

Estimating animal utilization densities using continuous-time Markov chain models

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Abstract

1. A long-standing goal in ecology is to describe an animal's home range or utilization density (UD) without complete knowledge of the animal's movement. There are a number of methods available to calculate a UD from telemetry data, but the most common methods limit the UD to cover areas where the animal was observed during tracking, and do not account for preferential use of different habitats (resource selection).
2. The limiting distribution of a continuous-time Markov chain (CTMC) matches the intuitive understanding of a UD for an animal following a CTMC movement model. By modelling continuous-time movement through discrete-gridded space we can infer environmental effects on animal movement and then predict a UD over the desired spatial area that captures preferential use of space.
3. The R packages `crawl` and `ctmcmove` allow ecologists to use telemetry data to predict the UD of an animal using the limiting distribution of a CTMC movement model.
4. We used data collected from Steller sea lions in Alaska to illustrate use of this method for investigating range-wide space use. Our findings show how these packages, and this method, can aid our understanding of space-use by predicting use outside the areas where animals were observed, avoiding barriers to movement, including environmental covariates and removing the release effect of telemetry studies. These results will be important for both conservation and management, particularly when determining critical habitat designation.

KEYWORDS

continuous-time Markov chain, limiting distribution, Steller sea lion, telemetry, utilization density

1 | INTRODUCTION

Animal tracking via telemetry devices has become routine in ecology and allows for the study of animal movement, resource selection, and space use (Hanks, Hooten, & Aldredge, 2015; Hooten, Johnson, McClintock, & Morales, 2017; Johnson, Hooten, & Kuhn, 2013). Telemetry data provide insight into animal movement, but may not depict complete coverage of animal activities or behavior. Consequently, a long-standing

goal in ecology has been to determine how one should define the home range or utilization density (UD) of an animal with incomplete knowledge of its path (Kie et al., 2010). Heuristically, UD's can be thought of as a probability density for the realization of an animal's location on a two-dimensional surface, that is, where an animal is likely to be found on a map if we relocate it sometime in the future (Hooten et al., 2017).

Kernel density estimation has become the most frequently used method for estimating the UD (Keating & Cherry, 2009; Kie et al.,

2010; Lavar & Kelly, 2008), with Brownian Bridge Movement Models gaining popularity in recent years (Horne, Garton, Krone, & Lewis, 2007; Kranstauber, Kays, LaPoint, Wikelski, & Safi, 2012; Tracey et al., 2014). These methods are popular and easy to implement with R packages; however, choice of smoothing parameter (Kie et al., 2010) and adjustments for environmental barriers (e.g., marine animals not crossing land or terrestrial animals not walking off a cliff) remain points of debate. Additionally, these methods typically restrict the UD within the area where the animal was observed and do not extrapolate to include other potential high-use areas nearby.

Whitehead and Jonsen (2013) recently proposed a method to calculate UDs from telemetry data by using the limiting distribution of a discrete-time Markov chain. This method is an improvement in calculating density estimates, but does not incorporate continuous-time nor habitat related covariates that may inform movement patterns.

When analysing animal telemetry data, the goal is often to relate the continuous movement of the animal to gridded environmental covariates. Hanks et al. (2015) proposed a continuous-time Markov chain (CTMC) to model an animal's movement through a discrete, gridded space. This process links animal movement to environmental covariates and allows for flexible modelling of an animal's response to potential drivers of movement.

In this paper, we describe a method to estimate the UD of an animal using a CTMC model that accounts for environmental barriers and preferential use of different habitats. We extend the approach of Hanks et al. (2015) to predict space use across the entire area of interest, instead of restricting the UD to where the animal was observed during the deployment period. We explain how this method works, show how it can be applied using the R packages `crawl` and `ctmcmove`, and demonstrate the method using telemetry data from Steller sea lions (SSL) (*Eumetopias jubatus*) in Alaska.

2 | CTMC MODELS OF ANIMAL MOVEMENT

A CTMC movement model is a stochastic process in which an animal transitions in continuous time between a set of discrete states, in this case, spatial grid cells. Movement through the cells is defined by the rate (λ_{ij}) at which an animal transitions from cell, i , to neighbouring cell, j . The time spent in cell i is exponentially distributed with rate $\bar{\lambda}_i = \sum_{j=1}^{n_i} \lambda_{ij}$, and once an animal leaves cell i the probability that it moves from cell i to cell j is $\lambda_{ij}/\bar{\lambda}_i$ (Kulkarni, 2010). Herein, transitions are only allowed between neighbouring grid cells (e.g., a rook's neighbourhood), but this is not a mathematical constraint, it can be extended as desired. Setting a rate $\lambda_{ij} = 0$ makes moving from cell i to cell j impossible, so the CTMC model can easily incorporate impassible terrain.

