

Unifying Population and Landscape Ecology with Spatial Capture-recapture

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Abstract

Spatial heterogeneity in the environment induces variation in population demographic rates and dispersal patterns, which result in spatio-temporal variation in density and gene flow. Unfortunately, applying theory to learn about the role of spatial structure on populations has been hindered by the lack of mechanistic spatial models and inability to make precise observations of population structure. Spatial capture-recapture (SCR) represents an individual-based analytic framework for overcoming this fundamental obstacle that has limited the utility of ecological theory. SCR methods make explicit use of spatial encounter information on individuals in order to model density and other spatial aspects of animal population structure, and have been widely adopted in the last decade. We review the historical context and emerging developments in SCR models that enable the integration of explicit ecological hypotheses about landscape connectivity, movement, resource selection, and spatial variation in density, directly with individual encounter history data obtained by new technologies (e.g., camera trapping, non-invasive DNA sampling). We describe ways in which SCR methods stand to revolutionize the study of animal population ecology.

Keywords

Density, landscape connectivity, landscape ecology, non-invasive sampling, population ecology, spatial capture-recapture, resource selection, spatial point process.

78

79 INTRODUCTION

80 Understanding factors influencing natural variation in population size and structure, demographic
81 rates, and movement has long been a central research focus for population ecologists. Despite well-
82 developed theories over the last half century demonstrating the importance of spatial structure in
83 shaping spatio-temporal population dynamics (e.g., Huffaker 1958, Hanski 1999, Elner et al. 2001), the
84 field of population ecology remains, by and large, unconcerned about within-population spatial
85 processes and their effects on populations. Ecologists routinely study such processes as how
86 individuals use space within their home range, how they perceive connectivity of the landscape,
87 interact with other individuals of the same or other species and how survival or recruitment might be
88 impacted by landscape heterogeneity. However, the population level implications of these processes
89 are not widely studied. Instead the focus is at the individual level, often by studying only a few
90 individuals, with no accounting for how those individuals are sampled from the population. Extending
91 inferences from the individual to the population is not straightforward and in some cases not even
92 possible without a formal statement of a population model linking the sample to the true state, and a
93 description of the sampling process.

94 Much of what drives the spatial ecological processes that give rise to spatio-temporal
95 population dynamics is the structure and configuration of the landscape (Turner et al. 2001). In fact,
96 linking landscape structure to ecological processes is the primary focus of landscape ecology. This focus
97 on how spatial structure influences ecosystem composition, structure, and function (Turner et al. 2001)
98 by definition, avoids any assumption about spatial homogeneity. When related to animal populations,
99 the tendency in landscape ecology is to focus on movement processes, specifically landscape
100 connectivity (Taylor et al. 1993) and resource selection functions (Chetkiewicz et al. 2009, McLoughlin
101 et al. 2010) rather than demographic rates and population state variables that are of interest in
102 population ecology. Population and landscape ecology offer alternative, yet equally important
103 approaches for understanding spatio-temporal dynamics, yet a consistent theory or quantitative
104 framework linking spatial landscape structure and population ecology does not yet exist.

105 The ecological theory underpinning landscape and population ecology is well-developed
106 (Tilman & Kareiva 1997; Hanski & Ovaskainen 2000, Hanski 2001, Turner et al. 2001, Kot 2001, Williams

107 et al. 2002; Gets & Saltz 2008; Allen & Singh 2016), but testing theoretical models and predictions
108 about spatial ecology in practice is both logistically and statistically challenging. One major impediment
109 is the lack of general mechanistic spatial models that can be applied to empirical data; this precludes
110 rigorous testing of theoretical predictions. Spatial point process models (Illian et al. 2008) provide a
111 natural framework for characterizing the spatial structure of populations assumed to be static and that
112 can be observed with a high degree of accuracy. However, point process models have not been widely
113 adopted in practical field studies of population ecology where individuals cannot be enumerated easily.
114 In practice, populations distributed widely in space must be studied by observing a sample of
115 individuals, sometimes only a very small fraction, at only a few time points and at only a few locations.
116 In some cases, individuals can be continuously monitored (e.g., by telemetry), but in general it is not
117 possible to observe the status of animals perfectly – either their demographic status, their location, or
118 even whether or not they are alive. This is one of the key considerations that has motivated the
119 development and widespread adoption of capture-recapture methods which are now ubiquitous in
120 ecology (Williams et al. 2002; Cooch & White 2006).

121 For decades, capture-recapture methods have been the cornerstone of ecological statistics as
122 applied to population biology (Nichols 1992, Williams et al. 2002). At their core, capture-recapture
123 models are the canonical class of models for “individual encounter history” data. These data are
124 obtained by capturing or encountering individuals (e.g., using camera traps, acoustic sampling, non-
125 invasive genetic sampling, or direct physical capture), marking them, and observing them over time.
126 Capture-recapture methods have had a profound influence on the study and understanding of
127 demography in wild populations (Karanth et al. 2006, Pradel et al. 2010), in advancing ecological theory
128 (Cooch et al. 2002), and informing modern conservation and wildlife management practices (Nichols
129 and MacKenzie 2004). While capture-recapture has become the standard sampling and analytical
130 framework for the study of population processes (Williams, Nichols & Conroy 2002) it has advanced
131 independent of and remained unconnected to the spatial structure of the population or the landscape
132 within which populations exist. Furthermore, capture-recapture does not invoke any spatially explicit
133 biological processes and thus is distinctly non-spatial, accounting neither for the inherent spatial
134 nature of the sampling nor of the spatial distribution of individual encounters. This precludes the study
135 of many important spatial processes and/or the emerging within-population spatial structure that is

136 arguably as important as demographic rates in population ecology. Recently developed *spatial* capture-
137 recapture (SCR) methods (Royle et al. 2014) couple a spatio-temporal point process with a spatially
138 explicit observation model which resolves these important criticisms and offers a significant advance in
139 our ability to quantify and study spatial processes using encounter history data. Spatial capture-
140 recapture represents an extension of classical capture-recapture and allows for both the spatial
141 organization of sampling devices and the spatial information that is inherent in essentially all studies of
142 animal populations, i.e., *spatial encounter histories*.

143 Although a relatively recent advance in the field of statistical ecology (Efford 2004), the past
144 decade has seen an explosive growth in SCR methodological development and applications (Box 1).
145 Spatial capture-recapture provides a quantitative framework that links ecological processes at the
146 individual and population levels. SCR promises the integration of models (hypotheses) of within-
147 population dynamics with "population level" parameters and dynamics. Thus, SCR has proven to be
148 more than simply an extension of a technique, but has emerged as a flexible framework that allows
149 ecologists to test hypotheses about a wide range of ecological theories including landscape and
150 network connectivity (Sutherland et al. 2015, Fuller et al. 2015), demography (Ergon & Gardner 2013,
151 Whittington and Sawaya 2015, Munoz et al, 2016), resource selection (Royle et al. 2013b, Proffitt et al.
152 2015), and movement and dispersal (Borchers et al. 2014, Lagrange et al. 2014, Schaub & Royle 2015,
153 Royle et al. 2016). While classical capture-recapture methods focus on population level quantities, SCR
154 models allow for the "downscaling" of population structure from coarse summaries (spatial and/or
155 demographic) into finer-scale components by the use of a spatially explicit individual-based point
156 process model. By connecting population level attributes to individual level attributes that are spatially
157 realistic, SCR unifies the fundamental concepts of population and landscape ecology, relating spatial
158 encounters of individuals to explicit descriptions of spatial structure and of how space is sampled (Box
159 2).

160 In this review, we describe the basic elements of spatial capture-recapture and how SCR
161 methods advance spatial population ecology by providing a unified framework that integrates
162 important concepts and elements of population ecology and landscape ecology. As such, the
163 framework allows for the study of density, movement, resource selection, landscape connectivity, and
164 other spatial population processes using ordinary encounter history data. Finally, we discuss new

165 directions in the study of animal populations that are made possible by the existence of spatially
166 explicit capture-recapture methods.

167 **THE ELEMENTS OF SPATIAL CAPTURE-RECAPTURE**

168 Traditional capture-recapture (CR) models were largely motivated by a formal statistical sampling view
169 of how individuals are encountered by sampling, with little or no direct consideration given to the
170 fundamental spatial nature of the sampling. As a result, traditional CR models represent, in essence,
171 “fish bowl” sampling – that is, a system that is devoid of any meaningful spatial context. This leads
172 immediately to several important technical concerns that arise in the application of traditional CR to
173 the study of animal populations which are necessarily spatially explicit.

