



# Mechanistic approaches to understanding and predicting mammalian space use: Recent advances, future directions

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9 **Mechanistic Approaches to Understanding and Predicting Mammalian Space-Use:**  
10 **Recent Advances, Future Directions**

11

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16 The coming of age of GPS telemetry, in conjunction with recent theoretical innovations  
17 for formulating quantitative descriptions of how different ecological forces and  
18 behavioral mechanisms shape patterns of animal space-use, has led to renewed interest  
19 and insight into animal home-range patterns. This renaissance is likely to continue as  
20 result of on-going synergies between these empirical and theoretical advances. In this  
21 article I review key developments that have occurred over the past decade that are  
22 furthering our understanding of the ecology of animal home ranges. I then outline what I  
23 perceive as important future directions for furthering our ability to understand and predict  
24 mammalian home-range patterns. Interesting directions for future research include: (1)  
25 improved insights into the environmental and social context of animal movement  
26 decisions and resulting patterns of space-use; (2) quantifying the role of memory in  
27 animal movement decisions; (3) examining the relevance of these advances in our  
28 understanding of animal movement behavior and space-use to questions concerning the  
29 demography and abundance of animal populations.

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33           Two inter-related questions that are often asked about species of management or  
34 conservation interest are: how is the spatial distribution of animals on a landscape likely  
35 to change as a result of changes in the environment? And how will this, in turn, affect its  
36 demography and abundance? Such questions regarding the distribution and abundance of  
37 animals in space and time are longstanding, and lie at the heart of wildlife ecology. Being  
38 able to provide meaningful answers to these questions is becoming increasingly  
39 important, however, as the impact of humans on the planet's ecosystems intensifies due  
40 to continuing habitat transformation, resource exploitation, and human-induced climate  
41 change. Here I review recent progress in measurements and analysis methods relevant to  
42 understanding mammalian home-range patterns. I then outline what I see as the next key  
43 steps for improving the ability to provide relevant scientific answers to ecologists and  
44 wildlife biologists about how mammalian home-range patterns and the resulting spatial  
45 distributions of animal populations are likely to change as environments change. Finally,  
46 I discuss the relevance of these advances in understanding animal home-range patterns  
47 for answering questions regarding the second related issue: the abundance of animal  
48 populations on current and future landscapes.

49           Mammals do not tend to move at random, but instead restrict their movements to  
50 particular areas (Seton 1909). This phenomenon underlies the concept of an animal's  
51 home range, defined by Burt (1943) as "that area traversed by an individual in its normal  
52 activities of food gathering, mating, and caring for the young." As a result, understanding  
53 the key factors underlying animal home-range patterns is therefore crucial to  
54 understanding how patterns of mammalian space-use will respond to changes in the  
55 environment. Prior to the 1950s, information on home ranges came from either direct

56 behavioral observations of animal movements, spatially-distributed trapping of animals  
57 over a period of time, or by following animal tracks on snow covered landscapes. The  
58 advent of radio-telemetry in the 1950s ushered in a new era of animal home-range  
59 analysis, enabling researchers to document systemically the patterns of space use by  
60 animals. Radio-telemetry was subsequently widely adopted in animal ecology and  
61 wildlife studies (see Macdonald et al. 1980 and Millspaugh and Marzluff 2001 for  
62 reviews).

63         The widespread adoption of radio-telemetry, in turn, spurred the development of  
64 methods for analyzing radio-telemetry data. In particular, a variety of density estimation  
65 methods for analyzing telemetry data were developed, including the bivariate normal,  
66 harmonic mean, and kernel, and nearest-neighbor convex hull (Getz and Wilmers 2004)  
67 home-range models (see Macdonald 1980; Worton 1987; and Kernohan et al. 2001 for  
68 reviews). These statistical methods convert spatial patterns of telemetry relocations into  
69 useful summary estimates and descriptors of home-range size, shape, and intensity of use.

70         A second important milestone in the study of animal home ranges was the  
71 introduction of Resource Selection Analysis (RSA) during the 1980s. In contrast to the  
72 descriptive statistical methods of home-range analysis that simply summarize observed  
73 spatial patterns of animal relocations, RSA seeks to identify key habitats or resources by  
74 analyzing the frequency at which habitats are used relative to some measure of their  
75 availability on a landscape (Fig. 1). RSA analyses can be conducted at a variety of spatial  
76 scales; however, here I focus on RSAs conducted at scale of individual home ranges, i.e.  
77 so-called third-order selection (*sensu* Johnson 1980), Thomas and Taylor 1990). Results  
78 from numerous studies have shown how the RSA approach can be used to identify

79 associations between animal home ranges and particular land-cover types, and other  
80 aspects of environmental heterogeneity, such as topography, resource availability, or  
81 habitat edges (see Manly et al. 1993; Boyce and McDonald 1999; Cooper and Millsbaugh  
82 2001; and Erickson et al. 2001 for reviews).

83         Mechanistic home-range analysis has been advanced as an alternative framework  
84 for analyzing animal home ranges (Moorcroft et al. 1999; Moorcroft and Lewis 2006). In  
85 contrast to conventional RSA analyses that are spatially implicit in nature (the RSA  
86 equations, in effect, assume that animals assumed to choose between habitats in a manner  
87 analogous to choosing different colored balls from a container, i.e. without regard to  
88 spatial proximity of habitat types -- see Moorcroft and Lewis 2006 and Moorcroft and  
89 Barnett 2008 for further discussion of this issue), mechanistic home-range models  
90 develop spatially explicit predictions for patterns of animal space use by modeling the  
91 process of individual movement (Millsbaugh and Marzluff 2001). The origins of these  
92 models lies in the mathematical analysis of correlated random walks (Skellam 1951;  
93 Okubo 1980; Kareiva and Shigesada 1983; Turchin 1998) that characterize the fine-scale  
94 movement behavior of individuals via a so-called redistribution kernel, which specifies  
95 probability of an animal moving from any given location to any other location in a  
96 specified time interval (Fig. 2a). In addition to the effects of habitat or resources  
97 considered in RSA, other behavioral and ecological factors influencing the movements of  
98 individuals can be incorporated into the redistribution kernel that defines the stochastic  
99 fine-scale movement process. For example, in a recent analysis of coyote (*Canis latrans*)  
100 home ranges in Yellowstone, Moorcroft et al. (2006), building on earlier work by Holgate  
101 (1971), Okubo (1980), and Lewis and Murray (2003), developed a “prey availability plus

102 conspecific avoidance” mechanistic home-range model in which individuals exhibit: (i) a  
103 foraging response to prey availability in which individuals decreased their mean step  
104 length in response to small mammal abundance, (ii) an avoidance response to encounters  
105 with foreign scent marks, (iii) an over-marking response to encounters with foreign scent  
106 marks. From the mathematical description of fine-scale movement behavior, it is then  
107 possible to derive probability density functions for the expected spatial pattern of home  
108 ranges that result from individuals moving on a landscape according to these underlying  
109 rules of movement. Fig. 2b shows the fit of the “prey availability plus conspecific  
110 avoidance” mechanistic home-range model to the observed spatial distribution of radio  
111 telemetry relocations of five adjacent coyote packs in Yellowstone National Park  
112 (Moorcroft et al. 2006; see also Moorcroft and Lewis 2006). As Fig. 2b illustrates, the  
113 model captures the influences of both resource availability and the presence of  
114 neighboring groups on the coyote home ranges within the region. Note that in linking the  
115 scent-mark and foraging responses of individuals to their resulting pattern home ranges,  
116 mechanistic home-range models are, in some sense, implicitly linking third-order  
117 selection (how an animal utilizes the different habitats in its home range) with fourth  
118 order selection (the way in which the animal uses each of the different habitats). For a  
119 discussion of orders of selection, see Johnson (1980).