The discrete-space representation of the CTMC movement path provides a natural framework for making inference about possible drivers of movement, represented as covariates in raster form, by setting the rate of movement from cell $i = 1, \dots, S$, to cell j as $\lambda_{ij} = \exp(\mathbf{x}_{ij}'\boldsymbol{\beta})$, where \mathbf{x}_{ij} contains covariates controlling the rate of movement from cell i to j and $\boldsymbol{\beta}$ is the associated vector of coefficients.

Hanks et al. (2015) consider two broad classes of covariates: (1) motility covariates ($x_{ij} = x_i$), which are dependent only on the landscape in cell i and are constant over all j , and (2) directional covariates of movement, in which x_{ij} are different for each neighbouring cell and capture directional bias in movement along covariate gradients. The motility covariates control the desire of an animal to stay in (or leave) a cell due to the current habitat (i.e., speed of movement through a cell), while directional drivers control attraction (or repulsion) to neighbouring cells due to improvement (degradation) in the neighbouring habitat relative to the current habitat.

This CTMC approach is similar to a resource selection analysis with the available resources defined as the neighbouring grid cells. The transition rate to each neighbouring cell contains information that defines preferential use of the resources in each cell. Estimates of $\boldsymbol{\beta}$, therefore, provide information about how animals are using the available habitat.

A number of species have barriers in their environment that they are unable to cross (e.g., marine mammals cannot swim across land). Modelling movement in discrete space allows us to put "holes" in the habitat grid that serve as barriers for movement (the probability of transition into a barrier cell = $\lambda_{ij} = 0$). By not allowing the movement path to cross a barrier, we can calculate a UD that respects impassible barriers to movement.

3 | INFERRING UDS FROM CTMC LIMITING DISTRIBUTIONS

Heuristically, the limiting distribution of the CTMC is the long-run distribution of the animal's location at some point far into the future. In the case of an animal moving through gridded space, the states are cells in the habitat grid and the limiting distribution is the probability that an animal is located in each cell at some point far in the future. This description of the limiting distribution matches how ecologists think of the UD, so, it stands to reason that it can be considered as the UD for an animal following a CTMC movement model.

The conditions under which a CTMC possesses a limiting distribution have been studied in many contexts (see section 4.6 of Kulkarni, 2010). The most general conditions that ensure a CTMC has a limiting distribution are that the CTMC is *irreducible* and *positive recurrent*. For our model, this means:

1. if a grid cell can be visited (e.g., not a barrier cell) then it can be accessed from any other grid cell given enough time (irreducible) and
2. after an animal leaves a cell, the probability that it will take an infinitely long time to return to that cell is zero (positive recurrence).

For the CTMC model of animal movement, these conditions are satisfied if the study area is not cut into sections where the animal cannot move from one section to another (1) and all other cells allow at least one move to a neighbouring cell (2). Mathematically, the second condition implies that $\bar{\lambda}_i > 0$ for any cells the animal can visit. In

a general sense, there can be no cells for which the animal remains forever once it enters, and the predicted space should not contain cells that would never be visited by the animal in question.

To aid in the calculation of the UD from a CTMC, it will be helpful to break the CTMC into two random processes, the embedded Markov chain, G_1, \dots, G_T , which is the time-ordered list of cells visited over the course of the deployment, and the times, τ_1, \dots, τ_T , that the animal spends in each cell. Because the CTMC model is irreducible and positive recurrent, the limiting distribution can be calculated as a weighted average

$$u_i = \frac{\alpha_i / \bar{\lambda}_i}{\sum_k \alpha_k / \bar{\lambda}_k}$$

of $\alpha = (\alpha_1, \dots, \alpha_S)$, which is the limiting distribution of the embedded Markov chain (Norris, 1997). Therefore, in the long run, the proportion of time that an animal spends in a cell is equal to the long-run probability (α_k) that it visits that cell (the limiting distribution of the embedded chain), multiplied by the expected amount of time $1/\bar{\lambda}_k$ it resides in that cell (residence time is exponentially distributed with rate $\bar{\lambda}_k$). This is just one solution for obtaining the limiting distribution and is a good explanation of the general idea. There are many approaches to finding the limiting distribution of a CTMC once the rate parameters (λ_{ij}) have been estimated (Moler & Van Loan, 2003). Our analysis uses the more numerically efficient method of Harrod and Plemmons (1984).

There are several benefits (not mutually exclusive) to estimating a UD using this limiting distribution method. As Whitehead and Jonsen (2013) note, using a limiting distribution removes the release effect. That is, over a small timeframe, an animal may not adequately explore all of the territory it would normally use because it can only move so far from where the researcher releases it. By removing the release effect, this approach allows predictive estimation of the UD because it estimates use in the long run, after the animal has had time to explore all of the study area. Consequently, high use areas can be predicted where the animal never visited, if the environmental conditions in those cells are good enough to eventually warrant a visit from the

animal. Finally, because the initial conditions are removed, estimated UD are directly comparable between animals of different telemetry deployment lengths. Essentially, the deployment length (i.e., release) effects have been removed since the UD for every animal is based on the same long-run time-scale. This method also links the movement of the animal to environmental covariates, consequently accounting for the animal's response to environmental drivers of movement when calculating the UD. This method for estimating a UD can now be implemented using the `ctmcmove` package in R.