174 One important deficiency with classical closed population models is the inability to directly
175 estimate animal *density* (D), arguably *the* state variable of interest in the vast majority of animal
176 monitoring studies (Krebs 1985, Turchin 1998). This is because, in almost all practical field applications,
177 it is not possible to precisely define the effective area sampled by a set of trapping devices due to
178 movement of individuals into and out of the region within which sampling occurs (Dice 1938; Hayne
179 1949; Wilson and Anderson 1985a,b). Secondly, the probability of encountering an individual is
180 necessarily heterogeneous among those individuals exposed to sampling. For example, individuals on
181 the periphery of a trapping grid should have lower probability of capture than individuals with home
182 ranges on the interior of the trapping grid (Figure 1). This heterogeneity in encounter probability has
183 long been known to induce negative bias in estimates of abundance (N), and hence density (K. Ullas
184 Karanth & Nichols, 1998; Otis, Burnham, White, & Anderson, 1978), and was one of the factors that
185 motivated the development of SCR methods (Efford, 2004). These (and other) technical limitations of
186 the non-spatial CR framework arise directly as a result of a lack of spatial explicitness. On the other
187 hand, SCR integrates models that describe the spatially explicit nature of sampling, how individuals are
188 distributed, and how they use space.

189 SCR models assume that a population of N individuals is sampled and that each individual has
190 associated with it a spatial location which represents its activity centre which can be expressed by its
191 X and Y coordinates as $\mathbf{s}_i = [s_{i,X}, s_{i,Y}]$. The collection of activity centres $\mathbf{s}_1, \dots, \mathbf{s}_N$ can be thought of
192 as the realization of a statistical point process (Illian et al. 2008), a class of probability models for

193 characterizing the spatial pattern and distribution of points. This is perhaps the key innovation of
194 spatial capture-recapture because it is this model that connects observations to much of the ecological
195 theory that can be addressed by SCR. To formalize the point process model it is necessary to describe
196 the probability distribution function of the point locations. The simplest possible point process model
197 is to assume that each of the N point locations are distributed uniformly in space (the “uniformity
198 assumption”):

$$199 \quad \mathbf{s}_i \sim \text{Uniform}(S) \quad (1)$$

200 where S is an explicit spatial region within which sampling of individuals occurs, and for which
201 inferences about density will be made. Formally this is referred to as the *state-space* of the point
202 process and is an essential component of a probabilistic characterization of potential activity centres,
203 which are equivalent to individuals in the SCR framework. One important distinction to be made
204 between SCR and classical CR methods is that the state-space S is an explicit component of the SCR
205 model. The state-space induces an explicit model of heterogeneous detection probabilities which may
206 affect inferences about density and, hence, population size.

207 The introduction of this statistical point process – that is, the association of a spatial coordinate
208 with each individual in the population – leads naturally to two distinct conceptually important and
209 powerful modifications of the classical capture-recapture framework which are at the core of the SCR
210 method: First, we can formulate a spatial model for the probability that an individual is captured in
211 *each* sample location or trap x_j for $j=1,2,\dots,J$, conditional on its activity centre rather than simply
212 whether an individual was captured at all in a sample occasion, as is the case in traditional CR.
213 Acknowledging the spatial structure of the traps means observations can be spatially indexed (Box 2,
214 top panel) so encounter histories describe *who* (i), *when* (k) and importantly *where* (j) individuals were
215 encountered, i.e. $y_{i,j,k}$. Often, these observations are assumed to be Bernoulli outcomes:

$$216 \quad y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k}), \quad (2)$$

217 where $p_{i,j,k}$ is the probability of encountering individual i in trap j , and occasion k . It is this model
218 which links the observations (spatially indexed encounters) to the underlying latent point process
219 describing biological pattern and process. At a minimum the encounter probability model depends on

220 the distance between the trap location (x_j) and the individual's activity centre (s_i) such as the half-
221 normal encounter model (Box 2, middle panel):

$$222 \quad p_{i,j,k} = p_{0,j,k} \times e^{-(1/2\sigma^2)d(x_j,s_i)^2} \quad (3)$$

223 where p_0 is the baseline encounter probability, the probability of encountering an individual at its'
224 activity centre, the parameter σ describes the rate at which detection probability declines as a
225 function of distance, and $d(x_j,s_i)$ is the Euclidean distance between trap j and the activity centre of
226 individual i (Box 2, middle panel). In a spatial capture-recapture analysis, the parameters to be
227 estimated are p_0 , σ and population size N or density D . We note that the parameter σ
228 accommodates individual heterogeneity in detectability but, unlike classical models of heterogeneity
229 (Otis et al. 1978; Dorazio & Royle 2003) the parameter represents an explicit source of heterogeneity,
230 due to the distance between individual activity or home range centres and traps.

231 The uniformity assumption yields what is usually referred to as a homogenous point process
232 model, although very general models of the point process are possible. For example, when spatially
233 referenced covariates, say $z(\mathbf{s})$, can be identified that result in spatially heterogeneous density
234 surfaces (Box 2, lower panel), then a standard inhomogeneous point process model posits that

$$235 \quad \Pr(\mathbf{s}) \propto \exp(\beta z(\mathbf{s})), \quad (4)$$

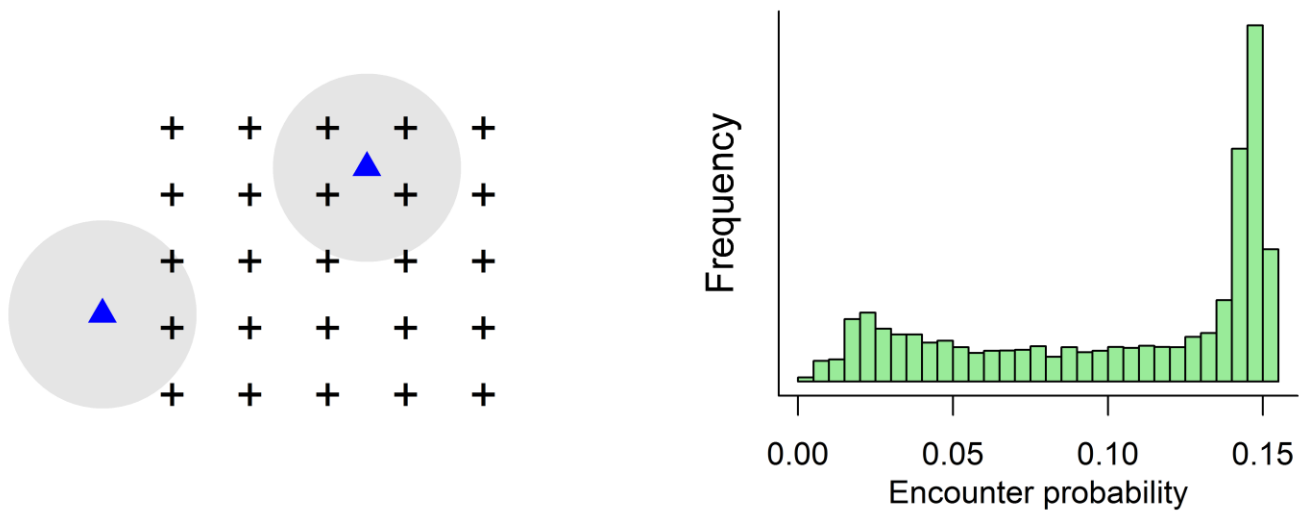
236 where the parameter β corresponds to an explicit hypothesis: "does density depend on the covariate
237 z ?"

238 Integrating the point process model with the CR sampling framework leads naturally to a direct
239 focus on inference about parameters of the underlying point process, instead of the abstract quantity
240 N which is devoid of spatial context. Under the SCR modelling framework, the goal is to estimate the
241 number of individuals (or activity centres) within any region of the *state-space* S . For example, we may
242 estimate density D , the number of activity centres per unit area of S , or produce predictions of the
243 number of points in any formal subset of S , or functions of the entire set of N points which might be
244 used to test for spatial randomness, clustering mechanisms (Reich & Gardner, 2014) or other point
245 process assumptions.