120

121

## RECENT DEVELOPMENTS

122 *GPS telemetry.*—One of the most significant developments in studies of animal  
123 home ranges has been the recent coming of age of Global Positioning System (GPS)-  
124 based telemetry. Satellite-based telemetry systems began appearing in the 1970s. The

125 first systems, such as ARGOS, used Doppler shift to identify an animal's spatial position.  
126 However, since the 1990s, this technology has been increasingly combined with, or  
127 replaced by, GPS-based telemetry systems that have higher positional accuracy  
128 (Tomkiewicz et al. 2010). GPS-based telemetry systems were initially only suitable for  
129 deployment on large terrestrial and marine vertebrates (e.g. Priede and French 1991,  
130 Rempel 1995, Ballard et al 1995, Bethke et al. 1996), but over the subsequent two  
131 decades, advances in GPS-based telemetry systems have enabled their deployment on  
132 species of ever-smaller body sizes such as white-tailed deer (*Odocoileus virginianus*)  
133 (Merrill et al. 1998), coyotes (Windberg et al. 1997), and more recently, Japanese  
134 macaques (*Macaca fuscata*) (Sprague et al. 2004) and lynxes (*Lynx lynx* and *Lynx*  
135 *canadensis*) (Krofel et al. 2006; Burdett et al. 2007). It takes several years of pilot and  
136 evaluation studies before GPS-based telemetry becomes an operational technology  
137 suitable for addressing particular scientific or management questions for a species For  
138 moose (*Alces alces*), the transition from pilot and evaluation studies (e.g. Rempel et al.  
139 1995; Moen et al. 1996) into an operational technology suitable for addressing particular  
140 scientific or management questions (e.g. Dussault et al. 2004, 2005a,b) took almost a  
141 decade. As GPS telemetry continues to mature, however, the transition between  
142 technology evaluation studies and operational deployment is getting shorter. For  
143 example, for elk (*Cervus elaphus*), evaluation studies of GPS telemetry were conducted  
144 in 2001 (e.g. Rumble et al. 2001; Biggs et al. 2001), and only a few years later were  
145 beginning to be used to answer scientific questions regarding elk movement (e.g. Boyce  
146 et al. 2003; Rumble et al. 2005). Thus, while GPS-telemetry systems have existed for two  
147 decades, I would argue that only in the past five years has its scientific potential begun to

148 be realized.

149       Now that GPS telemetry is becoming a mainstream technique for studying patterns  
150 of animal movement, it is providing a wealth of new information on patterns of animal  
151 space use and movement behavior. One of its most obvious benefits is the sheer volume  
152 of data that each collar yields. For example, the radio telemetry dataset used by  
153 Moorcroft et al. (2006) in the analysis of coyote home ranges shown in Fig. 2 consisted  
154 of approximately 2000 relocations, while modern GPS telemetry datasets are typically ten  
155 to a hundred times larger. For example, Fig. 3 shows a GPS telemetry dataset comprised  
156 of 140,000 locations of 29 brushtail possums (*Trichosurus vulpecula*) collected at 5-15  
157 minute intervals, recently collected by Todd Dennis and colleagues.

158       As the dataset shown in Fig. 3 exemplifies, the increase in data volume in GPS  
159 telemetry is primarily due to an increase in the temporal frequency with which  
160 relocations are obtained. This increased frequency of sampling does come at cost,  
161 however: the short battery life, and high price of GPS-telemetry collars means that GPS-  
162 telemetry studies typically have a shorter duration, and collars placed on fewer numbers  
163 of individuals compared to radio-telemetry collars.

164       The increased sampling frequency in GPS telemetry studies compared to  
165 conventional radio telemetry has yielded more detailed and spatially-resolved description  
166 of animal's pattern of space use (though see Fieberg and Börger, this issue). One  
167 reflection of this has been the increased temporal resolution of resource selection  
168 analyses; in particular, the move towards so-called step-selection RSA in which resource  
169 selection is examined on a per-step, or, more accurately, relocation-to-relocation, basis.  
170 Further details on step-selection RSA can be found in the section below. This has resulted



171 in a considerable increase in statistical power to detect the signatures of factors affecting  
172 fine-scale movements of individuals, and resulting insights into factors influencing  
173 movement behavior. For example, whereas Boyce et al.'s (2003) analysis of elk resource  
174 selection in Yellowstone used radio-telemetry measurements separated by ten to fourteen  
175 day intervals, Forester et al.'s (Forester 2005; Forester et al. 2007) analyses of elk  
176 resource selection in Yellowstone analyzed resource selection using GPS-telemetry data  
177 collected at five-hour intervals. Although both of the above analyses incorporated  
178 common landscape covariates such as cover type and topography, the analyses by  
179 Forester et al. also identified distance to forest edge and distance to roads as additional  
180 explanatory covariates for patterns of elk space-use, and quantified a clear crepuscular  
181 pattern of elk movements.

182       *Advances in analysis methods.*—Conventional resource-selection analysis (RSA)  
183 uses ratios of habitat utilization to an aggregate measure of habitat availability in order to  
184 identify habitats that animals use disproportionately relative to their occurrence on a  
185 landscape. Concurrent with the rise of GPS telemetry has been a shift towards step-  
186 selection RSA methods that assess animal habitat preferences at the scale of successive  
187 relocations. This trend began with a ground-breaking analysis of patterns of polar bear  
188 (*Ursus maritimus*) habitat use by Arthur et al. (1996) who argued that habitat availability  
189 should not be treated as a constant, but should vary in relation to the current location of  
190 an individual. Accordingly, in their analysis, Arthur et al. (1996) used a circle around the  
191 animal's current location whose radius corresponded to the maximum distance the animal  
192 could travel in the time interval between relocations to define a measure of habitat  
193 availability that was specific for each relocation in the dataset. This step-selection

194 methodology is well-suited to the increased temporal frequency of GPS telemetry data,  
195 and accordingly has been widely adopted in analyses of GPS-telemetry measurements.  
196 The estimates of habitat availability used in step-selection studies are also becoming  
197 increasingly sophisticated, and often now account for the probability of an animal  
198 moving a given distance within the sample interval. As I discuss later in this article,  
199 habitat availability also depends on what an animal remembers (--see also Spencer in this  
200 special section).

201       A second important methodological advance linked to the rise of GPS telemetry has  
202 been the incorporation of an animal's state into analyses of animal movement behavior.  
203 Whereas RSA approaches have shown that landscape attributes significantly influence  
204 animal movement decisions, focal studies have shown that the movements of animals are  
205 also strongly influenced by their internal physiological and behavioral states, such as  
206 hunger (e.g. Jung and Koong 1985), thirst (e.g. Senft et al. 1987), and fear (e.g. Mitchell  
207 and Lima 2002; Zollner and Lima 2005). The significance of an animal's internal  
208 physiological and behavioral state on its patterns of fine-scale movements has been  
209 inferred in two recent analyses of elk GPS-telemetry data. Morales et al. (2004), building  
210 on earlier work by Johnson et al. (2002), showed that state-based movement models, in  
211 which individuals switched probabilistically between a series of behavioral states that are  
212 associated with different distributions of step lengths or turning angles, provided a better  
213 fit to the observed patterns of fine-scale movement than models in which animal's fine-  
214 scale movement behavior was invariant. Similarly, Forester et al. (2007) showed that the  
215 movements of individual elk were significantly influenced both by current landscape  
216 attributes and the landscape attributes associated with previous relocations, implying the

217 existence of one or more internal state variables that individuals used to track the history  
218 of places previously visited by the animal.

