LOCATION ONLY AND USE-AVAILABILITY DATA

Estimating animal resource selection from telemetry data using point process models

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Summary

1. Analyses of animal resource selection functions (RSF) using data collected from relocations of individuals via remote telemetry devices have become commonplace. Increasing technological advances, however, have produced statistical challenges in analysing such highly autocorrelated data. Weighted distribution methods have been proposed for analysing RSFs with telemetry data. However, they can be computationally challenging due to an intractable normalizing constant and cannot be aggregated (i.e. collapsed) over time to make space-only inference.

2. In this study, we take a conceptually different approach to modelling animal telemetry data for making RSF inference. We consider the telemetry data to be a realization of a space–time point process. Under the point process paradigm, the times of the relocations are also considered to be random rather than fixed.

3. We show the point process models we propose are a generalization of the weighted distribution telemetry models. By generalizing the weighted model, we can access several numerical techniques for evaluating point process likelihoods that make use of common statistical software. Thus, the analysis methods can be readily implemented by animal ecologists.

4. In addition to ease of computation, the point process models can be aggregated over time by marginalizing over the temporal component of the model. This allows a full range of models to be constructed for RSF analysis at the individual movement level up to the study area level.

5. To demonstrate the analysis of telemetry data with the point process approach, we analysed a data set of telemetry locations from northern fur seals (*Callorhinus ursinus*) in the Pribilof Islands, Alaska. Both a space–time and an aggregated space-only model were fitted. At the individual level, the space–time analysis showed little selection relative to the habitat covariates. However, at the study area level, the space-only model showed strong selection relative to the covariates.

Key-words: animal telemetry, point process, resource selection, space–time, weighted distribution

Introduction

Analyses of animal resource selection functions (RSF) using data collected from relocations of individuals via remote telemetry devices have become commonplace. Technological advances, however, have produced statisti-cal challenges in analysing such highly autocorrelated data. There have been several recent proposals for making statistical inference for RSFs from autocorrelated data. Most of these proposals have been variations of the weighted distribution (Patil 2002) approach (McDonald, Manly & Raley 1990; Lele & Keim 2006; Christ, Ver Hoef & Zimmerman 2008; Johnson *et al.* 2008; Forester, Im & Rathouz 2009). However, see Hooten *et al.* (2010) and Hanks *et al.* (2011) for alternatives to the traditional

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weighted distribution. Johnson *et al.* (2008) illustrates that the weighted distribution approach generalizes the notion of resource selection, typically defined as habitat use relative to the proportion of habitat available, by considering observed spatial locations as 'habitat' with availability governed by a movement model and the previous location of the animal. See Aarts, Fieberg & Matthiopoulos (2013) for additional exploration of the notion of availability in RSF studies. The weighted distribution approach makes inference on selection by modelling animal use as a function of a movement model and an RSF. There are three drawbacks to the weighted distribution approach, however. First, these methods can be computationally challenging due to an intractable normalizing constant. Second, there is a dearth of software available to animal ecologists for fitting these models. Finally, selection can only be inferred at the level of individual movement. The weighted distribution models are designed to model selection of the animal's next location given the current location. There is no straightforward way to aggregate over time and model selection relative to the entire study area while simultaneously accounting for temporal autocorrelation. This may be desirable as often location times are of no biological interest because they are a function of the sampling rate programmed into the telemetry device by the researcher. Throughout the remainder of the paper, we will refer to aggregation over time to mean ignoring the times of observation and modelling only the spatial location of the points.

Spatial point processes have recently been proposed for general analysis of presence–absence data (Warton & Shepherd 2010; Aarts *et al.* 2012). Warton & Shepherd (2010) proposed the spatial Poisson process as a solution to the 'pseudo-absence problem' that also appears in resource selection studies. The pseudo-absence problem arises due to the fact that one can often determine which spatial locations an animal has used, but it may be impossible to know which locations were *available* for the animal to use and were passed over for the selected locations. Early resource selection methods recognized this fact and used a researcher-selected sample of locations (the *availability sample*) to compare with known used locations (see chapter 5 of Manly *et al.* 2002). Controversy concerning the interpretation of the estimated parameters ensued due to the fact that inference was based on how the researcher and animal each selected their locations (Keating & Cherry 2004; Johnson *et al.* 2006; Beyer *et al.* 2010). Warton & Shepherd (2010) and Aarts *et al.* (2012) illustrated, however, that availability samples could be interpreted as quadrature points for approximating integrals within RSF likelihoods. Therefore, there is no case–control interpretation for the RSF with respect to use and availability, and we are free to select our availability points deterministically to best approximate the point process likelihood. While the point process likelihood presented by Warton & Shepherd (2010) and Aarts *et al.* (2012) eliminates the availability

sampling problem for analysis of resource selection based on a landscape snapshot of use, telemetry data can contain substantial temporal autocorrelation that is not accounted for in spatial point process models previously used. Therefore, we propose the use of *space–time* point process models to account for this high autocorrelation.

By using space–time point process models, we take a conceptually different approach to analysing animal telemetry data for making RSF inference. Instead of considering the locations to be essentially a bivariate time series, as is the case with most movement-based weighted distribution models, we consider the telemetry data to be a realization of a space–time point process. The space–time point process models event occurrences (e.g. animal locations) in three dimensions: latitude, longitude and time. Under the space–time point process paradigm, the times of the relocations are also considered to be random rather than fixed. We view this as a more realistic model as there is often a random component to when telemetry locations are received. Even when devices are programed to record (and transmit) locations at specified times, there are usually some locations that will not be received by chance. These random components may be due to hypothesized sources such as animal state (e.g. sleeping) or habitat occupied (e.g. dense forest); however, this information is often not known to the researcher, thus a random process model of some kind is appropriate. Another benefit of using space–time models for telemetry data is that there is a theoretical basis for aggregating data over time to examine study area level selection. In fact, we will show that space–time point process models are a generalization of the weighted distribution models that Johnson *et al.* (2008) propose. Thus, even starting with a different motivation, we end up back at essentially the same place. However, by adding models for the arrival of location times, we can overcome the three main drawbacks of the weighted distribution RSF telemetry models: computational burden, lack of available software, and inability to aggregate over time.

