Modelling animal movement using the Argos satellite telemetry location error ellipse

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Summary

1. The Argos satellite telemetry system is popular for studying the movement and space use of marine animals. The life histories of marine mammals, in particular, result in a relatively large proportion of inaccurate locations, thus making analysis methods that do not account for location measurement error inappropriate for these data. Using a new Kalman filtering algorithm, Argos now provides locations and estimated error ellipses associated with each satellite fix, but to our knowledge, the location error ellipse has yet to be incorporated into analyses of animal movement or space use.

2. We first present an observation model utilizing the Argos error ellipse and then demonstrate how this observation model can be combined with a simple three-dimensional movement model in a state-space formulation to infer activity budgets and movement characteristics from location and dive data of two species of seal, the bearded seal (Erignathus barbatus) and the Hawaiian monk seal (Monachus schauinslandi). These example data sets are of variable quality and represent species that differ in both space use and latitudinal range relative to the polar orbits of Argos satellites. We also compare the results from our error ellipse model with those from an approximate (isotropic) error circle model.

3. We found the error circle to be a crude approximation of the actual anisotropic error ellipse for the higher quality bearded seal data, but inferences from the lower quality Hawaiian monk seal data were more robust to the choice of observation model. In both examples, we found the theoretical bivariate normal distribution corresponding to the error ellipse often failed to adequately explain the most extreme location outliers.

4. In practice, we suspect the inferential consequences of using traditional isotropic location quality classes or other crude approximations in lieu of the error ellipse will be largely case-dependent. We support the Argos recommendation that practitioners wishing to more properly account for location measurement error utilize the error ellipse in analyses. However, the continued presence of outliers using the new algorithm suggests practitioners should consider using a fat-tailed distribution derived from the error ellipse (e.g. bivariate t-distribution) or filtering extreme outliers during data pre-processing.

Key-words: animal location data, Erignathus barbatus, hierarchical model, measurement error, Monachus schauinslandi, movement model, state-space model, switching behaviour

Introduction

Since the late 1980s, the Argos satellite telemetry system has been routinely used in the study of marine mammals (e.g. McConnell 1986; Martin, Smith & Cox 1993; McConnell et al. 1999; Vincent et al. 2002; Jonsen, Flemming & Myers 2005) and other aquatic taxa (e.g. Jonsen, Myers & James 2006; Block et al. 2011; Douglas et al. 2012; Hoенner et al. 2012). Argos tags have proven invaluable for collecting animal location and behavioural data, but the life histories of marine animals result in a relatively large proportion of inaccurate locations. Failure to properly account for location measurement error can lead to spurious inferences about animal movement, space use and behaviour (e.g. Montgomery et al. 2010; Montgomery, Roloff & Ver Hoef 2011), and analysis methods that do not account for location measurement error (e.g. Blackwell 2003; Morales et al. 2004; Langrock et al. 2012) are inappropriate for Argos data. Complex state-space models that account for location measurement error have therefore been developed (e.g. Jonsen, Flemming & Myers 2005; Johnson et al. 2008), but these typically rely on ad hoc filters or auxiliary information about location quality classes.

Argos data have historically been analysed based on location quality class (3, 2, 1, 0, A, B and Z), with estimated error radii of <250 m for class 3, <500 m for class 2, <1500 m for class 1 and >1500 m for class 0 (Lopez et al. 2013). Until recently, classes A, B and Z provided no estimated error because the accuracy of these locations was ‘not guaranteed’ by Argos. At the expense of valuable (albeit noisy) data,
locations assigned to these lower quality classes are often ignored altogether (e.g. Boyd et al. 1998; Johnson et al. 2008), or partially discarded using filters based on speed (e.g. McComb, Chambers & Fedak 1992; Johnson et al. 2008; Patterson et al. 2010) or other biological thresholds (e.g. Douglas et al. 2012).

Lower quality Argos locations have been retained in analyses of animal movement using state-space models, but only when auxiliary information about the accuracy for these classes was available. For example, a single assessment of four Argos tags on captive grey seals in the United Kingdom (Vincent et al. 2002) has been the basis for modelling Argos location errors in many marine mammal telemetry studies (e.g. Jonsen, Flemming & Myers 2005; Johnson et al. 2008; Patterson et al. 2010; Silva et al. 2014). These studies justify the use of auxiliary information because they reasonably suspected the location quality classes provided by Argos were inadequate. Even when auxiliary data are available and appropriate for the specific tag, species and study area of interest, state-space models using location error radii assume errors in latitude and longitude are uncorrelated, typically using independent univariate normal or t-distributions for the error in each direction (e.g. Jonsen, Flemming & Myers 2005; Johnson et al. 2008; Silva et al. 2014; but see Patterson et al. 2010). However, the orientation of the uncertainty in Argos locations estimates is related (perpendicular) to the subsatellite ground track (Lopez et al. 2013), and the magnitude of the error typically varies with latitude due to the polar orbits of the satellites.

