CHAPTER 11

Home range estimation: examples of estimator effects

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11.1 Introduction

In the 19th century Darwin (1861) noted that animals tended to restrict their movements to a defined area, but the accepted definition of home range as an area regularly traversed by an individual for activities of food gathering, mating, and caring for the young, but excluding occasional sallies outside this area, was not formally described until much later (Burt 1943). Within a home range, animals demonstrate a certain familiarity with the area; they know the locations of principal shelters, resources, potential mates, and escape routes. Hence, home range can be viewed as the interaction between the environment and an animal's understanding of that environment; in essence, a cognitive map (Powell and Mitchell 2012). "Home range behavior" is the product of decision-making and the contribution of spatially distributed resources to an individual's fitness (Mitchell and Powell 2012), meaning that an animal is expected to use the minimum area that can sustain its energetic requirements (Harestad and Bunnel 1979). Although home range estimation methods are mathematical and statistical in nature, researchers attempting to understand the mechanistic and biological foundations of home range should keep in mind that an animal's home range reflects its requirements and decisions to fulfill those requirements. As a result, home ranges will differ among species, individuals within a species, and even within individuals over time

(Powell and Mitchell 2012) depending on shifting needs and changing resources. This variation in home range characteristics (i.e., size, shape, location, overlap) is related to intrinsic and extrinsic factors, such as body size-dependent metabolic needs (McNab 1963, Harestad and Bunnel 1979, Lindstedt et al. 1986), age and sex (Mech 1980, Cederlund and Sand 1994, Larter and Gates 1994), population density (Kilpatrick et al. 2001, Kjellander et al. 2004), habitat quality (Watson 2002, Campioni et al. 2013), food availability (Simon 1975, Jones 1990), environmental variability (Rivrud et al. 2010, Morellet et al. 2013, Kowalczyk et al. 2015), diet (Milton and May 1976, Rigamonti 1993, Zabel et al. 1995, Peery 2000), and breeding stage (Erikstad 1985, Vega Rivera et al. 2003, Beltran et al. 2010, van Beest et al. 2011). Because interactions among these factors and habitat-use are dynamic, home range estimates should be interpreted as a "snapshot," and are thus a useful tool for predicting future home range characteristics under similar conditions.

Raptors can provide valuable insight into the effect of these factors on an animal's home range characteristics because raptor species vary considerably in body size (Ferguson-Lees and Christie 2001), diet (Korpimäki and Marti 1995), and foraging behavior (Peery 2000). Breeding raptors are central place foragers (Orians and Pearson 1979); thus breeding season movements are dictated by the distribution of food resources (prey) that must be carried back to the nest (the central place) to feed nestlings. As a consequence, home range configuration is, in part, determined by prey abundance and habitat quality (Marquiss and Newton 1982, Village 1982, Bloom et al. 1993, Marzluff et al. 1997, Lapointe et al. 2013). Thus, home range size and configuration can capture important movement patterns among individuals that results from the juxtaposition of nesting territories and the spatial distribution of prey. A "nesting territory" is the part of a bird's home range that is defended against conspecifics (Odum and Kuenzler 1955), and is therefore a sub-unit of the home range characterized by agonistic behaviors.

Arctic-nesting raptors play a key role in tundra ecosystems as top predators, but studying them remains a challenge, in part because of their remote location (Sokolov et al. 2014). Further, Arctic raptors are often dependent on highly fluctuating food resources (Mindell et al. 1987, Gilg et al. 2009, Barichello and Mossop 2011), and changes in prey abundance or distribution can have important consequences on Arctic ecosystem food webs. Climate change has occurred more rapidly in Arctic ecosystems (Stocker 2014). Landscapes have been modified as a result (Hinzman et al. 2005), affecting primary productivity (Sturm et al. 2001) and population dynamics (Post et al. 2009). The study of home ranges of key species of Arctic ecosystems, such as the Gyrfalcon, can potentially provide insight into the way in which these species modify foraging behavior in response to a changing environment. Further, breeding opportunity, food abundance, and favorable environmental conditions in the Arctic occur during a brief period of time each breeding season, making it an interesting region to examine the temporal dynamics of home ranges.

Koskimies (2011) indicated that future studies on Gyrfalcons should focus on identification of environmental factors that limit density, including habitat use and home range. Since then, few studies have investigated Gyrfalcon home range (Burnham and Newton 2011, Eisaguirre et al. 2016). Although mean home range (95% kernel) size of breeding female Gyrfalcons varied considerably among individuals within a given population, it was similar across populations in Yukon Territory, Canada (mean = 421 km^2, n = 2, range = 284–758 km^2; Eisaguirre et al. 2016) and in Greenland (mean = 457 km^2, n = 6, range = 88–829 km^2; Burnham and Newton 2011). These results highlight the importance of using the same home range estimation methods when the goal is to make comparisons among studies. Using standardized approaches to study and characterize home ranges should improve our understanding of the effects of environmental factors on Gyrfalcon behavior and fitness.

The methods and interpretations highlighted in this chapter can be applied broadly to most raptor species. We focus on estimating breeding home range using three different approaches that produce different outputs from the same data set. Here we highlight: 1) Kernel Density Estimate (KDE), 2) Local Convex Hull (LoCoH), and 3) Biased Random Bridge (BRB). For migratory species, these estimation techniques can be applied similarly to wintering home ranges.

11.2 Data collection

Our understanding of factors that influence home range is, in large part, due to rapid advances in telemetry technology (Cagnacci et al. 2010) and analytical techniques. Although a wide range of animal tracking devices are readily available, the advantages and drawbacks of each type of device must be considered within the context of the research question (Robinson et al. 2010). Researchers must consider the tradeoffs among several factors: number of locations that can be collected daily (i.e., fix frequency), the precision of the locations, the weight and dimensions of the devices, and the human resources required to obtain a location. For example, geolocators are lightweight devices that estimate location using a light sensor to calculate day length and solar noon (Wilson et al. 1992, Lisovski et al. 2012). Geolocators are widely used to track long distance migration of seabirds and passerines because they are cost-effective and small (Burger and Shaffer 2008, Stutchbury et al. 2009). However, they are much less accurate and collect fewer daily fixes compared to other device types (one or two locations per day; mean error 185–200 km; Phillips

2004). They are excellent for answering broad scale questions where fine scale accuracy is not required, but cannot provide the accuracy required for home range studies.

Very High Frequency (VHF) radio transmitters and satellite/cellular transmitters equipped with an onboard Geographical Positioning System (GPS) provide data that are sufficiently accurate (Robinson et al. 2010) for estimating home ranges. VHF transmitters have the advantage of being lightweight and are small (0.5 g), but the technology is reliant on field technicians working to continuously relocate marked individuals on foot, by automobile, or aircraft (Seegar et al. 1996, Thorup et al. 2007), and then estimating location by direct observation or triangulation, which can also be inaccurate. Solar powered GPS Platform Terminal Transmitters (PTTs) and Global System for Mobile (GSM) loggers are light (17–25 g for the smallest devices), and can be deployed on raptors in the size range of Gyrfalcons and most other large raptor species (according to the < 3% of body weight standard suggested by Bird Banding Laboratory; USGS 2016). Note, however, the increasing concerns with regard to negative effects of backpack-style transmitters on adult and juvenal Gyrfalcons (McIntyre et al. 2009, Fuller et al. 2011, Eisaguirre et al. 2016). We suggest, as recommended by Steenhof et al. (2006), that researchers carefully consider and minimize the effects of radio marking falcons to ensure that any benefits gained from the study will outweigh costs to individual animals. Further research on Gyrfalcon home range and movement should take advantage of future developments in tracking technology and attachment methods to avoid negative effects on Gyrfalcons (Eisaguirre et al. 2016).