We begin our discourse with a review of the weighted distribution approach and transition to development of space–time point process models and demonstrate that by modelling random times of location, we obtain a space–time point process model from the weighted distribution model. Following this, using the marginal intensity of the locations in a space–time point process, we will develop some methods for mitigating temporal dependence in locations when using space-only Poisson process models for RSF inference (Warton & Shepherd 2010; Aarts *et al.* 2012). For both versions we provide numerical approximations that allow model fitting with standard or readily available statistical software. Finally, we demonstrate space–time and space-only RSF inference by performing each analysis on a data set of northern fur seal (*Callorhinus ursinus*) telemetry locations in the Bering Sea off the coast of Alaska. In the fur seal analysis, we illustrate that the basic models developed earlier in the paper can be

readily extended to accommodate more complex movement such as central place foraging.

Materials and methods

WEIGHTED DISTRIBUTION MODELS

The general form of a weighted distribution model for RSF inference is defined by the conditional distribution

$$g_u(\mathbf{s}, t | \boldsymbol{\theta}, \mathcal{H}_t) = \frac{w(\mathbf{s}, t; \boldsymbol{\theta}_w) g_a(\mathbf{s}, t | \boldsymbol{\theta}_a, \mathcal{H}_t)}{\int_{\mathcal{A}} w(\mathbf{u}, t; \boldsymbol{\theta}_w, \mathcal{H}_t) g_a(\mathbf{u}, t | \boldsymbol{\theta}_a, \mathcal{H}_t) \, d\mathbf{u}} \qquad \text{eqn 1}$$
$$= K_t^{-1} w(\mathbf{s}, t; \boldsymbol{\theta}_w) g_a(\mathbf{s}, t | \boldsymbol{\theta}_a, \mathcal{H}_t),$$

where g_u is the probability density of animal location (use distribution or UD) at time t, w is the RSF, g_a is the availability window based on the history, $\mathcal{H}_t$, of locations up to time t, $\mathcal{A}$ is the study area, and $\boldsymbol{\theta} = (\boldsymbol{\theta}_w, \boldsymbol{\theta}_a)$ is a vector of parameters.

Given a set of telemetry locations, $\mathbf{s}_1, ..., \mathbf{s}_n$, recorded at times $t_1, ..., t_n$, the log-likelihood function to be maximized is

$$L(\boldsymbol{\theta}) = \sum_{i=1}^{n} \log\{w(\mathbf{s}_i, t_i | \boldsymbol{\theta}_w)\} + \log\{g_a(\mathbf{s}_i, t_i | \mathcal{H}_{t_i}, \boldsymbol{\theta}_a)\} - \log\{K_{t_i}\}.$$
$$\text{eqn 2}$$

To be more specific, one can take, say, the standard exponential RSF, $w(\mathbf{s}_i, t_i | \mathcal{H}_{t_i}) = \exp\{\mathbf{x}_i'\boldsymbol{\alpha}\}$, and a Brownian motion motivated availability window, $g_a(\mathbf{s}_i, t_i | \mathcal{H}_{t_i}) = \exp\{-\beta d_i^2 \Delta_i^{-1}/2\}$, where $\mathbf{x}_i$ is a vector of environmental variables measurable at location $\mathbf{s}_i$ at time t_i, $\boldsymbol{\alpha}$ is a vector of resource selection coefficients, β controls the spread of the availability window, d_i is the distance from $\mathbf{s}_{i-1}$ to $\mathbf{s}_i$, and $\Delta_i = t_i - t_{i-1}$. Substituting these specifics into (2) gives the log-likelihood for a basic RSF model for telemetry data,

$$L(\boldsymbol{\theta}) = \sum_{i=1}^{n} \mathbf{x}_i'\boldsymbol{\alpha} - \beta \, d_i^2 \Delta_i^{-1} - \log K_{t_i}. \qquad \text{eqn 3}$$

Equation (3) is deceptively simple-looking except for the normalizing term that must be calculated for each observed location,

$$\log K_{t_i} = \log \int_{\mathcal{A}} \exp\{\mathbf{x}(\mathbf{u})'\boldsymbol{\alpha} - \beta d_i^2(\mathbf{u})\Delta_i^{-1}\}, \qquad \text{eqn 4}$$

where $d_i(\mathbf{u})$ is the distance between $\mathbf{u}$ and $\mathbf{s}_{i-1}$ for an location $\mathbf{u}$ in $\mathcal{A}$. One can see that models of this sort become very computationally demanding with custom coding necessary for parameter estimation. Thus, these models are generally inaccessible to a great majority of animal ecologists.

Some approximations have been proposed that aim to reduce the computational burden for weighted distribution RSF models. Initially, McCracken, Manly & Vander Heyden (1998) proposed a design-based sampling estimate of K_t for each observation time. Johnson *et al.* (2008) extended the design-based approximation with a more general importance sampling-based estimator. Even with this type of approximation, these models still remained out of reach for general practice due to lack of available software for implementing the methods.

SPACE−TIME POINT PROCESS MODELS

Space–time point processes have been used to model random events such as earthquakes (Ogata 1998), wildfires (Peng, Schoenberg & Woods 2005) and nesting of seabirds (Diggle, Kaimi & Abellana 2010) where the data collected are the locations and times, $(\mathbf{s}, t)$, of these events. Schoenberg, Brillinger & Guttorp (2002) present a basic overview of space–time point process models and analysis. A space–time point process is defined by its conditional intensity function $\lambda(\mathbf{s}, t | \mathcal{H}_t)$ (Fishman & Snyder 1976). In general terms, the conditional intensity governs the rate of event occurrences at location $\mathbf{s}$ and time t given the history of event occurrences, $\mathcal{H}_t$, up to time t. Mathematically, the conditional intensity can be defined as the limit of the expected count of event occurrences in the cube $B_{\delta} = (\mathbf{s} + \delta\mathbf{s}) \times (t + \delta t)$ as δ tends to zero, i.e.

$$\lambda(\mathbf{s}, t | \mathcal{H}_t) = \lim_{\delta \to 0} E[N(B_{\delta}) | \mathcal{H}_t]/|B_{\delta}|, \qquad \text{eqn 5}$$

where $N(B_{\delta})$ is the number of events occurring in B_{δ}.

