahs/100 km<sup>2</sup> is consistent with the impression that the MMNR provides important cheetah habitat in Africa. During most years, spatial distribution of vegetation greenness (proxy for ungulate habitat quality) accounted for important variation in encounter rates. The search-encounter design here could be applied to other regions for cheetah monitoring. While snap-shot estimates of population size across time are</p>

	useful for wildlife monitoring, open population models may better identify the mechanisms behind temporal changes.

SCHOLARONE™  
Manuscripts

1 *Original article*

2

3 **Challenges and opportunities in population monitoring of cheetahs**

4

5 Daniel W. Linden<sup>1\*</sup>, David S. Green<sup>2</sup>, Elena V. Chelysheva<sup>3</sup>, Salim Mandela Mandere<sup>3</sup>, and  
6 Stephanie M. Dloniak<sup>4</sup>

7 <sup>1</sup> NOAA National Marine Fisheries Service, Greater Atlantic Regional Fisheries Office,  
8 Gloucester, MA 01930, USA

9 <sup>2</sup> Institute for Natural Resources, Oregon State University, Corvallis, OR, 97331, USA

10 <sup>3</sup> Mara-Meru Cheetah Project, P.O. Box 1611, Sarit, Nairobi, Kenya

11 <sup>4</sup> Department of Integrative Biology, Michigan State University, East Lansing, MI, 45524, USA

12

13 \* Corresponding author: 55 Great Republic Drive, Gloucester, MA, 01922, USA;

14 daniel.linden@noaa.gov

15

16 \* These authors contributed equally.

17 **Abstract**

18 Population monitoring is key to wildlife conservation and management but is challenging at the  
19 spatial and temporal extents necessary for understanding changes. Non-invasive survey methods  
20 and spatial capture-recapture (SCR) models have revolutionized wildlife monitoring by  
21 providing the means to acquire data at large scales and the framework to generate spatially-  
22 explicit predictions, respectively. Despite opportunities for improved monitoring, challenges can  
23 remain in the study design and model fitting phases of an SCR approach. Here, we used a  
24 search-encounter design with multi-session SCR models to collect spatially-indexed photographs  
25 and estimate changes in density of cheetahs between 2005 and 2013–2016 in the Masai Mara  
26 National Reserve (MMNR) in Kenya. Our SCR models of cheetah encounters suggested little  
27 change in cheetah density from 2005 to 2013–2016, with some evidence that density fluctuated  
28 annually in the MMNR. The sampling period length (5 vs. 10 months) and timing (early, late,  
29 full year) over which spatial encounters were modeled did not alter inferences about density  
30 when sample sizes were adequate (>20 spatially distinct encounters). Our average density  
31 estimate of ~1.2 cheetahs/100 km<sup>2</sup> is consistent with the impression that the MMNR provides  
32 important cheetah habitat in Africa. During most years, spatial distribution of vegetation  
33 greenness (proxy for ungulate habitat quality) accounted for important variation in encounter  
34 rates. The search-encounter design here could be applied to other regions for cheetah  
35 monitoring. While snap-shot estimates of population size across time are useful for wildlife  
36 monitoring, open population models may better identify the mechanisms behind temporal  
37 changes.

38

39 **Keywords:** *Acinonyx jubatus*, cheetah, Masai Mara National Reserve, Mara-Serengeti  
40 ecosystem, non-invasive sampling, population monitoring, spatial capture-recapture

## 41 1. Introduction

42 Population monitoring is key to wildlife conservation and management but is challenging  
43 at the spatial and temporal extents necessary for understanding changes (Ellis et al. 2014).  
44 Monitoring over space and time requires a feasible scheme and persistence in both dedication  
45 and resources to obtain adequate information. Low replication in either dimension reduces the  
46 capacity to explain observed patterns or test hypotheses about perturbation, limiting the value of  
47 the monitoring data for informing conservation and management decisions (Yoccoz et al. 2001).  
48 The monitoring challenge has been particularly acute for wide-ranging, cryptic species that occur  
49 at low densities, such as carnivores. These life history features have historically made data  
50 collection and analysis difficult and reduced the opportunities for robust inference about  
51 population dynamics at relevant spatial and temporal scales (Karanth et al. 2006).

52 Non-invasive survey methods (Long et al. 2008) and spatial capture-recapture (SCR)  
53 models (Borchers and Efford 2008, Royle et al. 2014) have revolutionized wildlife population  
54 monitoring by providing the means to more easily acquire data at large scales and the framework  
55 to generate spatially-explicit predictions, respectively. In an SCR model, the locations of  
56 individual encounters (e.g., photographs, genetic material) are used to determine centers of  
57 activity for each observed individual, providing spatial information on the number of total  
58 individuals in the population and the probabilities of encountering them across the landscape.  
59 By formally linking the distributions of individuals and their movement ecology in a hierarchical  
60 framework, SCR models jointly estimate the ecological and observational processes that generate  
61 the spatial encounter data collected by large-scale monitoring designs, enabling robust inferences  
62 that are critical for conservation (Royle et al. 2018). These models have proven useful for  
63 estimating the density of wide-ranging carnivores, particularly in applications to large felids  
64 including tigers *Panthera tigris* (Royle et al. 2009), jaguars *Panthera onca* (Sollmann et al.  
65 2011), leopards *Panthera pardus* (Gray and Prum 2012) and cougars *Puma concolor* (Russell et  
66 al. 2012). Recently, the approach was illustrated using search-encounter surveys with African  
67 lions *Panthera leo* (Elliot and Gopaldaswamy 2017) and cheetahs *Acinonyx jubatus* (Broekhuis  
68 and Gopaldaswamy 2016). These applications have highlighted the potential of SCR as a  
69 monitoring tool, though rarely have studies spanned long enough timeframes to allow for  
70 examining temporal changes in population size or density at large scales (e.g., Chandler and  
71 Clark 2014).

72           Despite the opportunities for improved monitoring, challenges can remain in the study  
73 design and model fitting phases of a spatial capture-recapture approach. Sampling efforts may  
74 not yield enough unique spatial locations per individual to enable model fitting (Becker et al.  
75 2017), unless some type of auxiliary data is integrated (e.g., telemetry; Sollmann et al. 2013).  
76 Longer survey durations can be used to acquire more captures or encounters and improve  
77 parameter estimation (Dupont et al. 2019), at the expense of potentially violating assumptions  
78 regarding population closure (i.e., no births, deaths, immigrants/emigrants during sampling).  
79 The timing and duration of surveys will dictate the scope of the population being assessed,  
80 dependent on which individuals are available for sampling (e.g., residents vs. dispersers) and can  
81 meet assumptions of the observation process. Resource selection at one or more spatial scales  
82 can affect model inferences if not properly incorporated, particularly if it results in unmodeled  
83 heterogeneity in the encounter process (Royle et al. 2013, Linden et al. 2018). And small sample  
84 sizes, even when large enough to enable model fitting, may yet afford little power for  
85 accommodating relevant variation in one or more parameters which can reduce accuracy and  
86 precision of the resulting estimates (Sollmann et al. 2013). Most of these design and modeling  
87 considerations are important for any animal sampling and population estimation approach, and  
88 we note that explicitly modeling the sampling process does not necessarily obviate critical  
89 assumptions regarding how data were collected and what the data represent. For these reasons  
90 and others, it is prudent that researchers design robust monitoring schemes, use multiple lines of  
91 evidence, and temper any conclusions from monitoring data when making inferences that will  
92 guide conservation and management of large carnivore populations.

93           Here, we used a search-encounter design with SCR models (*sensu* Royle et al. 2011) to  
94 collect spatially-indexed photographs and estimate the changes in density of cheetahs between  
95 2005 and 2013–2016 in the Masai Mara National Reserve (MMNR) in southwestern Kenya.  
96 Cheetahs are currently listed globally as “vulnerable” with a decreasing total population (Durant  
97 et al. 2015, Durant et al. 2017) and while much of the current cheetah range exists outside of  
98 protected areas the populations within represent important strongholds for cheetah conservation  
99 (Durant et al. 2017). Few long-term studies have empirically estimated how cheetah populations  
100 are faring over time (Chauvenet et al. 2011, Durant et al. 2011), or have illustrated how changing  
101 landscapes around protected areas may be influencing wildlife within reserve boundaries.  
102 Carnivore populations in the MMNR have historically been high compared to other areas in sub-

103 Saharan Africa (Craft et al. 2015), and the Mara-Serengeti ecosystem is considered a stronghold  
104 for large carnivores in East Africa (Ogutu and Dublin 2002, Riggio et al. 2013). Yet,  
105 populations of wild herbivores in the MMNR have been declining over time (Ottichilo et al.  
106 2000, Ogutu et al. 2009, Ogutu et al. 2011), livestock often graze within reserve boundaries and  
107 anthropogenic disturbance has altered the behaviors and population numbers of other large  
108 carnivores (Boydston et al. 2003, Kolowski and Holekamp 2009, Green et al. 2018a), and  
109 rangelands around the MMNR are rapidly shifting into a matrix of urbanization and agriculture  
110 (Lamprey and Reid 2004, Løvschal et al. 2017).