246 For purposes of statistical estimation and inference, the activity centres are regarded as latent
247 variables (i.e., as in classical random effects or mixed models, Laird & Ware 1982). The point process
248 model is then precisely equivalent to the random effects distribution or prior distribution. The resulting
249 model is amenable to analyses by classical methods of statistical inference such as based on marginal
250 likelihood (Borchers & Efford 2008), in which the latent variables are removed from the likelihood by
251 integration, or Bayesian analysis by Markov chain Monte Carlo (MCMC; Royle & Young 2008), in which
252 the activity centres are explicitly estimated along with other unknown parameters and random
253 variables.

254 SCR models are now routinely applied to many taxa, across a wide variety of systems using a
255 range of sampling methodologies (Box 1). However, the utility of the model reaches far beyond simply
256 estimating density and includes the investigation of important questions about population and
257 landscape ecology which we describe next. Moreover, an enormous number of extensions to SCR
258 models can be accommodated, both to the structure of the ecological processes and the types of
259 observation method, including acoustic sampling (Dawson & Efford, 2009), sampling continuous space
260 instead of using traps (Royle, Kéry, & Guélat, 2011; Royle & Young, 2008), sampling continuous time
261 instead of having discrete sampling intervals (Borchers et al. 2014) and modeling population dynamics
262 such as survival and recruitment using individual level or state-space formulations of classical Jolly-
263 Seber and Cormack-Jolly Seber models (Gimenez et al. 2007; Gardner et al. 2010). We discuss some of
264 these extensions below.

265



266

267 **Figure 1.** Left: Two home ranges of individuals (gray circles) juxtaposed with a spatial sampling grid
268 (traps) illustrating the variable exposure to trapping based on home range location. Right: the implied
269 distribution of individual encounter probability for a population exposed to sampling by a regular grid
270 (taken from Royle et al. 2014, ch. 5).

271

272 **SCR – A DECADE OF DEVELOPMENT AND APPLICATION**

273 As SCR methods were first appearing more than 10 years ago, the motivation for their development
274 and use was exclusively as a technical device for resolving specific technical limitations of ordinary
275 capture-recapture (Fig. 1). More generally, SCR methods have proved to be a flexible framework for
276 making ecological processes explicit in models of individual encounter history data, and for studying
277 spatial processes such as individual movement, resource selection, space usage, landscape
278 connectivity, population dynamics, spatial distribution, density and inter- and intra-specific
279 interactions. Historically, researchers studied these questions independently, using ostensibly
280 unrelated study designs and statistical procedures.

281

282 ***SCR for resource selection***

283 SCR models provide a coherent framework for modeling both 2nd and 3rd order resource selection
284 (Johnson 1980; Box 3). Second order resource selection is defined as the processes by which

285 individuals select the location of their home range within a particular landscape. SCR models
286 parameterize an explicit representation of this selection process in the specification of the latent point
287 process model (individual activity centres s_1, \dots, s_N). While typical applications involve a relatively
288 simple homogeneous point process model in which activity centers are distributed independently and
289 uniformly over the state-space S , the SCR framework accommodates inhomogeneous point process
290 models in which the density of activity centers varies as a function of explicit covariates or flexible
291 spatial response surface models (Borchers & Kidney 2014) that affect density. Inhomogeneous point
292 process models show great promise for testing explicit hypotheses about 2nd order selection,
293 understanding mechanisms that influence species density distribution, and developing conservation
294 and management strategies with explicit abundance- or density-based objectives (Kendall et al. 2015,
295 Proffitt et al. 2015, Sun et al. 2015, Linden et al. 2016).

296 Third order resource selection – that is, selection that occurs within an individual’s home range
297 – can be modeled explicitly in SCR models by accommodating habitat structure in the vicinity of
298 sampling (or trap locations) as a covariate that affects the probability of encounter (Royle et al. 2013b).
299 Traditionally, resource selection was studied exclusively by telemetry, and more recently GPS, and
300 because of the high cost are often based on a small sample of individuals observed many times.
301 Conversely, SCR methods may produce a sample of many more individuals, and direct information
302 about population level resource selection from spatial encounter data. However, individuals in the
303 population often do not need to be physically captured to obtain this information by SCR methods
304 (e.g., by camera trapping). Thus, SCR provides an alternative, efficient, and cost effective framework
305 for studying the important population process of resource selection from individual encounter history
306 data for species that classical telemetry may not be viable and that is based on a larger sample of the
307 population.

308

309 ***SCR for modeling movement and dispersal***

310 The direct linkage of the SCR encounter probability model to movement of an individual within its
311 home range is one of the basic concepts of SCR (Royle & Young 2008; Borchers et al. 2014). However,
312 one of the key assumptions of most SCR methods to date is that the latent point locations which
313 represent the individual activity centers are static variables. In a sense this is a manifestation of type of

314 population “closure”; individuals are allowed to move around in space, but their expected location is
315 assumed not to change over the course of the study. Recent attention has been given to modifying the
316 underlying state point process model to accommodate temporal dynamics such as dispersal or
317 transience (Schaub & Royle 2014; Ergon & Gardner 2014). These models formally allow for the
318 estimation of survival probability that is free of biasing effects of dispersal whereas, classically, only
319 “apparent survival” has been estimated from standard capture recapture data (Schaub et al. 2004).
320 Even in populations where mortality or recruitment are absent, including a dynamic spatial process to
321 account for dispersal and transience is possible by coupling a latent movement model with a spatial
322 model of the encounter process (Royle et al. 2016). For example, to modify the point process model to
323 allow for an individual’s activity center to shift from time $t - 1$ to time t we might accommodate this
324 with a simple Markovian movement model where the difference between successive activity centers
325 has variance τ^2 :

326
$$\mathbf{s}_{i,t} | \mathbf{s}_{i,t-1} \sim Normal(\mathbf{s}_{i,t-1}, \tau^2 \mathbf{I})$$

327 Thus, SCR has a characterization as a state-space (Patterson et al. 2008) or hidden Markov model
328 (HMM; Langrock et al. 2012) with specific forms of observation model governed by spatial sampling
329 and an underlying latent process model that describes movement of individuals on the landscape. As a
330 result, SCR offers a general framework for the formal study of dispersal, transience, and other types of
331 movement from individual encounter history data.

332

333 ***Modeling landscape connectivity***

334 One of the core elements of SCR is the model for encounter probability which we described above as a
335 function of Euclidean distance between activity centers and sample locations (Box 2). However, the
336 Euclidean distance assumption implies a simplistic model of space usage – that individual home ranges
337 are symmetric and stationary. In practice, we expect individual home ranges to be influenced by local
338 landscape characteristics and structure. One approach for accommodating this landscape structure-
339 induced asymmetry in space use in SCR models is the relaxation of the Euclidean distance assumption.

340 This is achieved using an alternative distance metric that is related to the landscape through
341 which distance is being measured, thus allowing the degree of asymmetry to be estimated using a

342 model that relates the observed spatial pattern of observations explicitly to the measurable landscape
343 characteristics. For example, Royle et al. (2013a) suggested using least-cost path distance with the
344 exception that, rather than being defined *a priori* based on opinion as is customary (Zeller et al. 2012),
345 the resistance parameters are estimated using standard likelihood methods based on spatial encounter
346 histories (Box 4). This idea was extended by Sutherland et al. (2015) for highly structured dendritic
347 networks, an extreme yet intuitive conceptual setting for investigating the utility of this asymmetric
348 space use model. The major development is that the model of asymmetric space use can be used to
349 jointly estimate density and resistance parameters which are typically defined a priori based on
350 opinion (Zeller, McGarigal & Whitely 2012), yielding ecologically interesting and realistic individual
351 home range geometries which can be scaled up to the landscape level based on direct estimates of the
352 landscape structure-space use relationship (Box 4). What results is the important notion that ordinary
353 encounter history data that is extensively collected in ecological studies with relative ease can now be
354 used to formally characterize landscape connectivity within a framework of statistical inference.
355 Sutherland et al. (2015) defined several intuitive measures of landscape connectivity based on such
356 upscaling based on the SCR encounter probability model to the landscape scale. The asymmetric space
357 use model described here and in Box 4 in general, can be extended to multiple landscape
358 characteristics as would be done with any log-linear regression model, and requires only that the
359 landscape covariates are defined at the pixel level. While current applications have focused on river
360 networks (Fuller et al. 2016), the approach should be highly relevant for any species for which one or
361 more landscape features act to impede or facilitate movement (Morin et al. *in press*) (e.g., extreme
362 topographic variation, well-defined networks of roads and trails used by a species, Box 4). Moreover,
363 SCR offers a formal model-based solution for investigating the strength of landscape interactions,
364 avoiding the need to arbitrarily prescribe resistance values. The possibility exists to consider other non-
365 Euclidean distance metrics such as circuit distance (McRae et al. 2006) or flexible deformations of
366 geographic space (Sampson & Guttorp 1992).