The main advantage of GPS-accurate (±18 m for GPS-PTTs and ±3 m for GSM loggers) devices for home range studies is the capacity to collect multiple locations per day, in addition to options for programming diurnal and seasonal relocation schedules. Moreover, batteries often have sufficient capacity to track an individual for more than one annual cycle. Because of the high cost of these devices (typically between $1350 and $4200 in 2017), studies that have tracked raptors rarely deployed transmitters on more than 10 individuals (e.g., Strandberg et al. 2009, Fuller et al. 2011, Duerr et al. 2012, Lanzone et al. 2012, Lapointe et al. 2013, Sokolov et al. 2014). Note that Argos-PTTs have larger error around locations than GPS-PTTs. Argos location data are based on the Doppler effect and location points are of variable quality, with Argos error estimate being ≤250 m in the best of cases (CLS 2016). Interpretations based on relatively small sample sizes must be made carefully because extensive data on a few individuals may not be generalizable to the population (Fieberg and Börger 2012).

The number of locations required to reliably estimate home range depends on the range estimator. For non-parametric kernel estimators (discussed below), Seaman et al. (1999) suggest a minimum of 30 fixes, and preferably > 50. For minimum convex polygon (MCP), Bekoff and Mech (1984) suggested that the minimum sample size should be between 100 and 200 fixes. Sampling regime (i.e., number of locations/days) is therefore an important consideration. If a tracking device collects only one location per day over a short period of time (e.g., breeding season), the resulting data may be inadequate to reliably estimate a home range. We feel that four fixes per day provides adequate home range estimates for large Arctic breeding falcons and should prevent the negative effects of small sample size on home range estimation (Bekoff and Mech 1984), particularly if estimates of within-season home range estimation are important (e.g., use of space during discrete time periods such as pre-laying, incubation, or brood rearing).

11.3 Estimating home range

Choice of home range estimation method can explain as much of the variation in home range size as the ecological variables affecting it (Nilsen et al. 2007), thus selection of the optimal home range estimator should consider the question of interest (Table 11.1). For example, MCPs are considered inadequate by many (Burgman and Fox 2003, Börger et al. 2006, Laver and Kelly 2008), but the approach is easy to understand and can be applied for comparative purposes (e.g., Kjellander et al. 2004, Herfindal et al. 2005, van Beest et al. 2011, Williams et al. 2011, Sokolov et al. 2014). However, overestimation of home range size remains a major drawback associated with MCPs (Burgman and Fox 2003). On the other hand, although the ability for frequent collection of many fixes has improved considerably in recent years, in cases where fixes are collected over short time periods, successive locations may not be statistically independent (i.e., auto-correlated). Several estimators have been developed to account for auto-correlation among relocations (Walter et al. 2011, Walter et al. 2015). Among these are the local convex hull (LoCoH; Getz and Wilmers 2004, Getz et al. 2007), the single-linkage cluster (SLCA; Kenward et al. 2001), characteristic hull (CHAR; Downs and Horner 2009), kernel density estimator (KDE; Worton 1989), Brownian bridge (BB; Horne et al. 2007), and biased random bridge (BRB; Benhamou 2011). Thus, the choice of home range estimator should align with study objectives (Fieberg and Börger 2012), and consider the limitations inherent to the estimator (Table 11.1). In an extensive review of home range studies, Laver and Kelly (2008) indicated that studies involved in estimating home range often used sub-optimal methods and lacked sufficient information to reproduce them.

In the following section, we define the term utilization distribution (UD), demonstrate the use of three UD-based estimators (KDE, LoCoH,

Table 11.1 An overview of the advantages and drawbacks of most popular and pertinent home range estimation methods as well as their principal utility.

Home range estimator	Advantage(s)
Minimum convex polygon (MCP)[1,2]	Very simple to use. Free of distributional assumptions. Widely used; many comparable studies.
Kernel density estimators (KDE)[3,4,5]	Free of distributional assumptions (non-parametric). Flexible method; can be used in many situations.
Local convex hull (LoCoH)[6,7]	Produce consistent results with different sampling regimes. Convergence to true distribution as sample size increase. Identify unused area within a home range.
Brownian bridge (BB)[8]	Accounts for time and distance between locations.
Biased random bridge (BRB)[9]	Accounts for time and direction between locations. Smoothing parameters can be estimated from the data. Works well with serially correlated relocations.

References: 1) Hayne1949, 2) Powell 2000b, 3) Worton 1989, 4) Kernohan et al. 2001, 5) Seaman and Powell 1996, 6) Getz and Wilmers 2004, 7) Getz et al. 2007, 8) Horne et al. 2007, 9) Benhamou 2011

and BRB), and show how the choice of estimator can produce markedly different results. We used simulated data based on known movement patterns of an adult breeding female Peregrine Falcon (*Falco peregrinus*) equipped with a 22-g solar-powered PTT 100 (Microwave Telemetry Inc., Columbia, Maryland). The data set is restricted to a 30-day period (n = 323 locations) during the brood rearing period to characterize foraging behavior consistent with that observed for an Arctic-nesting falcon raising young.

A data set capable of estimating home range using the three methods illustrated in this chapter should contain the following fields: 1) Locations; must be two columns for both x and y positions (locations in this example are in Universal Transverse Mercator (UTM) coordinate system, but latitude and longitude could also be used); 2) Date and time; should be merged for transformation from successive point locations to trajectory between locations; 3) UTM zone (required only if the UTM coordinate system is used). This will be necessary to set a projection to the resulting home range estimates (See Table 11.2).

Drawback(s)	Utility
Crude outlines. Sensitive to extreme locations. Ignores all information provided by interior locations. Tends to overestimate home range. Sensitive to sample size before ~100 locations.	Comparative studies. Habitat selection.
Sensitive to bandwidth choice. Assumption of independence.	Analyze use of space by producing bounded UDs.
Sensitivity of the user-selected nearest-number-of-neighbors parameter, k.	Consider hard boundaries within the habitat. Habitat selection.
Requires short time interval between locations. Assumption of diffusive movement.Tends to overestimate areas where animal is immobile for long periods.	Includes principal movement corridors and hard boundaries in home range estimation.
Requires short time interval between locations.	Includes principal movement corridors and hard boundaries in home range estimation.

Table 11.2 Example of the data set required to estimate home range using kernel density estimate, local convex hull and biased random bridge methods. Each row is a Global Positioning System fix and each column is a variable. There is no ID field in this example because the table contains only re-location from a single individual. The coordinates (xcoo and ycoo) are given in Universal Transverse Mercator. Date (named "hour" in the data set) format is year-month-date hour:min:sec.

xcoo	ycoo	hour	utmzone
481036.11513	7801896.82561	2010-07-31 14:00:00	17N
481031.192258	7802287.31069	2010-07-31 16:00:00	17N
481031.192258	7802287.31069	2010-07-31 18:00:00	17N
481037.791804	7802287.17726	2010-07-31 20:00:00	17N
481024.592712	7802287.44414	2010-07-31 22:00:00	17N
481031.192258	7802287.31069	2010-08-01 00:00:00	17N

11.3.1 Utilization distribution

The utilization distribution (van Winkle 1975) is an extension of the home range concept first described by Burt (1943), and describes an animal's use of space as a probability density function that characterizes the chance that an animal will be found in any given location within the region defined as its home range. UDs are commonly represented by isopleths delineating regions in space with differing probabilities (or rates) of use. In turn, home ranges are typically depicted as the 95% isopleth of an unbounded UD, meaning that some relocations are excluded from the estimated home range. These excluded locations could be considered those that Burt (1943) referred to as occasional sallies outside the home range. The difficulty for those interested in estimating home range is selection of an estimator that properly excludes locations that are truly sallies beyond the bounds of a home range. Thus, selection of the appropriate estimator is critical to characterizing which points should be considered representative of an animal's exploratory movements, and which should be considered routine movements necessary for foraging and reproduction (Getz et al. 2007). Regardless of which home range estimator is used, it is important to remember that any illustration of an individual's home range is an approximation of an animal's use of space that is not constrained by fixed boundaries (Powell 2000).

11.3.2 Kernel density estimate (KDE)

Worton (1989) described a kernel method for the estimation of UDs from relocations of an animal. The approach recognizes that over time, places within an individual's home range that are used repeatedly (e.g., a nest site) accumulate many more fixes than places that are used rarely. Thus, the density of fixes within the vicinity of a nest site, for example, would be high, and the density of fixes in a rarely used location would be low. However, calculating an estimate of use depends on the form (i.e., shape and width) of the kernel, and this can pose a problem because several different kernel options are available (e.g., fixed versus adaptive, univariate versus bivariate bandwidth; Worton 1989, Seaman and Powell 1996). In general, kernel shape has little effect on output, but differences in bandwidth can result in markedly different outputs. It should come as no surprise that home range estimates depend on the kernel bandwidth (i.e., smoothing parameter h; Walter et al. 2011), and that comparisons of home range estimates among studies should take into consideration the form of the smoothing parameter (Kernohan et al. 2001).