The conditional intensity function is often broken into a product of separate intensity functions representing different components, say, purely spatial, purely temporal and space–time interactions (Schoenberg, Brillinger & Guttorp 2002). Using this approach, we can define a space–time point process model for telemetry locations.

$$\lambda(\mathbf{s}, t | \mathcal{H}_t) = \lambda_0(t) w(\mathbf{s}) g(\mathbf{s}, t | \mathcal{H}_t) \qquad \text{eqn 6}$$

where $\lambda_0(t)$ represents the baseline rate of telemetry location acquisition at time t, $w(\mathbf{s})$ represents a purely spatial component to location and $g(\mathbf{s}, t | \mathcal{H}_t)$ represents an interaction between spatial and temporal aspects of the model. It is not coincidence that w and g were chosen for the notation. If a space–time point process model with conditional intensity (6) is adopted and we condition on the observation times $t_1, ..., t_n$, we obtain (1) as the conditional distribution of $\mathbf{s}_1, ..., \mathbf{s}_n$ given the observation times (Diggle, Kaimi & Abellana 2010). Thus, (6) represents the unconditional distribution of observed locations *and* times.

SPACE−TIME POINT PROCESS INFERENCE

The general likelihood for a space–time point process over spatial area $\mathcal{A}$ and time interval $(0, T]$ is given by

$$L(\boldsymbol{\theta}) = \sum_{i=1}^{n} \log \lambda(\mathbf{s}_i, t_i | \mathcal{H}_{t_i}) - \int_{\mathcal{A}} \int_0^T \lambda(\mathbf{u}, t | \mathcal{H}_t) \, dt \, d\mathbf{u}, \qquad \text{eqn 7}$$

where $(\mathbf{s}_i, t_i)$ is the observed location and time of the ith event, $\mathcal{A}$ is again the two-dimensional study area, and the period of interest is $[0, T]$ (see Schoenberg, Brillinger & Guttorp 2002 and references therein). Specifically, if we assume the Brownian availability RSF model (3), with a constant baseline intensity of locations (i.e. $\log \lambda_0(t) = \alpha_0$), we obtain the log-intensity function

$$\log \lambda(s, t | \mathcal{H}_t) = \mathbf{x}(s)'\boldsymbol{\alpha} - \beta d(\mathbf{s})^2 \Delta(t)^{-1}/2, \qquad \text{eqn 8}$$

where $d(s)$ is the distance from $\mathbf{s}$ to the last observed location prior to t, $\Delta(t)$ is the difference between t and the time of last observation, and the covariate vector $\mathbf{x}$ now contains a one such that an intercept (α_0) is estimated. From this intensity function, we subsequently obtain the likelihood

$$L(\boldsymbol{\theta}) = \sum_{i=1}^{n} \left[\{ \mathbf{x}_i' \boldsymbol{\alpha} - \beta d_i^2 \Delta_i^{-1} \} - \int_{\mathcal{A}} \int_0^{\Delta_i} e^{\mathbf{x}(\mathbf{u})' \boldsymbol{\alpha} - \beta d_i(\mathbf{u})^2 \delta^{-1}} \, \mathrm{d}\delta \, \mathrm{d}\mathbf{u} \right].$$

eqn 9

If location acquisition is not possible continuously through the deployment (e.g. due to preprogrammed telemetry device sampling schedules), the temporal integral becomes a sum over the possible times with α_0 becoming the log probability of location acquisition at any of those times. It would appear that we have traded several two-dimensional integrals for several more difficult three-dimensional integrals and created an even more computationally burdensome model. That initial impression, however, is incorrect.

In order to calculate likelihood values for estimation of spatial Poisson process models, Berman & Turner (1992) proposed a quadrature method that makes use of common statistical software for fitting Poisson family generalized linear models (GLMs). Their method can be directly extended to the space–time case by choosing m quadrature points on multiple grids in time (indexed by k) and space within time (indexed by j, k) plus the n observed locations and times to produce the numerical approximation

$$L(\boldsymbol{\theta}) \approx \sum_{j,k} q_{jk} \{ z_{jk} \log \lambda(\mathbf{s}_{jk}, t_j | \mathcal{H}_{t_j}) - \lambda(\mathbf{s}_{jk}, t_j | \mathcal{H}_{t_j}) \}, \qquad \text{eqn 10}$$

where q_{jk} is the volume of the cube surrounding the (j,k) quadrature point and $z_{jk} = 1/q_{jk}$ if the (j,k) quadrature point belongs to the set of observations and $z_{jk} = 0$ if the (j,k)th point is one of the chosen grid points. Closer inspection of (10) reveals the approximation to be proportional to a weighted Poisson likelihood function with observations z_{jk} and weights q_{jk}. Thus, if $\log \lambda(\mathbf{s}, t | \mathcal{H}_t)$ is a linear function of the parameters, any GLM fitting software that allows noninteger Poisson observations can be used for maximization. Both Warton & Shepherd (2010) and Aarts *et al.* (2012) use this method for fitting *spatial* point process models to animal presence–absence data. Recently, Simpson *et al.* (2011) proposed an alternative version making use of Poisson regression with offsets rather than weights.

After the quadrature data (i.e. z_{jk}, q_{jk}, $\mathbf{s}_{jk}$, t_j and $\mathbf{x}_{jk}$) are created, analysis of several models and/or individuals can proceed quickly due to optimized GLM fitting routines in most statistical packages [e.g. the glm() function in the open-source R statistical software (R Development Core Team 2012)]. The same quadrature data set is used for all model fitting. In our experience, even when λ is not linear in the parameters, maximization of (10) proceeds much faster than maximization of (2). The weighted distribution likelihood requires a loop over sites within each time because the log normalizing constant is needed, whereas (10) can be evaluated in one vector operation.

MITIGATING TEMPORAL DEPENDENCE IN SPACE-ONLY RSF ANALYSIS

The space–time models presented in the previous sections illustrate that temporal correlation in telemetry data can be taken into account in a computationally efficient and practical way. However, as noted by Fieberg *et al.* (2010), these models measure selection at the level of individual movement, and broad-scale trends over many individuals can be missed. Larger extent space-only point process models such as those used in Warton & Shepherd (2010) and Aarts *et al.* (2012) have the ability to combine data from many individuals over large regions to examine

selection functions. In neither of those studies, however, were the locations considered to be (or simulated to be) temporally correlated. So, the question arises of whether or not we can use some theoretical aspects of space–time models to develop practical methods to mitigate the temporal correlation when analysing telemetry data with space-only point processes. In this section, we present a proposal which can be extended as warranted depending on the biology of the species of study.