219       *Biotelemetry.*—Although the analyses of Morales et al. (2004) and Forester et al.  
220 (2007) described above illustrate how the existence of different movement states for  
221 animals can be inferred from telemetry relocations, these approaches, are, in essence,  
222 inferring process from pattern, which as noted by Pielou (1977), is an inherently difficult  
223 exercise. For these reasons, obtaining direct measurements of the external conditions and  
224 physiological and behavioral condition of animals as they move is highly desirable for  
225 improving our understanding the underlying impacts of physiological and behavioral  
226 states on animal movement behavior. Beginning in the 1960s, researchers have deployed  
227 devices on free-living animals that are designed to provide information on the animal's  
228 physiological condition (e.g. heart rate, breathing rate, wing beat frequency, head  
229 position), as well as information on the external environment (e.g. air temperature, water  
230 temperature or depth). Such techniques are often referred to as either “biologging” or  
231 “biotelemetry” (Ropert-Coudert 2005; Cooke et al. 2004; Ropert-Coudert et al. 2010).  
232 Biotelemetry techniques were pioneered in the marine realm (e.g. Kooyman 1965) where  
233 direct animal observation is difficult, and they have provided important insights into the  
234 ecology of marine mammals and birds. Recent advances in electronics have led to the  
235 development of a wide variety of biosensors, including ones to measure food intake (via  
236 gut temperature, gut pH, or esophagus temperature sensor), energy expenditure (via  
237 heart-beat or wing-beat frequency sensors), and foraging behavior (via timed video-  
238 capture or sensors to detect head position) (Ropert-Coudert and Wilson 2005).

239       *Integrating resource selection and mechanistic analyses of home-range patterns.*

240 – As discussed earlier, the spatially-implicit nature of conventional RSA contrasts with  
241 the spatially-explicit nature of mechanistic home-range analysis, and thus appear to  
242 constitute alternate frameworks for analyzing patterns of animal space use (Moorcroft  
243 and Lewis 2006). However, subsequent developments in RSA analysis have enabled a  
244 reconciliation between RSA and mechanistic home-range models. Rhodes et al. (2005)  
245 recast Arthur et al.'s (1996) resource selection equation in terms of the probability of an  
246 animal moving from its current location to any subsequent location within the circle  
247 defining habitat availability for each relocation. Their motivation for doing so was to  
248 argue for a measure of habitat availability that took into account the fact that the  
249 probability of moving a given distance within the relocation time interval was likely to be  
250 a decreasing function of the distance moved. Moorcroft and Barnett (Moorcroft and  
251 Barnett 2008; Barnett and Moorcroft 2008) then showed that when written in this form,  
252 the equations used by Arthur et al. (1996) and Rhodes et al. (2005) in their RSAs  
253 constituted redistribution kernels. This result means that RSA equations can be used to  
254 derive a corresponding mechanistic movement model, yielding spatially-explicit  
255 predictions for the pattern of space use that results from the animal moving around a  
256 landscape with a given set of habitat preferences. Moorcroft and Barnett's analyses  
257 showed that, surprisingly, when an animal's habitat preferences are spatially localized  
258 (i.e. preferences are governed by local availability), the relative intensity of its space use  
259 at a given location is equal to the square of its preference for that location (Moorcroft and  
260 Barnett 2008) but, as the spatial scale of animal's habitat preference increases, the  
261 intensity of space use becomes proportional to its preference (Barnett & Moorcroft 2008).

262 *The role of memory in animal movement behavior.*—A key issue for developing

263 quantitative predictions of mammalian space use is formulating mathematical  
264 descriptions of the mechanisms responsible for the formation and maintenance of  
265 characteristic home ranges for animals. In mathematical terms, the formation of home  
266 range requires the existence of some form of centralizing tendency in the movement  
267 behavior of animals that localizes their movements to a particular portion of the  
268 landscape. While the existence and significance of these behaviours for patterns of  
269 animal space use has been known for decades within ecology and wildlife biology, the  
270 ability to formulate compact, mathematical representations of the process of home-range  
271 formation and maintenance is relatively new. In the mechanistic home-range models  
272 developed by Holgate (1971), Okubo (1980), Lewis and Murray (1993), and Moorcroft et  
273 al. (2006), this centralizing tendency arose from a bias in the movements of individuals  
274 towards a prescribed home-range center. Such formulations are arguably reasonable for  
275 species that have clear, identifiable centers of attraction, such as the den sites of  
276 carnivores. However, in mammal groups, such as ungulates and primates, that lack a  
277 well-defined center of attraction, other mechanisms must be responsible for the  
278 centralizing tendency of individuals and their resulting home ranges.

279         An important area of recent theoretical development with regard to the issue of  
280 home-range formation has been incorporating the effect of memory on animal movement  
281 behavior. In classical random walk models of animal movement (e.g. Patlak 1953; Okubo  
282 1980; Turchin 1991, 1998), the movements of individuals are unaffected by their history  
283 of previously visited locations. Note that some classical random-walk formulations (e.g.  
284 Patlak 1953) incorporate autocorrelation between successive movement directions, but  
285 this does not usually result in any spatial localization. However, in many mammals, it is

286 clear that the movements of individuals are influenced not only by their current  
287 environment, but also by their history of past movements (Powell 2000; see also Powell  
288 and Mitchell, and Spencer, this issue). As highlighted in recent reviews (e.g. Borger et al.  
289 2008; Smouse et al. 2010), the role of memory is a key issue in understanding the  
290 formation and maintenance of animal home ranges in many mammalian species. Indeed,  
291 it has been argued that an animal's cognitive map of its environment constitutes and  
292 defines its home range (Powell 2000, Powell and Mitchell this issue, Spencer this issue).  
293 In an early paper, Siniff and Jesson (1969) proposed a home-range simulation model in  
294 which individuals biased their movements towards locations that they had previously  
295 visited. More recently, Tan et al. (2001, 2002), building on earlier work by Sapozhnikov  
296 (1994, 1998), and Dalziel (2008), have analyzed the behavior of so-called "self-  
297 attracting" random walks in which individuals display an increased probability of moving  
298 towards previously visited locations. Their analyses showed that movement models of  
299 this kind result in individuals developing quasi-stable home ranges: over short timescales,  
300 the movements of an individual are largely confined to some characteristic area (i.e. a  
301 home range), whereas on longer timescales the center of the individual's home range  
302 drifts randomly around the landscape. Van Moorter et al. (2009) recently proposed an  
303 alternative formulation of animal memory in which an individual displays both an  
304 avoidance response to recently visited resource patches, and an attractive response  
305 towards resource patches that have been visited some time in the past. Their simulations  
306 indicated that both components of this movement process are necessary for the  
307 production of stable home ranges for individuals. Home-range models have also been  
308 proposed in the context of Levy flight models of animal movement, in which the

309 probability distribution of movement distances exhibited by an animal is ‘fat-tailed’  
310 (leptokurtic) (Gautestad and Mysterud 2004; Smouse et al. 2010). Spatial memory has  
311 also been incorporated into optimal foraging models to determine its impacts on the  
312 movement of individuals between resource patches and the conditions under which it  
313 gives rise to home ranges (see Spencer, this issue).

314

315

### FUTURE DIRECTIONS

316 *GPS telemetry.*—Analyses of animal habitat selection using hourly-to-daily scale  
317 GPS telemetry data, such as that by Forester et al. (2007), are undoubtedly advancing our  
318 understanding of the factors influencing fine-scale movement behavior of animals. This  
319 trend is likely to continue for some time as more GPS-collars are deployed and the  
320 resulting datasets analyzed. As datasets accumulate for more species with differing and  
321 diverse ecologies, the prospects for developing generalizations about the nature of  
322 mammalian home ranges and home-range movement behavior will increase.