Table 11.3 Principal R packages and functions used to estimate home range using kernel density estimate.

Package	**Function**	**Utility**
ks[1]	Hpi	Univariate plug-in selector
	kde	Kernel density estimator to build UD
	contourLevels /contourLines	Extraction of the home-range contours (isopleths)
adehabitatHR[2]	kernelUD	Kernel density estimator to build UD
	getverticesHR	Extraction of the home-range contours (isopleths)
Rgeos[3]	gArea	Calculate area of estimated home range

References: 1) Duong 2016, 2) Calenge 2011, 3) Bivand and Rundel 2017

First generation smoothing methods include *reference* (h_{ref}) and least square cross validation (h_{lscv}; Walter et al. 2011). The reference method has been criticized for over-smoothing, resulting in UDs that overestimate the spatial extent of an animal's home range. Although least squares cross validation (*lscv*) may minimize over-smoothing, Walter et al. (2011) point out that the approach has been poorly evaluated using high resolution GPS data. In addition, *lscv* presents convergence problems when datasets are large, and fixes are clumped, both of which are likely in data sets collected on breeding raptors. The plug-in (h_{pi}) method (Jones and Kappenman 1992), which was developed after the *reference* and *lscv* methods, provides better convergence and reasonable trade-offs between bias and variance (Jones et al. 1996, Duong and Hazelton 2003). However, the plug-in method can produce renditions of home ranges that appear fragmented. Thus, the choice of kernel method must consider the research question and the manner in which home range outputs will be interpreted (Worton 1995). The principal R packages and functions (R core team 2016) used to estimate home range using kernel density estimates are shown in Table 11.3 (see Calenge (2011) for more details).

11.3.2.1 Estimating home range using KDE

Once we load the data into R, naming it ‘loca’, we set the format for date and time. Although this is not mandatory for KDE, it will be necessary for BRB to account for time and direction between successive locations.

```
# set the right date/hour format
  loca$time = as.POSIXct(strptime(loca$time,
       format = ‘%Y-%m-%d %H:%M:%S’))
```

Now we attempt to estimate a 95% KDE home range first using h_{lscv} to illustrate problems with convergence, and follow-up using h_{ref}.

```
# try using hlscv
  kernLSCV<-kernelUD(SpatialPoints(loca[, 1:2]), h = “LSCV”)
```

We get a warning about convergence. Even by increasing hlim (i.e., the limit of the smoothing parameter, or bandwidth), the algorithm will not converge. We can illustrate that using the function **`plotLSCV`** as follows:

```
# plot kernLSCV
  plotLSCV(kernLSCV)
```

The plot (not shown) illustrates that the cross validation criterion (CV) cannot be minimized here (because the CV values continue to rise as h increases), which is the goal of LSCV function. Let’s try with h_{ref} bandwidth selector:

```
# try using href
  kernhref<-kernelUD(SpatialPoints(loca[, 1:2]), h = “href”)
```

With h_{ref} , the algorithm converges, so now we can estimate and plot (not shown) the 95% isopleth of the UD.

```
# estimate and plot the 95% isopleth
  kernhref <- getverticeshr(kernhref, percent = 95)
  plot(kernhref)
```

We can also calculate the area of the 95% isopleth using the function **`gArea`**, which returns the area in m^2.

```
# calculate the area of the 95% isopleth
  gArea(kernhref)
  # output
    514881400
```

Second-generation bandwidth selectors such as the plug-in method are thought to reduce problems associated with non-convergence. We will estimate home range using KDE, but this time using the plug-in method for smoothing *hpi* (using the R package ks). We will also illustrate how to build the gradient of use across the home range. The algorithm that defines the smoothing parameter (*h*) is a function of unknown target density. Hence, a pilot value is required to find the optimal smoothing parameter. This can be achieved by estimating the bandwidth that minimizes the Asymptotic Mean Squared Error (AMSE pilot; Wand and Jones 1994), the Sum of Asymptotic Mean Squared Error (SAMSE pilot; Duong and Hazelton 2003), or by using a single unconstrained bandwidth (*unconstr* pilot) or higher derivative order bandwidths (*dunconstr* and *dscalar* pilots; Chacón and Duong 2010).

```
# find PlugIn parameter value with Hpi
# choose between 4 different “pilots”
  h1 = Hpi(loca[,1:2], pilot = ’samse’, binned = T)
  h2 = Hpi(loca[,1:2], pilot = ’unconstr’, binned = T)
  h3 = Hpi(loca[,1:2], pilot = ’dunconstr’, binned = T)
  h4 = Hpi(loca[,1:2], pilot = ’amse’, binned = T)
```

We get similar results from SAMSE and AMSE, as well as *unconstr* and *dunconstr*. So, we estimate home range using KDE with h_{pi} using only SAMSE and *unconstr* pilots (Fig 11.1).

```
# hpi with samse pilot
  kernPI1 <- kde(loca[,1:2], H = h1)
  cont = contourLevels(kernPI1, cont = 95)
  line = contourLines(x = kernPI1$eval.points[[1]], y =
       kernPI1$eval.points[[2]], z = kernPI1$estimate,
       level = cont)
  sldf = ContourLines2SLDF(line)
  plot(sldf)
```

```
# convert contour lines into polygons to calculate area
# ignore warning, no need to define coordinate system for now
  sldf = SpatialLines2PolySet(sldf)
  sldf = PolySet2SpatialPolygons(sldf)
  gArea(sldf)
  # output
   58015136

# hpi with unconstr pilot
  kernPI2 <- kde(loca[,1:2], H = h2)
  cont = contourLevels(kernPI2, cont = 95)
  line = contourLines(x = kernPI2$eval.points[[1]], y =
       kernPI2$eval.points[[2]], z = kernPI2$estimate,
       level = cont)
  sldf = ContourLines2SLDF(line)
  plot(sldf)

# convert contour lines into polygons to calculate area
# ignore warning, no need to define coordinate system for now
  sldf = SpatialLines2PolySet(sldf)
  sldf = PolySet2SpatialPolygons(sldf)
  gArea(sldf)
  # output
  169848862
```

We now plot the UD within the home range using KDE and h_{pi} with SAMSE pilot. Various methods allow the illustration of UD from relocations, but our method consists of creating several different polygons (isopleths) and successively overlaying each isopleth as part of the plotting process. One advantage of this method is that the resulting home ranges of different isopleths are independently estimated, and can be imported easily into a Geographic Information System (GIS). The first step is to create the home ranges from different isopleths (e.g., 50% to 95%). Because of the high density of points around a nest, the algorithm sometimes cannot draw a polygon for 50% isopleth. If this is the case (Contour Lines [CL] too short), start with higher (55% or 60%).

```
# first create list of polygons of different isopleths
  SPDF = list()
  Levels = seq(95,50,by = -2.5)
  for (j in 1 : length(levels)){
    cat(j,"\n")
```

```
# extract every isopleth (contour line) of level j
  cont = contourLevels(kernPI1, cont = levels[j])
  line = contourLines(x = kernPI1$eval.points[[1]],
       y = kernPI1$eval.points[[2]], z = kernPI1$estimate,
       level = cont)
  sldf = ContourLines2SLDF(line)

# set projection (UTM) for polygons
  utm = names(sort(table(as.character(loca$utmzone)))[1])
  utm = gsub(‘N|S’, ‘’, toupper(utm))
  proj4string(sldf) = CRS(paste(“+ proj = utm +zone =”, utm,
       “ +datum = NAD83 + ellps.default = GCS”, sep = ‘’))

# convert contour lines into polygons
  sldf = SpatialLines2PolySet(sldf)
  sldf = PolySet2SpatialPolygons(sldf)

# list of every polygons made with each contour level
  SPDF[[j]] = sldf
  names(SPDF)[j] = levels[j]
  }
```

We can then overlap all the polygons within a single plot to visualize use of space within the 95% home range.