Beginning in 2011, the Argos system implemented a multi-model Kalman filter algorithm that provides an estimated location and error ellipse for all fixes provided by Argos (Lopez & Malardé 2011; Lopez et al. 2013). Argos strongly recommends use of the error ellipse because error radii only approximate the actual errors, which are clearly anisotropic due to the polar orbits of the satellites. The error ellipse also reduces dependence on prior information about location uncertainty for quality classes A and B (e.g. Vincent et al. 2002) and provides a natural framework for accounting for anisotropic errors in state-space models of animal movement. However, to our knowledge, the error ellipse has yet to be incorporated into movement models utilizing Argos data.

Here, we present an observation model that accounts for location uncertainty based on the Argos error ellipse, and this can be easily combined with a movement process model in a state-space formulation. We demonstrate how one can utilize this observation model in conjunction with a discrete-time movement model to infer activity budgets and movement characteristics from bearded seal location and dive data collected in the Bering and Chukchi seas near Alaska, USA. We provide an additional example using the Hawaiian monk seal, which resides closer to the Earth’s equator (i.e. further away from polar orbits) and exhibits movement behaviours that differ from bearded seals. We also compare the residual errors and inferences from our error ellipse model with those from an approximate (isotropic) error circle model.

Materials and methods

THE ARGOS LOCATION ERROR ELLIPSE

Along with the traditional location quality class, Argos location data now include an error ellipse corresponding to the $\sqrt{2}$-sigma ellipse of a bivariate normal distribution (Lopez & Malardé 2011; Lopez et al. 2013). Just as one would expect 63–2% of draws from a normal distribution to lie within $\sqrt{2}$ standard deviations of the mean, one would expect 63–2% of draws from a bivariate normal distribution to lie within its $\sqrt{2}$-sigma ellipse. For each location at time $t (x_t, y_t)$, the Argos error ellipse is characterized by a semi-major axis (metres), semi-minor axis (metres) and orientation (0° to 180° angle from North to the East; see Fig. 1). Because an error ellipse is provided for valid location qualities (3, 2, 1, 0, A and B), one can account for location measurement error without prior information or ad hoc filters. This can be accomplished using a bivariate normal error distribution based on the error ellipse:

$$(x_t, y_t) \sim N(\mu_t, \Sigma_t),$$

where $\mu_t = (\mu_x, \mu_y)$ is the true location at time $t$, and the location error variance-covariance matrix

$$\Sigma_t = \begin{pmatrix} \sigma_{x_t}^2 & \sigma_{x,y} \\ \sigma_{x,y} & \sigma_{y_t}^2 \end{pmatrix}$$

is derived from the components of the Argos error ellipse:

$$\sigma_{x_t}^2 = \left(\frac{M}{\sqrt{2}}\right)^2 \sin^2 c_t + \left(\frac{m}{\sqrt{2}}\right)^2 \cos^2 c_t,$$

$$\sigma_{y_t}^2 = \left(\frac{M}{\sqrt{2}}\right)^2 \cos^2 c_t + \left(\frac{m}{\sqrt{2}}\right)^2 \sin^2 c_t,$$

and

$$\sigma_{x,y} = \frac{M^2 - m^2}{2} \cos c_t \sin c_t,$$

where $M$ is the semi-major axis length, $m$ is the semi-minor axis length, and $c$ is the orientation of the error ellipse (Service Argos 2013). This bivariate normal error distribution may be readily used as an observation model within state-space formulations of animal movement or resource selection models.

APPLICATION TO BEARDED SEALS IN THE BERING AND CHUKCHI SEAS

Between 2009 and 2012, $N = 7$ bearded seals (*Erignathus barbatus*) were captured and deployed with Argos tags off the coast of Kotzebue, Alaska, USA. Bearded seals are large phocid seals that forage primarily on or near the bottom of continental shelf waters and are an important traditional resource for many indigenous communities in the Arctic. We utilized both location and dive activity data collected by the tags to characterize movement behaviour as resting ($R$), foraging ($F$) or transit ($T$). The dive activity data were binned into 6-h intervals and consisted of the proportion of time that each individual spent diving >4 m below the surface. Because our dive summary data were for 6-h intervals, but locations were obtained at irregular time intervals (≥45 s) dependent on the surfacing patterns of the seals, we estimated positions at the endpoints of each of these 6-h intervals and used Bayesian analysis methods to fit a discrete-time, multistate movement model.
We assume bearing spent diving transit, and we also expect directional persistence to be largest for and state-specific directional persistence $0 \leq \theta \leq \pi$ which is a wrapped Cauchy distribution with bearing 0.