367 368 **FUTURE DIRECTIONS OF SPATIAL CAPTURE-RECAPTURE**

369 The relevance of SCR methods is expanding rapidly because these techniques allow ecologists to
370 explicitly test hypotheses about the mechanisms that drive ecological phenomena as diverse as habitat

371 selection, persistence of rare species, community assembly, invasion, and genetic diversity. The
372 developments described above represent significant contributions to applied population ecology
373 despite their relative infancy, and we believe the potential for SCR in ecology has not yet been fully
374 realized. We highlight specific and potentially fruitful development areas for SCR that have the
375 potential to make further contributions with regard to wildlife population sampling, and/or developing
376 and testing ecological hypotheses.

377

378 ***Landscape management and corridor design***

379 It is possible to use SCR with individual encounter history data to inform landscape management
380 decisions such as corridor and reserve design. Because SCR models provide spatially explicit within-
381 population information about density, they provide objective inferences about where the population is
382 distributed in space and why. Therefore, SCR can serve as an empirical framework for characterizing
383 the utility of landscapes to populations. In particular, when combined with explicit models of
384 connectivity (previous section), spatially explicit metrics which integrate information about both
385 density and connectivity (Sutherland et al. 2015; Fuller et al. 2016; Morin et al. 2016) can be estimated,
386 thus providing information about quality of the landscape for maintaining connectivity and also for
387 maintaining source populations of important species.

388 Corridors are increasingly used as conservation tools, designed to facilitate movement of
389 individuals between habitat patches, or between two nodes or habitat blocks separated by some
390 distance (e.g., two protected areas) with the ultimate goal of maintaining landscape connectivity. In
391 the most general sense, corridor design involves defining a resistance value (i.e., resistance of the
392 landscape to animal movement) of each pixel in the landscape as a function of pixel characteristics,
393 and then subsequently selecting the lowest cost pixels, typically evaluated by estimating the
394 cumulative cost of moving from one area to another. The resistance of a landscape is approximated by
395 a 'cost' value, representing how difficult it is for an individual to move through a landscape. High
396 quality habits are more permeable to movement and infer lower ecological costs (i.e., they provide
397 increased survival and reproduction) relative to lower quality habitat. Resistance values are most often
398 based on subjective expert opinion or data from previously published studies (Zeller et al. 2012). These
399 user defined resistance models have been tested based on limited inference from few radiomarked

400 individuals (Driezen et al. 2007). However, examples exist of deriving resistance values from
401 occurrence probability from occupancy models (Walpole et al. 2012) or using a variety of different
402 threshold values based on the most traversable habitat from radio-marked individuals (Poor et al.
403 2012). Of importance is that these applications fail to utilize the information from animal movements
404 to directly estimate landscape resistance values.

405 We are aware of only one application of using capture-recapture data for formal inference
406 about landscape resistance for a species (Fuller et al. 2016), which was based on the Ecological
407 distance SCR model (Royle et al. 2013a, Sutherland et al. 2015). Further, corridor conservation has
408 been devoid of explicit consideration of local population density. SCR models allow for the
409 simultaneous estimation of the two processes that are most critical to the conservation of spatially-
410 structured populations, density and connectivity. Morin et al. (in press) derived a model-based
411 estimator of landscape connectivity (i.e., density-weighted connectivity) that estimates both the spatial
412 distribution and connectivity of individuals across a landscape. Spatial optimization approaches that
413 maximize density-weighted connectivity would identify areas on the landscape that support the
414 highest number of individuals and best landscape connectivity and would therefore have the greatest
415 potential for application in corridor conservation and landscape management.

416

417 ***Modeling spatial interactions***

418 The latent point process describing the spatial distribution of individuals is a central component of SCR
419 methods. Parameterization of this point process allows encounter history data to be used to develop
420 models that explicitly address theories related to competition, including territoriality (Reich & Gardner
421 2014) and maintenance of coexisting species and species diversity. Extending the point process model
422 to account for dependencies among multiple species simultaneously occupying a landscape may
423 provide an analytic framework for the empirical study of inter and intra-specific competition and
424 landscape level spatial structure in species assemblages. This should have enormous relevance in
425 understanding host-pathogen and disease in natural systems where transmission depends on local
426 interactions of individuals and local density. Where individuals live and who they interact with are
427 fundamental elements contributing to the dynamics of disease and pathogen systems.

428 ***Acoustic sampling***

429 Acoustic sampling is emerging as a promising technology for sampling vocal species such as birds,
430 anurans, marine mammals, and primates, and the application of these methods is increasing rapidly
431 (Marques et al. 2009; Blumstein et al. 2011). Information on signal strength and/or direction gives
432 imperfect information about the source of the vocalization although statistically pinpointing the source
433 has been recognized as being analogous to inference about the activity center in SCR methods, and
434 therefore SCR has been adapted to accommodate data obtained by acoustic sampling methods
435 (Dawson & Efford 2009; Efford et al. 2009; Borchers et al. 2015; Stevenson et al. 2015; Kidney et al.
436 2016). It seems probable that these technologies will become the *de facto* sampling method in bird
437 population studies due to the increasing affordability of the technology.

438

439 ***Uncertain identity***

440 Given the widespread adoption of non-invasive sampling technologies, which may only yield partial
441 information on the identity of individual samples, it will become important to accommodate
442 uncertainty in individual identity in to studies of animal populations that use individual encounter
443 histories. There has been considerable attention paid to the problem of uncertain identity in capture-
444 recapture (Link et al. (2010), Bonner & Holmberg (2013), McClintock et al. (2013)). However, such
445 methods have developed in the context of classical capture-recapture methods which ignore the
446 spatial information inherent in most animal population sampling studies. On the other hand, for most
447 populations we should expect that the spatial location of samples should be informative about the
448 uncertain identity of those samples (Chandler & Royle 2013, Chandler & Clark 2014, Royle 2015,
449 Augustine et al. 2016). That is, all other things being equal, spatial samples that are in close spatial
450 proximity to one another should more likely be of the same individual than samples that are far apart.
451 Thus, dealing effectively with an uncertain identity of an individual is fundamentally a spatial problem
452 for which SCR offers a solution.

453 Methods of accommodating uncertain identity and partially marked populations are promising
454 avenues for the formal integration of citizen science data collection with population ecology studies
455 based on capture-recapture. SCR facilitates the use of citizen science in studies of population ecology
456 because citizen science schemes naturally produce abundant information about individual location,
457 potentially useful in spatial mark-resight and similar SCR models. Thus, involving citizens in data

458 collection will produce large quantities of confirmations of species and their locations, but potentially
459 no individual identity of the observations.

460 **CONCLUSIONS**

461 Two technological advances have influenced the present and future of animal population ecology in a
462 way that we believe is more profound than any advance in quantitative ecology since the invention of
463 computers. First is the development of new technologies for obtaining spatial encounter information
464 on individuals (Box 1). These technologies have revolutionized applied population ecology.
465 Simultaneous to the development of these new field techniques has been the increasing spatialization
466 of ecological process models seen in the advancing fields of landscape ecology and metapopulation
467 ecology, along with the increasing utilization of statistical point process models throughout population
468 ecology. SCR lies at the convergence of these two technological advances, combining a spatially explicit
469 observation model that describes data collected using new technologies such as noninvasive genetics
470 or camera trapping, with spatially explicit models describing how individuals are distributed across a
471 landscape.

472 Estimating abundance or population size is one of the most important problems in applied
473 ecology permitting the evaluation of sophisticated questions in population dynamics (Krebs 1984,
474 Williams et al. 2002, Sutherland et al. 2013) and providing necessary information for the conservation
475 and management of important species (Karanth & Nichols, 2002). SCR has become the standard
476 method for obtaining such information for many species, and is now routinely used to estimate
477 abundance of populations of conservation concern including species such as tigers (Royle et al. 2009),
478 grizzly bears (Efford & Mowat 2014; Kendall et al. 2015), wolverines (Magoun et al. 2011, see Box 1)
479 and jaguars (Sollmann et al. 2011). These and many other species are extremely difficult to capture and
480 so non-invasive sampling combined with SCR methods are perfectly suited to study these species.
481 Moreover, many populations exist in such low densities that obtaining sufficient sample sizes of
482 individuals can be challenging, and thus making the most efficient use of all data, and in particular,
483 spatial recaptures which are discarded by ordinary capture-recapture, is critically important.