111 Our initial SCR modeling efforts suggested a >50% decline in cheetah density between  
112 2005 and 2013 (Green et al. 2014). Broekhuis and Gopalaswamy (2016) provided a 2014  
113 population estimate for cheetahs within the greater Mara using a similar survey and SCR  
114 modeling approach; their results conflicted with our suggestion of a decline. We fit more  
115 extensive data from a multi-year survey effort (2005, 2013–2016) conducted during a longer  
116 sampling window (10 months) with sample sizes that afforded additional model complexity. In  
117 particular, we incorporated a resource selection function relating the probability of encounter to  
118 annual variance in green vegetation (i.e., Normalized Difference Vegetation Index [NDVI]) as an  
119 approximation to habitat quality for ungulate prey (Pettorelli et al. 2005, Bro-Jorgensen et al.  
120 2008). We hypothesized that cheetahs would be encountered more frequently in areas with high  
121 variation where vegetation changed drastically across the year in response to moisture (e.g., short  
122 grass), compared to low variance regions with relatively constant conditions (e.g., riparian forest  
123 or bare ground). We also compared inferences between 5-month (both an early and late season)  
124 and 10-month sampling periods to explore tradeoffs in the acquisition of encounters while trying  
125 to meet population closure assumptions. Our additional years of monitoring and subsequent  
126 modeling indicate that the Mara cheetah population may exhibit annual fluctuations due to  
127 movement between the MMNR, adjacent conservancies, and the Serengeti National Park,  
128 highlighting the importance of conservation and management efforts in those areas surrounding  
129 the reserve.

130

## 131 2. Materials and Methods

### 132 2.1 Study area and data collection

133 Our study took place in the 1510 km<sup>2</sup> Masai Mara National Reserve in southwestern  
134 Kenya (Figure 1). The MMNR is predominantly comprised of open grassland interspersed with  
135 riparian areas, supporting a high density and diversity of resident herbivores, which are also  
136 joined seasonally by migrant populations of wildebeest *Connochaetes taurinus*, zebra *Equus*  
137 *quagga*, and Thomson's gazelle *Eudorcas thomsonii* from the Serengeti National Park to the  
138 southwest and the Loita plains to the northeast (Bell 1971, Stelfox et al. 1986, Sinclair and  
139 Norton-Griffiths 1995). The MMNR is bounded by the border with Tanzania and the Serengeti  
140 National Park to the south, and is surrounded in all other directions by community conservancies,  
141 pastoralist communities, small towns, and agricultural lands (Figure 1). There are no fences or  
142 barriers encompassing the MMNR, and wildlife regularly move beyond its political borders.

143 We systematically searched for cheetahs in the MMNR from January to October in 2005  
144 and each year during 2013–2016 by dividing the MMNR into 6 sampling blocks roughly equal in  
145 size (Figure S1). Searches occurred between 0500 and 1900 h, during which time observers (1  
146 or 2) drove throughout one block looking for cheetahs in a single vehicle, periodically stopping  
147 and scanning the surrounding landscape with binoculars (Caro 1994). Main roads were followed  
148 when convenient but considerable time was spent off-road to cover all accessible areas of each  
149 block; survey effort was calculated as the number of hours spent searching a block on a given  
150 date. When a cheetah was sighted, we drove within 50 m of an individual or group of  
151 individuals and photographed both sides of each animal and recorded geographic coordinates,  
152 sex and age class. We identified each individual using the distinct pelage and tail ring patterns  
153 (Caro and Durant 1991, Chelysheva 2004) and limited our modeling to adults (not dependent on  
154 mother).

155 We acquired spatial raster data from the Famine Early Warning System Network hosted  
156 by the USGS/EROS Data Center (<https://earlywarning.usgs.gov/fews/>). The data included  
157 250 m resolution grids with 10-day NDVI values observed across each year (36 for a given year)  
158 for a region spanning most of East Africa. We calculated the standard deviation in NDVI value  
159 within a given year to approximate the seasonal variation within a given grid cell. Notable  
160 features that are apparent in every year include the vegetation along the Mara and Talek Rivers  
161 (Figure S2).



162

163 *2.2 Spatial capture-recapture model*

164 Similar to previous applications of spatial capture-recapture using unstructured search-  
 165 encounter designs (Russell et al. 2012, Broekhuis and Gopaldaswamy 2016), we divided our study  
 166 area (the MMNR) into a grid with a sufficiently low resolution (2-km  $\times$  2-km cells) to create  
 167 spatial encounter histories for individual cheetahs. We defined the number of encounters  $y_{ij}$  for  
 168 individual  $i$  in grid cell  $j$  as a Poisson-distributed random variable:

$$169 \quad y_{ij} \sim \text{Poisson}(\lambda_{ij}g_{ij})$$

170 Here,  $\lambda_{ij}$  is the mean encounter rate for an individual having its activity center ( $s_i$ ) within a given  
 171 grid cell, and  $g_{ij}$  is a detection function describing how encounter rate decreases as the distance  
 172 ( $d_{ij}$ ) increases between the location of an individual's activity center and the coordinates of grid  
 173 cell  $j$ . We chose a Gaussian encounter probability model such that  $g_{ij} = \exp(-d_{ij}^2/2\sigma_{sex}^2)$ , where  
 174  $\sigma_{sex}$  is a scale parameter representing the standard deviation of a bivariate normal distribution  
 175 used to approximate space usage (Royle et al. 2014), which was allowed to vary by sex  
 176 (Sollmann et al. 2011, Broekhuis and Gopaldaswamy 2016).

177 The mean encounter rate  $\lambda_{ij}$  was modeled as a function of several variables specific to an  
 178 individual and grid cell. We considered differences among years to account for potential factors  
 179 related to observers and the space-use of individual cheetahs in a given year. We also considered  
 180 two grid cell covariates for  $\lambda_{ij}$ : 1) the annual variance in NDVI for each year (standardized within  
 181 the year to have mean = 0 and unit variance); and 2) the log-transformed fraction of hours spent  
 182 searching a grid cell, given its location within 1 of the 6 search blocks. We included quadratic  
 183 functions for NDVI that were year-specific to accommodate resource selection by cheetahs in  
 184 response to spatial-temporal differences in vegetation within the Mara across years. The effect  
 185 of search effort was constrained similar to a Poisson offset, though we estimated a regression  
 186 coefficient instead of assuming it was 1. Finally, we allowed the encounter rate to vary by sex,  
 187 with an effect estimated for males. As such, we modeled the log-linear encounter rate ( $\lambda_{ij}$ ) as:

$$188 \quad \log(\lambda_{ij}) = \alpha_0 + \alpha_{1,yr} + \alpha_{2,yr} \text{NDVI}_{yr[i],j} + \alpha_{3,yr} \text{NDVI}_{yr[i],j}^2 + \alpha_4 \text{EFFORT}_{yr[i],j} + \alpha_5 \text{SEX}_i$$

189 Here,  $\alpha_0$  is the baseline encounter rate on the log scale for an individual female captured in 2005;  
 190  $\alpha_{1,yr}$  is a vector of year-specific coefficients for differences in encounter rates of individuals  
 191 observed in later years ( $yr[i] = 2013, 2014, 2015, \text{ or } 2016$ );  $\alpha_{2,yr}$  and  $\alpha_{3,yr}$  are vectors of year-

192 specific coefficients for the linear and quadratic effects, respectively, of the variance in NDVI for  
 193 each grid cell in each year;  $\alpha_4$  is a coefficient describing the relationship between encounter rate  
 194 and search effort in a given grid cell and year; and  $\alpha_5$  is the difference in encounter rate for males  
 195 compared to females.