4 | TUTORIAL

This tutorial illustrates how to use existing R packages to estimate a UD using telemetry data and environmental covariates. We initially modelled the telemetry data using the R package `crawl` (Johnson, 2016) with subsequent steps of the CTMC model implemented in `ctmcmove` (Hanks, 2016). The general steps to accomplish this are: (1) create covariate rasters; (2) create a quasi-continuous movement path from the telemetry data using `crawl`; (3) adjust the movement path to avoid any barriers; (4) estimate CTMC model parameters using `ctmcmove`; and (5) calculate the UD. See Appendix S1 for step-by-step code.

For this example, we used telemetry data (Wildlife Computers SPLASH tags) from adult female SSL, tagged over-winter in the Aleutian Islands, Alaska, USA. The data include location estimates (latitude/longitude), with a corresponding date/time, location class (an error estimate for each Argos location), and whether or not the SSL was hauled-out on land (drytime).

4.1 | Create covariate rasters

The raster grid extent and resolution was the same for all animals (1 km) and covered the central Aleutian Islands (Figure 1). We used bathymetry (Alaska Regional Office 2017), slope, distance to the closest SSL haul-out or rookery site (Fritz, Sweeney, Towell, & Gelatt,

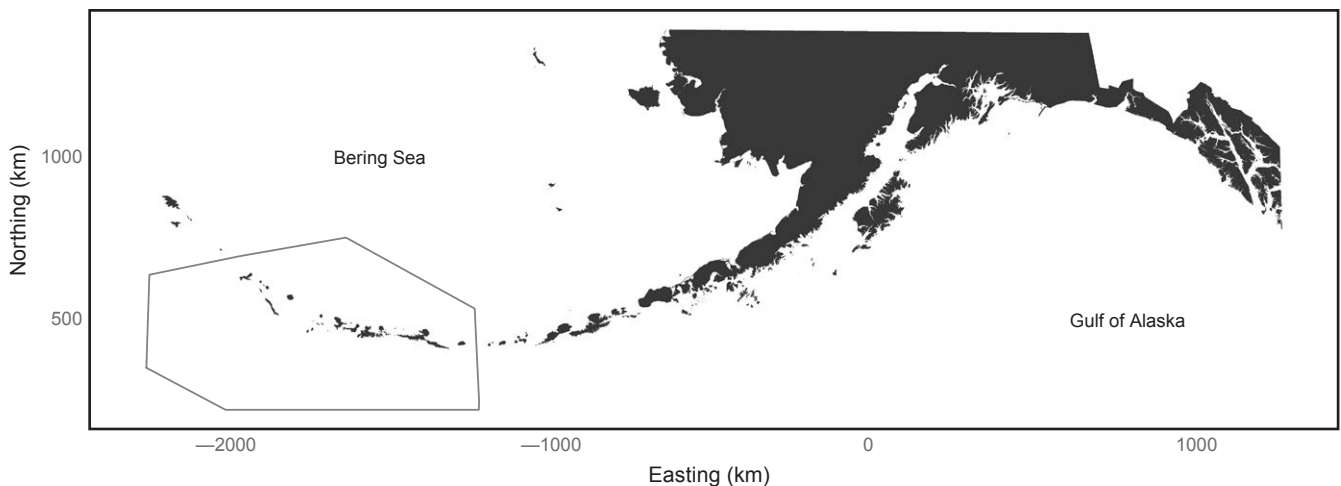


FIGURE 1 Study area: Central Aleutian Islands, Alaska, USA

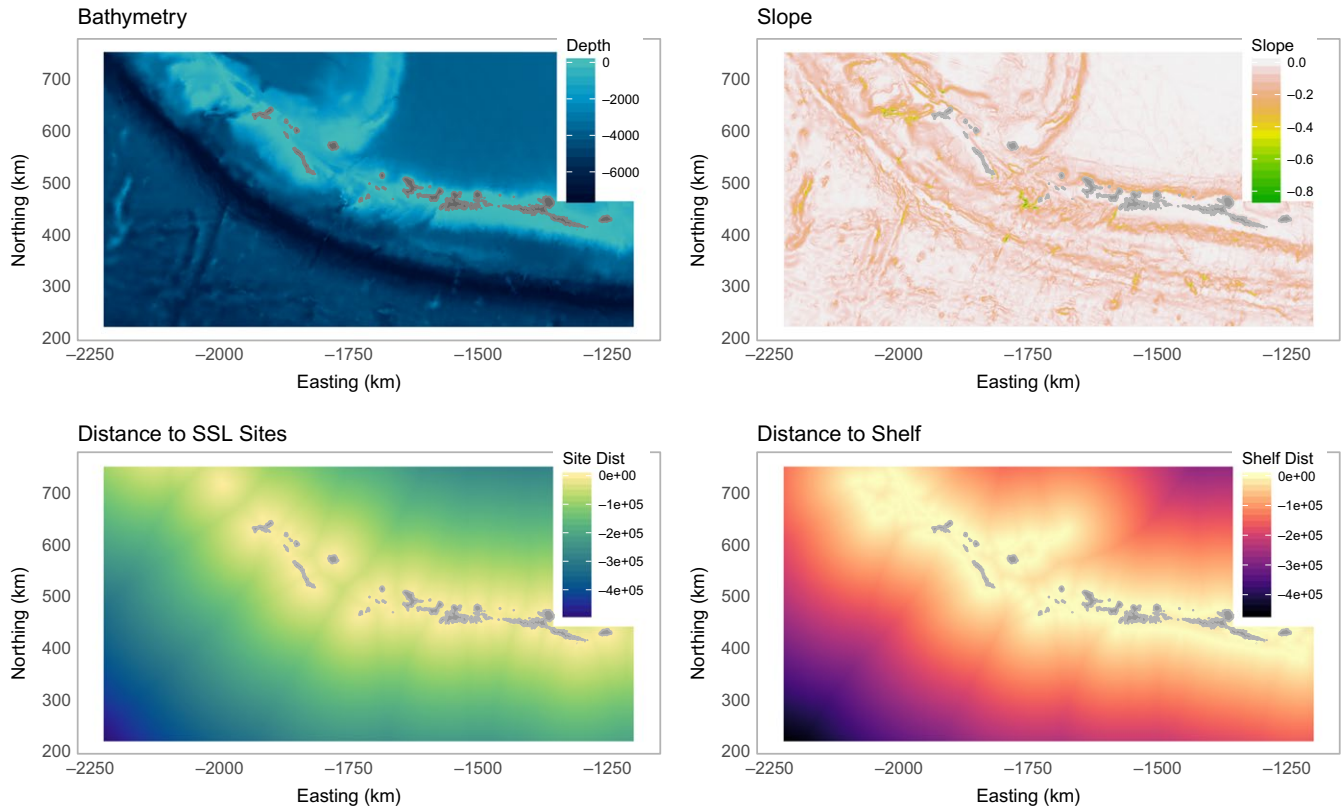


FIGURE 2 Environmental variables used as covariates in the analysis of Steller sea lion movement in the central Aleutian Islands, Alaska

2016), and distance to the continental shelf as our environmental covariates (Figure 2).

We loaded the environmental covariate rasters into `r` using the `raster` package and made two raster stack objects representing the directional (`grad.stack`) and motility covariates (`loc.stack`), respectively.

```
# Read in raster covariates and stack them together
grad.stack <- stack(bathy,slope,siteDist,shelfDist)
loc.stack<-stack(int,bathy,slope,siteDist,shelfDist)