323 While GPS telemetry is now delivering large volumes of data on animal home-  
324 range movements, it is not without limitations (Hebblewhite and Haydon 2010). First,  
325 due to the constraints on battery longevity, the high cost of GPS collars, and the relatively  
326 high failure rate of deployed collars, the duration and number of animals with active  
327 collars is often lower than in telemetry studies using conventional radio collars. As a  
328 result, the ability to reliably characterize generalized differences in the movement  
329 behavior of individuals of ages, or sexes, and differences between years is often limited.  
330 Second, while GPS telemetry typically provides higher temporal resolution than either  
331 radio telemetry or ARGOS-based telemetry, it does not yield the complete path of an

332 individual through its environment (such as that obtained through tracking studies), and  
333 thus the accuracy of the implied animal movement trajectories of animals arising from  
334 relocations remains a concern, particularly when collars are programmed to deliver  
335 relatively infrequent relocations in order to preserve battery life. Third, a key issue in any  
336 ecological study is the extent to which information collected at a given temporal and  
337 spatial scale is relevant to other scales (Levin 1992). In this context, an important and, as  
338 yet, unanswered issue is the extent to which the improvements in our understanding of  
339 the fine-scale movement behavior of animals made possible by GPS-telemetry data will  
340 inform the ability of ecologists and wildlife biologists to understand and predict the long-  
341 term, large-scale patterns of space use by animals. Hebblewhite and Haydon (2010)  
342 detailed the benefits and limitations of GPS telemetry.

343       *Environmental Covariates.*—Another critical factor determining the value of GPS  
344 telemetry data is the availability of corresponding information about the animal's  
345 environment as it moves across a given landscape. A key source of information on  
346 landscape characteristics has been the increasing availability of data layers derived from  
347 remote sensing. Explanatory variables used in resource selection studies have typically  
348 used simple categorical classifications of land cover types (e.g. Johnson 1980; Manly et  
349 al. 1993). Whereas some more recent studies have included more relevant information  
350 about the environment, such as estimates of forage productivity derived from measures of  
351 vegetation greenness (Carroll et al. 2001; Ryan et al. 2006; Mueller et al. 2008), the  
352 majority of analyses still use “off-the-shelf” land cover classifications that may be weakly  
353 related to the actual habitat requirements of the species being studied, and its temporal  
354 resolution may not be well-matched to the frequency at which relocations are collected



355 and the rate at which the environment changes, Thus, the exploitation of remote-sensing  
356 data for explanatory environmental variables in studies of animal home ranges is still in  
357 its infancy.

358       One significant hurdle has been that virtually all of the remote-sensing data  
359 products used in analyses of animal space-use have been derived from optical remote  
360 sensing data, consisting of reflectance values in the visible and near infra-red  
361 wavelengths for each spatial location. Optical remote sensing measurements can be used  
362 to discriminate basic land-cover classes and to calculate estimates of vegetation  
363 greenness, but are unable to measure directly other landscape characteristics important  
364 for animals, such as structure of forest canopies, or the presence of downed logs in forest  
365 understory. Ongoing developments in active remote sensing methods-- so called because  
366 they involve the transmission of signal and measurement of the return signal -- offer a  
367 promising source of additional information about the landscapes that animals inhabit. In  
368 particular, LIght Detection and Ranging (LIDaR), which provides measurements of forest  
369 canopy height and vertical canopy structure (Dubayah et al. 2000; Hyde et al. 2006), and  
370 Radio Detection and Ranging (Radar), which provides information on aspects of  
371 vegetation structure, such as above-ground biomass and basal area, and also on moisture  
372 levels in the canopy and in the soil (Treuhaft and Siqueira 2000; Fransson et al., 2000;  
373 Treuhaft et al. 2003; Quiñones and Hoekman, 2004; Saatchi et al., 2007). Another  
374 significant development is the increasing availability of remotely-sensed imaging  
375 spectrometry, which yields a continuous reflectance spectrum for each pixel rather than  
376 reflectance values in a few specific wavelengths. The principal advantage of imaging  
377 spectrometry (also known as hyperspectral remote sensing) over conventional optical

378 remote sensing is its increased ability to discriminate vegetation types including, in some  
379 cases, the ability to detect the presence of particular species of plants that have distinctive  
380 reflectance spectra (e.g. Vane and Goetz 1993; Lewis et al. 2001; Asner 2008). Whereas  
381 the benefits of these new forms of data remains to be seen, it seems likely that the most  
382 promising new datasets in the near term will be ones coming from airborne deployed  
383 instruments that can provide information on habitat structure and composition at meter  
384 and sub-meter scales rather than the coarser-resolution datasets that come from  
385 instruments deployed on satellite platforms Kampe et al. (2010).

386         The second significant hurdle in generating environmental covariates has been the  
387 technical and biological expertise necessary to translate the raw remote sensing data into  
388 meaningful ecological information for a given species of interest, such as food  
389 availability, cover from predators, or nest or den-site availability. Although the tools and  
390 methodologies for doing this have become cheaper and easier to use, it still requires a  
391 significant investment to learn how to analyze and process remote sensing measurements,  
392 and also, in many cases, significant expense to purchase the necessary imagery. As a  
393 result, the use of remote sensing imagery in analyses of animal space-use patterns has  
394 largely been confined to the use of standard data products, such as basic habitat  
395 classifications, vegetation indices, and estimates of percent cover. In some cases, these  
396 have been combined with field sampling to develop custom maps for particular species,  
397 for example, the coyote small mammal biomass shown in Fig. 2, and the forage maps for  
398 elk in Yellowstone National Park (Forester et al. 2007, Anderson et al. 2008). However, I  
399 argue here that exploiting the full richness of environmental information available from  
400 remote sensing to understand animal spatial distribution better will require moving

401 beyond standard remote sensing data products such as general land cover classifications.  
402 Many species are known to have particular ecological requirements, and thus, what is  
403 needed is for animal ecologists and wildlife biologists to develop customized data layers  
404 that measure key habitat attributes for the species of interest, rather than simply relying  
405 on the generalized landscape attributes available in standard remote sensing data  
406 products.

407       *Biotelemetry.*—Improved understanding of the connections between an animal's  
408 movements, other components of its behavior such as foraging, and its physiological  
409 condition will be important bridges to link the movement ecology of animals with the  
410 demography of animal populations. Commercial telemetry devices for marine animals  
411 now typically include sensors for measuring temperature, depth, and saltwater  
412 immersion; however, the rate of adoption in telemetry studies of terrestrial mammals has  
413 been relatively slow (Ropert-Coudert and Wilson, 2005): telemetry collars for terrestrial  
414 animals typically have only a basic activity sensor to indicate whether an animal is  
415 moving or not, although some newer GPS- and ARGOS-based telemetry collars also  
416 contain a temperature and activity sensor.

417       The principal limitations on the use of biotelemetry are twofold. First, the cost of  
418 the units limits the number of units deployed on animals, resulting in small sample sizes.  
419 Second, the increased battery consumption arising from powering the various sensors  
420 limits the duration of a biotelemetry collar deployments (Cagnacci et al. 2010). Thus,  
421 whereas the trend towards increasing use of biotelemetry will likely continue, it seems  
422 likely that the constraints imposed by sensor cost and the negative impacts of additional  
423 sensors on collar battery life will mean that, for the time being at least, the use of

424 biotelemetry sensors will be confined to targeted studies involving small numbers of  
425 animals. One interesting area for potential future growth is crossover technologies from  
426 human biotelemetry. For example, a number of biomedical companies are developing  
427 minimally invasive implantable biosensors for long-term measurement of blood glucose  
428 levels in humans (Newman and Turner 2005). Because such sensors are usually tested on  
429 animal subjects before being approved for human use, similar sensors could be deployed  
430 easily on wild animal subjects. An interesting study relevant to assessing the value of  
431 such approaches is an ongoing study of polar bear movement behavior  
432 (<http://www.polarfield.com/blog/polar-bear-project/>) in which internal temperature and  
433 activity sensors are being used to relate their foraging behavior to resulting animal  
434 condition.