484 While SCR methods were developed originally as a tool for inference about animal density from
485 capture-recapture data (Efford, 2004) motivated by the need to address specific technical limitations
486 of ordinary capture recapture methods (Fig. 1), they have proven to be more than simply an extension

487 of technique. Spatial capture recapture has profoundly affected the manner in which capture-
488 recapture is used in studies of animal populations because they allow testing of explicit hypotheses of
489 core elements of population and landscape ecology by formally integrating technical descriptions of
490 these processes with encounter history data obtained by sampling animal populations. SCR models
491 include an explicit model of density and thus relationships can be modeled between density and
492 landscape features or other population attributes. For example, SCR models can be used to test
493 hypotheses related to density dependence in animal populations, such as the relationship between
494 density and home range size (Efford et al. 2015). In addition, understanding movement of individuals
495 over the landscape is a key objective throughout ecology, and SCR enables the formal integration of
496 explicit movement, dispersal, and survival models with models of density and other population
497 characteristics (Ergon & Gardner 2015; Schaub & Royle 2015). Because SCR models are spatially
498 explicit, we believe it is possible to consider explicit modeling of population dynamic rates as a function
499 of local density. Finally, landscape connectivity is a fundamental element of landscape ecology and
500 explicit models of connectivity can be integrated directly with models of spatial encounter history data
501 within the SCR framework to provide population-level estimates of connectivity parameters.
502 Sutherland et al. (2015) and Fuller et al. (2016) develop SCR models in highly structured landscapes and
503 demonstrate formal inference for an explicit model of landscape connectivity and resistance,
504 estimated from individual encounter history data from a capture-recapture study of mink.

505 SCR is not only revolutionizing how population and landscape ecology questions can be
506 addressed but also in the way we observe populations. For example, use of scat dogs to sample space
507 using unstructured area searches is extremely practical for studying many species and this method has
508 grown rapidly in recent years. When data are obtained in this manner, it is imperative that the spatial
509 structure of sampling be accounted for and SCR accommodates this by explicitly using GPS search lines
510 in place of trap locations. Acoustic sampling (Dawson & Efford 2009) is a promising new technology for
511 sampling birds and many other species. However, without a spatially explicit model that describes both
512 the sampling and underlying process, it is not possible to connect observed acoustic encounter data to
513 meaningful biological parameters such as population density. Finally, SCR has potential as the
514 framework for integrating individual encounter data with inexpensive, broad scale auxiliary data such

515 as from occupancy studies (Chandler & Clark 2014; Whittingham & Chandler *in press*) and potentially
516 even citizen science programs.

517 At the core of science is the notion of testing theories by confronting models with data. At the
518 level of the population this has been recognized as a promise of capture-recapture for several decades
519 (Nichols 1992), but the use of capture-recapture has not been widely used to address questions related
520 to within-population spatial structure and population dynamics. However, SCR achieves this promise,
521 by integrating a formal spatial model describing how individuals are distributed over a landscape, with
522 a formal spatial model for how the population is sampled. SCR enables testing explicit spatial
523 mechanisms and processes and improves understanding of spatial ecology from individual encounter
524 history data. SCR incorporates elements of population structure and dynamics and explicit spatial and
525 landscape structure to provide a quantitative framework that unifies population and landscape
526 ecology.

527

528 REFERENCES

529

530 Allen, A.M. & Singh, N.J. (2016). Linking movement ecology with wildlife management and
531 conservation. *Front. Ecol. Evol.*, 12, Jan 2016.

532

533 Augustine, B., Royle, J.A., Kelly, M., Satter, C., Alonso, R., Boydston, E. & Crooks, K. (2016). Spatial
534 capture-recapture with partial identity: an application to camera traps. bioRxiv, p.056804.

535

536 Blumstein, D. T., Mennill, D. J., Clemins, P., Girod, L., Yao, K., Patricelli, G., *et al.* (2011). Acoustic
537 monitoring in terrestrial environments using microphone arrays: applications, technological
538 considerations and prospectus. *J. Appl. Ecol.*, 48, 758–767.

539

540 Bonner, S. & Holmberg, J. (2013). Mark-recapture with multiple, non-invasive marks. *Biometrics*, 69,
541 766-775.

542

543 Borchers, D.L. & Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture-
544 recapture studies. *Biometrics*, 64, 377-385.

545

546 Borchers, D. L. & Kidney, D. (2014). Flexible density surface estimation for spatially explicit capture-
547 recapture surveys Technical Report, University of St Andrews.

548

- 549 Borchers, D., Distiller, G., Foster, R., Harmsen, B. & Milazzo, L. (2014). Continuous-time spatially
550 explicit capture–recapture models, with an application to a jaguar camera-trap survey. *Methods Ecol.*
551 *Evol.*, 5, 656-665.
- 552
- 553 Borchers, D.L., Stevenson, B.C., Kidney, D., Thomas, L. & Marques, T.A. (2015). A unifying model for
554 capture–recapture and distance sampling surveys of wildlife populations. *J. Am. Stat. Assoc.*, 110, 195-
555 204.
- 556
- 557 Chandler, R.B. & Royle, J.A. (2013). Spatially explicit models for inference about density in unmarked
558 or partially marked populations. *Ann. Appl. Stat.*, 7, 936-954.
- 559
- 560 Chandler, R.B. & Clark, J.D. (2014). Spatially explicit integrated population models. *Methods Ecol.*
561 *Evol.*, 5, 1351-1360.
- 562
- 563 Chetkiewicz C. B. & Boyce, M.S. (2009). Use of resource selection functions to identify conservation
564 corridors. *J. Appl. Ecol.*, 46, 1036–1047.
- 565
- 566 Cooch, E.G., Cam, E. & Link, W. (2002). Occam's shadow: Levels of analysis in evolutionary ecology--
567 where to next? *J. Appl. Stat.*, 29, 19-48.
- 568
- 569 Cooch, E. & White, G. (2006). Program MARK: a gentle introduction. Available in pdf format for free
570 download at <http://www.phidot.org/software/mark/docs/book>.
- 571
- 572 Converse, S.J., Block, W.M. & White, G.C. (2006). Small mammal population and habitat responses to
573 forest thinning and prescribed fire. *Forest Ecol. Manag.*, 228, 263-273.
- 574
- 575 Dawson, D.K. & Efford, M.G. (2009). Bird population density estimated from acoustic signals. *J. Appl.*
576 *Ecol.*, 46, 1201-1209.
- 577
- 578 Dice, L.R. (1938). Some census methods for mammals. *J. Wildl. Manage.*, 2, 119-130.
- 579
- 580 Dorazio, R.M. & Royle, J.A. (2003). Mixture models for estimating the size of a closed population when
581 capture rates vary among individuals. *Biometrics*, 59, 351-364.
- 582
- 583 Driezen K., Adriaensen F., Rondini C., Doncaster C.P. & Matthysen E. (2007). Evaluating least-cost
584 model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs
585 (*Erinaceus europaeus*). *Ecol. Model.*, 209, 314–322.
- 586
- 587 Efford, M. G. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598-610.
- 588