The marginal distribution for the spatial portion of a space–time point process is a complex point process model with interacting points. Moreover, the interaction term is also random. Therefore, we propose considering a space-only Poisson process approximation for analysis of the spatial component. Following Illian *et al.* (2012), we construct a covariate to help account for interaction between points. In order to construct an appropriate covariate, we use the fact that a space–time Poisson process (i.e. $\lambda(\mathbf{s}, t | \mathcal{H}_t) = \lambda(\mathbf{s}, t)$) has a marginal space-only process with intensity function $\lambda(\mathbf{s}) = \int_0^T \lambda(\mathbf{s}, t) \mathrm{d}t$ (Illian *et al.* 2008). The marginal intensity function derived from (8) is given by

$$\begin{aligned} \lambda(\mathbf{s}) &= e^{\mathbf{x}(\mathbf{s})' \boldsymbol{\alpha}} \sum_{i=1}^{n} \int_0^{\Delta_i} e^{-\beta d_i(\mathbf{s})^2 \delta^{-1}} \, \mathrm{d}\delta \\ &= e^{\mathbf{x}(\mathbf{s})' \boldsymbol{\alpha}} \sum_{i=1}^{n} \tilde{G}_i(\mathbf{s}) \\ &= e^{\mathbf{x}(\mathbf{s})' \boldsymbol{\alpha}} G(\mathbf{s}), \end{aligned} \qquad \text{eqn 11}$$

While $\tilde{G}_i(\mathbf{s})$ has no closed form solution, we can see that it is still a kernel centred on observed location $\mathbf{s}_{i-1}$ that is essentially the average of normal kernels. Thus, the sum, $G(\mathbf{s})$, is a smooth variable kernel density function of the observed location. Thus, we can construct a covariate from an unnormalized (i.e. $\int_{\mathbf{u}} G(\mathbf{u}) \mathrm{d}\mathbf{u} = n$) variable kernel utilization distribution estimate to serve as a surrogate for point interactions in the space-only analysis. Now, in order to model data pooled over h individuals, note that a combination of Poisson processes is also a Poisson process with intensity $\lambda(\mathbf{s}) = \sum_h \lambda_h(\mathbf{s})$. Thus, assuming an identical RSF between individuals, we can obtain a pooled intensity from (11) using $\lambda(\mathbf{s}) = e^{\mathbf{x}(\mathbf{s})' \boldsymbol{\alpha}} \sum_h G_h(\mathbf{s})$, where $G_h(\mathbf{s})$ is the variable kernel density estimate for animal h.

With respect to inference, the Berman (10) or Simpson *et al.* (2011) quadrature scheme could be used for a space-only model as well. But, a simpler approach (Illian *et al.* 2012) is to use the grid defined by $\mathbf{x}(\mathbf{s}_j)$, evaluate each $G_h(\mathbf{s}_j)$ on the covariate raster grid, count the total number of points over all animals, y_j, within each cell and model y_j as a Poisson variable with log mean

$$\log \lambda_j = \mathbf{x}(\mathbf{s}_j)' \boldsymbol{\alpha} + \beta \log G^*(\mathbf{s}_j), \qquad \text{eqn 12}$$

where $G^*(\mathbf{s}) = \sum_h G_h(\mathbf{s})$ is our constructed covariate. We added the coefficient β into the linear predictor even though it is not present in $\lambda(\mathbf{s})$ above to help restore some uncertainty due to the fact that the $G^*(\mathbf{s})$ is random. Illian *et al.* (2012) also add a spatially correlated random effect, $\eta(\mathbf{s})$, to the model (12) in order to capture other latent clustering effects not captured by the constructed cluster covariate. This is something we suggest and make use of later in out fur seal analysis. With the spatial random effect, it is necessary to find software that can analyse generalized linear mixed models.

There is one small caveat in using the proposed Poisson process approximation. Selection effects are contained in the $G^*(\mathbf{s})$

estimate. Thus, $\log G^*(\mathbf{s})$ may be collinear with $\mathbf{x}(\mathbf{s})$ obscuring $\boldsymbol{\alpha}$ inference. To remove the effects of selection within the utilization distribution $G^*(\mathbf{s})$, we suggest using the residuals of $\log G^*(\mathbf{s})$ regressed on $\mathbf{x}(\mathbf{s})$. By using the residuals, the constructed covariate discounts observations close together in time, but not necessarily in space. Two observations may be near each other in space, but if there is a large time gap between them, the kernel surface will be flatter underneath them (Fig. 1e). The following section on northern fur seal selection illustrates how this method can be used.

NORTHERN FUR SEAL RESOURCE SELECTION

In order to demonstrate the proposed point process methods, we analysed data from a telemetry study of female northern fur seals in the Pribilof Islands, Alaska. In this section, our goal is to not only illustrate the methods with real data, but to show that these models are very flexible and we can easily add terms to the model to better fit the biology of our species as well as our method of data collection. Here, we present two specific space–time and space-only models, but we would like to impress upon the reader how adaptable these models can be in various situations. In the space–time model, we illustrate how we can make a dynamic model in which movement changes over the length of deployment, while the space-only analysis illustrates inference for pooled data with selection measured relative to the study area as a whole.

During summer months, female northern fur seals are central place foragers that alternate between foraging trips lasting several days and remaining at the rookery to nurse pups (Gentry 1998). The Pribilof population of fur seals has been declining c. 6–7% per year for several decades (Towell, Ream & York 2006), necessitating a better understanding of space use and habitat preference for conservation needs. We were interested in assessing resource selection at two different scales. First, using the space–time models, we examined selection at the individual movement scale. Following that analysis, we used the space-only point process models to assess selection at the scale of our study area (eastern Bering Sea continental shelf; see Fig. 1).