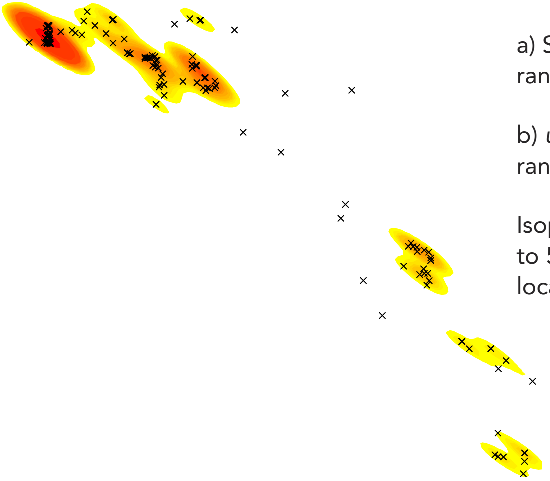
```
# set shading colours for every contour lines
  cols = colorRampPalette(c(“yellow”,”red”))
  cols = cols(length(SPDF))

# borders of every isopleths
  bord = “NA”

# export results on a single plot by overlapping polygons
  plot(SPDF[[1]],col = cols[1],border = bord, axes = F,
        main = “KDE_hpi_SAMSE”)
  for (i in 2 : length(SPDF)){
    plot(SPDF[[i]],col = cols[i],border = bord, add = T)
  }

# optional: add fixes and scalebar
  points(loca[, 1:2],pch = 4,cex = 0.75)
  scalebar(d = 10000,type = ”bar”,label = c(“0”,”“,”10km”))
```

a) SAMSE pilot



b) *unconstr* pilot

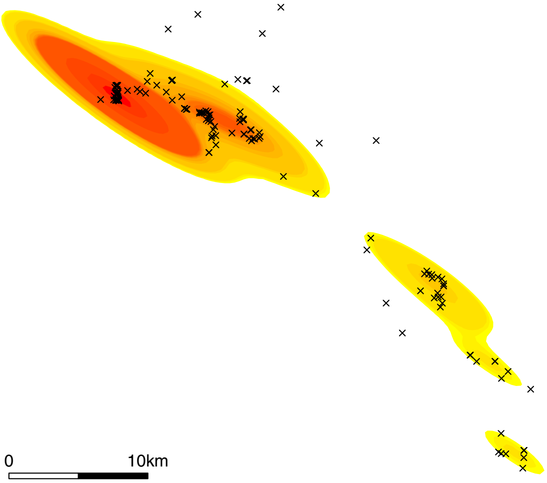


Figure 11.1 Home range estimation of an example data set (n = 323 locations) using kernel density estimate with plug-in bandwidth and

a) SAMSE pilot (95% home range size = 57 km^2)

b) *unconstr* pilot (95% home range size = 169 km^2).

Isopleths from 95% (yellow) to 50% (red) as well as relocations (x) are depicted.

11.3.3 Local convex hull (LoCoH)

Local convex hull (LoCoH) is a non-parametric kernel method that was developed because some parametric kernel methods (e.g., symmetric bivariate Gaussian) can overestimate use of space relative to hard boundaries common to many natural systems within an animal's home range (Getz et al. 2007). LoCoH is a generalization of the MCP estimator and consists of constructing convex hulls (i.e., local convex polygons) for each relocation and its nearest neighbors, and then merging the hulls from smallest to largest to create isopleths (Getz et al. 2007). The UD is produced by structuring the hulls according to isopleths ranked by utilization; i.e., the 10% isopleth contains 10% of the points and represents a higher utilization than the 100% isopleth that contains all the points (Calenge 2011). The principal R packages and functions (R core team, 2016) used to estimate home range using Local convex hull methods are shown in Table 11.4.

The R package adehabitatHR (Calenge 2011) offers three approaches to estimating LoCoH home ranges:

1. Fixed k LoCoH (Getz and Wilmers 2004), in which convex hulls are constructed from *k*-1 nearest neighbors. Hulls are merged from smallest to largest (Fig. 11.2a). Getz et al. (2007) suggested a heuristic value of $k = \sqrt{n}$ values (where n is the number of points in the set), but warned against the negative effects of small sample size on this value.

2. Fixed r LoCoH (Getz et al. 2007), in which convex hulls are created from all points within *r* distance of the root point to create a "sphere of influence" of radius *r*. When merging hulls, the hulls are first sorted by the value of *k* generated for each hull (the number of points contained in the hull), and then by the area of the hull (Fig. 11.2b). To define the *r* parameter, Getz et al. (2007) suggested using half of the maximum of all the nearest neighbor distances associated with the data, but also warned against the effect of sample size on this value.

3. Adaptive LoCoH (Getz et al. 2007) in which convex hulls are created from the maximum number of nearest neighbors such that the sum of the distances from the nearest neighbors is less than or equal to *d*. The hulls are first sorted by the value of *k* generated for each hull and then by the area of the hull (Fig. 11.2c). Getz et al. (2007) suggested that the maximum distance between two points among all points in the data set is the optimal *a* parameter value and is not affected by sample size.

Table 11.4 Principal R packages and functions used to estimate home range using local convex hull methods.

Package	**Function**	**Utility**
adehabitatHR[1]	LoCoH.k[2]	Fixed k Local convex hull method
	LoCoH.r[3]	Fixed r Local convex hull method
	LoCoH.a[3]	Adaptive Local convex hull method
	LoCoH.k.area/ LoCoH.r.area/ LoCoH.a.area	Investigate relationship between home range size (area) and a/k/r value
rgeos[4]	gArea	Calculate area of estimated home range

References: 1) Calenge 2011, 2) Getz and Wilmers 2004, 3) Getz et al. 2007, 4) Bivand and Rundel 2017.

11.3.3.1 Estimating home range using LoCoH

The first step is to transform the data set into an object of class *Spatial Points* data frame. This is a requirement of LoCoH methods in adeHabitatHR.

```
# transform locations to spatial point objects
  loca_pt<-SpatialPoints(loca[, 1:2])
```

We will first use fixed k LoCoH. Before estimating home range, we must define k-value $k = \sqrt{n}$, where n is the number of points in the set (Getz et al. 2007). Alternatively, we can also investigate the relationship between k-value and home range size to find optimal k-value (function **`LoCoH.k.area`**) although the analysis will take considerably longer to run. Then, we can estimate the home range using **`k-LoCoH`**.

```
# define k
  k=sqrt(length(loca_pt))

# HR with LoCoH using k-value proposed by Getz et al.(2007)
  Hullk<-LoCoH.k(loca_pt,k = k)

# include UD in HR estimate using r-LocoH
  plot(Hullk, col = colorRampPalette(c(“red”,”yellow”))
       (length(Hullk)), border = ‘NA’, axes = F,
       main = “k-LoCoH”)
```

```
# optional: add fixes and scalebar
  points(loca_pt, pch = 4,cex = 0.75)
  scalebar(d = 10000, type = "bar",label = c("0","","10km"))
```

The resulting plot shows many polygons within the home range (Fig. 11.2a), each representing a different isopleth. To calculate home range size, you must identify the largest (and final) polygon. You can also associate a polygon to its color using function **`cbind`**.

```
# associate polygons of different isopleth to colors
  attributs = Hullk@data
  color = colorRampPalette(c("red","yellow"))(length(Hullk))
  dat = cbind(attributs, color)
  dat

# calculate area of largest polygon (last in list, 323)
  gArea(Hullk[323,])
  # output
    237803334
```