- 589 Ellner, S.P., McCauley, E., Kendall, B.E., Briggs, C.J., Hosseini, P.R., Wood, S.N., *et al.* (2001).
590 Habitat structure and population persistence in an experimental community. *Nature*, 412, 538-543.
591
- 592 Efford, M. G., Dawson, D.K. & Borchers, D.L. (2009). Population density estimated from locations of
593 individuals on a passive detector array. *Ecology*, 90, 2676-2682.
594
- 595 Efford, M.G. & Mowat, G. (2014). Compensatory heterogeneity in spatially explicit capture–recapture
596 data. *Ecology*, 95, 1341-1348.
597
- 598 Efford, M.G., Dawson, D.K., Jhala, Y.V. & Qureshi, Q. (2015). Density-dependent home-range size
599 revealed by spatially explicit capture–recapture. *Ecography*, 39, 676-688.
600
- 601 Ergon, T. & Gardner, B. (2013). Separating mortality and emigration: modelling space use, dispersal
602 and survival with robust-design spatial capture–recapture data. *Methods Ecol. Evol.*, 5, 1327-1336.
603
- 604 Fuller, A.K., Sutherland, C.S., Royle, J.A. & Hare, M.P. (2015). Estimating population density and
605 connectivity of American mink using spatial capture-recapture. *Ecol. Appl.*, 26, 1125-1135.
606
- 607 Gardner, B., Reppucci, J., Lucherini, M. & Royle, J.A. (2010). Spatially explicit inference for open
608 populations: estimating demographic parameters from camera-trap studies. *Ecology*, 91, 3376-3383.
609
- 610 Getz, W.M. & Saltz, D. (2008). A framework for generating and analyzing movement paths on
611 ecological landscapes. *Proc. Natl. Acad. Sci. U.S.A.*, 105, 19066-19071.
612
- 613 Gopaldaswamy, A.M., Royle, J.A., Hines, J.E., Singh, P., Jathanna, D., Kumar, N. & Karanth, K.U.,
614 2012. Program SPACECAP: software for estimating animal density using spatially explicit capture–
615 recapture models. *Methods Ecol. Evol.*, 3, 1067-1072.
616
- 617 Gimenez, O., Rossi, V., Choquet, R., Dehais, C., Doris, B., Varella, H., *et al.* (2007). State-space
618 modelling of data on marked individuals. *Ecol. Modell.*, 206, 431-438.
619
- 620 Gustafson, E.J. & Gardner, R.H. (1996). The effect of landscape heterogeneity on the probability of
621 patch colonization. *Ecology*, 77, 94-107.
622
- 623 Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press, 266 pp.
624
- 625 Hayne, D.W. (1949). Calculation of size of home range. *J. Mammal.*, 30, 1-18.
626
- 627 Huffaker, C.B. (1958). Experimental studies on predation: dispersion factors and predator–prey
628 oscillations. *Hilgardia*, 27, 343–383.

- 629
630 Illian, J., Penttinen, A., Stoyan, H. & Stoyan, D. (2008). *Statistical Analysis and Modelling of Spatial*
631 *Point Patterns* (Vol. 70). John Wiley & Sons.
632
633 Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource
634 preference. *Ecology*, 61, 65-71.
635
636 Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures
637 and recaptures. *Ecology*, 79, 2852-2862.
638
639 Kārantā, K.U. & Nichols, J.D. eds. (2002). *Monitoring Tigers and Their Prey: a Manual for*
640 *Researchers, Managers, and Conservationists in Tropical Asia*. Centre for Wildlife Studies.
641
642 Karanth, K.U., Nichols, J.D., Kumar, N. & Hines, J.E. (2006). Assessing tiger population dynamics
643 using photographic capture–recapture sampling. *Ecology*, 87, 2925-2937.
644
645 Kendall, K.C., Macleod, A.C., Boyd, K.L., Boulanger, J., Royle, J.A., Kasworm, W.F., *et al.* (2016).
646 Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak Ecosystem. *J. Wildl.*
647 *Manage.*, 80, 314-331.
648
649 Kidney, D., Rawson, B.M., Borchers, D.L., Stevenson, B.C., Marques, T.A. & Thomas, L. (2016). An
650 efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia.
651 *PLOS ONE*, 11, p.e0155066.
652
653 Kot, M. (2001). *Elements of Mathematical Ecology*. Cambridge University Press, 453 pp.
654
655 Krebs, C. J. 1985. *Ecology*, 3rd ed. Harper & Row.
656
657 Lagrange, P., Pradel, R., Bélisle, M. & Gimenez, O. (2014). Estimating dispersal among numerous sites
658 using capture–recapture data. *Ecology*, 95, 2316-2323.
659
660 Laird, N.M. & Ware, J.H. (1982). Random-effects models for longitudinal data. *Biometrics*, 38, 963-
661 974.
662
663 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. & Morales, J.M. (2012). Flexible and
664 practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology*, 93, 2336-
665 2342.
666
667 Linden, D.W., Fuller, A.K., Royle, J.A. & Hare, M.P. (2016). Estimating the occupancy-density
668 relationship for a low density carnivore. *J. Appl. Ecol.* (in press).

- 669
670 Link, W.A., Yoshizaki, J., Bailey, L.L. & Pollock, K.H. (2010). Uncovering a latent multinomial:
671 analysis of mark–recapture data with misidentification. *Biometrics*, 66, 178-185.
672
- 673 MacArthur, R.H. & MacArthur, A.T. (1974). On the use of mist nets for population studies of birds.
674 *Proc. Natl. Acad. Sci. U.S.A.*, 71, 3230-3233.
675
- 676 Magoun, A.J., Long, C.D., Schwartz, M.K., Pilgrim, K.L., Lowell, R.E. & Valkenburg, P. (2011).
677 Integrating motion-detection cameras and hair snags for wolverine identification. *J. Wildl. Manag.*, 75,
678 731-739.
679
- 680 Marques, T.A., Thomas, L., Ward, J., DiMarzio, N. & Tyack, P.L. (2009). Estimating cetacean
681 population density using fixed passive acoustic sensors: an example with Blainville’s beaked whales. *J.*
682 *Acoust. Soc. Am.*, 125, 1982-1994.
683
- 684 McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering
685 ecological dynamics in resource selection functions. *J. An. Ecol.*, 79, 4-12.
686
- 687 McClintock, B.T., Conn, P.B., Alonso, R.S. & Crooks, K.R. (2013). Integrated modeling of bilateral
688 photo-identification data in mark–recapture analyses. *Ecology*, 94, 1464-1471.
689
- 690 McRae, B.H. (2006). Isolation by resistance. *Evolution*, 60, 1551-1561.
691
- 692 Morin, D.J., Fuller, A.K., Royle, J.A. & Sutherland, C. (2016). Model-based estimators of density and
693 connectivity to inform conservation of spatially-structured populations. *Ecosphere* (in press)
694
- 695 Muñoz, D.J., Miller, D.A., Sutherland, C. & Grant, E.H.C. (2016). Using spatial capture-recapture to
696 elucidate population processes and space-use in herpetological studies. *J. Herpetol.* (in press)
697
- 698 Nichols, J.D. (1992). Capture-recapture models. *BioScience*, 42, 94-102.
699
- 700 Nichols, J.D., Pollock, K.H. & Hines, J.E. (1984). The use of a robust capture-recapture design in small
701 mammal population studies: a field example with *Microtus pennsylvanicus*. *Acta Theriol.*, 29, 357-365.
702
- 703 Nichols, J.D. and MacKenzie, D.I., 2004. Abundance estimation and conservation biology. *An. Biod.*
704 *Cons.*, 27, 437-439.
705
- 706 Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture
707 data on closed animal populations. *Wildl. Monogr.*, 62, 3-135.
708

- 709 Ovaskainen, O. (2004). Habitat-specific movement parameters estimated using mark-recapture data and
710 a diffusion model. *Ecology*, 85, 242-257.
- 711
- 712 Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008). State-space
713 models of individual animal movement. *Trends Ecol. Evol.* 23, 87-94.
- 714
- 715 Poor, E.E., Loucks, C., Jakes, A. & Urban, D.L. (2012). Comparing habitat suitability and connectivity
716 modeling methods for conserving pronghorn migrations. *PLOS ONE*, 7, p.e49390.
- 717
- 718 Pradel, R., Choquet, R., Lima, M.A., Merritt, J. & Crespin, L. (2010). Estimating population growth rate
719 from capture-recapture data in presence of capture heterogeneity. *J. Agric. Biol. Environ. Stat.*, 15, 248-
720 258.
- 721
- 722 Proffitt, K.M., Goldberg, J.F., Hebblewhite, M., Russell, R.E., Jimenez, B.S., Robinson, H.S., *et al.*
723 (2015). Integrating resource selection into spatial capture-recapture models for large carnivores.
724 *Ecosphere*, 6, 1-15.
- 725
- 726 Reich, B.J. & Gardner, B. (2014). A spatial capture-recapture model for territorial species.
727 *Environmetrics*, 25, 630-637.
- 728
- 729 Royle, J.A. (2015). Spatial capture-recapture with partial identity. *arXiv preprint arXiv:1503.06873*.
- 730
- 731 Royle, J.A. & Young, K.V. (2008). A hierarchical model for spatial capture-recapture data. *Ecology*, 89,
732 2281-2289.
- 733
- 734 Royle, J.A., Chandler, R.B., Sollmann R. & Gardner, B. (2014). *Spatial Capture-Recapture*. Academic
735 Press/Elsevier. 612 pages.
- 736
- 737 Royle, J.A., Chandler, R.B., Gazenski, K.D & Graves, T.A. (2013a). Spatial capture-recapture models
738 for jointly estimating population density and landscape connectivity. *Ecology*, 94, 287-294.
- 739
- 740 Royle, J.A., Chandler, R.B., Sun C.C. & Fuller, A.K. (2013b). Integrating resource selection information
741 with spatial capture-recapture. *Methods Ecol. Evol.*, 3, 545-554.
- 742
- 743 Royle, J.A., Kery, M. & Guelat, J. (2011). Spatial capture-recapture models for search-encounter data.
744 *Methods Ecol. Evol.*, 2, 602-611.
- 745
- 746 Royle, J.A., Fuller, A.K. & Sutherland, C. (2016). Spatial capture-recapture models allowing Markovian
747 transience or dispersal. *Popul. Ecol.*, 58, 53-62.
- 748