196 We considered encounters separated by  $\geq 5$  days to represent independent events with  
 197 regards to individual movement and encounter probability and, therefore, thinned 18–35% of the  
 198 total encounters in a given year to help meet model assumptions. A similar design-based  
 199 thinning is sometimes necessary in resource selection studies when temporal autocorrelation in  
 200 the locational fix data (e.g., collected via telemetry or GPS technology) is not explicitly modeled  
 201 (Manly et al. 2002). Adult male cheetahs regularly form coalitions with other males (Caro and  
 202 Collins 1987) and we observed them doing so in the MMNR (~60% of male sightings involved  
 203 coalitions). Despite this, we treated each sighting as an independent observation given that  
 204 coalitions were sometimes observed to exhibit fission-fusion dynamics and that the  
 205 independence assumption for activity centers has been shown to be robust to departures (Reich  
 206 and Gardner 2014).

207 We modeled the distribution of latent activity centers using an inhomogeneous point  
 208 process (Borchers and Efford 2008) to estimate variation in cheetah density over the years. We  
 209 expanded the 2-km resolution grid of the MMNR to include a 20-km buffer (Figure S1), which  
 210 was large enough to ensure a negligible encounter probability at the edges (Royle et al. 2014);  
 211 we also excluded the northwest escarpment, which was likely to have restricted cheetah  
 212 movement (Broekhuis and Gopalaswamy 2016). The total state space,  $S$ , of the point process  
 213 therefore included 1,381 discrete grid cells for a total area of 5,524 km<sup>2</sup>. The intensity of the  
 214 point process (i.e., the expected density) within a grid cell  $j$  in a given year was a log-linear  
 215 function:

$$216 \quad \log(E(D_{j,\text{yr}})) = \beta_0 + \beta_{1,\text{yr}}$$

217 Here,  $\beta_0$  is the log-scale expected cheetah density in 2005, while  $\beta_{1,\text{yr}}$  is a vector of year-specific  
 218 regression coefficients that estimate differences in expected density in later years (yr = 2013,  
 219 2014, 2015, or 2016). Conditional on the expected density for the year in which an individual  
 220 was encountered ( $\text{yr}_i$ ), the probability of an individual's activity center being located within a  
 221 given grid cell was defined as:

$$222 \quad \Pr(s_i = j | \boldsymbol{\beta}, y_{r_i}) = \frac{E(D_{j,yr})}{\sum_j E(D_{j,yr})}$$

223 The marginal likelihood of the observations for each individual are then computed by integrating  
224 over all possible grid cells.

225

### 226 *2.3 Model fitting and sample period comparison*

227 We fit the model using the multi-session sex-structured SCR framework in the R package  
228 `oSCR` (Sutherland et al. 2016, Sutherland et al. 2019) which maximizes the Poisson-integrated  
229 likelihood (Borchers and Efford 2008) and provides maximum likelihood estimates of model  
230 parameters. In addition to the parameters previously described, `oSCR` allows for estimating a  
231 sex ratio ( $\psi$ ). With specification of sex-specific parameters in various SCR model components,  
232 estimates of  $\psi$  are a function of the observed sex ratios of encountered individuals during each  
233 session (here, session = year) and differences in encounter probability, if any, between sexes.

234 We compared several sampling periods (early 5 months, full 10 months, late 5 months) to  
235 examine how differences in the observed data and parameter estimates affected population  
236 inferences. The early period spanned Jan–May and corresponded to a mostly hot and dry season  
237 that turns into long and heavy rains by May. The late period spanned Jun–Oct and corresponded  
238 to the cool season that follows the heavy rain season, during which widespread green vegetation  
239 supports a massive ungulate migration (Bell 1971, Sinclair and Norton-Griffiths 1995). This late  
240 period was similar to the 3-month sampling design (August–October) used by Broekhuis and  
241 Gopaldaswamy (2016). The full 10-month sampling period spanned most of the year (Jan–Oct)  
242 and, while facilitating more observations and larger sample sizes of individuals and spatial  
243 encounters, was likely to violate the assumption of population closure to a greater degree than  
244 the 5-month periods. Aside from differences in the density estimates across time we were  
245 particularly interested in how other model parameters might change with variation in the number  
246 and type of spatial encounters, including the estimated NDVI relationships with encounter rate,  
247 sex ratios, and individual movement scale.

248

### 249 3. Results

250 Monitoring efforts resulted in >7000 hours spent searching for and recording observations of  
251 cheetahs in the MMNR during 2005 and 2013–2016. The average number of hours searched  
252 each year was 1443 (range: 1086–1694) for the 10-month sampling period, which split into 623  
253 (range: 513–790) for the early 5-month period and 820 (range: 573–989) for the late 5-month  
254 period (Table 1). Compared to either 5-month period, the increased sampling effort for the full  
255 10 months always resulted in greater numbers (within a given year) of unique individuals  
256 encountered (median across years: full = 32, early = 20, late = 23), total encounter events (full =  
257 101, early = 40, late = 60), and spatially distinct encounters (full = 58, early = 18, late = 28).  
258 The observed sex ratios were variable depending on the year and sampling period, though on a  
259 whole the median ratio was 1:1. We plotted the unique individuals encountered each year  
260 according to the midpoint ordinal date of their encounters (mean of first and last dates seen),  
261 indicating the sampling period(s) in which they were observed (Figure 2). The patterns indicated  
262 similar ratios of females to males observed during all sampling period definitions.

263 The spatial capture-recapture models indicated similar patterns in density variation over  
264 time (Table 2;  
265 Figure 3), though fluctuations were mostly small relative to the uncertainty. The density  
266 estimates from 2005 had very large confidence intervals for the 5-month sampling periods due to  
267 small sample sizes. The full period density estimate (with 95% CI) for 2005 was 1.67 (1.05–  
268 2.65) cheetahs/100 km<sup>2</sup>. During 2013–2016, mean estimated density ranged from 0.61 (0.34–  
269 1.10) cheetahs/100 km<sup>2</sup> in 2013 to 1.67 (1.00–2.80) cheetahs/100 km<sup>2</sup> in 2014, and estimates  
270 matched closely across sampling periods within a given year. Precision of the density estimates  
271 was better for the 10-month sampling period, particularly with regards to the coefficients of  
272 variation (Table S1). Regardless of the sampling period, density estimates with a CV <0.30  
273 could be achieved with >20 spatially distinct encounters (Figure 4).

274 The relationships between encounter rate and NDVI variance were variable across years  
275 and across sampling periods within a year (Table 2; Figure 5). For most years and sampling  
276 periods, the maximum encounter rates occurred at mid to high values of relative NDVI variance.  
277 The early period in 2016 was the primary exception, suggesting higher encounter rates for  
278 cheetahs in low variance areas during Jan–May. The hours spent searching a grid cell (given the  
279 survey block within which it was located) had a strong positive relationship with encounter rate,

280 and average encounter rates were higher in later years (2013–2016) compared to 2005.  
281 Encounter rates were lower for males than females across all sampling periods, with the  
282 strongest evidence of an effect for the full sampling period ( $\alpha_5 = -0.408$  [SE: 0.162]). The scale  
283 parameter of the half-normal distance function indicated more variation across sampling periods  
284 than between sexes; estimates were smaller during the early 5-month period ( $\sigma_F = 4.9$  km [4.2–  
285 5.6 km];  $\sigma_M = 4.9$  km [4.1–5.8 km]) compared to the late 5-month period ( $\sigma_F = 7.6$  km [6.4–8.9  
286 km];  $\sigma_M = 8.8$  km [7.3–10.7 km]), with the full 10-month period falling between ( $\sigma_F = 7.0$  km  
287 [6.4–7.8 km];  $\sigma_M = 6.8$  km [6.1–7.7 km]).

288 The sex ratios were estimated to be largely even across all years and sampling periods as  
289 none of the logit-scale estimates were significantly different from 0 (Table 2), suggesting that the  
290 probability of an individual being a male did not vary considerably from ~0.50. While mean  
291 estimates of  $\psi$  ranged from  $-0.65$  to  $0.56$  on the logit scale (suggesting a range in  $\text{Pr}(\text{sex}=\text{M})$  of  
292  $0.34$  to  $0.64$ ), the large standard errors indicated these differences were not meaningful.