```

We included a barrier to movement in the form of a rasterized coastline map (Figure 3) for use when calculating the transition matrix. `Water` is the raster showing where the SSL are *allowed* to move. `Land` (`1-Water`) is the raster of barrier cells.

```
# Create transition matrix with 4 possible directions
trans = transition(water, prod,4)
```

```
# identify locations of each land grid cell
holes <- which(land@data@values==1)
```

4.2 | Fit continuous-time correlated random walk movement model

We used the telemetry data to fit a quasi-continuous continuous-time correlated random walk (CTCRW) path for each animal.

```
# Fit CTCRW model
```

```
temp.fit <- crwMLE( mov.model=~1, err.model=list
(x=~A_loc_class-1), activity=~I(1-DryTime), data=data)
```

4.3 | Simulate CTCRW path for imputation

Because we do not observe the entire quasi-continuous path of the animal, we integrate over the uncertainty in the continuous path using the stacked weighted likelihood approach of Hanks and Hughes (2016). In this approach, several (M) paths are simulated from the fitted CTCRW model, and the CTMC model is fit to all M paths as if they were independent, but with each observation being assigned a weight of $1/M$. Hanks and Hughes (2016) showed that the results of the stacked weighted likelihood approach are nearly identical to those of multiple imputation, which has been the premier method of inference in the presence of missing data (Nakagawa & Freckleton, 2011; Scharf, Hooten, & Johnson, 2017). This allows one to account for uncertainty in the continuous-space path of the animal. First, we simulated multiple paths using the CTCRW fitted model and a set of regular time intervals (Step 2) and then we adjusted them by projecting the CTCRW paths that crossed land onto the nearest valid path that stayed in the water using the land raster and transition matrix that was created in Step (1) (Figure 3).

```
# simulate path and adjust for barriers
```

```
samp <- crwPostIS(simObj, fullPost = FALSE)
```