Fifteen adult female northern fur seals with dependent pups were instrumented at rookeries on St. Paul Island, Alaska (57·1°N, 170·3°W), in early August 2010. Each fur seal was equipped with an Mk10-F or Mk10-AF tag (Wildlife Computers, Redmond, WA, USA), which use Fastloc GPS technology to record at sea locations and have time–depth recorder capabilities. GPS locations were recorded at 15-min intervals when the animal was on the surface or on land. To facilitate instrument recovery, each female was also equipped with a VHF tag (Advanced Telemetry Systems, Isanti, MN, USA). Instruments were attached directly to the dorsal pelage using quick-set epoxy. To remove erroneous locations, GPS locations were filtered based on a maximum transit rate of 3 m/s using the algorithm described in Freitas *et al.* (2008; implemented via R package argosfilter). Finally, to remove issues related to differing deployment length between animals in a highly dynamic habitat environment, we analysed data from only the first foraging trip for each animal in this analysis so that the data could meaningfully aggregated over time. We provide some discussion later concerning data pooling in general. Locations are illustrated in Fig. 1(a).

We selected three habitat covariates in our study area for which to asses resource selection (Fig. 1). The first is average net primary productivity (NPP) for August 2010 (Behrenfeld & Falkowski 1997; data available from http://www.science.oregon state.edu/ocean.productivity/). Second, we obtained average sea surface temperature (SST) for the month of August 2010 (available from http://oceancolor.gsfc.nasa.gov/). Finally, we included walleye pollock (*Theragra chalcogramma*) number caught per unit effort (CPUE) data from groundfish trawl surveys conducted by the National Marine Fisheries Service, NOAA (data available at http://www.afsc.noaa.gov/RACE/groundfish/survey_data/). Walleye pollock are a primary prey species for northern fur seals. In order to make all the covariates compatible, all habitat data were projected to the same 9 km resolution grid (Fig. 1) using the R statistical software with the sp, rgdal, gstat and raster packages. Although this is not strictly necessary, this step greatly eases construction of the quadrature data set.

In order to infer habitat importance at the scale of individual movement, we fitted the space–time point process model (7) separately to each animal using the space–time version of the Berman–Turner method (10). The conditional intensity model fitted was

$$\log \lambda(\mathbf{s}, t | \mathcal{H}_t) = \mathbf{x}(\mathbf{s})'\boldsymbol{\alpha} + \beta_1 \kappa_B(\mathbf{s}, t) + \beta_2 t + \beta_3 d_r(\mathbf{s}) + \beta_4 d_r(\mathbf{s})t,$$

eqn 13

where $\mathbf{x}(\mathbf{s})$ is the vector of spatial covariates and location $\mathbf{s}$, $\kappa_B(\mathbf{s}, t) = -d(\mathbf{s})^2\Delta(t)^{-1}/2$ is the Brownian availability window, $\Delta(t)$ is the time gap from t to the last observation, $d(\mathbf{s})$ is the distance from $\mathbf{s}$ to the last observed location and $d_r(\mathbf{s})$ is the distance from the rookery. In addition to the selection and Brownian motion portions of the model, we added a 'distance from home' portion, via $d_r(\mathbf{s})$, which is allowed to change through time with an interaction term. This was added because female northern fur seals are central place foragers that leave the rookery and return to feed their pups at the end of their trips. Thus, the animal moves away (i.e. repelled) from the rookery at the beginning of the trip, but, is then attracted to the rookery towards the end of the trip. A simple Brownian availability would be insufficient to capture this aspect of their movement (Hanks *et al.* 2011).