Estimating home range using r-LoCoH is similar to k-LoCoH but we use the function **`LoCoH.r`** (after defining r-value; Fig 11.2b). The suggested r-value is the maximum of all the nearest neighbor distances associated with the data (Getz et al. 2007). Here again, you can investigate the relationship between r-value and home range size to find optimal r-value (function **`LoCoH.r.area`**).

```
# use get.knn to get nearest neighbour of each point
# then define r
  r<-get.knn(as.data.frame(loca_pt))
  r<-(max(r$nn.dist,na.rm = T))/2

# HR with r-LoCoH using r-value proposed by Getz et al.
# (2007)
  Hullr<-LoCoH.r(loca_pt,r = r)

# include UD in HR estimate using r-LocoH
  plot(Hullr, col = colorRampPalette(c("red","yellow"))
       (length(Hullr)), border = 'NA', axes = F,
       main = "r-LoCoH")

# optional: add fixes and scalebar
  points(loca_pt,pch = 4,cex = 0.75)
  scalebar(d = 10000,type = "bar",label = c("0","","10km"))
```

```
# associate polygons of different isopleth to colors
  attributs = Hullr@data
  color = colorRampPalette(c("red","yellow"))(length(Hullr))
  dat = cbind(attributs, color)
  dat

# calculate area of largest polygon (last in list, 323)
  gArea(Hullr[323,])
  # output
    196944436
```

Estimating home range using a-LoCoH is again similar but this time with function **`LoCoH.a`** (after defining a-value; Fig 11.2c). The suggested a-value is the maximum nearest neighbor distance between any two points in the dataset (Getz et al. 2007). Here again, we can investigate the relationship between a-value and home range size to find optimal a-value (function **`LoCoH.a.area`**).

```
# define a
  a<-max(spDists(loca_pt),latlong = F)

# HR with a-LoCoH using a-value suggested by Getz et al.
# (2007)
  Hulla<-LoCoH.a(loca_pt, a = a)

# include UD in HR estimate using r-LocoH
  plot(Hulla, col = colorRampPalette(c("red","yellow"))
       (length(Hulla)), border = 'NA', axes = F,
       main = "a-LoCoH")

# optional: add fixes and scalebar
  points(loca_pt,pch = 4,cex = 0.75)
  scalebar(d = 10000,type = "bar",label = c("0","","10km"))

# associate polygons of different isopleth to colors
  attributs = Hulla@data
  color = colorRampPalette(c("red","yellow"))(length(Hulla))
  dat = cbind(attributs, color)
  dat

# calculate area of largest polygon (last in list, 323)
  gArea(Hulla[323,])
  # output
    221291166
```

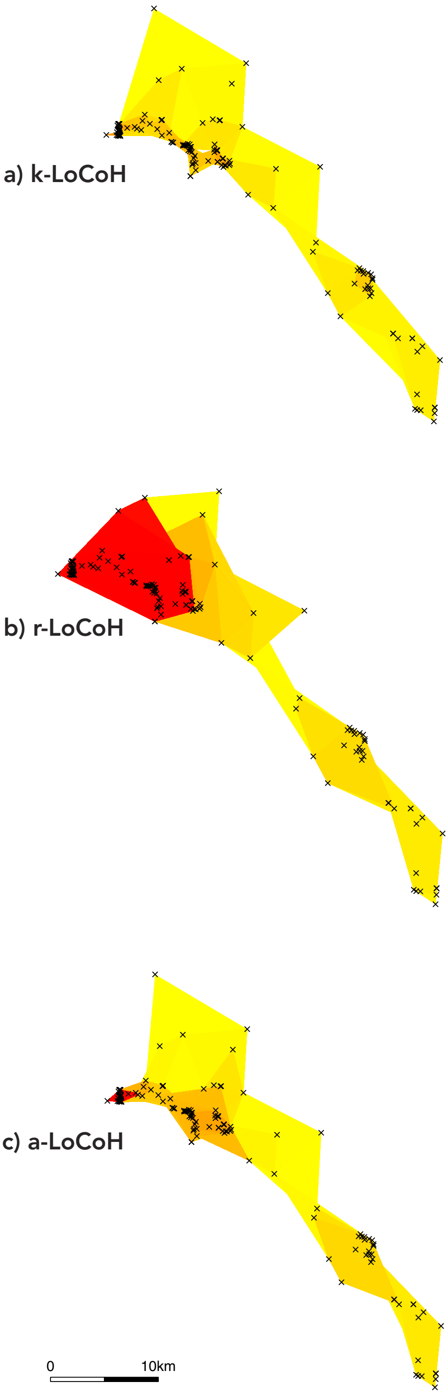


Figure 11.2 Home range estimation of an example data set (n = 323 locations) using LoCoH methods. The colors represent a utilization distribution gradient from high (red) to low (yellow) utilization.

a) Fixed k local convex hull with isopleths from 100% (area = 237 km^2) to 5%.

b) Fixed r local convex hull with isopleths from 100% (area = 197 km^2) to 83%.

c) Adaptive local convex hull with isopleths from 100% (area = 221 km^2) to 63%.

Relocations (x) are depicted.

11.3.4 Biased random bridge

The biased random bridge (BRB) home range estimator is a movement-based kernel density estimator (Benhamou 2011). It is derived from the Brownian Bridge method (BB) that estimates UDs using time between start and end locations (Horne et al. 2007). Both methods are useful when the goal is to illustrate space use between locations independent of location density. As a consequence BB and BRB can characterize hard boundaries and movement corridors within the estimated home range. However, the theoretical foundation of BB (Brownian motion) is inconsistent with the concepts of home range and habitat selection (Benhamou 2011). BRB addresses this problem by incorporating a biased random bridge equation that accounts for directional (i.e., biased) movement as well as stationary behavior. This method is therefore useful for central place foragers, including raptors that routinely engage in directional travel from breeding sites to and from foraging sites (Orians and Pearson 1979).

BRB divides each segment in a track (i.e., the Euclidian distance between two known locations) into several sub-segments by inserting new points at regular intervals between each relocation, and then generating a kernel function on known and interpolated points (Calenge 2011). BRB involves a variable smoothing parameter that depends on the time spent between a known relocation and an interpolated relocation: the smoothing parameter is small when the relocation is known and becomes larger as the interpolated time between the known relocation and the interpolated locations increase (Calenge 2011).

The principal R packages and functions (R core team, 2016) used to estimate home range using biased random bridges are shown in Table 11.5. The smoothing factor for BRB is affected by parameters that can be estimated from the data (Papworth et al. (2012); but see Calenge (2011) and Benhamou (2011) for more details on these parameters).

1. T_{max} (Upper recording time threshold): the maximum duration (in seconds) allowed for a step built by successive relocations. All steps characterized by duration greater than T_{max} are not taken into account in the calculations. The key role of T_{max} is to filter out track segments that are likely to involve significant changes in direction of movement (Benhamou 2011). In our data set, most consecutive locations are within 4 hours, with longer intervals when the falcon is less active (e.g., brooding nestlings or roosting). Thus, we set T_{max} to 4 hours to ensure that all segments represented by activity are included in the analysis. Note that this parameter has significant impact on the resulting home range size (Fig. 11.3).

Table 11.5 Principal R packages and functions used to estimate home range using biased random bridge method.

Package	**Function**	**Utility**
adehabitatLT[1]	as.ltraj	Transform locations in steps (bursts) to build BRB
adehabitatHR[2]	BRB.likD	Estimates the diffusion coefficient using the maximum likelihood method.
	BRB.D	Estimates the diffusion coefficient using plug-in method.
	BRB	Estimates UD using Biased random bridge[3]
	getverticesHR	Extracts the home-range contours (isopleths)
rgeos[4]	gArea	Calculates area of estimated home range

References: 1) Calenge 2006, 2) Calenge 2011, 3) Benhamou 2011, 4) Bivand and Rundel 2017

2. D: diffusion coefficient (squared "units" per second, where "units" denote the units of the relocation coordinates). In contrast to the BB method that assumes a constant diffusion coefficient, BRB uses a diffusion coefficient that can change during the tracking period (i.e., habitat-specific diffusion coefficients). There is a possibility to include a data frame with relative diffusion coefficients of the animal in different components of the habitat.

3. L_{min}: the minimum distance (in units of the coordinates) between successive relocations, defining intensive use or resting. Note that the GPS measurement-error should be considered when defining L_{min}. If a step is shorter than L_{min}, the animal will be considered to be stationary and the step will be filtered out by the BRB algorithm.

4. h_{min}: the minimum smoothing parameter (in units of the relocations coordinates), applied to all recorded relocations. According to Benhamou and Cornélis (2010), h_{min} should at least equal the standard deviation of the location errors and be large enough to include potential locations in the same patch as the recorded location.