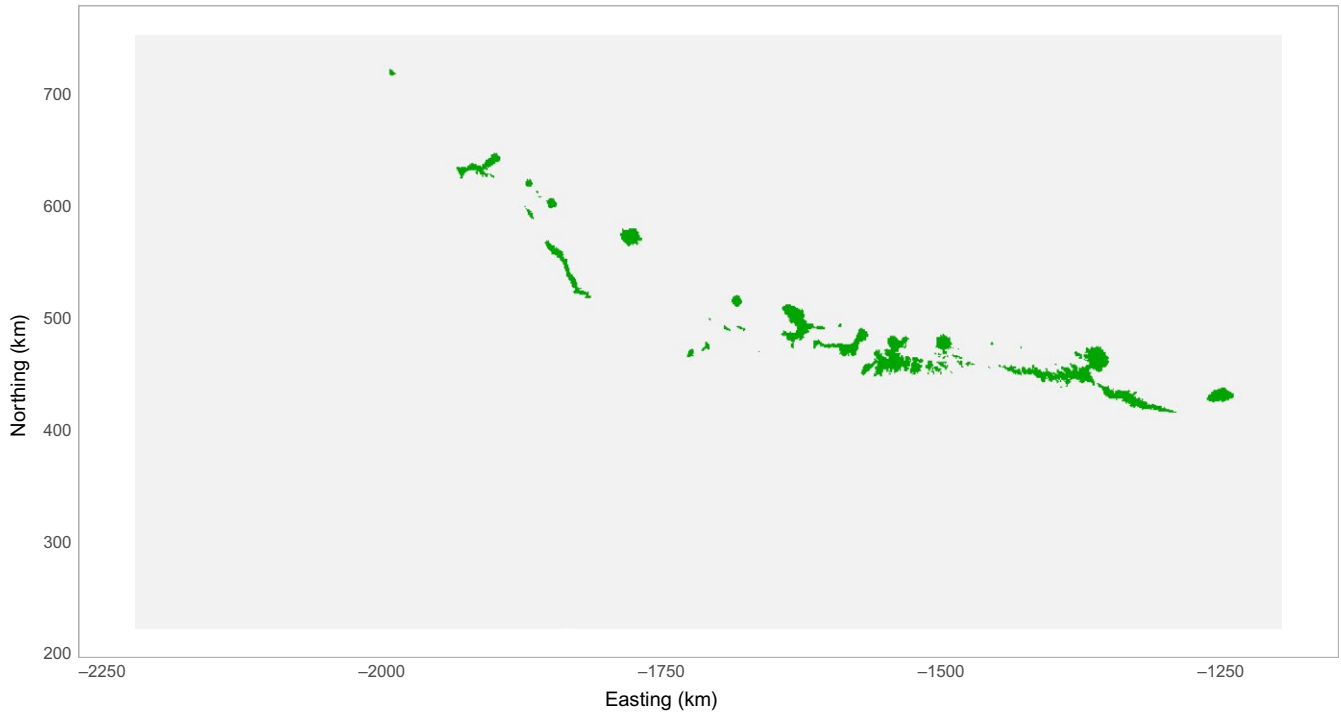


FIGURE 3 Raster grid showing barriers to movement (islands) for Steller sea lions in the central Aleutian Islands, Alaska

```
samp <- cbind(samp[[1]][,c(1,3)],t=samp[[3]]) #pull
out xy coords and time
newpath <- fix_path(samp[,1:2],samp[,3],land,trans)
%>% data.frame(.)
```

4.4 | Fit CTMC model

For each simulated path, the discrete space path, G_1, \dots, G_T , is extracted along with cell residence times, τ_1, \dots, τ_T , using the `path2ctmc` function in `ctmcmove`. Hanks et al. (2015) showed that inference on CTMC parameters can be made by rewriting the CTMC likelihood into a form proportional to a Poisson Generalized Linear Model (GLM) likelihood. The necessary transformation of each CTMC path is facilitated through the `ctmc2glm` function. Finally, we fit the model using the standard GLM functions in R. See the full code in Appendix S1.

```
path <- list(t=newpath$time,xy=newpath[,1:2])
ctmc <- path2ctmc(path$xy,path$t,grad.stack,zero.
idx=holes)
glm.data <- ctmc2glm(ctmc,loc.stack,grad.stack,zero.
idx=holes)

# fit GLM
fit <- glm(z~bathy+slope+d2site+d2shelf+bathy.loc+
slope.loc+ d2site.loc+d2shelf.loc,family="poisson",
offset=log(tau), data=glm.data)
```

Gradient-based drivers of movement explain how directional bias in animal movement rates are related to the environment (our

`grad.stack` object). A significantly negative value for bathymetry, for example, would suggest that animals move towards deeper water. Location-based drivers of movement show how speed of movement is affected by environmental conditions (`loc.stack`). For example, a significantly negative coefficient value for `bathy.loc`, would suggest that the animal moves more slowly in deeper waters (Figure 4).