- 749 Sampson, P.D. & Guttorp, P. (1992). Nonparametric estimation of nonstationary spatial covariance
750 structure. *J. Am. Stat. Assoc.*, 87, 108-119.
- 751
- 752 Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. (2004). Estimating survival and temporary
753 emigration in the multistate capture-recapture framework. *Ecology*, 85, 2107-2113.
- 754
- 755 Schaub, M. & Royle, J.A. (2014). Estimating true instead of apparent survival using spatial Cormack-
756 Jolly-Seber models. *Methods Ecol. Evol.*, 5, 1316-1326.
- 757
- 758 Schwartz, M.K., Luikart, G. & Waples, R.S. (2007). Genetic monitoring as a promising tool for
759 conservation and management. *Trends Ecol. Evol.*, 22, 25-33.
- 760
- 761 Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T., Tôrres, N.M. & Silveira, L. (2011).
762 Improving density estimates for elusive carnivores: accounting for sex-specific detection and
763 movements using spatial capture-recapture models for jaguars in central Brazil. *Biol. Cons.*, 144, 1017-
764 1024.
- 765
- 766 Sollmann, R., B. Gardner, A.W. Parsons, J.J. Stocking, B.T. McClintock, T.R. Simons, & O'Connell,
767 A.F. (2013). A spatial mark-resight model augmented with telemetry data. *Ecology*, 94, 553-559.
- 768
- 769 Stevenson, B.C., Borchers, D.L., Altwegg, R., Swift, R.J., Gillespie, D.M. & Measey, G.J. (2015). A
770 general framework for animal density estimation from acoustic detections across a fixed microphone
771 array. *Methods Ecol. Evol.*, 6, 38-48.
- 772
- 773 Sun, C.C., Fuller, A.K. & Royle, J.A. (2014). Trap configuration and spacing influences parameter
774 estimates in spatial capture-recapture models. *PLOS ONE*, 9, e88025.
- 775
- 776 Sutherland, C., Fuller, A.K. & Royle, J.A. (2015). Modelling non-Euclidean movement and landscape
777 connectivity in highly structured ecological networks. *Methods Ecol. Evol.*, 6, 69-177.
- 778
- 779 Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., *et*
780 *al.* (2013), Identification of 100 fundamental ecological questions. *J. Ecol.*, 101, 58–67.
- 781
- 782 Taberlet, P. & Luikart, G. (1999). Non-invasive genetic sampling and individual identification. *Biol. J.*
783 *Linn. Soc.*, 68, 41-55.
- 784
- 785 Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity is a vital element of landscape
786 structure. *Oikos*, 68, 571-572.
- 787

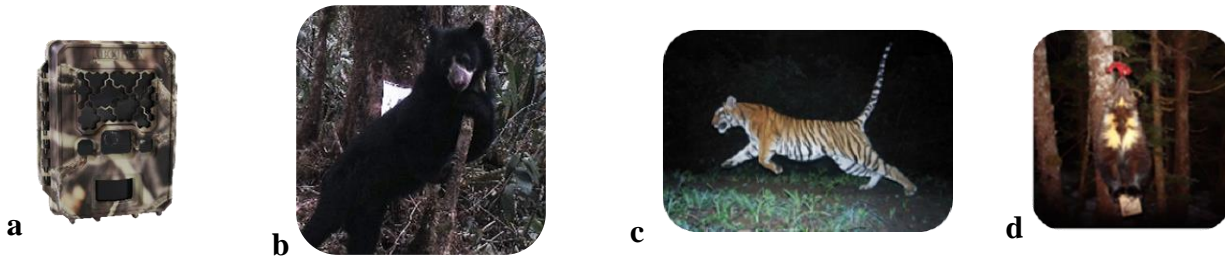
- 788 Tilman, D. & Kareiva, P.M. (1997). Spatial ecology: the role of space in population dynamics and
789 interspecific interactions (Vol. 30). Princeton University Press.
- 790
- 791 Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population*
792 *Redistribution in Animals and Plants* (Vol. 1). Sunderland: Sinauer Associates.
- 793
- 794 Turner, M.G., Gardner, R.H. & O'Neill, R.V. (2001). *Landscape Ecology in Theory and Practice*. New
795 York: Springer.
- 796
- 797 Walpole A.A., Bowman J., Murray D.L., & Wilson P.J. (2012). Functional connectivity of lynx at their
798 southern range periphery in Ontario, Canada. *Land. Ecol.*, 27, 761–773
- 799
- 800 Whittington J. & Sawaya, M.A. (2015). A comparison of grizzly bear demographic parameters
801 estimated from non-spatial and spatial open population capture-recapture models. *PLOS ONE*, 10,
802 e0134446.
- 803
- 804 Whittington, J., Hebblewhite, M. & Chandler, R.B. (2017). Generalized spatial mark-resight models
805 with an application to grizzly bears. *J. Appl. Ecol.*, (in press).
- 806
- 807 Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002). *Analysis and Management of Animal Populations*.
808 Academic Press.
- 809
- 810 Wilson, K.R. & Anderson, D.R. (1985a). Evaluation of a nested grid approach for estimating density. *J.*
811 *Wildl. Manag.*, 49, 675-678.
- 812
- 813 Wilson, K.R. & Anderson, D.R. (1985b). Evaluation of a density estimator based on a trapping web and
814 distance sampling theory. *Ecology*, 66, 1185-1194.
- 815
- 816 Zeller, K.A., McGarigal, K. & Whiteley, A.R. (2012). Estimating landscape resistance to movement: a
817 review. *Land. Ecol.*, 27, 777-797.
- 818
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Box 1 – New technologies for generating spatial encounter data

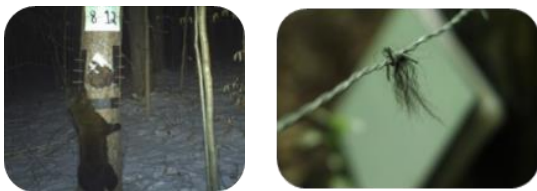
The advent of new field-based methodologies for individual identification allows researchers to collect spatial encounter information on individual animals without the need for physically capturing and marking individuals. Additionally, many of the methods are amenable to citizen science approaches (Dickinson et al. 2010) whereby non-professional scientists are engaged in the collection of data (e.g., camera traps, hair snares), providing increased spatial extent of sampling.

Camera Traps: With improvements in camera technology, there are many commercially available cameras (a) with superior digital technology that provide still photographs and videos to capture species that are elusive and otherwise difficult to capture. Individuals can be identified from photographs for species that possess distinctive natural marks (e.g., Andean bears (b), tigers (c), wolverines (d), bobcats, jaguars, snow leopards, and others).

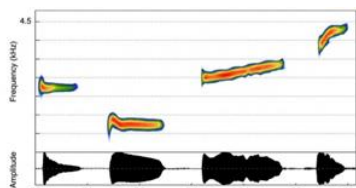


Non-Invasive Genetic Sampling (NGS): NGS allows for the identification of individuals without direct observations via the extraction of DNA from samples. Genetic data can be collected from scat, hair, feathers, shed skin, saliva, and urine. Two common methods of obtaining genetic samples are by using devices that snag hair (i.e., hair snares) (a) and scat detection dogs (b). These methods have been employed on marine and terrestrial mammals (e.g., right whales, black bear, fisher, American mink).

a) Hair Sampling



b) Scat sampling



Bioacoustics: Spatially separated microphones or hydrophones can be used to detect species that produce sounds for biological purposes such as defending territories, social calling, and mate attracting. Recent advances in bioacoustics technologies and signal detection and recognition algorithms of spectrographs (left) permit the collection of sounds from species such as mammals, birds, and marine mammals.