In order to specify space–time quadrature points $(\mathbf{s}_{jk}, t_j)$ and associated weights q_{jk} in (10), we used the following method. First, for the temporal portion, observed times were augmented with a grid of hourly time points. For each of the time points, t_j an interval length $l_j = (t_{j+1} - t_{j-1})/2$ was calculated. For the spatial component, we first calculated the empirical velocities for each of the observed locations. Following this, we determined the maximum velocity attained by the animal in each of the intervals defined by the 0–20, 20–40, 40–60, 60–80 and 80–100 percentiles of the observed time gaps in the location record. This was done to keep the range of spatial grid points for time t_j within reason if there is a big time gap from the last known location. Animals can attain large velocities for short distances and if just the overall maximum velocity was used to define the jth grid, for large time gaps, it would be unreasonably large. Next, for each t_j, we calculated Δ_j, the difference between t_j and the time of the last observed location. Then, Δ_j was classified according to the time gap percentile ranges, and the maximum empirical velocity v_j was chosen for that range. Finally, we selected the smallest 4 km resolution spatial grid $\mathbf{s}_{jk}$ centred on the last observed location which contained the circle with radius equal to $v_j\Delta_j$. Going beyond this spatial range is unlikely to benefit the numerical approximation because the conditional intensity surface is c. 0 due to the Brownian availability window. We chose 4 km resolution for the quadrature grids to try and capture some of the habitat variation for small
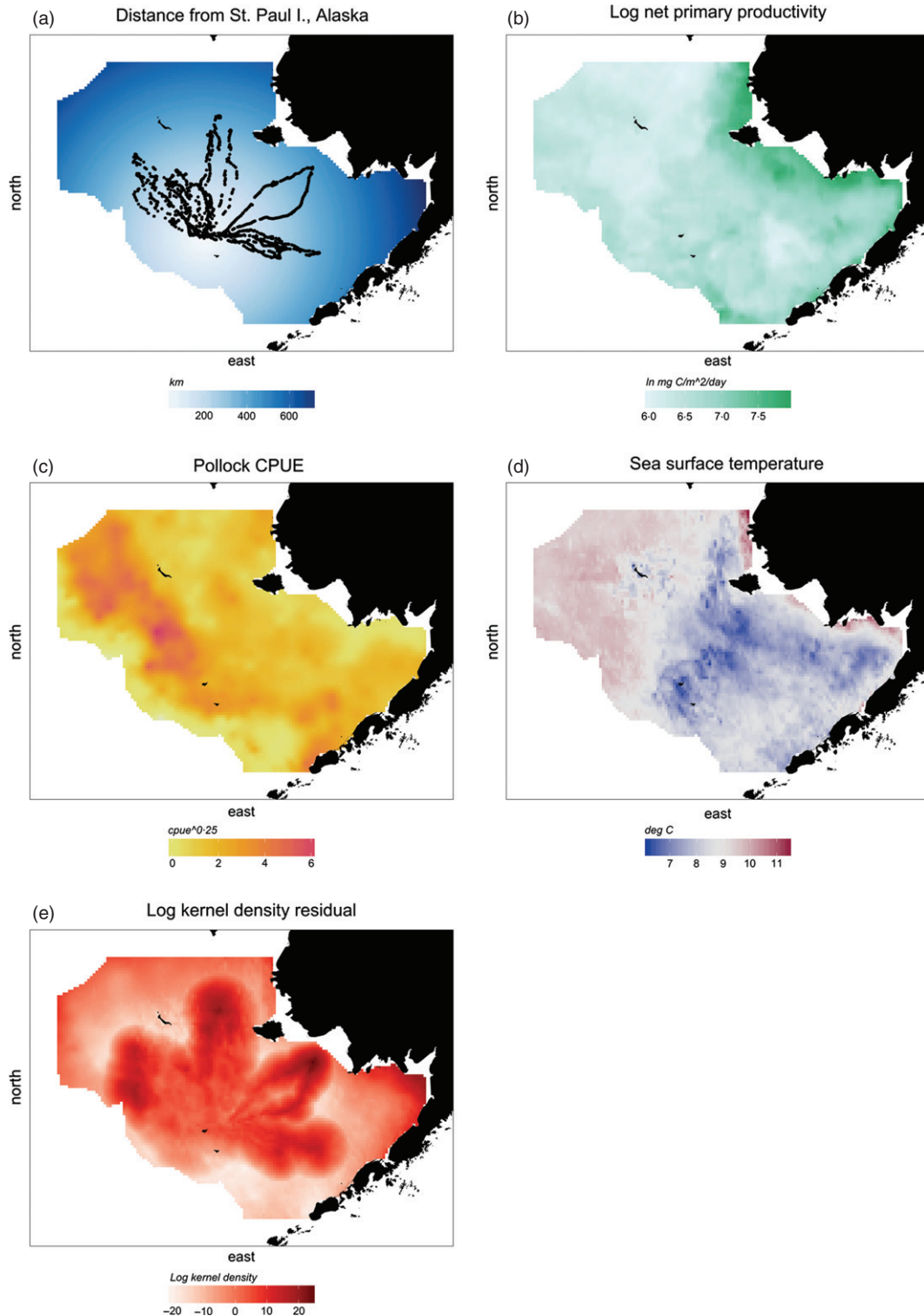
Fig. 1. Variables for resource selection analysis in lactating female northern fur seals. The study area depicted in each subplot is the eastern Bering Sea shelf, off the coast of Alaska. Individual locations are shown in subplot (a). The distance variable (a) was used for modelling movement away and back to the rookery in the individual space–time analysis via a time × distance interaction. In the space-only analysis, distance was considered to be inversely related to availability. The other habitat variables, (b) net primary productivity, (c) walleye pollock CPUE and (d) sea surface temperature, were investigated for selectivity during foraging trips.

scale movements near habitat grid (9 km resolution) boundaries, as well as, the shape of the Brownian availability. Because our spatial coordinates are in metres, each grid cell centred on $\mathbf{s}_{jk}$ has

area $a_{jk} = 4000^2$. If t_j corresponds to one of the observed times, then there is one additional $\mathbf{s}_{jk}$ associated with the observed location. If that was the case, then $a_{jk} = 4000^2/2$ for both the

observed location and the grid cell containing the observed location. Now for each quadrature point $(\mathbf{s}_{jk}, t_j)$, we have the weight $q_{jk} = l_j a_{jk}$ which is equal to the volume of the cube containing $(\mathbf{s}_{jk}, t_j)$. For each quadrature point $(\mathbf{s}_{jk}, t_j)$, we evaluated the quadrature covariates $\mathbf{x}(\mathbf{s}_{jk})$, $\kappa_B(\mathbf{s}_{jk}, t_j)$, $d(\mathbf{s}_{jk})$, and $d_r(\mathbf{s}_{jk})$. For inference, we used the native R function glm() with the weights argument equal to the vector of q_{jk}.

In contrast to selection with respect to individual movement, we also analysed the fur seal selection with respect to the study area as a whole by using a space-only point process model. To mitigate the effects of serial correlation of animal locations, we used the Brownian motion–derived space-only model (11) as inspiration but augmented it to make it possible to estimate the parameters with readily available software. First, the space-only intensity model fitted to the data set as a whole was

$$\log \lambda(\mathbf{s}) = \mathbf{x}(\mathbf{s})'\boldsymbol{\alpha} + \beta_1 \log G^*(\mathbf{s}) + \beta_2 d_r(\mathbf{s}) + \eta(\mathbf{s}), \qquad \text{eqn 14}$$

where $G^*(\mathbf{s}) = \sum_{h=1}^{15} G_h(\mathbf{s})$, $G_h(\mathbf{s})$ is a variable kernel density map constructed from all locations of the animal h, and $\eta(\mathbf{s})$ is a spatially correlated normal random effect. To obtain the individual kernel density maps, $G_h(\mathbf{s})$, we placed a two-dimensional independent normal kernel with bandwidth $b = 5510\sqrt{t_{i+1} - t_i}$ over each observed location $\mathbf{s}_i$. Each kernel was evaluated on each of the 9 km centroids of the habitat grid, $\mathbf{s}$ then summed at each $\mathbf{s}$ to obtain individual kernel density maps, $G_h(\mathbf{s})$. The chosen bandwidth corresponds to a Brownian availability window with 95% of the mass within 10·8 km of center for time gaps of 1 h. That is the displacement that would be observed if a seal averaged a speed of 3 m s^{-1} for 1 h, the often assumed maximum sustained speed in pinniped telemetry studies. We then calculated the constructed covariate $G^*(\mathbf{s}) = \sum_{h=1}^{15} G_h(\mathbf{s})$. The log $G^*(\mathbf{s})$ surface was regressed against the habitat covariates to obtain the residuals for use in the space-only analysis. Finally, we used an intrinsic conditionally autoregressive (ICAR or CAR) spatial model with rook neighbourhood structure for $\eta(\mathbf{s})$ (Banerjee, Carlin & Gelfand 2004).