For our discrete-time, multistate hierarchical movement process model, movement behaviour state $z_{nt} \in \{R,F,T\}$ was estimated based on step length ($s_{nt}$), bearing ($\phi_{nt}$), and the proportion of time spent diving >4 m below the surface ($a_{nt}$) for each 6-h time step $t = 1, \ldots, T_n$ and individual $n = 1, \ldots, 7$. Between tag deployment in the summer and the annual moult during the following spring, the number of time steps per seal ($T_n$) ranged from 774 to 1201 ($\sum_{n=1}^{7} T_n = 7191$).

Following McClintock et al. (2013), we assume step length $s_{nt} | z_{nt} = i \sim$ Weibull ($a_{nt}, b_{nt}$):

$$f(s_{nt} | z_{nt} = i) = \frac{b_{nt}}{a_{nt}} \left(\frac{s_{nt}}{a_{nt}}\right)^{b_{nt}-1} \exp\left[-\left(\frac{s_{nt}}{a_{nt}}\right)^{b_{nt}}\right]$$

for state-specific scale parameter $a_{nt} > 0$ and shape parameter $b_{nt} > 0$.

We assume bearing $\phi_{nt} | z_{nt} = i \sim$ wCauchy ($\phi_{nt-1}, r_{nt}$):

$$f(\phi_{nt} | z_{nt} = i) = \frac{1}{2\pi} \frac{1 - r_{nt}^2}{1 + r_{nt}^2 - 2r_{nt}\cos(\phi_{nt} - \phi_{nt-1})}$$

which is a wrapped Cauchy distribution with bearing $0 \leq \phi_{nt} < 2\pi$ and state-specific directional persistence $0 \leq r_{nt} < 1$, where logit ($r_{nt}$) $\sim N(\rho_r, \sigma_{\rho_r}^2)$.

We expect average step length to be smaller for resting and larger for transit, reflecting these expectations at a maximum sustainable speed of 2 m s$^{-1}$ (Williams & Kooyman 1985; Lesage, Hammill & Kovacs 1999), we constrain the scale parameter for the state-dependent Weibull distributions for step length at both the population level:

$\exp(\theta_R) \sim \text{Unif}(0, 3000)$

$\exp(\theta_F) \sim \text{Unif}(0, \exp(\theta_T))$

$\exp(\theta_T) \sim \text{Unif}(\exp(\theta_F), 43\,200)$

and the individual level:

$\log(\theta_{R,n}) \sim TN(-\infty, \log(3000)) \left(\theta_R, \sigma_{\theta_R}^2\right)$

$\log(\theta_{F,n}) \sim TN(-\infty, \log(\theta_{R,n})) \left(\theta_F, \sigma_{\theta_F}^2\right)$

$\log(\theta_{T,n}) \sim TN(\log(\theta_{F,n}), \log(43\,200)) \left(\theta_T, \sigma_{\theta_T}^2\right)$

where $TN(l,a)$ is the normal distribution truncated at $l$ and $u$, and 3000 m was our expected maximum step length for the resting state (given bearded seals may drift while resting at sea or hauling out on ice). For each state, we right truncated the Weibull distribution for step length at 43 200 m (the maximum possible horizontal displacement when travelling at 2 m s$^{-1}$ for 6 h). We also constrained directional persistence such that logit$^{-1}(\rho_R) \sim \text{Unif}(0, 1)$, logit$^{-1}(\rho_F) \sim \text{Unif}(0, \logit^{-1}(\rho_T))$, logit$^{-1}(\rho_T) \sim \text{Unif}(0.75, 1)$, logit$(\rho_{T,n}) \sim N(\rho_{T,n}, \sigma_{\rho_{T,n}}^2)$, logit$(\rho_{R,n}) \sim TN(-\logit(\rho_{T,n})) \left(\rho_{R,n}, \sigma_{\rho_{R,n}}^2\right)$, and logit$(\rho_{F,n}) \sim TN(\logit(0.75), \infty) \left(\rho_{F,n}, \sigma_{\rho_{F,n}}^2\right)$, where 0.75 was selected to inform a relatively strong directional persistence when in the transit.
state. To model switches between behaviour states, we assign a first-order Markov categorical distribution, \( z_n \sim \psi_{z_n} \), where \( \psi_{z_n} \) is the probability of switching from state \( k \) at time \( t - 1 \) to state \( i \) at time \( t \), and \( \sum \psi_i = 1 \).