4.5 | Calculate UD from CTMC output

The coefficient estimates from the GLM (Table 1) explain directional bias in the movement patterns (`grad.stack` coefficients) and how absolute animal movement rates are related to the environment (`loc.stack` coefficients). These coefficients can be used to get a rate matrix (R) for the entire raster grid. The elements of this rate matrix are the estimated CTMC transition rates λ_{ij} . The `get.UD` function calculates the limiting distribution of the Markov Chain using the rate matrix (R). The limiting distribution is an estimate of the proportion of time the animal spends in each cell and is consequently an estimate of the UD.

```
# Rate matrix & stationary distribution
R <- get.rate.matrix(fit, loc.stack, grad.stack,
zero.idx=holes)
pi <- get.UD(R)
```

When considering critical habitat designation or species management, it may be important to understand the space use of a population of animals, rather than knowing that of one individual. To look at the

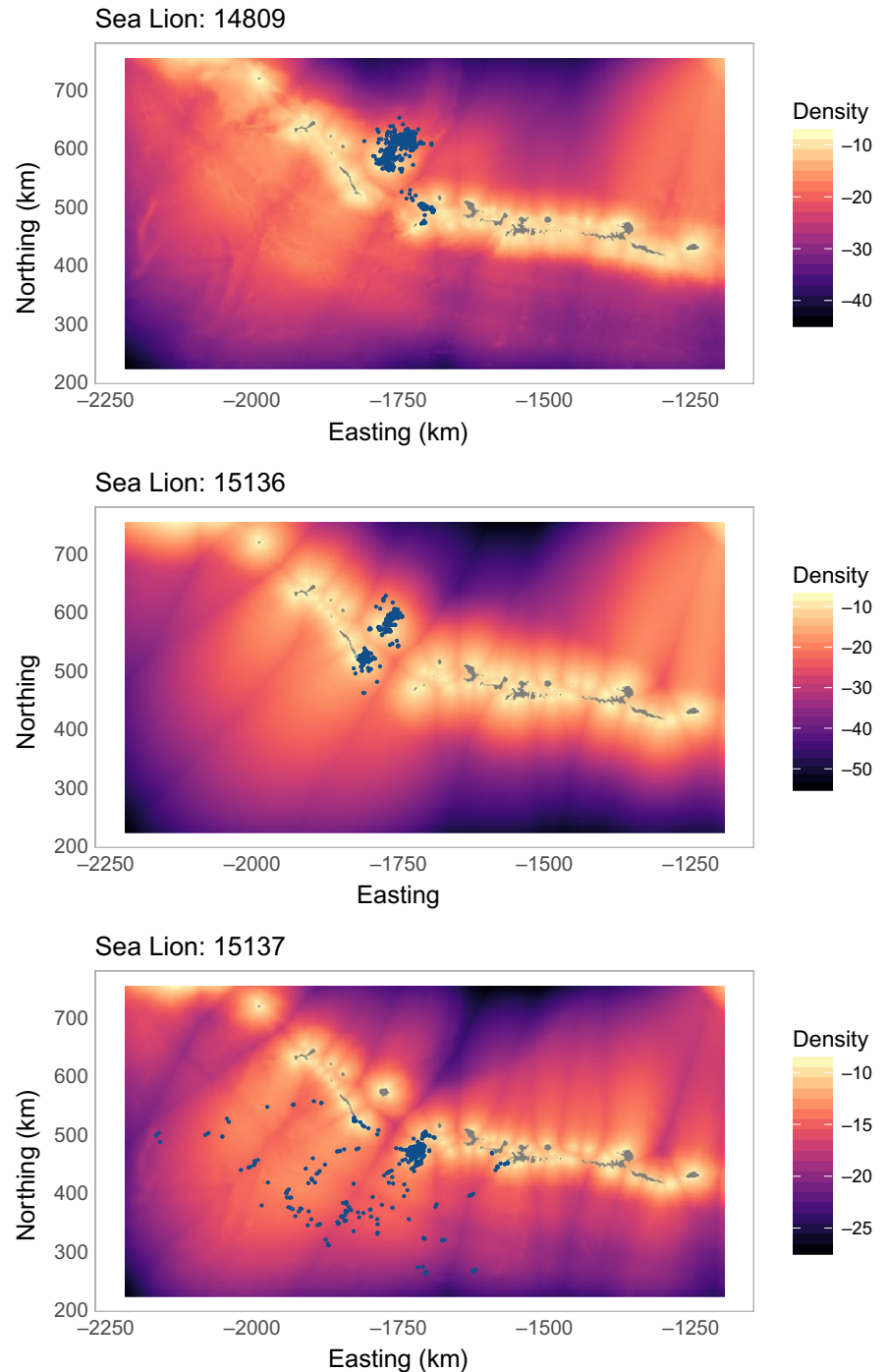


FIGURE 4 Utilization densities for Steller sea lions in the central Aleutian Islands, Alaska. Blue points are the telemetry locations used in the movement model for each sea lion

space use of all three SSLs together, we combined the individual UD rasters (Figure 4) into one 'population-level' UD (Figure 5).

```
allUD <- mosaic(ud15136, ud15137, ud14809, fun=sum)
```

Calculating individual UDs before combining them allows for individual variation in habitat preferences to influence the combined UD. This is ideal for species with high levels of individual variation in movement patterns (e.g., SSL and harbour seals). If the study species does not have high individual variation, or if a general population-mean UD is desired, then the `glm.data` for individuals could be combined before fitting the GLM.