435         Another growing area is deploying sensors that provide information on an animal's  
436 social environment. The social context in which animals live affects patterns of space use  
437 in many animal populations (Rubenstein and Wrangham 1986). Until recently, obtaining  
438 such information required detailed observational studies of focal animal subjects. The  
439 social environment of animals can be estimated using conventional and GPS-based  
440 telemetry systems (e.g. Haydon et al. 2008); however, the accuracy of the information  
441 regarding the social environment is limited due to the number of collars deployed, and  
442 the temporal frequency and spatial accuracy of the relocations (Prange et al. 2006).

443         One promising approach to the study of animal social environments is the  
444 deployment of proximity tags. As their name implies, these can be attached to an animal  
445 and then used to detect the presence of other tagged animals within a given distance of  
446 the individual. A number of pilot studies have evaluated proximity tag technology in

447 several species, including brushtail possums (Ji et al. 2005; Douglas et al. 2006),  
448 raccoons *Procyon lotor* (Prange et al. 2006), and lions *Panthera pardus* (Tambling and  
449 Belton 2009). Fig. 4 shows the contrasting patterns in the frequency and duration of  
450 contacts between two pairs of raccoons collected by Prange and colleagues (2006). Thus  
451 far, studies using proximity tags have focused on estimating animal-to-animal contact  
452 rates, a key factor influencing rates of disease transmission (Ji et al. 2005; Douglas et al.  
453 2006; Prange et al. 2006), and patterns of mating behavior (e.g. Douglas et al. 2006).  
454 More generally, however, proximity tag measurements such as those shown in Fig. 4  
455 offer a new source of measurements for understanding the social environment in which  
456 animals live and move, and thus the promise of new insights into patterns of group  
457 formation, relatedness and social cohesion in ungulates, primates, and social carnivores  
458 (e.g. Tambling et al. 2009), and into impacts of these social interactions on movement  
459 decisions of individuals.

460 As with GPS telemetry, the ability to gain insight into animal social structure from  
461 proximity tag deployments will require new methods of analysis. Alongside the  
462 methodological advances in analyzing animal home ranges that have occurred over the  
463 past decade have been methodological advances in the analysis of animal social structure.  
464 In particular, Social Network Analysis (SNA), a branch of graph theory that characterizes  
465 social groups as networks of nodes connected by social ties, is providing a theoretical  
466 framework for understanding the patterns of association seen in Fig. 4a,b. SNA has been  
467 used over several decades in the social sciences to study human social interactions (e.g.  
468 Wasserman and Faust 1994), but is now being applied to the study of animal interactions  
469 (see Croft et al. 2008; Wey et al. 2008; and Coleing 2009 for reviews). For example, Fig.

470 4c shows an example of a network graph that reveals the group structure of a population  
471 of red deer in Scotland. An important long-term challenge will be integrating these  
472 approaches used to quantify patterns of animal grouping that ignore the effects of spatial  
473 position, with the kinds of spatially-explicit approaches used to study the dynamics of  
474 animal movement and space use described earlier (though see Gueron and Levin 1993;  
475 Turchin et al. 1998; and Eftimie et al. 2000).

476 *Making mechanistic home range analysis easier and simpler.*— Though  
477 conceptually simple, the process of translating models of individual-based model of  
478 animal movement behavior into corresponding predictions for the resulting expected  
479 pattern of space use is, in practice, quite challenging. The simplest approach, directly  
480 simulating the underlying stochastic movement process on a computer, requires  
481 programming expertise, and, even with modern computers, is computationally expensive,  
482 requiring multiple simulations of the underlying stochastic movement model. The  
483 alternative approach, of formulating partial differential equations (PDEs) that  
484 approximate the outcome of the underlying movement process (see Mechanistic home  
485 range analysis section), is computationally more efficient, which makes model fitting  
486 easier and offers the possibility of mathematical insight into the connection between  
487 underlying movement behavior of individuals and resulting patterns of space use.  
488 However, the PDE-based approach requires familiarity with formulating and solving  
489 systems of differential equations that is not part of the training of most ecologists and  
490 wildlife biologists. As with RSA, broadening the use of mechanistic movement models in  
491 studies of animal movement is likely to require the development of more user-friendly  
492 software that simplifies the process of formulating mechanistic movement models for

493 animals and fitting them to observational datasets.

494 *The roles of memory in observed home-range patterns.*—As noted earlier, there has  
 495 been considerable progress on developing mathematical understanding of how memory  
 496 may influence the movement behavior of animals and their resulting patterns of space  
 497 use. However, because memory is, for the most part, a latent process, that is, a process  
 498 whose impacts we observe, but are unable to measure directly (except in controlled  
 499 laboratory settings), understanding the roles that memories play in determining actual  
 500 animal spatial distributions is inherently challenging.

501 By way of example, suppose an animal moves along a one-dimensional  
 502 landscape, and in the absence of memory it moves at random with mean squared  
 503 displacement  $D_0$ . Suppose further that the animal's probability of moving per unit time  
 504 decreases as a function of its familiarity with a given area, whereas its familiarity with a  
 505 given area increases as a function of its utilization and its existing familiarity with the  
 506 area, and familiarity decays over time. These assumptions yield the following equations  
 507 for the expected space-use  $u(x,t)$  and its familiarity  $f(x,t)$  with each location  $x$  at time  $t$ :

508

$$509 \quad \frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} [D(x,t)u(x,t)], \quad \text{where } D(x,t) = \frac{D_0 \alpha}{\alpha + f(x,t)}. \quad (\text{Eq. 1})$$

510

$$511 \quad \frac{\partial f(x,t)}{\partial t} = u(x,t)[l + M(f(x,t))] - \mu f(x,t) \quad (\text{Eq. 2})$$

512 where the parameter  $\alpha$  governs the sensitivity of the animal's displacement per unit time  
 513 to its familiarity with an area, the parameters  $l$  and  $\mu$  respectively determine the rate at  
 514 which the animal's familiarity with an area increases as a function of its visitation rate

515 and the rate at which its familiarity with an area decays over time, and the function  
516  $M(f(x,t))$  determines how familiarity is reinforced by previous visits. With regard to the  
517 latter issue, if we assume that rate of memory reinforcement increases in proportion to  
518 prior familiarity with the area, up to some maximum familiarity  $f_{max}$  (i.e.  $M(f(x,t)) =$   
519  $\max(mf(x,t), f_{max})$ ), then the above movement model gives rise to stable, well-defined  
520 home ranges for individuals (Fig. 5).

521         The model description above is formulated and motivated in terms of an animal's  
522 response to its internal memory, modeled as a dynamic state variable that tracks its  
523 familiarity with different places on the landscape. Whereas the equations can be  
524 appropriately viewed in the above terms, Eq.s (1)-(2) were actually advanced under a  
525 different biological premise: as a model for carnivore home ranges in which individuals  
526 scent mark as they move (Eq. (2), and how the presence of familiar scent marks affects  
527 the movements of individuals (Eq. (1); see Briscoe et al. (2002) and Moorcroft and Lewis  
528 (2006) for further details.

529         That two distinct biological processes, one involving movement responses to  
530 internal memory, the other movement responses to external environmental stimuli, can  
531 give rise to identical patterns of space use emphasizes the challenges of distinguishing the  
532 effects of memory on animal movement behavior from other factors affecting animal  
533 movement. The latent, unobservable nature of memory places animal ecologists in the  
534 situation of trying to infer process from pattern, an inherently difficult exercise (Pielou  
535 1977). The above example highlights the challenge of distinguishing the effects of  
536 memory from the olfactory responses exhibited by many animals such as carnivores;  
537 however, similar challenges are likely to arise in separating out the effects of responses to



538 habitat heterogeneity, especially aspects of habitat heterogeneity that are, at present,  
539 unmeasured. Thus, although considerable progress has been made over the past decade  
540 in developing mathematical models of animal movement that incorporate memory, the  
541 challenge of how to elucidate, and to quantify the ways in which memories actually affect  
542 patterns of animal space use on real landscapes remains. What are the characteristic  
543 timescales over which animals utilize different forms of memory? And what are the  
544 signatures of these different forms of memory on patterns of animal spatial distribution?  
545 Progress in answering these questions is likely to require a creative multi-faceted  
546 approach that draws upon not only telemetry measurements, but also behavioral  
547 observations, and insights gained from field manipulation experiments and laboratory  
548 studies where animal movement behavior and decision-making can be examined under  
549 controlled conditions (Bailey et al 1996).