#### 294 4. Discussion

295 Effective wildlife population monitoring spans enough time and space to detect change or  
296 variation that may require further investigation or be targeted for management action. In  
297 addition to adequate spatial and temporal extents, the sampling intensity needs to produce  
298 enough observations to ensure reasonable precision from statistical models designed to estimate  
299 population parameters. Our spatial capture-recapture models of cheetah encounters suggested  
300 little change in cheetah density from 2005 to 2013–2016 in the Masai Mara National Reserve,  
301 though there was some evidence that density fluctuated annually in recent years. The sampling  
302 period length (5 vs. 10 months) and timing (early, late, full year) over which spatial encounters  
303 were included in the modeling did not substantially alter inferences about density when sample  
304 sizes were adequate (e.g.,  $\geq 20$  spatially distinct encounters). This suggests some flexibility in the  
305 design of search-encounter surveys for monitoring cheetahs over large landscapes.

306 We estimated an average cheetah density of  $\sim 1.2$  cheetahs/100 km<sup>2</sup>, consistent with the  
307 impression that the MMNR provides important habitat for cheetahs in Africa. Cheetah density  
308 varies extensively throughout the current species range, from 0.02 cheetahs/100 km<sup>2</sup> in areas of  
309 low productivity (Belbachir et al. 2015) to  $>2$  cheetahs/100 km<sup>2</sup> in the highly productive  
310 Serengeti (Durant et al. 2011, Durant et al. 2017). Broekhuis and Gopalaswamy (2016) used a

311 similar search encounter design with SCR modeling and estimated a mean cheetah density of  
312  $\sim 1.3$  cheetahs/100 km<sup>2</sup> in the MMNR and surrounding conservancies in 2014, which is  
313 consistent with our 2014 estimate from the late period (1.35 cheetahs/100 km<sup>2</sup>). Our additional  
314 years of monitoring indicated that density in some years may be nearly half that which was  
315 estimated in 2014.

316 Long-term studies of cheetah population trends in the Mara-Serengeti ecosystem have  
317 indicated a relatively stable density in recent years (Chauvenet et al. 2011, Durant et al. 2011). If  
318 the density fluctuation we estimated during 2013–2016 represents a real ecological phenomenon,  
319 as opposed to sampling variability, then our comparison with 2005 is difficult to interpret, given  
320 that this single year could have represented either ebb or flow for the cheetah population. It  
321 could also be argued that none of our density estimates are meaningfully different from each  
322 other. Therefore, it is unclear whether cheetah density has declined in the MMNR during the  
323 past 10+ years. This uncertainty highlights the value of long-term monitoring programs, but also  
324 of monitoring designs that can estimate population size with useful precision. Our population  
325 modeling was limited to adult cheetahs and many individuals were encountered during only a  
326 portion of the year (Figure 2), therefore, population fluctuation in the MMNR is likely due to  
327 variable movement between the reserve and surrounding areas (e.g., Serengeti National Park).  
328 The magnitude of individual movements in cheetahs could make annual density an erratic  
329 statistic for an area the size of the MMNR (1510 km<sup>2</sup>), especially in the presence of non-resident,  
330 “floater” males (Caro 1994). Density estimation from SCR modeling is generally robust to  
331 transient individuals, though such movement dynamics could be explicitly modeled (Royle et al.  
332 2016).

333 Based on the estimate of  $\sigma$  from the distance function (Royle et al. 2014), the mean 95%  
334 space use or home range area ranged from  $\sim 450$  to  $\sim 1,500$  km<sup>2</sup> in the MMNR. Cheetah home  
335 ranges can be similar in size for males and females and overlap in areas where prey are non-  
336 migratory (Broomhall et al. 2003). In contrast, where ungulate prey are migratory, home ranges  
337 are comparatively larger with males forming small territories and females exhibiting roving  
338 behaviors (Caro 1994). Although there is a seasonal influx of migrant herbivores into the  
339 MMNR each year (Bell 1971, Stelfox et al. 1986, Sinclair and Norton-Griffiths 1995), resident  
340 herbivores are also present year-round in relatively high numbers. Thus, movements by cheetahs  
341 in the MMNR may be better predicted by interspecific competition with other large carnivores

342 (Broekhuis et al. 2013) or the direct and indirect effects of people, rather than habitat suitability  
343 or prey populations. We caution any interpretation of the 95% space use approximation given  
344 the circular assumption of the bivariate normal distribution for  $\sigma$  (Royle et al. 2014). In addition,  
345 cheetah space use has been shown to be highly concentrated within a small portion of the home  
346 range (~14% of the total area), even for individuals that otherwise occupy large areas (Marker et  
347 al. 2008).

348         Several differences between our study and that of Broekhuis and Gopalaswamy (2016)  
349 warrant discussion, given the similarity in our approaches to collecting and modeling spatial  
350 encounters of cheetahs in the Mara. First, Broekhuis and Gopalaswamy (2016) modeled the  
351 daily encounter probability over 3 months of sampling, while we summed our encounters over  
352 the relevant sampling period (5 or 10 months) and treated the counts as a Poisson random  
353 variable; given the low rates of encounter, these choices should have had a negligible influence  
354 (Royle et al. 2014). Second, our calculations of effort differed and the approach of Broekhuis  
355 and Gopalaswamy (2016) using summation of GPS search tracks was preferable. We did not  
356 have GPS track records for 2005 and instead attempted to systematically search pre-defined  
357 sections (i.e., blocks) of the MMNR for various lengths of time; such a definition of effort is  
358 approximate at best, though blocks were searched thoroughly when visited. Third, we observed  
359 a fairly even sex ratio of cheetahs that remained constant over the 5 years of surveys and is  
360 consistent with previous research in the Mara-Serengeti (Kelly et al. 1998). The extremely  
361 skewed ratio (F:M = 5:1) observed by Broekhuis and Gopalaswamy (2016) was potentially an  
362 artefact of a low sample size and short survey duration (3 months), though it should also be noted  
363 that over half of their survey effort was in the conservancies to the north of the MMNR. Finally,  
364 Broekhuis and Gopalaswamy (2016) estimated a large difference in the scale parameter ( $\sigma$ )  
365 between females and males while our estimates indicated no strong evidence of a difference; it  
366 could be noted, however, that our largest mean difference occurred for the late period (Jun–Oct),  
367 the period that overlapped the timing of their survey the closest. Despite the contrasting details,  
368 the close similarity in our cheetah density estimates provides empirical support to the robustness  
369 of SCR modeling (Royle et al. 2014).

370         Improvements to the design of our search-encounter survey could make the effort more  
371 efficient and useful in other parts of the species range. We thinned almost 1/3 of our observed  
372 cheetah encounters before fitting the SCR models because of uneven effort across space and



373 time. Ideally, areas would be searched with regular periodicity to ensure that inferences  
374 regarding individual movement matched in temporal scale at all spatial locations. This is  
375 typically the case for other common methods of collecting spatial encounters (e.g., camera  
376 trapping), where traps are operated on regular intervals (Royle et al. 2014). The problem of  
377 sampling regularity would be most acute for transient individuals; for example, 5 consecutive  
378 days of effort in a given location could yield a very different collection of encounters than 5 days  
379 spread across several months. Integrating more complex movement processes and explicitly  
380 modeling the spatiotemporal dependence in movement could make use of all encounters  
381 regardless of sampling design (Borchers et al. 2014). Uneven spatial sampling makes the  
382 interpretation of posterior density surfaces from SCR models especially problematic and prone to  
383 artefacts (Efford 2018a), relegating the identification of “hot spots” (e.g., Broekhuis and  
384 Gopalaswamy 2016) to random error. Finally, the ability to traverse the landscape and get close  
385 enough to individuals for high quality photographs could limit the application of this survey to  
386 certain regions (e.g., protected areas and open habitats). While long-range camera lenses may  
387 provide expanded opportunities for monitoring, it could still be difficult to clearly photograph  
388 both sides of every individual at great distances, ultimately increasing identification uncertainty  
389 (Augustine et al. 2018).

390 Other aspects of cheetah population ecology could be modeled with different or more  
391 complex analytical approaches to the individual encounter data we generated with the surveys.  
392 Our primary objective was a comparison between 2005 and 2013–2016, so we focused on  
393 understanding how best to estimate density within a given year (or seasonal period), while  
394 accommodating the sparse data from 2005. We hypothesized that individual space use and, thus,  
395 encounter probability would vary by habitat attributes and used NDVI variance as a proxy for  
396 ungulate habitat quality (Pettorelli et al. 2005, Bro-Jorgensen et al. 2008); in most years and  
397 seasonal periods, the spatial distribution of NDVI variance accounted for important variation in  
398 encounter rates. An open population model (Kendall et al. 1997) would allow for estimating  
399 survival and temporary emigration and potentially enable more comprehensive inferences than  
400 “snap-shot” density estimates (Harmsen et al. 2017). While open-population SCR models  
401 provide the opportunity to integrate spatial explicitness into estimation and prediction (e.g.,  
402 Green et al. 2018b), the Bayesian frameworks typically used for fitting such models are  
403 notoriously slow and computationally demanding for complex spatiotemporal inferences. New



404 approaches using maximum likelihood and hidden Markov models could provide promising  
405 alternatives (Efford 2018b, Glennie et al. 2019). Snap-shot estimates of population size across  
406 time are useful for wildlife monitoring, but understanding the mechanisms behind population  
407 changes can facilitate better conservation and management decision making (Harmsen et al.  
408 2017).