We take the same inferential approach as Illian *et al.* (2012) for estimating model parameters in the space-only model by using the Poisson count approximation (12) and the R package INLA to summarize the Bayesian posterior distribution of the parameters. Due to the inclusion of the spatial random effect $\eta(\mathbf{s})$, maximum likelihood inference is exceedingly difficult and we prefer a Bayesian approach. It is also possible to perform this inference via Markov Chain Monte Carlo (MCMC). The INLA package uses numerical integration to perform the necessary calculations and is virtually no more difficult than fitting a standard Poisson GLM model. We used all default vague prior settings in INLA for this analysis.

Results

The estimated selection coefficients and 95% confidence intervals for the space–time analysis are presented in Fig. 2 for each female. There appears to be no striking pattern among all of the individuals with estimates of selection coefficients on both sides of zero for every covariate. There does appear to be one outlying individual that seemed to select high NPP locations. However, it is uncertain due to the large confidence interval. We calcu-

lated population average estimates for each of the coefficients using averages weighted by the estimated variances. These are (SE estimates in parentheses) NPP: -0.51 (0·20), SST: -0.15 (0·12) and Pollock field: -0.13 (0·12). Thus, there seems to be evidence for negative selection of high NPP at the population level; however, there does not seem to be evidence for any population-level selection for SST and pollock CPUE.

Table 1 gives the posterior median estimates for the space-only study area scale selection analysis. There is significant negative selection for both SST and NPP and positive selection for pollock CPUE. Figure 3(a) illustrates the posterior median fitted values for the portion of the model related to known habitat variables ($\log w(\mathbf{s}) = \mathbf{x}(\mathbf{s})'\boldsymbol{\alpha}$) that is > 0. These are preferential locations relative to the availability surface, $\log\ g(\mathbf{s}) = \beta_1 \log G(\mathbf{s}) + \beta_2 d_r(\mathbf{s}) + \eta(\mathbf{s})$. Note, we have placed $\eta(\mathbf{s})$ in the availability portion of the model, but it is possible that it also contains selection effects of latent habitat variables for which we are unaware. That being the case, we prefer to place this term in $g(\mathbf{s})$ and denote $w(\mathbf{s})$ to be the RSF of known habitat variables. Figure 3(b) shows the posterior median availability surface.

Discussion

In this paper, we proposed practical methods for making RSF inference at two different scales while accounting for serial correlation in telemetry locations. Previous weighted distribution methods, while well motivated, have some drawbacks that we have addressed with the use of point process modelling methods. Although, developed from a different paradigm, the space–time point process model is simply a generalization of the weighted distribution model of Johnson *et al.* (2008) created by modelling times of observations in addition to the locations themselves. Using a data set from a northern fur seal telemetry study, we illustrated that this method can be readily used on multiple animals due to the computational savings and available software. Code written in R to build the quadrature data for all animals took <10 min to run and each GLM model completed the fitting process in under a minute.

The first issue with utilizing weighted distribution models for selection inference is that they are computationally expensive, currently requiring custom likelihood coding and optimization. By using space–time point process models with the Berman quadrature method, only quadrature points and weights need to be calculated using a custom method. Once these are determined, however, any number of models with different covariate combinations can be quickly analysed with standard GLM software. In fact, models that contain nonparametric functions of the covariates can be fit with the R package mgcv. We investigated such models for the fur seal data, but determined that those nonparametric functions were unnecessary. And, we determined this very quickly and dismissed those models using the built-in cross-validation selection proce-
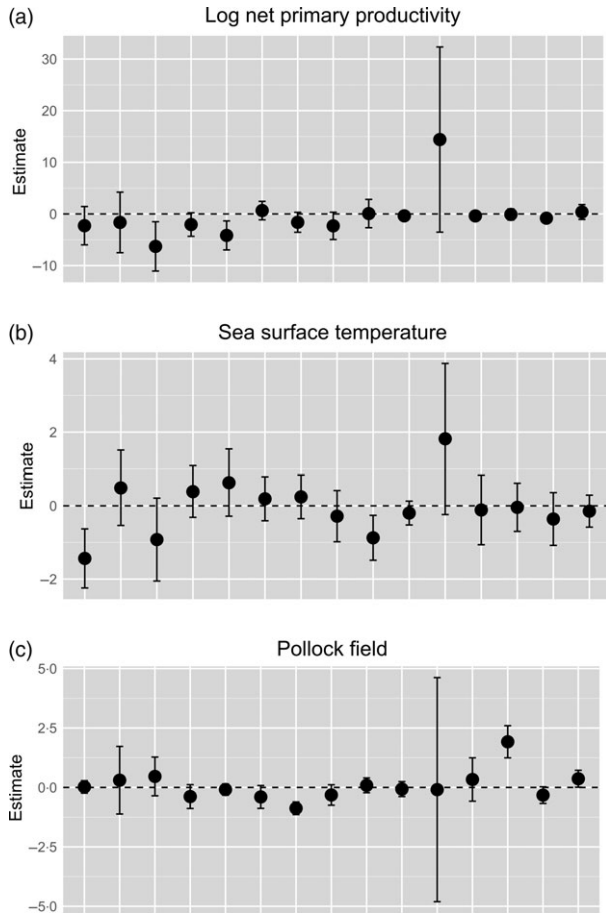
Fig. 2. Resource selection coefficient estimates for space–time point process analysis. Points represent coefficient estimates for each of the 15 individuals and error bars are 95% confidence intervals. The habitat variables examined in the model were (a) log net primary productivity, (b) sea surface temperature and (c) pollock CPUE$^{0.25}$. The dotted horizontal line is placed at zero for orientation to no selection.

Table 1. Space-only analysis selection coefficient estimates

	Mean	SD	Lower 95% CI	Upper 95% CI
Intercept	45·39	1·65	42·22	48·68
NPP	−3·22	0·18	−3·58	−2·87
SST	−3·67	0·11	−3·89	−3·45
pollock field	3·14	0·08	2·98	3·30
$\log G^*(\mathbf{s})$	1·67	0·04	1·60	1·75
distance	−0·08	0·005	−0·08	−0·07

The first and second columns are the estimated posterior means and standard deviations. The third and fourth columns are the lower and upper bounds of the 95% Bayesian credible intervals. SST, sea surface temperature; NPP, net primary productivity.

dure within MGCV. The level of coding to fit a nonparametric weighted distribution model would be a large impediment to many animal ecologists.