550        *Linking Studies of Animal Movement and Demography.*— Although understanding  
551 how changes in the environment will affect home-range patterns and the resulting spatial  
552 distribution of animals is a central issue in animal ecology and wildlife studies, an often  
553 more pressing concern is understanding how changes in the environment will affect  
554 species' demography and population abundance. The conventional approach to analyzing  
555 environment-demography relationships within species has been to look for associations  
556 between demographic rates (such as fecundity, juvenile survival, and adult survival), and  
557 population-level estimates of environmental covariates, such as winter-time temperature,  
558 or forage availability. For example, Catchpole et al. (2000) used logistic regression to  
559 show that both March rainfall and winter storm severity significantly influence  
560 survivorship of both males and females of Soay sheep (*Ovis aries*) on a Scottish Island.

561 Similar methods have been used to identify environmental correlates of demographic  
562 rates in a variety of mammalian species.

563         This approach for analyzing environment-demography relationships, shown in  
564 Fig. 6a, has two important limitations. First, this approach does not distinguish between  
565 the direct effects of environmental conditions on demography and the indirect effects of  
566 environmental conditions arising from environmentally-induced changes in the  
567 movement behavior and resulting home ranges of animals. As noted in a number of  
568 recent articles (Both et al. 2006; van der Graaf et al. 2006; Post and Forchhammer 2008;  
569 Post et al. 2008), the effects of climate variability and change on population demography  
570 acting via changes in the movement behavior are particularly significant in migratory  
571 animals, such as caribou, reindeer and musk oxen, in which the timing of large-scale  
572 movements in relation to seasonal shifts in climate and food availability has strong  
573 impacts on ensuing rates of fecundity and survivorship.

574         Second, in relating the demographic fate of individuals to a population-level  
575 average environmental condition, the traditional approach to analyzing environment-  
576 demography relationships shown in Fig. 6a averages over the differing environmental  
577 conditions that individuals actually experienced. In cases such as the relatively small  
578 insular populations studied by Catchpole et al. (2000), this assumption may not be  
579 unreasonable. However, in situations where the environmental conditions experienced by  
580 animals differs significantly among individuals (for example, the widely dispersed  
581 population of elk in Yellowstone National Park), using population-level average  
582 environmental conditions in an analysis of individual demographic performance will

583 change, and in some cases hide, causal relationships that exist between the actual  
584 conditions experienced by individual animals and their subsequent demography.

585         Until recently, there was no real way to address the above concerns regarding the  
586 analysis of environment-demography relationships. However, the increasing availability  
587 of measurements of animal locations and spatially- and temporally-resolved  
588 environmental data opens the way to linking demographic performance to environmental  
589 conditions and an animal's social environment at the scale of individual animals, rather  
590 than at the population level (Fig. 6b). Fig. 6b emphasizes that the availability of  
591 information on the movements of individuals is central to the ability to conduct such  
592 integrated analyses because: (1) it makes it possible to disaggregate population-level  
593 average landscape and climate information appropriately into corresponding individual-  
594 level environmental covariates, which can then be related to subsequent individual rates  
595 of fecundity and survival; (2) the analysis framework shown in Fig. 6b explicitly  
596 distinguishes between the direct effects of climate on survival, and those that have been  
597 mediated by changes in movement behavior and resulting home-range patterns. Analyses  
598 of this form would, in effect, integrate analyses of a population's demography with  
599 analyses of its spatial distribution. A natural framework for such analyses would be a  
600 hierarchical generalized linear mixed model (GLMM) approach incorporating both  
601 relocation data and demography data as key observables (see Bolker et al. 2008 for a  
602 discussion of GLMMs). Although such analyses would be more complex in nature, their  
603 broader scope offers the promise of developing a more accurate and consistent picture of  
604 how changes in the environment affect the movement behavior of individuals and their  
605 subsequent demographic fates.

606

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- 908

909 Figure legends

910

911 Figure 1. Schematic illustrating the resource selection analysis (RSA) approach to  
912 analyzing patterns of animal space-use. (a) Shaded squares represent an idealized  
913 landscape comprised of three equally abundant habitat types. Black lines represent the  
914 movement trajectory of an individual as it traverses the landscape with points  
915 representing fixed-interval relocations of the individual. Since the three habitat types that  
916 comprise the landscape plotted in (a) are equally abundant, in the absence of preference,  
917 equal numbers of relocations would be expected to be obtained in each habitat, as  
918 indicated by the hatched bars in panel (b). The actual distribution of relocations, indicated  
919 by the solid bars in panel (b), shows that the individual exhibits a preference for the dark  
920 grey habitat type.

921

922 Figure 2 (a) Schematic illustrating the underlying model of individual movement  
923 behavior that underpins a mechanistic home-range model. The movement trajectory of  
924 individuals is characterized as a stochastic movement process, defined in terms of  
925 sequences of movements between successive relocations ( $i = 1, \dots, m$ ) of distance  $\rho_i$  and  
926 directions  $\varphi_i$  drawn from statistical distributions of these quantities that are influenced by  
927 relevant factors affecting the movement behavior of individuals. (b) Colored contour  
928 lines showing fit of a mechanistic home-range model to relocations (filled circles)  
929 obtained from five adjacent coyote packs in Lamar Valley Yellowstone National Park. As  
930 described in the text, the PA+CA mechanistic home-range model used in this study  
931 incorporates a foraging response to small mammal prey availability plus a conspecific  
932 avoidance response to the scent-marks of individuals in neighboring packs. Also shown  
933 are the home-range centers for each of the packs are also (triangles), and the grayscale

934 background indicates small mammal prey density ( $\text{kg ha}^{-1}$ ) across the landscape  
935 (Moorcroft and Lewis 2006).

936  
937 Figure 3. Example of a GPS-telemetry dataset collected by Todd Dennis and colleagues  
938 on brushtail possums. The dataset consists of more than 140,000 relocations collected at  
939 5-15 minute intervals over two-year period. The figure shows 13,000 relocations of for a  
940 single individual and the color indicates the time of relocation. Todd Dennis (unpublished  
941 data).

942  
943 Figure 4. (a) and (b): Total number and daily duration (in seconds) of contacts recorded  
944 by proximity detectors during a 2-week period in summer 2004 for 2 pairs of raccoons in  
945 northeastern Illinois, USA. The vertical bars indicate the total duration of contacts for  
946 both members of each pair, while the open and closed circles show total number of  
947 contacts for both members of each pair. (c) Visualization of the social environment of red  
948 deer on the island of Rum, Scotland. The closed circles indicate different individuals and  
949 the lines between pairs of closed circles indicate when the two individuals were observed  
950 in the same group six or more times during the 26 census observation periods. The  
951 network plot indicates the existence of groups of individuals who interact strongly with  
952 one another, but interact weakly with individuals in other groups. From Prange et al.  
953 (2006) (panels a and b), and Croft et al. (2008) (panel c).