409

## 410 **5. Acknowledgements**

411 We thank the Kenya Wildlife Service; National Commission for Science, Technology  
412 and Innovation (NACOSTI, Kenya); Narok County Government; the Office of the President of  
413 Kenya; the Senior Warden of the Masai Mara National Reserve, and Mr. Brian Heath (CEO,  
414 Mara Conservancy) for the permissions to carry out this research. We also thank Kay E.  
415 Holekamp for providing assistance in the field and we thank the many local guides for  
416 information about cheetah activity in the Mara. SMD was supported by grants from the Lakeside  
417 Foundation, Mr. Paul L. Davies II, and Dalbit Petroleum Ltd. DSG was supported by a Graduate  
418 Research Fellowship from the National Science Foundation. EVC was supported by the Cheetah  
419 Conservation Fund, Namibia, and Roman Wildlife Foundation. This research is presented in  
420 memory of Mr. Paul L. Davies II.

421

## 422 **6. References**

- 423 Augustine, B. C., J. A. Royle, M. J. Kelly, C. B. Satter, R. S. Alonso, E. E. Boydston, and K. R.  
424 Crooks. 2018. Spatial capture-recapture with partial identity: An application to camera  
425 traps. *Annals of Applied Statistics* 12:67-95.
- 426 Becker, M. S., S. M. Durant, F. G. R. Watson, M. Parker, D. Gottelli, J. M'soka, E. Droge, M.  
427 Nyirenda, P. Schuette, S. Dunkley, and R. Brummer. 2017. Using dogs to find cats:  
428 detection dogs as a survey method for wide-ranging cheetah. *Journal of Zoology*  
429 302:184-192.
- 430 Belbachir, F., N. Pettorelli, T. Wachter, A. Belbachir-Bazi, and S. M. Durant. 2015. Monitoring  
431 rarity: the critically endangered Saharan cheetah as a flagship species for a threatened  
432 ecosystem. *Plos One* 10:e0115136.
- 433 Bell, R. H. 1971. A grazing ecosystem in the Serengeti. *Scientific American* 225:86-93.

- 434 Borchers, D., G. Distiller, R. Foster, B. Harmsen, and L. Milazzo. 2014. Continuous-time  
435 spatially explicit capture–recapture models, with an application to a jaguar camera-trap  
436 survey. *Methods in Ecology and Evolution* 5:656-665.
- 437 Borchers, D. L. and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for  
438 capture-recapture studies. *Biometrics* 64:377-385.
- 439 Boydston, E. E., K. M. Kapheim, H. E. Watts, M. Szykman, and K. E. Holekamp. 2003. Altered  
440 behaviour in spotted hyenas associated with increased human activity. Pages 207-219 *in*  
441 *Animal Conservation forum*. Cambridge University Press.
- 442 Bro-Jorgensen, J., M. E. Brown, and N. Pettorelli. 2008. Using the satellite-derived normalized  
443 difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding  
444 antelope: the importance of scale. *Oecologia* 158:177-182.
- 445 Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald. 2013. Risk avoidance  
446 in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*  
447 82:1098-1105.
- 448 Broekhuis, F. and A. M. Gopalaswamy. 2016. Counting Cats: Spatially Explicit Population  
449 Estimates of Cheetah (*Acinonyx jubatus*) Using Unstructured Sampling Data. *Plos One*  
450 11:e0153875.
- 451 Broomhall, L., M. Mills, and J. Du Toit. 2003. Home range and habitat use by cheetahs  
452 (*Acinonyx jubatus*) in the Kruger National Park. *Journal of Zoology* 261:119-128.
- 453 Caro, T. 1994. *Cheetahs of the Serengeti Plains: group living in an asocial species*. University of  
454 Chicago Press.
- 455 Caro, T. and D. Collins. 1987. Male cheetah social organization and territoriality. *Ethology*  
456 74:52-64.
- 457 Caro, T. and S. Durant. 1991. Use of quantitative analyses of pelage characteristics to reveal  
458 family resemblances in genetically monomorphic cheetahs. *Journal of Heredity* 82:8-14.
- 459 Chandler, R. B. and J. D. Clark. 2014. Spatially explicit integrated population models. *Methods*  
460 *in Ecology and Evolution* 5:1351-1360.
- 461 Chauvenet, A. L., S. M. Durant, R. Hilborn, and N. Pettorelli. 2011. Unintended consequences of  
462 conservation actions: managing disease in complex ecosystems. *Plos One* 6:e28671.
- 463 Chelysheva, E. 2004. A new approach to cheetah identification. *Cat news* 41:27-29.

- 464 Craft, M. E., K. Hampson, J. O. Ogutu, and S. M. Durant. 2015. Carnivore communities in the  
465 greater Serengeti ecosystem. Pages 419-450 in A. R. E. Sinclair, K. L. Metzger, S. A. R.  
466 Mduma, and J. M. Fryxell, editors. Serengeti IV: sustaining biodiversity in a coupled  
467 human-natural system. The University of Chicago Press, Chicago, USA.
- 468 Dupont, P., C. Milleret, O. Gimenez, and R. Bischof. 2019. Population closure and the bias-  
469 precision trade-off in spatial capture–recapture. *Methods in Ecology and Evolution*  
470 10:661-672.
- 471 Durant, S., N. Mitchell, A. Ipavec, and R. Groom. 2015. *Acinonyx jubatus*. The IUCN Red List  
472 of Threatened Species 2015. e. T219A50649567.
- 473 Durant, S. M., M. E. Craft, R. Hilborn, S. Bashir, J. Hando, and L. Thomas. 2011. Long-term  
474 trends in carnivore abundance using distance sampling in Serengeti National Park,  
475 Tanzania. *Journal of Applied Ecology* 48:1490-1500.
- 476 Durant, S. M., N. Mitchell, R. Groom, N. Pettoelli, A. Ipavec, A. P. Jacobson, R. Woodroffe, M.  
477 Böhm, L. T. B. Hunter, M. S. Becker, F. Broekhuis, S. Bashir, L. Andresen, O.  
478 Aschenborn, M. Beddiaf, F. Belbachir, A. Belbachir-Bazi, A. Berbash, I. Brandao de  
479 Matos Machado, C. Breitenmoser, M. Chege, D. Cilliers, H. Davies-Mostert, A. J.  
480 Dickman, F. Ezekiel, M. S. Farhadinia, P. Funston, P. Henschel, J. Horgan, H. H. de  
481 Iongh, H. Jowkar, R. Klein, P. A. Lindsey, L. Marker, K. Marnewick, J. Melzheimer, J.  
482 Merkle, J. M'soka, M. Msuha, H. O'Neill, M. Parker, G. Purchase, S. Sahailou, Y. Saidu,  
483 A. Samna, A. Schmidt-Küntzel, E. Selebatso, E. A. Sogbohossou, A. Sultant, E. Stone,  
484 E. van der Meer, R. van Vuuren, M. Wykstra, and K. Young-Overton. 2017. The global  
485 decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of*  
486 *the National Academy of Sciences* 114:528-533.
- 487 Efford, M. G. 2018a. Density surfaces in secr 3.1. [http://www.otago.ac.nz/density/pdfs/secret-](http://www.otago.ac.nz/density/pdfs/secret-densitysurfaces.pdf)  
488 [densitysurfaces.pdf](http://www.otago.ac.nz/density/pdfs/secret-densitysurfaces.pdf) Last Accessed 23 Feb 2018.
- 489 Efford, M. G. 2018b. openCR: Open Population Capture-Recapture. R package version 1.3.2.  
490 <https://cran.r-project.org/package=openCR>.
- 491 Elliot, N. B. and A. M. Gopalaswamy. 2017. Toward accurate and precise estimates of lion  
492 density. *Conservation Biology* 31:934-943.