11.3.4.1 Estimating home range using BRB

The first step is to extract direction of travel (i.e., trajectory) between relocations. This allows the BRB algorithm to integrate movement direction into the estimation of home range.

```
# extract the trajectory from fixes
  loc.ltraj <- as.ltraj(xy = loca[,1:2],
       date = loca$time, id = 1, typeII = TRUE)
```

We can then estimate home range using BRB. Before doing so, we estimate diffusion parameter D using function **`BRB.likD`**. We will set T_{max} = 4 hours, L_{min} = 50 meters and h_{min} = 500 meters.

```
# estimate diffusion parameter D
  vv <- BRB.likD(loc.ltraj, Tmax=4*60*60, Lmin=50)
```

We then estimate the UD within our home range using BRB. The first step is to create home ranges of varying isopleths (i.e., from 50% to 95%). Creating independent projected polygons from these home range estimates will allow the user to export them to GIS software and overlap home ranges with a map of the habitat. Because of the high density of points around the nest, the algorithm sometimes cannot draw a polygon for 50% isopleth. If this is the case (CL too short), start with higher (55% or 60%).

```
# estimate UD
  BRB <- BRB(loc.ltraj, D = vv, Tmax = 4*60*60, Lmin = 50,
       type = “UD”, hmin=500, grid = 500, extent = 3)

# first create list of polygons of different isopleths
  SPDF = list()
  Levels = seq(95,50,by = -2.5)
  for (j in 1 : length(levels)){
    cat(j,”\n”)

# extract every isopleth (contour line) of level j
  cont = contourLevels(kernPI1, cont = levels[j])
  line = contourLines(x = kernPI1$eval.points[[1]],
       y = kernPI1$eval.points[[2]], z = kernPI1$estimate,
       level = cont)
  sldf = ContourLines2SLDF(line)
```

```
# set projection (UTM) for polygons
  utm = names(sort(table(as.character(loca$utmzone)))[1])
  utm = gsub(‘N|S’, ‘’, toupper(utm))
  proj4string(sldf) = CRS(paste(“+ proj = utm + zone =”, utm,
        “ + datum = NAD83 + ellps.default = GCS”, sep = ‘’))

 # extract every isopleth of level j
   verBRB <- getverticeshr(BRB,percent = levels[j])
# list of every polygons made with each contour level
  SPDF[[j]] = verBRB
  names(SPDF)[j] = levels[j]
  }
```

We then overlap all the polygons within the same plot to visualize use of space within the 95% home range (Fig. 11.3b).

```
# set shading colours for every contour lines
  cols = colorRampPalette(c(“yellow”,”red”))
  cols = cols(length(SPDF))

# borders of every isopleth
  bord = ‘NA’

# export results on a single plot by overlapping polygons
  plot(SPDF[[1]],col = cols[1],border = bord, axes = F,
        main = “ BRB_Tmax = 4 hours “)
  for (i in 2 : length(SPDF)){
    plot(SPDF[[i]],col = cols[i],border = bord, add = T)
  }

# optional: add fixes and scalebar
  points(loca[, 1:2],pch = 4,cex = 0.75)
  scalebar(d = 10000,type = ”bar”,label = c(“0”,””,”10km”))
```

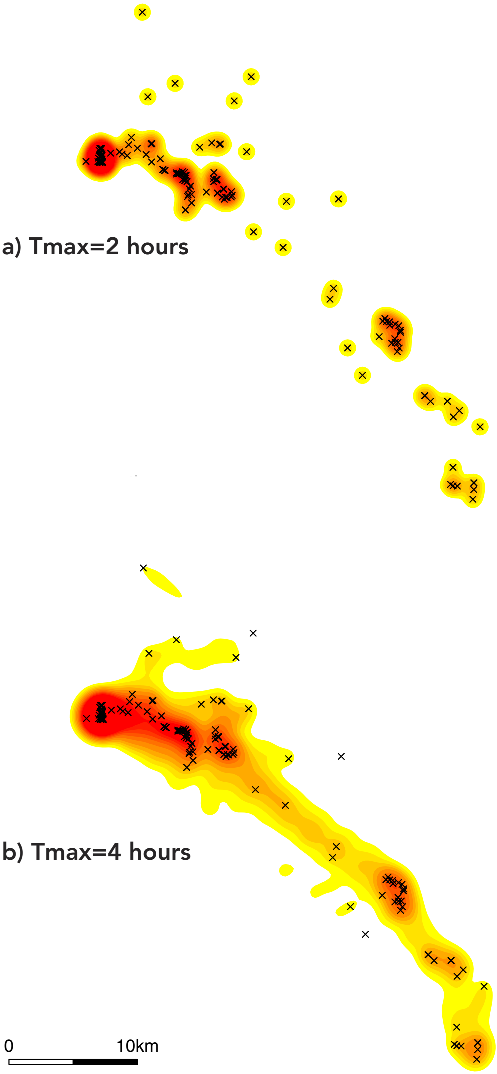


Figure 11.3 Home range estimation of an example data set (n = 323 locations) using biased random bridge with T_{max} set as:

a) 2 hours (95% home range size = 99 km^2);

b) 4 hours (95% home range size = 229 km^2).

Isopleths from 95% (yellow) to 50% (red) as well as relocations (x) are depicted.

11.4 Interpreting the output

Home range estimates obtained with KDE, LoCoH and BRB differ in size and degree of fragmentation (Figs. 11.1, 11.2 and 11.3, and see Table 11.6 for a summary of the outputs).

11.4.1 KDE

Home range estimates using kernel density estimation with h_{pi} varied with the choice of pilot, despite the fact that choice of pilot has little, if any, biological relevance. Resulting home range outputs are either over-smoothed, resulting in an overestimation of used areas (especially around the nest; Fig. 11.1b), or highly fragmented, resulting in multiple patches (Fig. 11.1a). However, in our example, predictions of core ranges (i.e., 50% home ranges) were consistent regardless of which smoothing parameter was used.

11.4.2 LoCoH

Unless specified otherwise, LoCoH methods produce UDs based on all isopleths from the smallest to largest (i.e., 100% isopleth). In our example, k-LoCoH produced isopleths from 5% to 100% (Fig. 11.2a), r-LoCoH produced isopleths from 83% to 100% (Fig. 11.2b), and a-LoCoH produced isopleths from 63% to 100% (Fig. 11.2c). Thus the method used to construct and arrange the convex hulls is important (e.g., identifying frequently used patches such as foraging sites and the nesting site), even though overall characterization of home range estimates remained relatively stable in our example. The main difference among the three LoCoH methods used is delimitation of areas of highly used (i.e., red and orange) patches. Home range size showed little variation (from 197 km^2 for r-LoCoH to 237 km^2 for k-LoCoH; Fig. 11.2) in our example. Here again, subjective, visual choice for the best method based on successive trials is an option, but Getz et al. (2007) argued that adaptive LoCoH (a-LoCoH) is the best method unless there are good biological reasons to use fixed k or fixed r. Although Local convex hull methods produced geometrically shaped polygons that appear unnatural, the method was useful for characterizing home ranges that were not fragmented and portrayed space use between the nest and principal foraging areas (Fig. 11.2).

11.4.3 BRB

The biased random bridge method was able to depict principal movement corridors (bridges) in home range estimates, but only when T_{max} was set to represent the sampling regime (i.e., locations every 4 hours; Fig. 11.3b). The resulting home range is contiguous, includes movement corridors and principal foraging sites, and over-smoothing does not appear to be a problem (i.e., estimates reflect the underlying data). However, setting $T_{max} < 4$ resulted in a fragmented home range without travel corridors, (Fig. 11.3a), and was similar to the KDE using h_{pi} with samse pilot (Fig. 11.1a). The simulated data used for our examples were based on the movement data from a falcon breeding within the Coxe Islands at the northern end of the Melville Peninsula in Nunavut, Canada. Our interpretation is based on direct knowledge of the landscape, location of the nesting site, and reproductive status, including brood size and age of nestlings, and we are confident that our interpretation of travel corridors between foraging areas (small islands of highly productive tundra within marine habitat) and the nesting site is consistent with the output. We emphasize that knowledge of the species' biology, as well as knowledge of the context of individuals (e.g., breeding status and surrounding landscape) can help considerably when judging which approach to home range estimate is most suitable.