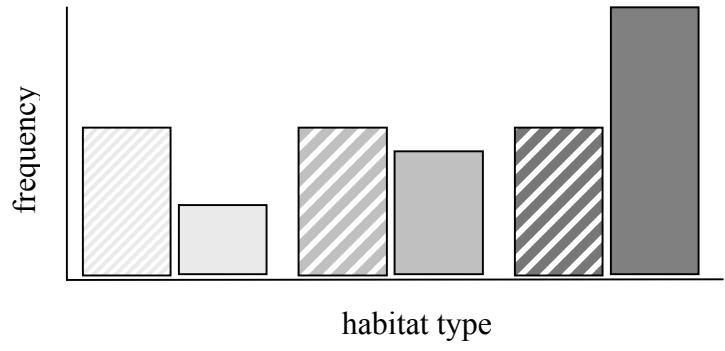
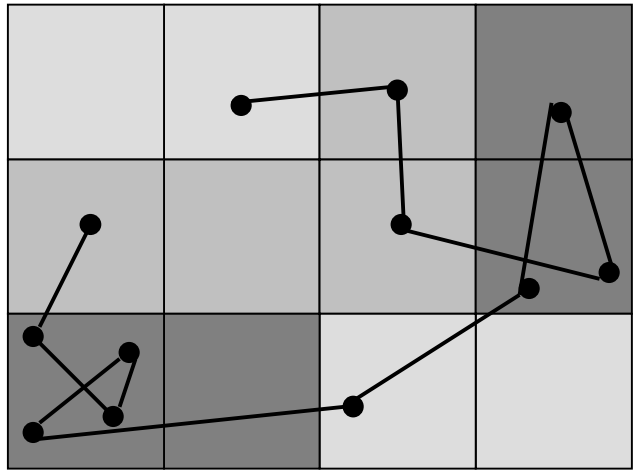
954  
955 Figure 5. Solution of Eq.s (1) and (2) in one space dimension ( $x$ ) showing the formation  
956 of a characteristic home-range  $u(x,t)$  for an individual that arises due to the animal  
957 developing familiarity  $f(x,t)$  with the landscape as it moves,


958


959 Figure 6. Schematic diagrams illustrating the conventional approach to analyzing animal  
960 distribution and abundance (panel a), and a proposed integrated method of analysis (panel  
961 b). The shade of each box indicates the relevant scale of the different forms of data:  
962 relocation-level (dark gray), individual-level (light grey), population-level (white).

963

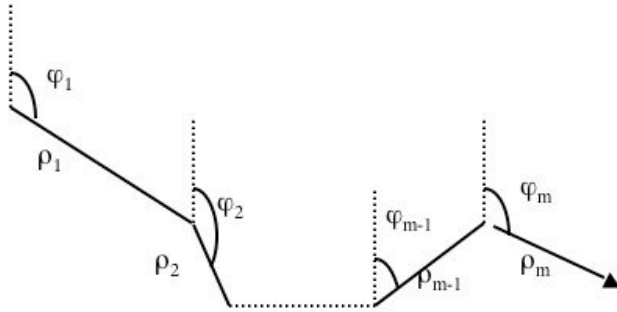
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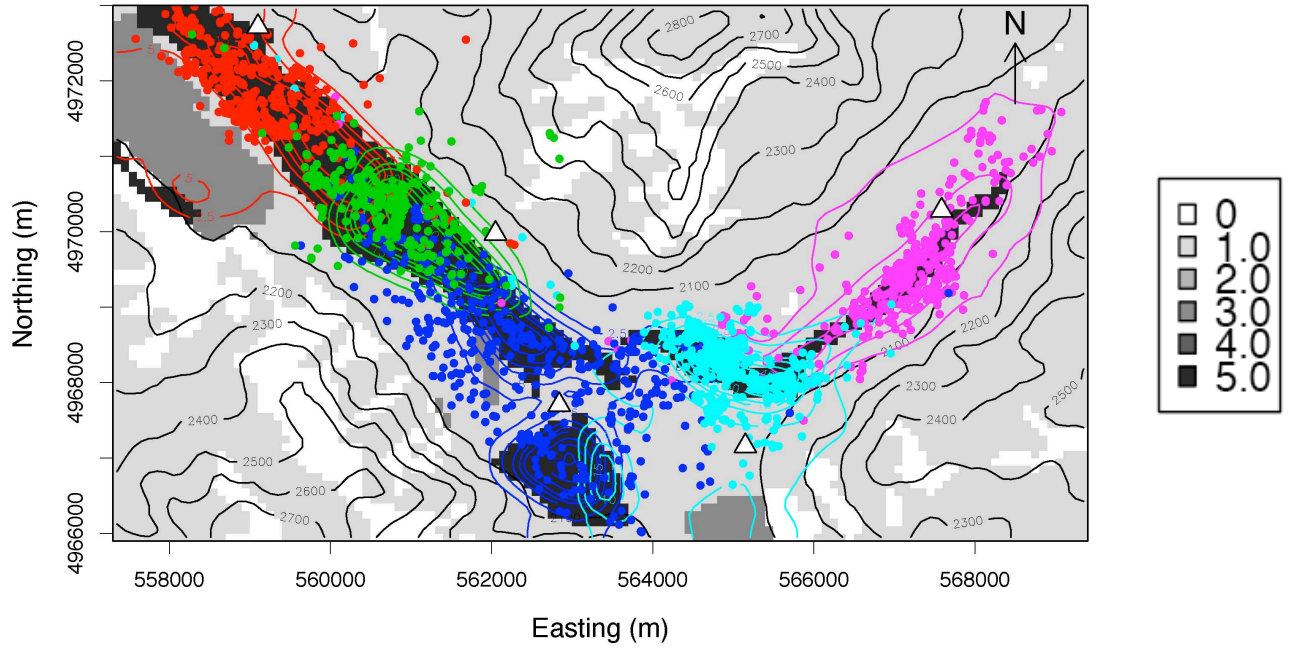
expected: 

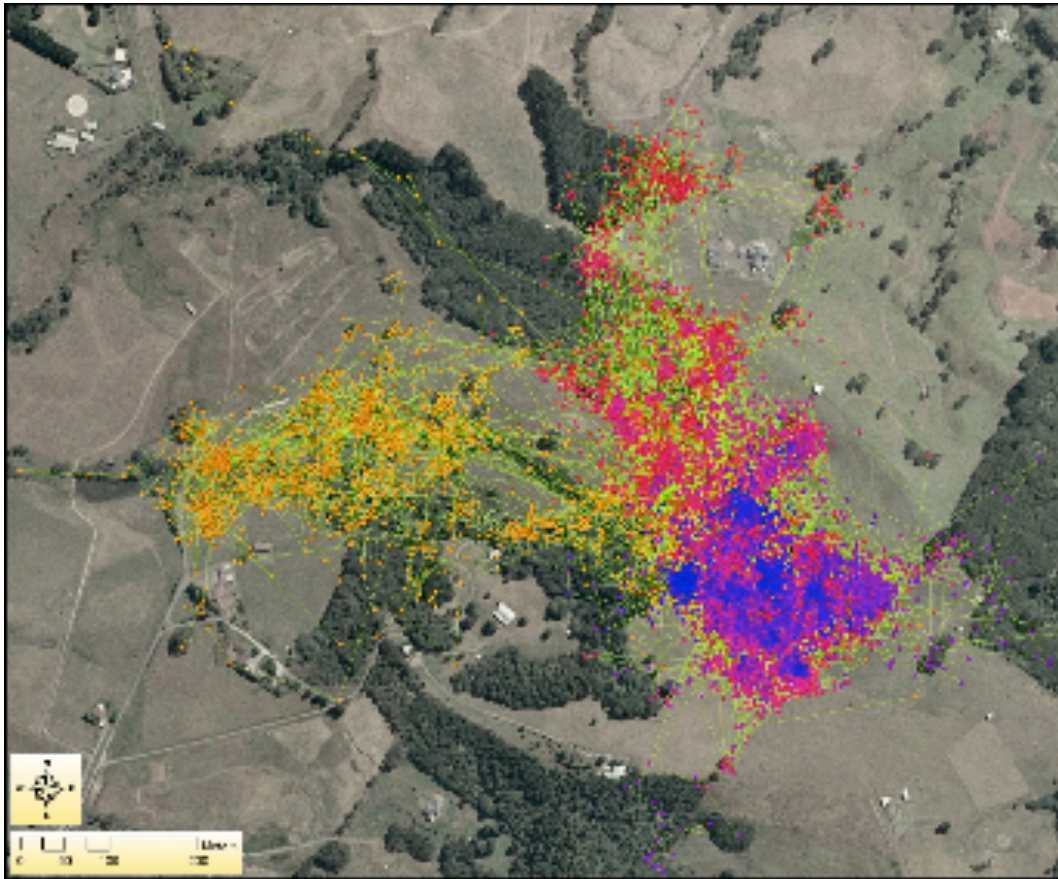
observed: 