Although movement behaviour state assignment could be based solely on horizontal movement characteristics (e.g. Morales et al. 2004; Jonsen, Fleming & Myers 2005; McClintock et al. 2012), we wished to incorporate the additional information about behaviour states provided by the dive summary data (sensu McClintock et al. 2013). Assuming independence between step length and bearing, we incorporated \( \alpha_{0k} \) into a joint conditional likelihood:

\[
f(x, \phi, \omega, z; \theta) = \prod_{n=1}^N \prod_{t=1}^{T_n} f(\omega_n|0, z_n) f(\phi_{n,t}|\theta, z_n) f(z_{n,t-1}|0, z_{n,t-1})
\]

where \( \theta \) denotes the set of all model parameters. Given the nature of the Argos platform, animal behaviour leading to limited or irregular exposure to the satellites, and limited bandwidth for transferring data, dive behaviour received from the tags are not continuous and are subject to missing or incomplete records. We assume a priori that any missing or incomplete dive activity data are equally likely to have arisen from the resting, foraging, or transit states; some dive data were missing for seals tagged during 2009 because extra (GPS location) data collected only in that year consumed a portion of the data uplinks to the Argos satellites. We further assume a priori that diving activity is equally likely to have arisen from the foraging or transit states:

\[
f(\omega_n|0, \theta, z_n = \hat{i}) = \text{Beta}(\nu_{\hat{i}}, \delta_{\hat{i}})
\]

for \( i = R, F, T \), where \( \nu_{\hat{i}} = \nu_T \) and \( \delta_{\hat{i}} = \delta_T \). Time spent <4 m below the surface is assumed to be indicative of the resting state, and time spent >4 m below the surface is assumed to be indicative of the foraging and transit states (Fig 2). Similar to McClintock et al. (2013), we therefore assigned the priors \( \nu_T \sim \text{Unif}(0, \delta_T) \), \( \nu_{\hat{i}} \sim \text{Unif}(1, 10) \), \( \delta_T \sim \text{Unif}(1, 10) \), and \( \delta_{\hat{i}} \sim \text{Unif}(0, 0.5) \).

For the observation process model, the location data consisted of the observed locations \( (x_{n,t}, y_{n,t}) \) for individual \( n = 1, \ldots, N \); time step \( t = 1, \ldots, T_n \); and observation \( t = 1, \ldots, K_{n,t} \) (where time steps with \( K_{n,t} = 0 \) have no observed locations). The number of observations per seal \( \Sigma_{t=1}^{T_n} K_{n,t} \) ranged from 6425 to 8999 (\( \Sigma_{n=1}^{N} K_{n,t} = 52303 \)). Similar to Jonsen, Fleming & Myers (2005) and McClintock et al. (2012, 2013), we assumed that individuals travel in a straight line between times \( t - 1 \) and \( t \). The temporally irregular observed \( (x_{n,t}, y_{n,t}) \) and true \( (\mu_{n,t}, \nu_{n,t}) \) locations were then related to the temporally regular locations \( (X_{n,t}, Y_{n,t}) \) via:

\[
f(0, X_0, Y_0, x, \phi, z; \Sigma, \omega) \propto \prod_{n=1}^{N} \prod_{t=1}^{T_n} f(X_{n,t}|0, z_n) f(\phi_{n,t}|\theta, z_n) f(\omega_n|0, z_n) f(z_{n,t-1}|0, z_{n,t-1})
\]

\[
\times \prod_{n=1}^{N} \prod_{t=1}^{T_n} f(x_{n,t-1}, y_{n,t-1}|Y_{n,t}, X_{n,t}) f(\phi_{n,t}|\theta, x_{n,t}, y_{n,t}) f(x_{n,t}, y_{n,t}|\omega_n, z_n) f(z_{n,t}|0, z_{n,t-1})
\]

Any missing dive activity data were imputed within the MCMC algorithm. After initial pilot tuning and burn-in of 100 000 iterations, we ran four parallel chains of 1 250 000 iterations (thinned every 1000 iterations) for posterior summaries. Analysis of pre- and post-processing were performed in R via the C interface (R Core Team 2012; see Data S1 for source code).
and data). For comparison, we then performed an identical analysis using the isotropic Argos error circle, where

\[
\Sigma_{i,j} = \begin{pmatrix}
\sigma_{i,j}^2 & 0 \\
0 & \sigma_{i,j}^2
\end{pmatrix},
\]

and \(r_{i,j} = \sqrt{M_{i,j}/P_{i,j}}\) is the Argos error radius for the \(i\)th observation during time step \(t\) for individual \(l\) (see Fig. 1). The error radius is generally a crude approximation (see Fig. 1) and is provided by Argos ‘for convenience only’ to help users classify locations based on their accuracy (López et al. 2013). Both analyses required about 165 h on a dedicated Linux server (8 Intel Xeon X5675@3.07 GHz processors, 12 Gb RAM). Standard chain diagnostics provided no evidence of lack of convergence.