- 493 Ellis, M. M., J. S. Ivan, and M. K. Schwartz. 2014. Spatially explicit power analyses for  
494 occupancy-based monitoring of wolverine in the U.S. Rocky Mountains. *Conservation*  
495 *Biology* 28:52-62.
- 496 Glennie, R., D. L. Borchers, M. Murchie, B. J. Harmsen, and R. J. Foster. 2019. Open population  
497 maximum likelihood spatial capture-recapture. *Biometrics* XX:XXX. doi:  
498 10.1111/biom.13078.
- 499 Gray, T. N. E. and S. Prum. 2012. Leopard density in post-conflict landscape, Cambodia:  
500 Evidence from spatially explicit capture-recapture. *Journal of Wildlife Management*  
501 76:163-169.
- 502 Green, D. S., L. Johnson-Ulrich, H. E. Couraud, and K. E. Holekamp. 2018a. Anthropogenic  
503 disturbance induces opposing population trends in spotted hyenas and African lions.  
504 *Biodiversity and Conservation* 27:871-889.
- 505 Green, D. S., D. W. Linden, E. V. Chelysheva, and S. M. Dloniak. 2014. Estimating changes in  
506 cheetah density and distribution in the Mara-Serengeti ecosystem with spatial capture-  
507 recapture (SCR). The Wildlife Society 21st Annual Conference, Pittsburgh, PA. DOI:  
508 10.13140/RG.2.2.34678.86086.
- 509 Green, D. S., S. M. Matthews, R. C. Swiers, R. L. Callas, J. Scott Yaeger, S. L. Farber, M. K.  
510 Schwartz, and R. A. Powell. 2018b. Dynamic occupancy modelling reveals a hierarchy of  
511 competition among fishers, grey foxes and ringtails. *Journal of Animal Ecology* 87:813-  
512 824.
- 513 Harmsen, B. J., R. J. Foster, E. Sanchez, C. E. Gutierrez-González, S. C. Silver, L. E. T. Ostro,  
514 M. J. Kelly, E. Kay, and H. Quigley. 2017. Long term monitoring of jaguars in the  
515 Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of  
516 carnivores. *Plos One* 12:e0179505.
- 517 Karanth, K. U., J. D. Nichols, N. S. Kumar, and J. E. Hines. 2006. Assessing tiger population  
518 dynamics using photographic capture–recapture sampling. *Ecology* 87:2925-2937.
- 519 Kelly, M. J., M. K. Laurenson, C. D. FitzGibbon, D. A. Collins, S. M. Durant, G. W. Frame, B.  
520 C. Bertram, and T. Caro. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*)  
521 population: the first 25 years. *Journal of Zoology* 244:473-488.
- 522 Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using  
523 capture–recapture data with Pollock’s robust design. *Ecology* 78:563-578.

- 524 Kolowski, J. and K. Holekamp. 2009. Ecological and anthropogenic influences on space use by  
525 spotted hyaenas. *Journal of Zoology* 277:23-36.
- 526 Lamprey, R. H. and R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara:  
527 what future for pastoralism and wildlife? *Journal of Biogeography* 31:997-1032.
- 528 Linden, D. W., A. P. K. Sirén, and P. J. Pekins. 2018. Integrating telemetry data into spatial  
529 capture–recapture modifies inferences on multi-scale resource selection. *Ecosphere*  
530 9:e02203.
- 531 Long, R. A., P. MacKay, J. Ray, and W. Zielinski. 2008. Noninvasive survey methods for  
532 carnivores. Island Press, Washington, DC, USA.
- 533 Løvschal, M., P. K. Bøcher, J. Pilgaard, I. Amoke, A. Odingo, A. Thuo, and J.-C. Svenning.  
534 2017. Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Scientific*  
535 *Reports* 7:41450.
- 536 Manly, B., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. Resource selection  
537 by animals: statistical analysis and design for field studies. Second edition. Kluwer Press,  
538 New York, New York, USA.
- 539 Marker, L., A. Dickman, M. G. Mills, R. Jeo, and D. W. Macdonald. 2008. Spatial ecology of  
540 cheetahs on north-central Namibian farmlands. *Journal of Zoology* 274:226-238.
- 541 Ogutu, J. and H. Dublin. 2002. Demography of lions in relation to prey and habitat in the Maasai  
542 Mara National Reserve, Kenya. *African Journal of Ecology* 40:120-129.
- 543 Ogutu, J. O., N. Owen-Smith, H. P. Piepho, and M. Y. Said. 2011. Continuing wildlife  
544 population declines and range contraction in the Mara region of Kenya during 1977-  
545 2009. *Journal of Zoology* 285:99-109.
- 546 Ogutu, J. O., H. P. Piepho, H. Dublin, N. Bhola, and R. S. Reid. 2009. Dynamics of Mara–  
547 Serengeti ungulates in relation to land use changes. *Journal of Zoology* 278:1-14.
- 548 Ottichilo, W. K., J. De Leeuw, A. K. Skidmore, H. H. Prins, and M. Y. Said. 2000. Population  
549 trends of large non-migratory wild herbivores and livestock in the Masai Mara  
550 ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology* 38:202-216.
- 551 Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005.  
552 Using the satellite-derived NDVI to assess ecological responses to environmental change.  
553 *Trends in Ecology & Evolution* 20:503-510.

- 554 Reich, B. J. and B. Gardner. 2014. A spatial capture-recapture model for territorial species.  
555 *Environmetrics* 25:630-637.
- 556 Riggio, J., A. Jacobson, L. Dollar, H. Bauer, M. Becker, A. Dickman, P. Funston, R. Groom, P.  
557 Henschel, and H. de Iongh. 2013. The size of savannah Africa: a lion's (Panthera leo)  
558 view. *Biodiversity and Conservation* 22:17-35.
- 559 Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture.  
560 Academic Press, Waltham, MA, USA.
- 561 Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013. Integrating resource selection  
562 information with spatial capture-recapture. *Methods in Ecology and Evolution* 4:520-530.
- 563 Royle, J. A., A. K. Fuller, and C. Sutherland. 2016. Spatial capture-recapture models allowing  
564 Markovian transience or dispersal. *Population Ecology* 58:53-62.
- 565 Royle, J. A., A. K. Fuller, and C. Sutherland. 2018. Unifying population and landscape ecology  
566 with spatial capture-recapture. *Ecography* 41:444-456.
- 567 Royle, J. A., K. U. Karanth, A. M. Gopalaswamy, and N. S. Kumar. 2009. Bayesian inference in  
568 camera trapping studies for a class of spatial capture-recapture models. *Ecology* 90:3233-  
569 3244.
- 570 Royle, J. A., M. Kéry, and J. Guelat. 2011. Spatial capture-recapture models for search-  
571 encounter data. *Methods in Ecology and Evolution* 2:602-611.
- 572 Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K.  
573 S. McKelvey. 2012. Estimating abundance of mountain lions from unstructured spatial  
574 sampling. *Journal of Wildlife Management* 76:1551-1561.
- 575 Sinclair, A. R. E. and M. Norton-Griffiths. 1995. Serengeti: dynamics of an ecosystem.  
576 University of Chicago Press.
- 577 Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. A. Jacomo, N. M. Torres, and L.  
578 Silveira. 2011. Improving density estimates for elusive carnivores: Accounting for sex-  
579 specific detection and movements using spatial capture-recapture models for jaguars in  
580 central Brazil. *Biological Conservation* 144:1017-1024.
- 581 Sollmann, R., B. Gardner, R. B. Chandler, D. B. Shindle, D. P. Onorato, J. A. Royle, and A. F.  
582 O'Connell. 2013. Using multiple data sources provides density estimates for endangered  
583 Florida panther. *Journal of Applied Ecology* 50:961-968.