(A)

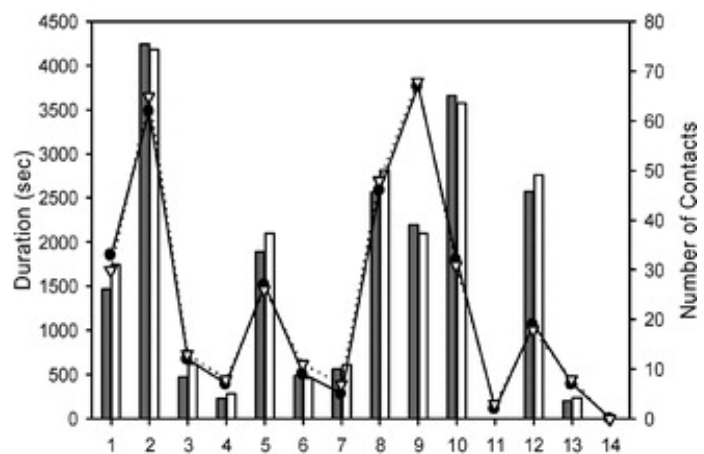


(B)

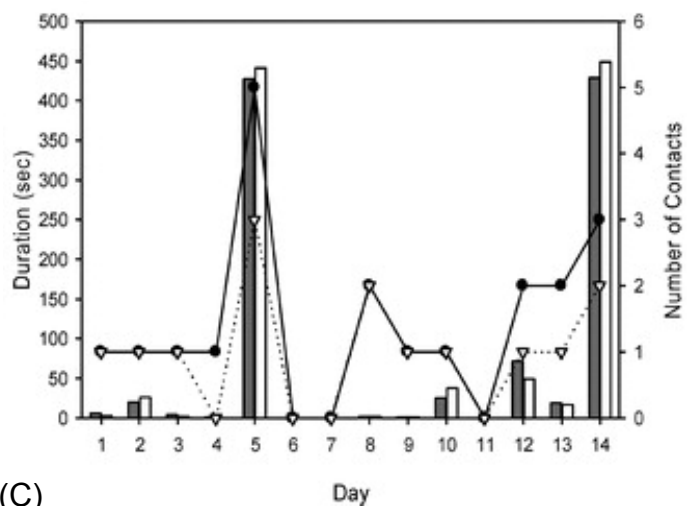




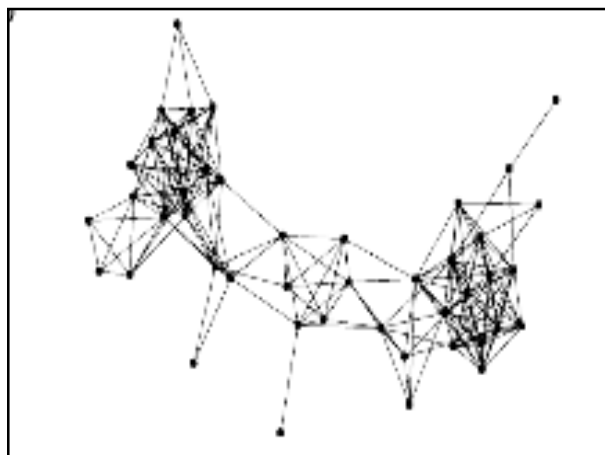
(A)



(B)

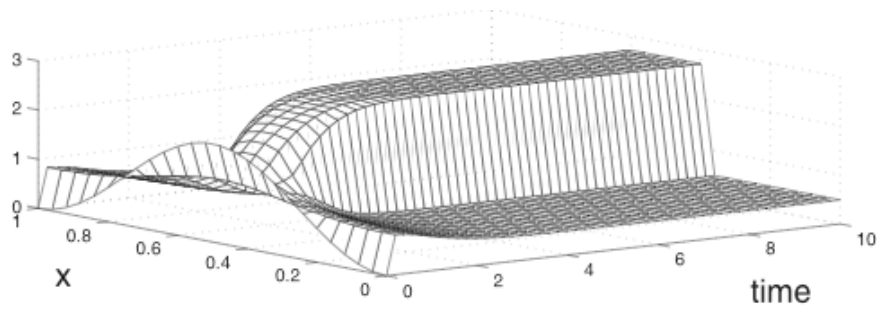


(C)

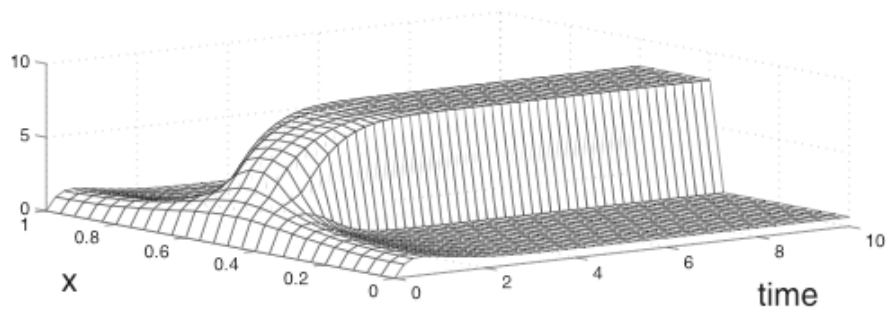




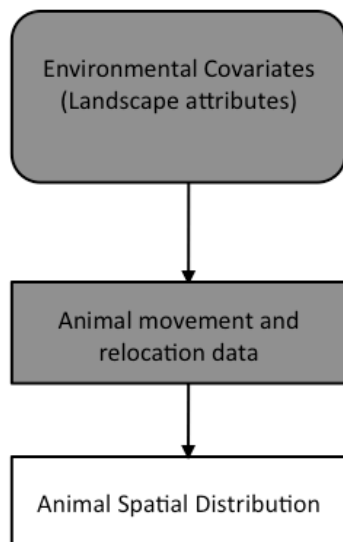
Pattern of space use  $u(x,t)$



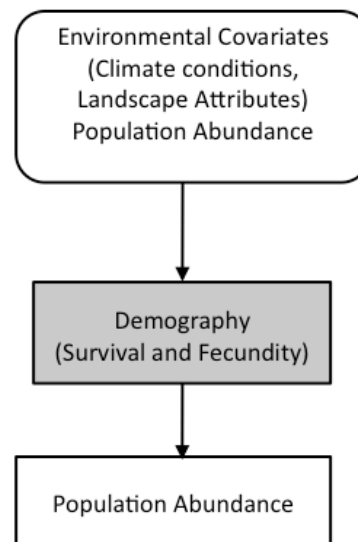
Familiarity  $f(x,t)$



(A) Space-use Analysis



Demographic Analysis



■ Relocation level    ■ Individual level    □ Population level

(B) Proposed Framework for integrated Analyses of Demography and Space Use