APPLICATION TO HAWAIIAN MONK SEALS

For comparison to our bearded seal results, we conducted a very similar analysis of monk seal (Monachus schauinslandi) location and dive data collected in the Northwestern Hawaiian Islands, USA. The data were collected from \(N = 10\) individuals between June 2008 and May 2012. The dive activity data were binned into 6-h intervals, but for this study consisted of the proportion of time that each individual spent diving >10 m below the surface. However, because monk seal movements tend to be less transitory with short foraging trips (relative to bearded seals), we found 6-h intervals were too coarse to accurately characterize these finer grain movements using our discrete-time model. We therefore selected 3-h time steps and simply divided the 6-h dive data evenly between the corresponding 3-h intervals (e.g. if seal \(n\) respectively spent 60% and 70% of the first and second 6-h interval >10 m below the surface and then we assumed \(t_{n,1} = 0 \cdot 6, t_{n,2} = 0 \cdot 6, t_{n,3} = 0 \cdot 7\) and \(t_{n,4} = 0 \cdot 7\)).

The number of 3-h time steps per seal (\(T_n\)) ranged from 407 to 2152 (\(\sum_{i=1}^{10} k_{n,i} = 11 181\) ). The number of observations per seal (\(\sum_{i=1}^{10} k_{n,i}\)) ranged from 684 to 2519 (\(\sum_{i=1}^{10} k_{n,i} = 13 050\) ). All other model specifications were identical to our bearded seal model, except for modified constraints corresponding to 3-h time steps: \(\exp(x_{k}) \sim \text{Unif}(0,1500), \log(a_{n,k}) \sim \text{Ta}(\log(1000), (\sigma_x^2))\), \(\exp(x_\theta) \sim \text{Unif}(0,21 600)\) and \(\log(a_{n,\theta}) \sim \text{Ta}(\log(10), (\sigma_x^2))\). For initial locations \((x_{n,0}, y_{n,0})\), we assigned a joint uniform prior over the region of the Pacific Ocean encompassing the Hawaiian submarine ridge. Our MCMC algorithm, the number of chains and the length of chains were the same as for our bearded seal analysis. Both analyses required about 110 h on a dedicated Linux server (8 Intel Xeon X5675@3.07 GHz processors, 12 Gb RAM). Standard chain diagnostics provided no evidence of lack of convergence.

Results

BEARDED SEAL ANALYSIS

The error ellipses were overwhelmingly oriented towards the \(x\)-axis, with mean semi-major axis \(M = 11 252\) m (median = 4174 m, SD = 36 190), semi-minor axis \(m = 493\) m (median = 239 m, SD = 4894) and orientation \(c = 90^\circ\) (median = 89°, SD = 20), while the mean error radius was 1755 m (median = 1010 m, SD = 11 278). Only 5% of locations had ellipses oriented towards the \(y\)-axis. Figure 3 illustrates the observed locations, location uncertainty, predicted movement path and behavioural state assignments for a single bearded seal from the error ellipse and error circle analyses. The estimated activity budgets (Table 1) and parameter estimates (see Appendix S2 for detailed posterior summaries) were somewhat different between the error ellipse analysis and the error circle analysis. The most significant differences were in the estimated activity budgets and the magnitude of the degrees of freedom term accounting for additional error that was not adequately explained by the error ellipse or circle (\(\gamma\)). Although estimated resting activity budgets were affected little by the observation error model, we found significant differences between the estimated budgets for foraging and transit. For example, we estimated the population-level foraging budget as \(0 \cdot 66 (95\% \text{ HDI} 0 \cdot 65–0 \cdot 68)\) using the error ellipse and \(0 \cdot 63 (95\% \text{ HDI} 0 \cdot 62–0 \cdot 64)\) using the error circle. We estimated posterior median \(\gamma = 0 \cdot 82 (95\% \text{ HDI} 0 \cdot 81–0 \cdot 83)\) from the error ellipse analysis and \(\gamma = 1 \cdot 63 (95\% \text{ HDI} 1 \cdot 61–1 \cdot 66)\) from the error circle analysis, suggesting the error circle tended to (spuriously) explain additional error along the semi-minor axis of the corresponding error ellipse (see Fig. 1). We also found the error circle allowed for slightly more correlated movements during the resting state, with population-level logit \((-1)(x_{\theta}) = 0 \cdot 00 (95\% \text{ HDI} 0 \cdot 00–0 \cdot 01)\) using the error ellipse and logit \((-1)(x_{\theta}) = 0 \cdot 03 (95\% \text{ HDI} 0 \cdot 00–0 \cdot 10)\) using the error circle. Hence, the isotropic error circle is clearly only a crude approximation to the actual error ellipse for these data.