Table 11.6 Summary table of the size and degree of fragmentation of home range estimates using the seven methods highlighted in the examples.

Method	95% HR Size (km²) *	Fragmentation
KDE-SAMSE pilot	57	high
KDE-*unconstr* pilot	169	low
Fixed k LoCoH	237	none
Fixed r LoCoH	197	none
Adaptive LoCoH	221	none
BRB-Tmax=2 hours	99	high
BRB-Tmax = 4 hours	229	low

* LoCoH estimates are given as 100% HR for comparative purpose because 95% isopleth is not precisely defined for each three methods.

11.5 Conclusion

Home range estimation is an abstraction of true space use by animals (Hemson et al. 2005), and home range analysis is a means to visualize the effect of multiple factors on an individual's movement behavior for a specific period of time. Because home range is a spatial representation of an animal's behavior within the surrounding habitat, it is important that an understanding of a species' biology drives the modeling process (Powell and Mitchell 2012). The objective of home range modeling is to provide greater understanding of the ways in which the behavior of wild animals fulfills their needs, and it is critically important that statistical methods make realistic assumptions about the way in which an animal behaves in its environment (Worton 1995). Consequently, because all animals behave differently, there is no single, best estimator for all species or research questions. Our examples show how the choice of home range estimator and appropriate selection of smoothing parameters can have considerable influence on home range estimates. For this reason, selection of a home range estimator should be conducted carefully after preliminary analysis of the data.

Because Gyrfalcons have specific needs for nest selection (Booms et al. 2010) and potentially forage in multiple cover types with a patchy distribution of resources, a suitable home range estimator for this species must be able to characterize frequently used patches and travel corridors among patches, without including areas that are not used. Based on our data, we suggest that biased random bridge home range estimator best fulfills those requirements. However, deciding which estimator to use and subsequent interpretation of the output must be done with caution (particularly when sample size is small). In this regard, there is considerable opportunity to share tracking data among studies through databases such as MoveBank (http://www.movebank.org/about/index.html) to resolve methodological differences and to increase sample size (i.e., number of individuals).

Comparative studies are especially important because they can shed light on factors that drive intraspecific variation in home range. Understanding the way in which home range varies in time, space, and within and among species is fundamental to gaining insight into aspects of a species' ecology such as habitat preferences (Williams et al. 2011), carrying capacity (Ryan and Jamieson 1998), and risk of extinction (Woodroffe and Ginsberg 1998). Given the rate of change that has occurred in Arctic ecosystems, these aspects are increasingly important for conservation of Arctic residents such as Gyrfalcons. Further, future studies involving Gyrfalcon home range should include estimates of habitat-specific abundance and distribution of principal prey species (see Chapter 8) because it is well known that fluctuations in prey abundance can have an effect on demography (Nielsen 1999, Mossop 2011). Yet, it is still unclear how these fluctuations in prey distribution (see Chapter 9) affect Gyrfalcons' home range.

Literature cited

Barichello, N., and D. Mossop. 2011. The overwhelming influence of Ptarmigan abundance on Gyrfalcon reproductive success in the central Yukon, Canada. Pages 307–322 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.

Bekoff, M., and L. D. Mech. 1984. Simulation analyses of space use: home range estimates, variability, and sample size. Behavior Research Methods, Instruments, & Computers 16:32–37.

Beltran, J. W., J. M. Wunderle Jr., and W. J. Arendt. 2010. Changes in home range of breeding and post-breeding male Pearly-eyed Thrashers in the Luquillo Mountains of Puerto Rico. Ornithological Neotropical 21:409–423.

Benhamou, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PLoS ONE 6:e14592.

Benhamou, S., and D. Cornélis. 2010. Incorporating Movement Behavior and Barriers to Improve Kernel Home Range Space Use Estimates. Journal of Wildlife Management 74:1353–1360.

Bivand,R., and C. Rundel. 2017. rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3–22. https://CRAN.R-project.org/package=rgeos

Bloom, P. H., M. D. McCrary, and M. J. Gibson. 1993. Red-shouldered Hawk home-range and habitat use in southern California. Journal of Wildlife Management 57:258–265.

Booms, T. L., F. Huettmann, and P. F. Schempf. 2010. Gyrfalcon nest distribution in Alaska based on a predictive GIS model. Polar Biology 33:347–358.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

Burger, A. E., and S. A. Shaffer. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264.

Burgman, M. A., and J. C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation 6:19–28.

Burnham, K. K., and I. Newton. 2011. Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. Ibis 153:468–484.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365:2157–2162.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calenge, C. 2011. Home range estimation in R: the adehabitatHR package. Office national de la classe et de la faune sauvage. Saint Benoist, Auffargis, France.

Campioni, L., M. d. M. Delgado, R. Lourenço, G. Bastianelli, N. Fernandez, and V. Penteriani. 2013. Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. Oecologia 172:371–385.

Cederlund, G., and H. Sand. 1994. Home-Range Size in Relation to Age and Sex in Moose. Journal of Mammalogy 75:1005–1012.

Chacón, J. E., and T. Duong. 2010. Multivariate plug-in bandwidth selection with unconstrained pilot bandwidth matrices. Test 19:375–398.

CLS. 2016. Argos user's manual 2007–16. http://www.argos-system.org/manual/. Accessed 11 January 2017.

Darwin, C. 1861. On the origins of species. 3rd edition. Murray, London, UK.

Downs, J. A., and M. W. Horner. 2009. A characteristic-hull based method for home range estimation. Transactions in GIS 13:527–537.

Duerr, A. E., T. A. Miller, M. Lanzone, D. Brandes, J. Cooper, K. O'Malley, C. Maisonneuve, J. Tremblay, and T. Katzner. 2012. Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. PLoS ONE 7:e35548.

Duong, T., and M. Hazelton. 2003. Plug-in bandwidth matrices for bivariate kernel density estimation. Journal of Nonparametric Statistics 15:17–30.

Eisaguirre, J. M., T. L. Booms, P. F. Schempf, and S. B. Lewis. 2016. Gyrfalcon home ranges and movements on the Yukon-Kuskokwim Delta, Alaska. Journal of Raptor Research 50:109–114.

Erikstad, K., Einar. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. Ornis Scandinavica 16:181–190.

Ferguson-Lees, J., and D. A. Christie. 2001. Raptors of the world. Houghton Mifflin Harcourt. New York, New York, USA.

Fieberg, J., and L. Börger. 2012. Could you please phrase "home range" as a question? Journal of Mammalogy 93:890–902.

Fuller, M. R., P. F. Schempf, and T. L. Booms. 2011. Developing Gyrfalcon surveys and monitoring for Alaska. Pages 275–282 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.

Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS ONE 2:e207.

Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489–505.

Gilg, O., B. T. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634–2652.

Harestad, A. S., and F. L. Bunnel. 1979. Home range and body weight – a reevaluation. Ecology 60:389–402.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home range analyses with least squares cross validation. Journal of Animal Ecology 74:455–463.

Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen, and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology 265:63–71.

Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, and H. P. Huntington. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Climatic Change 72:251–298.

Horne, J. S., O. Edward, S. Garton, M. Krone, and J. Lewis. 2007. Analyzing animal movement using brownian bridges. Ecology 88:2354–2363.

IPCC, 2013. Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T. F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley (eds.)]. Cambridge University Press, Cambridge, UK, and New York, New York, USA.

Jones, E. N. 1990. Effects of forage availability on home range and population density of *Microtus pennsylvanicus*. Journal of Mammalogy 71:382–389.

Jones, M., and R. Kappenman. 1992. On a class of kernel density estimate bandwidth selectors. Scandinavian Journal of Statistics 19:337–349.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.

Kenward, R. E., R. T. Clarke, K. H. Hodder, and S. S. Walls. 2001. Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. Ecology 82:1905–1920.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79:949–954.

Kjellander, P., A. J. Hewison, O. Liberg, J. M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. Oecologia 139:478–485.

Korpimäki, E., and C. D. Marti. 1995. Geographical trends in trophic characteristics of mammal-eating and bird-eating raptors in Europe and North America. Auk 4:1004–1023.