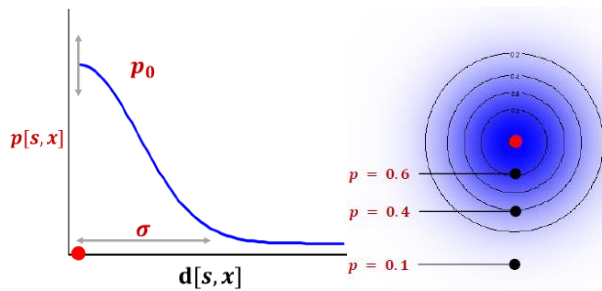
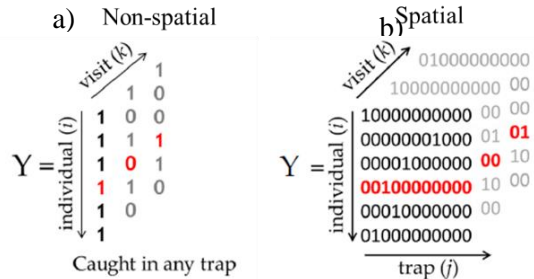
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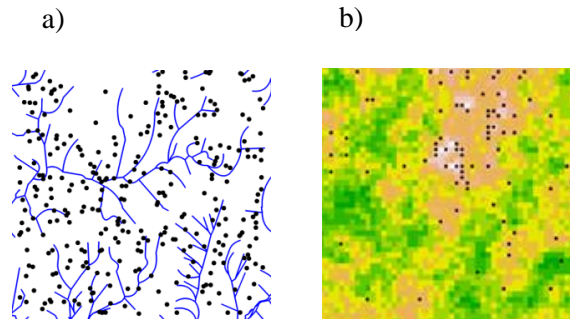
Box 2 – Core elements of spatial capture-recapture

Spatial encounter history data: Classical capture-recapture summarize spatial data and records only *when* each individual is encountered (a). In practice, data are reduced from a richer 3-d data structure - a record of *when* and *where* each individual was captured (b). Such spatial pattern data are informative about spatial population processes.



Encounter probability model: SCR models describe encounter probability as a function of the distance between a sample location and s , the individual's activity center (the half-normal form is shown to the left). The spatial scale parameter σ accommodates individual heterogeneity in detection due to the juxtaposition of individuals with detectors.

Spatially explicit point process model: Encounter histories are modelled conditional on a latent point process describing the spatial distribution of individuals. The null model of uniformity (a) is typically applied and robust to violations. More realistic models allow individuals to be distributed explicitly according to some covariate (b).



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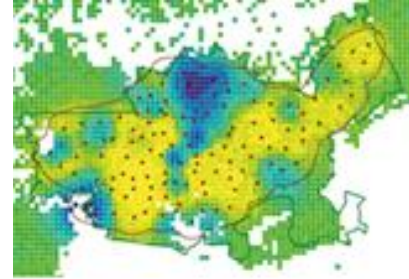
Box 3 – Modeling resource selection with SCR

Resource selection is a multi-scale process (Johnson 1980), determining the range of a species (1st order selection), the distribution of individuals within their range (2nd order), and the use of habitat by an individual within its home range or territory (3rd order). SCR methods allow for explicit modeling of both 2nd and 3rd order resource selection from encounter history data produced from standard capture-recapture methods such as camera trapping, scat and hair sampling for DNA and live trapping.

2nd order resource selection is the process that governs the placement or location of individual activity centers. SCR models accommodate explicit models for the probability distribution of activity centers s_i , referred to as inhomogeneous point process models, in which the intensity function depends on landscape or habitat structure:

$$\log(D(s)) = \beta_0 + \sum \beta_k X_{sk}$$

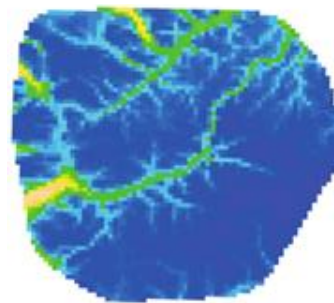
At right, mapped tiger density (from Gopalaswamy et al. 2012).



3rd order resource selection affects the SCR encounter probability model (Royle et al. 2013). For some spatially explicit covariate $z(x)$, the probability of encounter can be modeled as a function of both distance and measured covariate with parameter to be estimated:

$$p(x|s) \propto \exp(\alpha * z(x) - \text{dist}(x, s)).$$

This corresponds to the kernel of standard resource selection models, providing a framework for formal integration of capture-recapture data with data from telemetry studies. At right, estimated encounter probability surface for a black bear population if a trap were placed at a pixel relative to the encounter probability at a pixel of average elevation (from Royle et al. 2013).



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Box 4: Estimating landscape connectivity

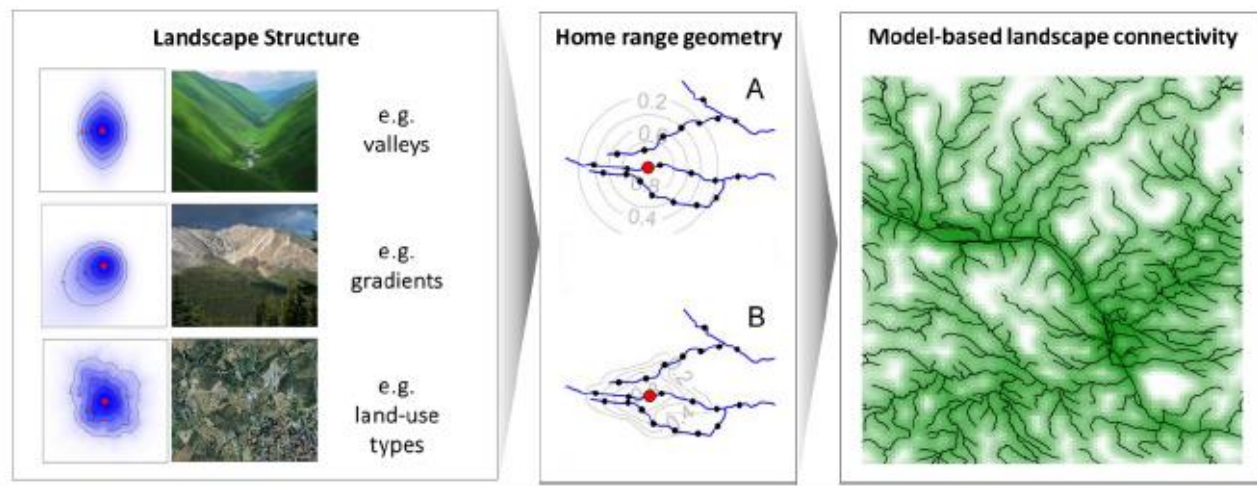
Landscape structure influences local movements such that, during monitoring, the pattern of individual observations around its activity center is likely to deviate from the assumption of a circular home range. Understanding patterns of space use, and thus estimating encounter rates without bias, requires that the structure of ecological landscapes is explicitly accounted for. Using a least cost path approach, SCR allows the estimation of one or more resistance parameters, δ , characterizing how movement is influenced by landscape structure. Euclidean distance in Eqn. 3 and Box 2 is replaced by *ecological distance*, d_{ecol} , the length of the least cost path between two points (v_0 and v_T):

$$d_{ecol}(v_0, v_T) = \min_{\mathcal{L}_1, \dots, \mathcal{L}_W} \sum_{a=0}^{T-1} \text{cost}(v_a, v_{a+1}) \times d_{euc}(v_a, v_{a+1}),$$

where $\mathcal{L}_w(v_0, v_T) = \{v_0, \dots, v_T\}$ denotes any path consisting of T adjacent lines connecting adjacent pixels, and $\text{cost}(v_a, v_{a+1})$ is a cost function which is a log linear function of the average pixel-specific covariate values:

$$\log(\text{cost}(v_a, v_{a+1})) = \delta \frac{z(v_a) + z(v_{a+1})}{2}.$$

Estimation of the resistance parameter provides a direct measure of the strength of species–landscape interactions which has important implications. First, this is a model for asymmetric space use that simultaneously relaxes assumptions of symmetry and stationarity, allowing *home range geometry* to vary depending on location and local landscape structure. Secondly, for a known landscape, the probability of use for any pixel on the landscape can be computed given an individual’s location, i.e., individual local connectivity, and it follows therefore that the composite local connectivity surfaces for any collection of activity centers provides a *model-based landscape connectivity* surface informed by the estimate of the species-landscape parameter.



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