Based on estimated population-level activity budgets for the error ellipse analysis, the majority of 6-h time steps were devoted to foraging activity (Table 1). Individual seals exhibited activity budgets ranging from 0-12 to 0-16 for resting, 0-56 to 0-76 for foraging and 0-11 to 0-31 for transit. We expected to see some variability in activity budgets and movement characteristics because the study period overlapped with the ‘summer’ (before 30 September), ‘fall’ (1 October to 31 December) and ‘winter’ (after 1 January). We did find some differences in time allocations to the different states, with resting increasing from...
summer to winter and transit decreasing from summer to winter (Table 1). These differences support the notion that adult bearded seals migrate from the north into the Bering Sea as seasonal sea ice accumulates. Adult bearded seals appear to have high winter site fidelity, and their winter movements are restricted (P. Boveng, unpublished data). This analysis.
provides additional insight to suggest a decrease in resting behaviour during the summer season and a slight increase in foraging behaviour during the winter season.

Compared to transitory movements, resting and foraging movements exhibited significantly shorter step lengths and less directional persistence. Also as expected, the resting state exhibited significantly smaller proportions of time spent diving below 4 m (Fig. 4). Based on population-level state transition probabilities, individuals were more likely to remain in the transit state (posterior median $\psi_{T,T} = 0.92$, 95% HPDI: 0.90–0.93) or foraging state ($\psi_{F,F} = 0.85$, 95% HPDI: 0.84–0.87) than the resting state ($\psi_{R,R} = 0.32$, 95% HPDI: 0.29–0.36). This indicates bearded seals were less likely to remain in the resting state for extended periods during our study. For example, the estimated probability of a bearded seal remaining in the resting state for an entire 24-h period was $\psi_{R,R}^4 = 0.01$.

**MONK SEAL ANALYSIS**

The monk seal location error ellipses had mean semi-major axis $M = 7435$ m (median = 3013 m, SD = 27 450), semi-minor axis $m = 843$ m (median = 496 m, SD = 1113) and orientation $c = 88°$ (median = 85°, SD = 42), while the mean error radius was 1858 m (median = 1250 m, SD = 2149). With 30% of locations having ellipses oriented towards the $y$-axis, these more equatorial fixes tended to yield error ellipses that were ‘more circular’ (i.e., shorter semi-major axis with longer semi-minor axis) and less often oriented along the $x$-axis relative to the bearded seal data (see Fig. 1). Figure 5

![Fig. 4](image-url)  
**Fig. 4.** Estimated bivariate densities of bearded seal step length and proportion of time step spent diving below 4 m. Separate densities were estimated for three distinct movement behaviour states (‘resting’, ‘foraging’ and ‘transit’), where darker shades indicate higher relative densities. Results are from two separate analyses using (a) the Argos error ellipse and (b) the Argos error circle. Time steps are 6 h.
illustrates the observed locations, location uncertainty, predicted movement path and behavioural state assignments for a single monk seal in the Northwestern Hawaiian Islands, USA, from separate analyses using (a) the Argos error ellipse and (b) the Argos error circle. Observed locations are connected by a line in light blue, and the location error ellipses/circles appear in light yellow. Estimated movement states for the predicted locations correspond to ‘resting’ (red), ‘foraging’ (green) and ‘transit’ (blue) movement behaviour states and are connected by a black line. Uncertainty in the state assignments (<95% posterior probability) are indicated by hollow circles within predicted locations. Uncertainty in predicted locations is indicated by 95% credible bands (dashed lines).

Fig. 5. Observed locations, location uncertainty, predicted locations and estimated movement behaviour states for a single monk seal in the Northwestern Hawaiian Islands, USA, from separate analyses using (a) the Argos error ellipse and (b) the Argos error circle. Observed locations are connected by a line in light blue, and the location error ellipses/circles appear in light yellow. Estimated movement states for the predicted locations correspond to ‘resting’ (red), ‘foraging’ (green) and ‘transit’ (blue) movement behaviour states and are connected by a black line. Uncertainty in the state assignments (<95% posterior probability) are indicated by hollow circles within predicted locations. Uncertainty in predicted locations is indicated by 95% credible bands (dashed lines).
were devoted to foraging activity (Table 2). Individual seals exhibited activity budgets ranging from 0.04 to 0.22 for resting, 0.39 to 0.92 for foraging and 0.00 to 0.53 for transit. Similar to the bearded seal results, resting and foraging movements exhibited significantly shorter step lengths and less directional persistence in relation to the transit state. The resting state similarly exhibited significantly smaller proportions of time spent diving below 10 m (Fig. 6). Based on

Table 2. Estimated proportion of 3-h time steps assigned to three movement behaviour states (‘resting’, ‘foraging’ and ‘transit’) for 10 monk seals in the Northwestern Hawaiian Islands, USA, from two separate analyses utilizing the Argos location error ellipse or circle. State assignments are based on both location and dive data for each time step.

| Behaviour state | Argos error ellipse | Argos error circle |
|-----------------|---------------------|--------------------|
|                 | Time allocation     | 95% HPDI           | Time allocation     | 95% HPDI           |
|                 | Lower   | Upper | Lower   | Upper |
| Resting         | 0.10    | 0.09  | 0.11    | 0.12  |
| Foraging        | 0.80    | 0.79  | 0.81    | 0.81  |
| Transit         | 0.10    | 0.08  | 0.11    | 0.10  |