Koskimies, P. 2011. Conservation biology of the Gyrfalcon (*Falco rusticolus*) in northern Fennoscandia. Pages 95–124 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume II. The Peregrine Fund, Boise, Idaho, USA.

Kowalczyk, N. D. , R. D. Reina, T. J. Preston, and A. Chiaradia. 2015. Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. Oecologia 178:967–979.

Lanzone, M. J., T. A. Miller, P. Turk, D. Brandes, C. Halverson, C. Maisonneuve, J. Tremblay, J. Cooper, K. O'Malley, R. P. Brooks, and T. Katzner. 2012. Flight responses by a migratory soaring raptor to changing meteorological conditions. Biology Letters 8:710–713.

Lapointe, J., L. Imbeau, J. A. Tremblay, C. Maisonneuve, and M. J. Mazerolle. 2013. Habitat use by female Peregrine Falcons (*Falco peregrinus*) in an agricultural landscape. Auk 130:381–391.

Larter, N. C., and C. C. Gates. 1994. Home-range size of wood bison: effects of age, sex, and forage availability. Journal of Mammalogy 75:142–149.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. Journal of Wildlife Management 72:290–298.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67:413–418.

Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn. 2012. Geolocation by light: accuracy and precision affected by environmental factors. Methods in Ecology and Evolution 3:603–612.

Marquiss, M., and I. Newton. 1982. A radio-tracking study of the ranging behaviour and dispersion of European sparrowhawks *Accipiter nisus.* Journal of Animal Ecology 51:111–133.

Marzluff, J. M., B. A. Kimsey, L. S. Schueck, M. E. McFadzen, M. S. Vekasy, and J. C. Bednarz. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. Condor 99:567–584.

McIntyre, C. L., D. C. Douglas, and L. G. Adams. 2009. Movements of juvenile Gyrfalcons from western and interior Alaska following departure from their natal areas. Journal of Raptor Research 43:99–109.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97:133–140.

Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. Journal of Mammalogy 61:261–267.

Milton, K., and M. L. May. 1976. Body weight, diet and home range area in primates. Nature 259:459–462.

Mindell, D., J. Albuquerque, and C. White. 1987. Breeding population fluctuations in some raptors. Oecologia 72:382–388.

Mitchell, M. S., and R. A. Powell. 2012. Foraging optimally for home ranges. Journal of Mammalogy 93:917–928.

Morellet, N., C. Bonenfant, L. Börger, F. Ossi, F. Cagnacci, M. Heurich, P. Kjellander, J. D. Linnell, S. Nicoloso, and P. Sustr. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology 82:1326–1339.

Mossop, D. H. 2011. Long-term studies of Willow Ptarmigan and Gyrfalcon in the Yukon Territory: A collapsing 10-year cycle and its apparent effect on the top predator. Pages 323–335 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and ptarmigan in a changing world, volume I. The Peregrine Fund, Boise, Idaho, USA.

Nielsen, Ó. K. 1999. Gyrfalcon predation on ptarmigan: numerical and functional responses. Journal of Animal Ecology 68:1034–1050.

Nilsen, E. B., S. Pederson, and J. D. C. Linnell. 2007. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635–639.

Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72:128–137.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 *in* D. J. Horn, G. R. Stairs, and R. D. Mitchell, editors. Analysis of ecological systems. Ohio State University Press, Columbus, Ohio, USA.

Papworth, S. K., N. Bunnefeld, K. Slocombe, and E. J. Milner-Gulland. 2012. Movement ecology of human resource users: using net squared displacement, biased random bridges and resource utilization functions to quantify hunter and gatherer behaviour. Methods in Ecology and Evolution 3:584–594.

Peery, M. Z. 2000. Factors affecting interspecies variation in home-range size of raptors. Auk 117:511.

Phillips, R., A. 2004. Accuracy of geolocation estimates for flying seabirds. Marine Ecology Progress Series 266:265.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, and T. T. Høye. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–103 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Colombia University Press, New York, New York, USA.

Powell, R. A., and M. S. Mitchell. 2012. What is a home range? Journal of Mammalogy 93:948–958.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rigamonti, M. M. 1993. Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. Pages 25–39 *in* Lemur social systems and their ecological basis. Springer, New York, New York, USA.

Rivrud, I. M., L. E. Loe, and A. Mysterud. 2010. How does local weather predict red deer home range size at different temporal scales? Journal of Animal Ecology 79:1280–1295.

Robinson, W. D., M. S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R. H. Diehl, T. H. Kunz, S. Mabey, and D. W. Winkler. 2010. Integrating concepts and technologies to advance the study of bird migration. Frontiers in Ecology and the Environment 8:354–361.

Ryan, C. J., and I. G. Jamieson. 1998. Estimating the home range and carrying capacity for takahe (*Porphyrio mantelli*) on predator-free offshore islands: implications for future management. New Zealand Journal of Ecology 22:17–24.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Seegar, W. S., P. N. Cutchis, M. R. Fuller, J. J. Surer, V. Bhatnagar, and J. G. Wall. 1996. Fifteen years of satellite tracking development and application to wildlife research and conservation. Johns Hopkins APL Technical Digest 17:401–411.

Simon, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology 56:993–998.

Sokolov, V., N. Lecomte, A. Sokolov, M. L. Rahman, and A. Dixon. 2014. Site fidelity and home range variation during the breeding season of peregrine falcons (*Falco peregrinus*) in Yamal, Russia. Polar Biology 37:1621–1631.

Steenhof, K., K. K. Bates, M. R. Fuller, M. N. Kochert, J. O. McKinley, and P. M. Lukacs. 2006. Effects of radiomarking on Prairie Falcons: attachment failures provide insights about survival. Wildlife Society Bulletin 34:116–126.

Strandberg, R., R. H. Klaassen, M. Hake, P. Olofsson, and T. Alerstam. 2009. Converging migration routes of Eurasian Hobbies *Falco subbuteo* crossing the African equatorial rain forest. Proceedings of the Royal Society of London B: Biological Sciences 276:727–733.

Sturm, M., C. Racine, and K. Tape. 2001. Climate change: increasing shrub abundance in the Arctic. Nature 411:546–547.

Stutchbury, B. J., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. Science 323:896–896.

Thorup, K., I. A. Bisson, M. S. Bowlin, R. A. Holland, J. C. Wingfield, M. Ramenofsky, and M. Wikelski. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. Proceedings of the National Academy of Sciences 104:18115–18119.

USGS. 2016. Auxiliary Marking Authorization. Bird banding laboratory. Canadian Wildlife Service. http://www.pwrc.usgs.gov/. Accessed 01 February 2017.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771–785.

van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118–123.

Vega Rivera, J., W. McShea, J. Rappole, and S. Hackett. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120:632–644.

Village, A. 1982. The home range and density of kestrels in relation to vole abundance. Journal of Animal Ecology 51:413–428.

Walter, W. D., J. W. Fischer, S. Baruch-Mordo, and K. C. VerCauteren. 2011. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step. Modern Telemetry 12:249–268.

Walter, W. D., D. P. Onorato, and J. W. Fischer. 2015. Is there a single best estimator? Selection of home range estimators using area-under-the-curve. Movement Ecology 3:DOI 10.1186.

Wand, M. P., and M. C. Jones. 1994. Multivariate plug-in bandwidth selection. Computational Statistics 9:97–116.

Watson, J. W. 2002. Comparative home ranges and food habits of Bald Eagles nesting in four aquatic habitats in western Washington. Northwestern Naturalist 83:101–108.

Williams, P. J., R. J. Gutiérrez, and S. A. Whitmore. 2011. Home range and habitat selection of Spotted Owls in the central Sierra Nevada. Journal of Wildlife Management 75:333–343.

Wilson, R. P., J. J. Ducamp, W. G. Rees, B. M. Culik, and K. Niekamp. 1992. Estimation of location: global coverage using light intensity. Pages 131–134 *in* I. M. Priede and S. M. Swift, editors. Wildlife telemetry: remote monitoring and tracking of animals. University of Chicago Press, Chicago, Illinois, USA.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128.

Worton, B., J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

Zabel, C. J., K. McKelvey, and J. P. Ward Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). Canadian Journal of Zoology 73:433–439.