This would result in the calculation of one UD that estimates the average space use for the population. The method can be applied to as many individuals as necessary. Some demonstration code has been added to the appendix for calculating cellwise standard errors of the estimated UD; however, this is computationally expensive for large study areas.

5 | CONCLUSIONS AND FUTURE DIRECTIONS

This work demonstrates a method to calculate a UD using the limiting distribution of a CTMC. The resulting UD avoids barriers to movement,

	SSL: 14809	SSL: 15137	SSL: 15136
Intercept	-0.23 (SE) 0.01	0.07 (SE) 0.009	-0.31 (SE) 0.02
Bathymetry	-0.51 (SE) 0.22	-0.16 (SE) 0.05	0.05 (SE) 0.14
Slope	1436 (SE) 583	-2.13 (SE) 141.0	525.9 (SE) 277.2
Site Dist.	0.09 (SE) 0.01	0.092 (SE) 0.01	0.16 (SE) 0.02
Shelf Dist.	0.04 (SE) 0.01	-0.02 (SE) 0.01	-0.02 (SE) 0.02
Bathy.loc	-2.66 e⁻⁴ (SE) 3.35 e⁻⁵	-3.22 e⁻⁵ (SE) 3.92 e⁻⁶	-4.88 e⁻⁵ (SE) 2.45 e⁻⁵
Slope.loc	-1.02 (SE) 0.22	-0.26 (SE) 0.05	-0.17 (SE) 0.11
siteDist.Loc	2.49 e⁻⁶ (SE) 3.46 e⁻⁷	3.91 e⁻⁶ (SE) 7.50 e⁻⁷	1.12 e⁻⁵ (SE) 1.46 e⁻⁶
shelfDist.Loc	-1.33 e⁻⁵ (SE) 1.45 e⁻⁶	-4.54 e⁻⁶ (SE) 8.28 e⁻⁷	-1.42 e⁻⁵ (SE) 2.47 e⁻⁶

Bold font indicates significance.

TABLE 1 Coefficient estimates from GLM looking at the effect of environmental variables on Steller sea lion (SSL) movement