Fig. 6. Estimated bivariate densities of monk seal step length and proportion of time step spent diving below 10 m. Separate densities were estimated for three distinct movement behaviour states (‘resting’, ‘foraging’ and ‘transit’), where darker shades indicate higher relative densities. Results are from two separate analyses using (a) the Argos error ellipse and (b) the Argos error circle. Time steps are 3 h.
population-level state transition probabilities, individuals were more likely to remain in the transit state (posterior median $\psi_{T,T} = 0.95$, 95% HPDI: 0.94-0.97) or foraging state ($\psi_{F,F} = 0.95$, 95% HPDI: 0.94-0.96) than the resting state($\psi_{R,R} = 0.63$, 95% HPDI: 0.59-0.67). This indicates monk seals were less likely to remain in the resting state for extended periods during our study. For example, the estimated probability of a monk seal remaining in the resting state for an entire 24-h period was $\psi_{R,R} = 0.02$. Foraging trips tended to be both preceded ($\psi_{F,R} = 0.36$, 95% HPDI: 0.32-0.39) and followed ($\psi_{F,R} = 0.04$, 95% HPDI: 0.04-0.05) by short periods of resting. As expected, movements were generally confined to the shallows surrounding the high peaks of the Hawaiian submarine ridge and thus much shorter and less transitory than for bearded seals.

These data suffered from frequent missing location and dive activity data that we suspect were attributable to poorer satellite coverage near the equator and tag duty cycling that prioritized battery life. For example, we frequently observed periods (several hours to days) of missing data that we believe resulted from long periods mostly at sea (during which data could not be transmitted) or hauled out (during which transmissions ceased after 2 h to preserve battery life). We found these missing data periods were more frequently assigned to the transit state relative to periods without missing data (see Appendix S3). In our model, the wrapped Cauchy distribution for bearing had greater density potential for the transit state (because of the constraint $\rho_T > \logit (0.75)$), and the right-truncated Weibull distribution for the transit state had greatest density potential towards the upper limit for step length (because of the constraint $\sigma_x < \sigma_T$). Thus, we suspect the estimated movement characteristics of the transit state were exaggerated (and the transit state activity budgets were likely overestimated) due to the prevalence of missing data.

**Discussion**

We have presented a method by which the Argos error ellipse can be incorporated into the analysis of animal location data. Despite substantial measurement error, we demonstrated how this observation process model can be combined with a simple three-dimensional movement model to infer the activity budgets of two species of seal that differ in both space use and latitudinal range relative to the polar orbits of the Argos satellites. Although inferences from our Hawaiian monk seal example were robust to the choice of observation model, we found the error ellipse to be a crude approximation of the actual anisotropic error ellipse for the bearded seal data (particularly along the x-axis). For the monk seals, the lower quality of the data, less transitory area-restricted search-type of movement and more circular error ellipses likely contributed to the similarity of the error ellipse and circle analyses. Despite the deleterious effects of the error circle approximation likely being mitigated by the predominantly north–south movements of the bearded seals, we found some significant differences between the error ellipse and circle analyses using these higher quality data. In practice, we suspect the inferential consequences of using the error circle (or traditional isotropic location quality classes) in lieu of the error ellipse will be largely case-dependent.

In our bearded seal example, although the properties associated with each movement behaviour state were consistent with those expected for resting, foraging and transit, biological interpretations of movement characteristics and activity budgets should be made with care. Because time steps were specified at 6-h intervals (the resolution of the dive summary data), state switching within intervals was likely. Such mid-interval switches may have somewhat blurred the step length, bearing and dive proportion distributions for the three states. For the 10% of time steps with 40–60% of the time spent diving ($0 \cdot 4 < \theta_{d,4} < 0 \cdot 6$), it is evident that some combination of resting and foraging likely occurred if the step length is relatively short (see Fig. 4). The potential for mid-interval switches between foraging and transit is particularly difficult to assess; to more accurately identify foraging, one would need to incorporate dive shape or biotelemetry information about feeding, such as stomach temperature (e.g. Austin et al. 2006). Because bearded seals do not appear to frequently rest for periods much greater than 6 h, finer resolution dive summary data would be required to better characterize resting movements and state transitions.