Spatio-temporal scaling is another issue for which weighted distribution models are inflexible. If selection at the level of individual movement is all that is of interest, then the weighted distributions can work well for estimating selection while accounting for autocorrelation. However, weighted distribution models cannot be rescaled or aggregated over time because fixed and known location times are one of the model assumptions. The point process approach does not condition on known times and therefore has the ability to scale from individual movement all the way to a completely spatial model where time is aggregated. We conjecture that the vast majority of the envisioned space–time models will not have closed form solutions for the $G(\mathbf{s})$ term that results from temporal aggregation, the point process framework itself provides continuity for building models along the spectrum of scales. There are few methods that provide the analyst the ability to choose the temporal scale of inference postdata collection while also accounting for autocorrelation. At the present time, we are only aware of one other (Hooten *et al.* 2012).

In analysing the fur seal data, we have shown that depending on the spatial scale in question, there can be differences in selection. This comes as no surprise and has been previously noted. Johnson (1980) describes four hierarchical levels of selection for an animal: (i) geographical range, (ii) home range, (iii) habitat within home range and (iv) structures within habitats. Depending on the biology of the animal in question, there may be strong selection at higher levels but not lower levels in that hierarchy. While examining the individual tracks from the fur seal data, we noted that even animals that had a negative selection coefficient for pollock CPUE tended to have tracks fully contained in higher pollock CPUE regions relative to the study area as a whole. This represents the bigger picture that Fieberg *et al.* (2010) note can be missed (Aarts, Fieberg & Matthiopoulos 2013). The fact that there is little or no selection at the movement level, and strong selection at the study area level implies that the fur seals are making selections at a larger spatial and temporal extent than what is immediately around them while they are foraging. Perhaps memory or previous experience tells them where to go before they leave the rookery and they make very few decisions en route along that preconceived path. Call *et al.* (2008) have noted that female fur seals can follow very similar paths on subsequent foraging trips as well as paths similar to other females from the same rookery.

We leave the reader with some discussion on the open topic of pooling individuals to make population-level inference. In the space–time analysis of individuals, population-level inference was made via weighted averages of coefficients, while in the space-only analysis a single model was fitted to pooled data. Thus, a common RSF is assumed for the space-only analysis (i.e. α is the same for all animals). This is not the case for space–time analysis as the weighted average estimator estimates the population average in the presence of uncertainty. Here, we used a simple weighted average to obtain population inference, but certainly, a more complex summary of individual estimates could be used (e.g., Hanks *et al.* 2011). However, in order for the
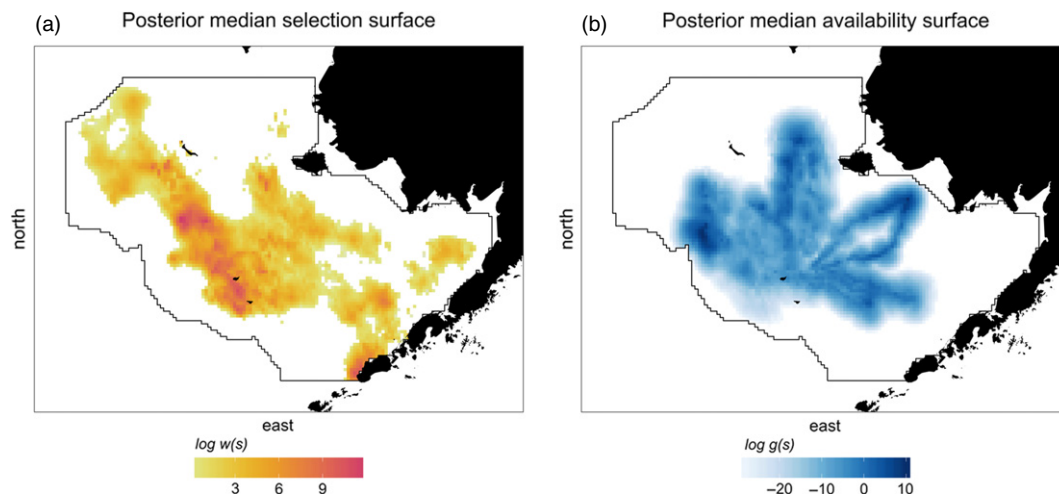
Fig. 3. Posterior median surfaces for the selection, $\log w(\mathbf{s}) = \mathbf{x}(\mathbf{s})'\boldsymbol{\alpha}$, and availability, $\log g(s) = \beta_1 G(\mathbf{s}) + \beta_2 d_r(\mathbf{s}) + \eta(\mathbf{s})$, components of the space-only model. In (a), only those location for which $\log w(\mathbf{s}) \geq 0$ are shown to illustrate regains of positive selectivity.

weighted average to be interpretable, the individual estimates of $\boldsymbol{\alpha}$ must be compatible over the deployments. This is the main reason that we restricted our fur seal analysis to the first trip for each individual. As the summer progressed, the habitat changed in ways which selection is most likely not compatible to that earlier in the season. Thus, to analyse the full data set for all animals over their entire deployment length, separate models should be fit to those periods for which the researcher believes the selection process is consistent between animals. This can be accomplished in the space–time models via interaction terms between the habitat variables and time variables. In the space-only analysis, the easiest method would be to analyse separate data sets for each period of interest, however, Bell & Grunwald (2004) provide some methodology for analysing replicated point patterns that could be used in a joint analysis over all periods. It is important to note for both space–time and space-only methods as long as selection is compatible over the union of all deployment times, both methods make adjustments to account for an unequal amount of data between individuals. In the space–time model, this is accomplished via differing standard errors between individuals, while in the space-only model, the calculated $G(\mathbf{s})$ surface summed over individuals accounts for apparent high use in a particular area due to a long deployment of an individual. In this sense, the $G^*(\mathbf{s})$ surface serves as an offset in the Poisson regression. In addition, it is also possible to fit the space-only model to each individual and use a weighted combination if that is desired.

Acknowledgements

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