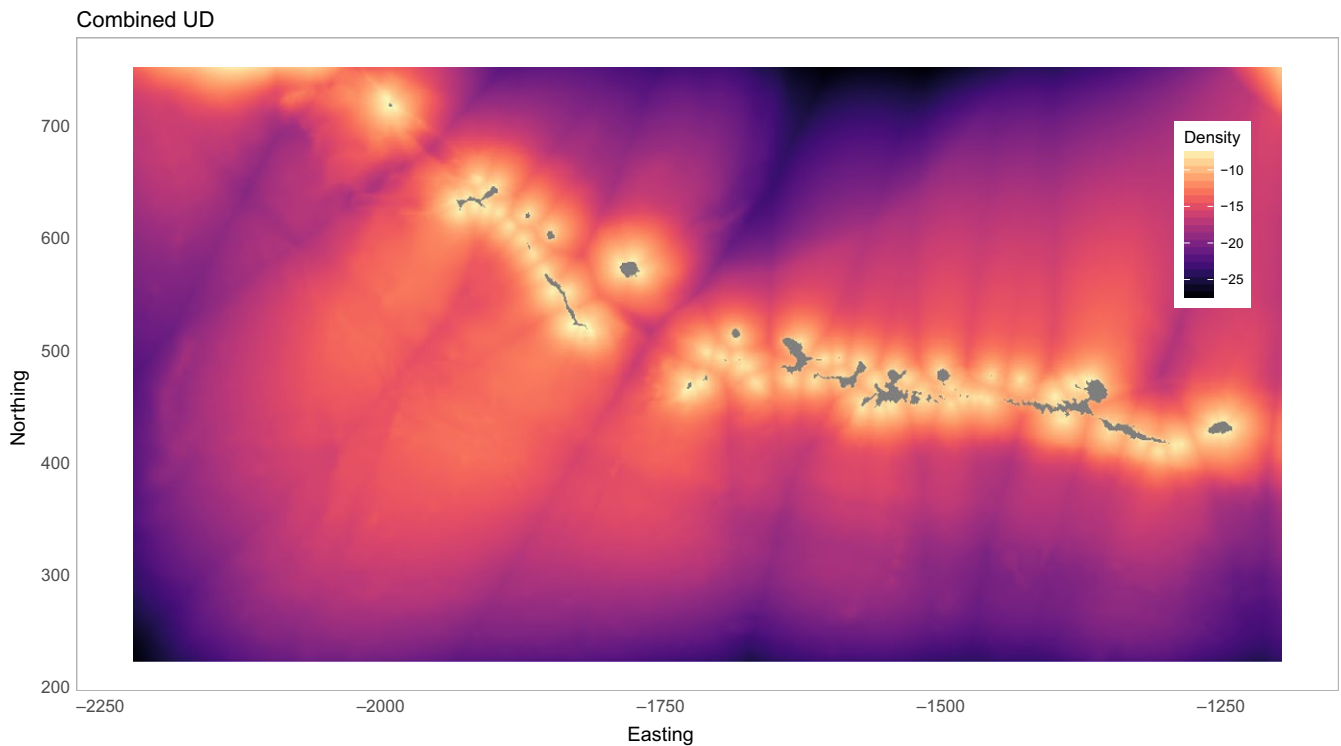


FIGURE 5 Combined UD for all three Steller sea lions in the central Aleutian Islands, Alaska

estimates use over the entire area of interest, accounts for the influence of covariates and movement on space use, and is not sensitive to initial conditions (release effect) or short observation periods.

Avoiding barriers in the calculation of a UD is a large step forward in the analysis of animal space use. Because we have a CTMC moving through discrete “states” (grid cells) we need a transition probability between each state. When we know where the barriers are located (e.g., islands on a map) we can set the probability of transition into the barrier cells equal to zero, preventing movement into those cells and excluding them completely from the calculation of the UD. Traditionally, barriers to movement were removed post-hoc after a home range or UD was calculated. Our method avoids this and allows for a more accurate representation of space use and home range size.

The `fix_path` function moves any predicted location estimates from the `crawl` model off land; however, some of the islands in this region are very small or skinny. The small size resulted in consecutive locations occurring on both sides of the island and thus allowed the path to cross back and forth over these small areas. We predicted locations every 20 min through a 1 km raster grid. If it is important to keep the path completely off of land, then use a raster resolution and prediction interval that reflects the size and shape of the barriers to be avoided.

Recent studies (Bevanda, Fronhofer, Heurich, Müller, & Reineking, 2015) have shown that landscape configuration has a strong effect on the size of individual home ranges. By incorporating environmental covariates into our model, we were able to account for the individual’s response to the landscape when estimating the

UD. The transition rate of the CTMC process to each neighbouring cell (available resources) contains information that defines preferential use of the resources in each cell and therefore provides information about how animals are using the available (or potentially available) habitat. Consequently, this method of calculating a UD is more similar to resource selection or mechanistic home range modelling (Moorcroft, 2012; Moorcroft, Lewis, & Crabtree, 2006) than to statistical UD calculations like kernel density estimation. However, this model is essentially using the movement model to make predictions at unvisited locations, therefore, researchers should be warned that the usual cautions concerning prediction beyond the data still apply. As with any analysis, our ability to predict an animal's UD hinges on the assumption that our observations are a representative sample. Particular care should be taken with telemetry data from animals with seasonal changes in movement behaviour. For example, the UD estimate resulting from telemetry data collected from a migratory animal only during winter months is an estimate of space use during winter months, and not throughout the entire year. Similarly, if animal movement behaviour is highly heterogeneous, then the predictive power of the UD will increase with the number of animals tracked. In addition, attention should be paid to environmental variables in other sections of the study area. If the values of the variables are different in far reaches of the study area then the fitted UD will be an extrapolation just as in any fitted regression model or GLM.

Stellar sea lions are multiple central place foragers and may therefore use the entire study area we selected at some time during the year (Raum-Suryan, Rehberg, Pendleton, Pitcher, & Getall, 2004). In the case of animals that are true central place foragers (or those with a well-defined home range), the entire study area may not actually be used by every animal and the predicted space should be adjusted accordingly. We chose to use static variables as our environmental covariates, but any variable that can be turned into a raster grid can be used in the model. For example, if one is willing to assume known locations for central attractors (rookeries, foraging hot spots), one simply needs to use distance and/or direction to that location(s) as a covariate layer. Hanks et al. (2015) used prey kill sites as attractors for CTMC analysis of mountain lion (*Puma concolor*) movement. If the location of central attractor is unknown the covariate becomes latent, which makes model fitting more challenging, but not impossible. Future research might involve basis function formulations for covariates in that case. Hanks et al. (2015) also considers a model where two individuals interact in their movements, however, determining the limiting distribution in this case may be challenging.

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AUTHORS' CONTRIBUTIONS

D.J. and K.W. conceived the idea; D.J. and E.H. designed the methodology; K.W. acquired the data, performed the analyses, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Telemetry data were collected by NOAA Fisheries, Alaska Fisheries Science Center. The data and complete R script can be found in this git repository: <https://github.com/kenady/ctmcUD-MEE>; <https://zenodo.org/badge/102527929.svg>.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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