The results from our monk seal example warrant additional care in interpretation. The finer scale of monk seal movements implies mid-interval switches were certainly still possible despite the shorter 3-h time step used for this analysis. With 47% of the time steps missing both location and dive data (compared with 3% for the bearded seal data), we suspect the high frequency of missing data periods resulted in overestimation of the transit state activity budget using our multistate movement behaviour model (see Appendix S3). This illustrates an important limitation of using multistate movement models with frequent missing data, but we shall limit discussion of this point given our specific focus here on the application of the Argos error ellipse for handling measurement error. While we included this example to demonstrate the use of the Argos error ellipse for data collected close to the equator (i.e. far away from the polar orbits of the satellites), a more realistic observation model that better explains the missing data component would likely yield more reliable inferences about monk seal activity budgets from these data. Incorporating movement models with behaviour data is a relatively new approach within the marine mammal field, and the amount and duration of missing data can be a challenge to overcome. The duty cycles for these tags were not optimized for fitting multistate movement models, but for this purpose in the future, we would recommend prioritizing regular location and higher resolution dive activity data. Breed et al. (2011) demonstrated that complex multistate movement models can produce misleading inferences when the scale of movement is small relative to observation error and frequency, and they provide guidelines for programming tags that will aid practitioners wishing to collect data that are better suited to these models.
We note that although the computation times were long in our examples (4–7 days), this is not attributable to our use of the Argos error ellipse. Rather, the long run times were necessitated by the complexity of our discrete-time, population-level multistate movement model and our use of MCMC to fit the model in a Bayesian framework. The bivariate normal and bivariate t-distributions derived from the error ellipse are no more complex than other commonly used error distributions. Individual-level models, simpler discrete-time models or movement models formulated in continuous time would not necessarily require the long run times when using our observation models based on the error ellipse. For example, the continuous-time correlated random walk model of Johnson et al. (2008) is currently being implemented with the bivariate normal error ellipse model for an upcoming release of the R package crawl (Johnson 2013); this model is fit using maximum-likelihood and is generally very fast.

Boyd & Brightsmith (2013) suggest the Argos error ellipse may be inadequate for describing location errors, although their study was limited to two transmitters from fixed locations. For animal tracking in particular, Lopez et al. (2013) acknowledge that their algorithm can underestimate the actual positioning error as a consequence of non-normal (e.g. heavy tailed) error distributions and inconsistent frequency measurement noise. Nevertheless, Silva et al. (2014) generally found less error in Argos positions obtained using the new multimodel Kalman filter algorithm relative to the older nonlinear least squares algorithm, but they did not incorporate the error ellipse and instead used independent t-distributions for each Argos location class based on Vincent et al. (2002). The bivariate t-distribution used in our example allows for additional location measurement error not explained by the error ellipse. Our estimates for the bivariate t degrees of freedom (\(\nu\)) suggest a bivariate normal distribution is inadequate, but similar to Jonsen, Flemming & Myers (2005), our discrete-time model is unable to partition the additional error between that attributable to outliers and discretization of the movement path into temporally regular time steps.

The inadequacy of the bivariate normal error distribution indicates the error ellipse fails to perfectly explain the Argos location measurement error. This is best illustrated by the obvious outliers in Figs 3(a) and 5(a), where several clearly erroneous locations have error ellipses with virtually no support within the plausible region of movement. Such errors can have deleterious effects when fitting movement models, even when fat-tailed error distributions are used in hopes of mitigating their influence. Finding the traditional location quality class provided by Argos to be similarly inadequate for explaining such errors, previous studies have used auxiliary data and t-distributions to help minimize their effects (e.g. Jonsen, Flemming & Myers 2005; Johnson et al. 2008; Patterson et al. 2010; Silva et al. 2014). We are unsure as to why such egregious errors still occur in the error ellipse data provided by Argos using the new Kalman filtering algorithm, but until these errors are corrected (or can be appropriately modelled), practitioners might still consider using a conservative filter (e.g. McConnell, Chambers & Fedak 1992; Freitas et al. 2008) to eliminate the extreme outliers prior to analysis.

Although inferences were robust to the choice of observation model in our example using lower quality monk seal data, we reiterate that there is no theoretical justification for the Argos error circle; the error radius is merely provided as an approximation ‘for convenience’ (Lopez et al. 2013). Compared to the relatively crude error circle, the error ellipse is theoretically justified and requires (virtually) no additional effort to implement, and we support the Argos recommendation that practitioners wishing to more properly account for location measurement error utilize the error ellipse in lieu of both the error circle and the traditional location quality class. While we hope technological developments will ‘one day’ or ‘someday’ render location measurement error a non-issue, the methods presented here can be useful in the meantime, as well as for revisiting historical data sets. Reprocessing of previous Argos data using the new Kalman filtering algorithm (which produces the error ellipse and radius) is currently available back to 1 January 2008 (Service Argos 2013).

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Data accessibility

Data from this analysis are available in Supporting Information (Data S1).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Markov chain Monte Carlo algorithm and BUGS/JAGS pseudo-code.

Appendix S2. Posterior summaries.

Appendix S3. Posterior state assignments for monk seals based on missing location and dive activity data.

Data S1. Source code and data for implementing the Markov chain Monte Carlo algorithm.