- 584 Stelfox, J. G., D. G. Peden, H. Epp, R. J. Hudson, S. W. Mbugua, J. L. Agatsiva, and C. L.  
585 Amuyunzu. 1986. Herbivore dynamics in southern Narok, Kenya. *The Journal of*  
586 *Wildlife Management* 50:339-347.
- 587 Sutherland, C., J. A. Royle, and D. W. Linden. 2016. oSCR: Multi-Session Sex-Structured  
588 Spatial Capture-Recapture Models. R package version 0.30.1.  
589 <https://github.com/jaroyale/oSCR>.
- 590 Sutherland, C., J. A. Royle, and D. W. Linden. 2019. oSCR: A Spatial Capture-Recapture R  
591 Package for Inference about Spatial Ecological Processes. *Ecography* 42:1–11. doi:  
592 10.1111/ecog.04551.
- 593 Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space  
594 and time. *Trends in Ecology & Evolution* 16:446-453.
- 595

596 **Tables**

597 Table 1. Summary of monitoring effort and adult cheetah encounters in the Masai Mara National  
 598 Reserve during 2005 and 2013–2016, used in the spatial capture-recapture modeling. Results  
 599 from the 3 sampling periods (early 5 months [Jan–May], full 10 months [Jan–Oct], and late 5  
 600 months [Jun–Oct]) include the hours spent searching, the number of unique individuals  
 601 encountered (n) and broken down by sex (F:M), and the number of encounter events (y).  
 602 Spatially distinct encounters occur across >1 grid cell and by definition involve recapture of an  
 603 individual. For example, in 2005 there were 23 individuals encountered during the early 5-  
 604 month period but only 8 (4 female; 4 male) were encountered in >1 grid cell.

Months	Year	Hrs	Total encounters		Spatially distinct encounters	
			n (F:M)	y>0	n (F:M)	y>1
5 (Jan–May)	2005	513	23 (12:11)	34	8 (4:4)	11
	2013	790	12 (6:6)	34	6 (3:3)	18
	2014	530	20 (10:10)	40	13 (8:5)	19
	2015	705	24 (11:13)	68	12 (6:6)	39
	2016	578	20 (12:8)	41	7 (6:1)	16
10 (Jan–Oct)	2005	1086	26 (14:12)	47	14 (7:7)	21
	2013	1535	20 (10:10)	73	13 (9:4)	46
	2014	1465	34 (14:20)	112	26 (12:14)	73
	2015	1694	32 (13:19)	142	19 (10:9)	92
	2016	1438	32 (17:15)	101	22 (12:10)	58
5 (Jun–Oct)	2005	573	11 (7:4)	13	2 (0:2)	2
	2013	745	15 (10:5)	39	8 (6:2)	22
	2014	935	30 (13:17)	72	17 (5:12)	39
	2015	989	23 (10:13)	74	12 (7:5)	45
	2016	860	27 (14:13)	60	14 (9:5)	28



605 Table 2. Parameter estimates from the spatial capture-recapture models of adult cheetah  
 606 encounters in 2005 and 2013–2016 in the Masai Mara National Reserve, fit to data from the  
 607 early period (Jan–May), full period (Jan–Oct), and late period (Jun–Oct). Estimates are on the  
 608 scale of the appropriate link function, either log ( $\alpha$ ,  $\beta$ ) or logit ( $\psi$ ), except for  $\sigma_{sex}$  which is in  
 609 units of km.

Process	$\theta$	Covariate	early (Jan–May)		full (Jan–Oct)		late (Jun–Oct)	
			Estimate	SE	Estimate	SE	Estimate	SE
Encounter	$\alpha_0$	Intercept	−3.690	0.376	−4.073	0.308	−5.170	0.760
	$\alpha_{1,2013}$	Year	1.308	0.459	0.761	0.319	1.725	0.790
	$\alpha_{1,2014}$		0.732	0.450	0.976	0.302	1.757	0.780
	$\alpha_{1,2015}$		1.118	0.408	0.998	0.303	1.679	0.781
	$\alpha_{1,2016}$		1.271	0.441	0.808	0.306	1.105	0.786
	$\alpha_{2,2005}$	NDVI×Year	1.287	0.485	0.378	0.233	−0.555	0.386
	$\alpha_{2,2013}$		1.230	0.392	0.742	0.255	0.632	0.344
	$\alpha_{2,2014}$		−1.710	0.491	−0.197	0.155	0.217	0.197
	$\alpha_{2,2015}$		0.944	0.334	0.738	0.219	0.542	0.296
	$\alpha_{2,2016}$		−0.412	0.245	0.148	0.147	0.828	0.298
	$\alpha_{3,2005}$	NDVI <sup>2</sup> ×Year	−0.923	0.397	−0.372	0.225	−0.243	0.382
	$\alpha_{3,2013}$		−0.666	0.389	−0.721	0.284	−0.880	0.443
	$\alpha_{3,2014}$		−1.567	0.457	−0.616	0.175	−0.654	0.231
	$\alpha_{3,2015}$		−0.380	0.227	−0.257	0.145	−0.124	0.187
	$\alpha_{3,2016}$		−0.405	0.219	−0.124	0.124	−0.234	0.211
	$\alpha_4$	Effort	0.842	0.149	0.682	0.129	0.686	0.149
	$\alpha_5$	Sex (= male)	−0.482	0.264	−0.408	0.162	−0.506	0.239
Distance scale	$\sigma_F$	Female	4.863	0.345	7.036	0.360	7.562	0.637
	$\sigma_M$	Male	4.853	0.426	6.817	0.414	8.820	0.861
Density	$\beta_0$	Intercept	−2.207	0.299	−2.708	0.239	−2.720	0.686
	$\beta_{1,2013}$	Year	−1.511	0.423	−0.666	0.332	−0.804	0.739
	$\beta_{1,2014}$		−0.497	0.395	−0.143	0.297	−0.195	0.713
	$\beta_{1,2015}$		−0.884	0.364	−0.409	0.298	−0.680	0.718
	$\beta_{1,2016}$		−0.894	0.385	−0.312	0.300	−0.270	0.717
Sex ratio	$\Psi_{2005}$	Pr(M)×Year	0.247	0.452	0.130	0.406	−0.391	0.659
	$\Psi_{2013}$		0.148	0.586	0.174	0.453	−0.649	0.565
	$\Psi_{2014}$		0.278	0.473	0.526	0.356	0.296	0.391
	$\Psi_{2015}$		0.300	0.419	0.499	0.365	0.254	0.436
	$\Psi_{2016}$		−0.197	0.473	0.033	0.361	−0.029	0.410

## 610 **Figures**

611 Figure 1. The location of cheetah monitoring in the Masai Mara National Reserve (MMNR) in  
612 southwestern Kenya (35.125° E, 1.44° S). Other conservation areas (shaded) surround the  
613 MMNR, including the Serengeti National Park in Tanzania to the south. Note, the solid line  
614 indicating the political border between Kenya and Tanzania contains no fences or barriers and is  
615 open to movement by wildlife. Map data © OpenStreetMap contributors, CC BY-SA.

616  
617 Figure 2. The midpoint ordinal date of encounter for each individual cheetah (females = dark,  
618 males = light) and the sampling periods in which they were encountered in the Masai Mara  
619 during 2005 and 2013–2016. Note, any individuals with encounters that spanned the full period  
620 (10 months) were included in the spatial capture-recapture models for all 3 periods. The  
621 midpoint was defined as the mean of the first and last dates an individual was seen.

622  
623 Figure 3. Mean estimates (with 95% CI) of cheetah density (#/100 km<sup>2</sup>) in the Masai Mara  
624 National Reserve in 2005 and 2013–2016 from spatial capture-recapture models fit using 5  
625 months (early and late periods) and 10 months of surveys.

626  
627 Figure 4. Relationship between number of spatially distinct encounters and coefficients of  
628 variation (CVs) for density estimates from the spatial capture-recapture models. Spatially  
629 distinct encounters occur across >1 grid cell and by definition involve recapture of an individual.

630  
631 Figure 5. Predicted relationships (with 95% CI) between NDVI variance and cheetah encounter  
632 rate during 2005 and 2013–2016 from spatial capture-recapture models using 5 months (early  
633 and late periods) and 10 months of surveys. Values for NDVI variance were standardized to  
634 have mean 0 and unit variance within each year. Ticks at bottom indicate observed values at  
635 pixel locations within the MMNR.

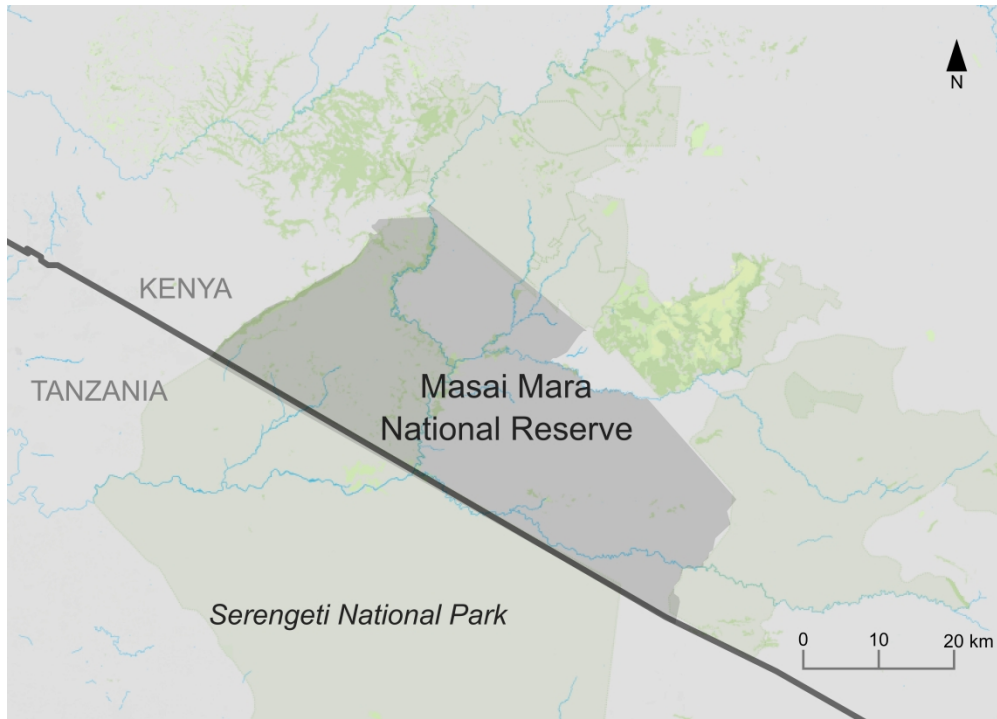


Figure 1

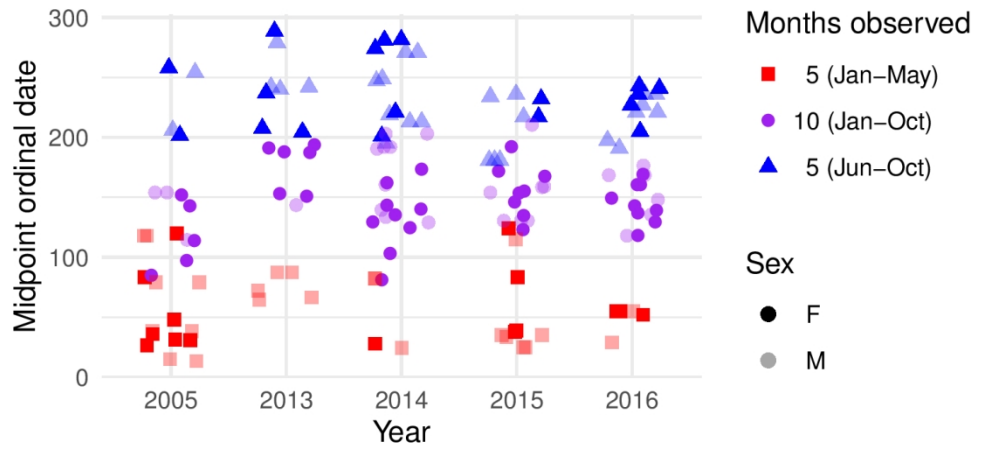


Figure 2

131x60mm (300 x 300 DPI)

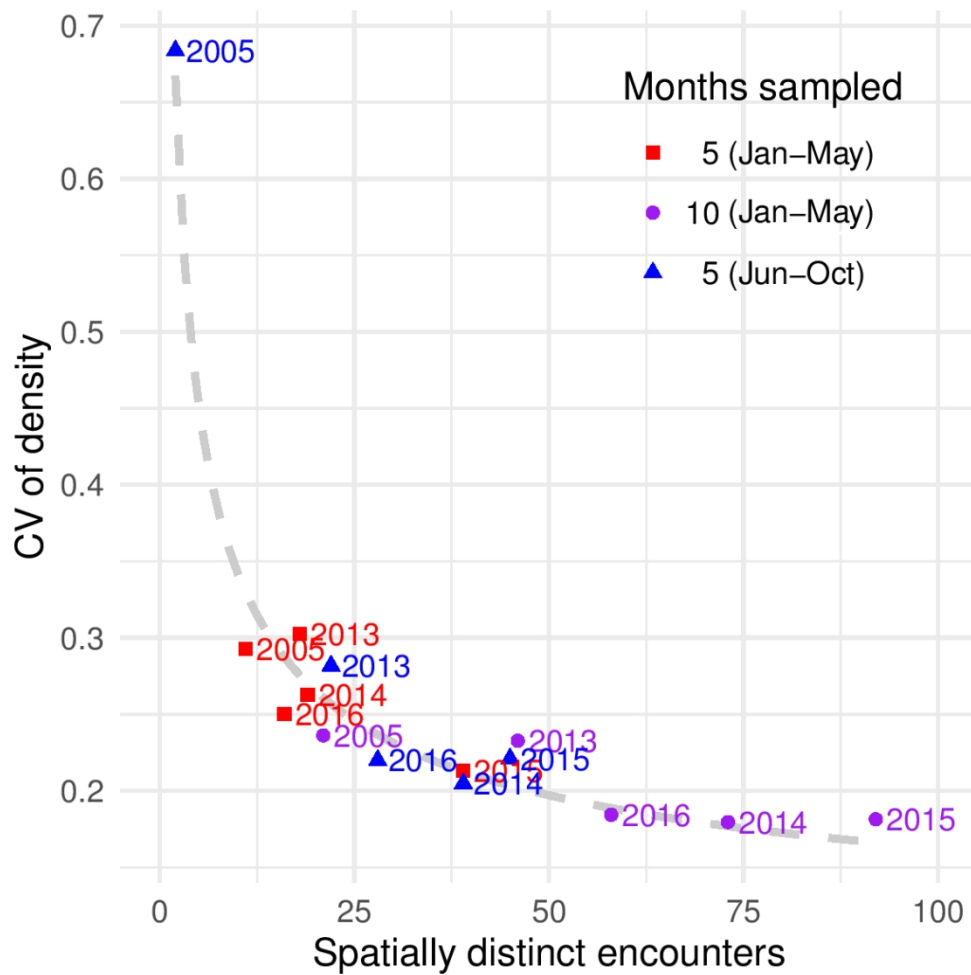


Figure 4

101x101mm (300 x 300 DPI)

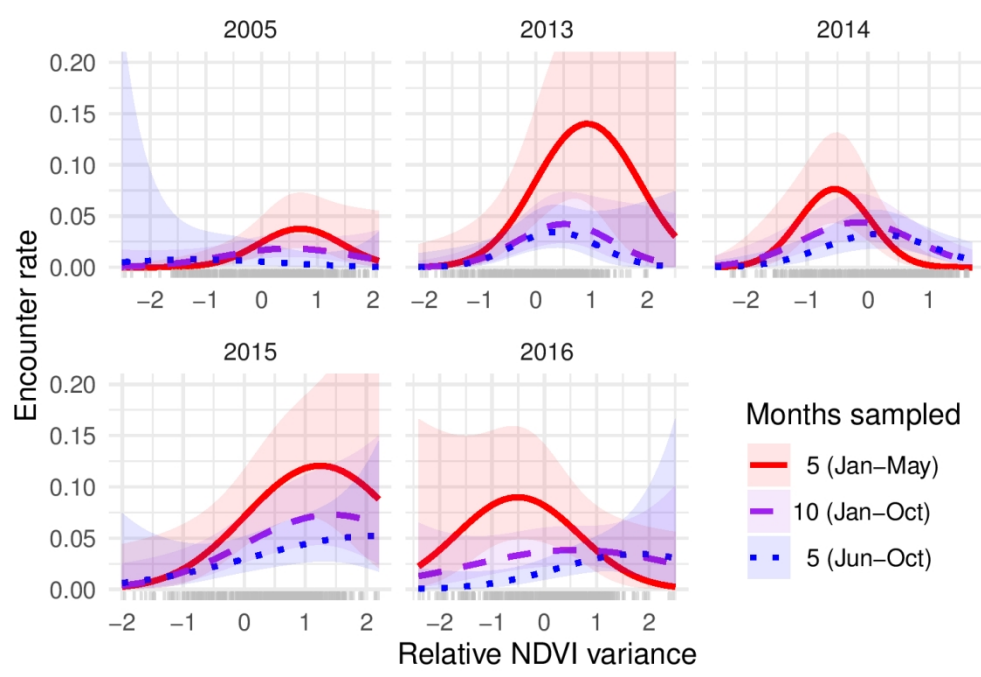


Figure 5

131x91mm (300 x 300 DPI)