

Robust hierarchical state–space models reveal diel variation in travel rates of migrating leatherback turtles

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Summary

1. Biological and statistical complexity are features common to most ecological data that hinder our ability to extract meaningful patterns using conventional tools. Recent work on implementing modern statistical methods for analysis of such ecological data has focused primarily on population dynamics but other types of data, such as animal movement pathways obtained from satellite telemetry, can also benefit from the application of modern statistical tools.

2. We develop a robust hierarchical state–space approach for analysis of multiple satellite telemetry pathways obtained via the Argos system. State–space models are time-series methods that allow unobserved states and biological parameters to be estimated from data observed with error. We show that the approach can reveal important patterns in complex, noisy data where conventional methods cannot.

3. Using the largest Atlantic satellite telemetry data set for critically endangered leatherback turtles, we show that the diel pattern in travel rates of these turtles changes over different phases of their migratory cycle. While foraging in northern waters the turtles show similar travel rates during day and night, but on their southward migration to tropical waters travel rates are markedly faster during the day. These patterns are generally consistent with diving data, and may be related to changes in foraging behaviour. Interestingly, individuals that migrate southward to breed generally show higher daytime travel rates than individuals that migrate southward in a non-breeding year.

4. Our approach is extremely flexible and can be applied to many ecological analyses that use complex, sequential data.

Key-words: Bayesian, *Dermochelys coriacea*, measurement error, process uncertainty, random walk.

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Introduction

The resolution of important ecological hypotheses requires advanced statistical tools that can accommodate data with astonishingly complex structures of artefactual noise and biological variability. Recent implementation of state–space and hierarchical Bayes modelling approaches for the extraction of ecological signals from complex data have rested in the domain of population ecology (de Valpine & Hastings 2002; Clark *et al.* 2005), but such tools have much to contribute to other areas of ecology (Jonsen, Myers & Mills Flemming 2003; Wikle 2003; Morales *et al.* 2004). Here

we illustrate how the inference of behaviour from remotely sensed animal tracking data benefits from the use of these modern statistical methods.

Understanding migratory behaviour of marine species is exceedingly challenging because of the expense and logistics involved in tagging multiple individuals and the general paucity of suitable statistical tools for the appropriate analysis of animal tracking data. The first challenge is being overcome now that large data sets of remotely sensed movement patterns are available for a variety of marine species (e.g. LeBoeuf *et al.* 2000; Block *et al.* 2001; James, Ottensmeyer & Myers 2005c). The challenge of developing suitable statistical tools is being addressed by the recent adaptation of state–space models and other Bayesian methods for analysis of time-series movement data (Jonsen *et al.* 2003; Sibert, Musyl & Brill 2003; Morales *et al.* 2004; Jonsen, Mills Flemming & Myers 2005).

Remotely sensed data such as those obtained from Argos satellite transmitters are a time-series of locations characterized by irregularly timed and serially correlated observations with strongly non-Gaussian errors that vary from one location to the next (Jonsen *et al.* 2005). These features require robust state–space methods that are powerful and flexible enough to allow researchers to estimate behavioural parameters and biological variability directly from inherently noisy and complex data. When multiple data sets exist, a hierarchical Bayesian approach is optimal because it can account for multiple and complex sources of variability in the data (Clark 2005) and improves estimation from information-poor individual data sets (Gelman *et al.* 2004). Our goal here is to illustrate how a robust state–space model, fitted into a hierarchical Bayes context, can be used to estimate aspects of the movement behaviour of the leatherback turtle (*Dermochelys coriacea* Vandelli 1761) from Argos satellite data. We emphasize that our approach can also be modified to suit other sequential data types, models and questions. The leatherback turtle is a cosmopolitan marine species that, in the Atlantic, undertakes migrations from sub-Arctic to tropical waters and back within a year (James *et al.* 2005c). Females nest on tropical beaches every 2–3 years, whereas males may mate annually, but all individuals complete the migration annually. This species is now critically endangered (IUCN 2004), due in part to interactions with commercial fisheries (Spotila *et al.* 2000; Ferraroli *et al.* 2004). Recent satellite telemetry data sets document important details of the migration routes of these turtles (Ferraroli *et al.* 2004; Hays, Houghton & Myers 2004b) and highlight previously unknown regions where there is potentially high vulnerability to fishing activities (James *et al.* 2005c). Very little, however, is known about the leatherback's behaviour during migration, although data from dive recorders indicate a preference for remaining near the surface during the day vs. a preference for deeper strata during the night (Hays *et al.* 2004b; James, Eckert, & Myers 2005a). A strong diel difference in depth preference may be associated with diel variation in foraging or navigation behaviours and is therefore likely to have implications for travel rates during the day and night periods. We use a robust hierarchical Bayes state–space model to test the hypothesis that leatherback travel rates are faster during the day, when turtles are predominantly near the surface, than at night, when turtles dive more frequently (Hays *et al.* 2004a; James *et al.* in press). Leatherbacks undertake return migrations from high-latitude foraging areas to tropical waters and back (James, Myers & Ottensmeyer 2005b). Consequently, we analyse three distinct phases of this migratory cycle (Fig. 1) and compare estimates of the ratio of day-to-night travel rates from Argos satellite telemetry data on adult male, female and juvenile leatherbacks. A secondary goal of our analyses is to examine potential differences in travel rates between both males vs. females and individuals in a breeding year vs. those in an interbreeding year. Finally, we illustrate the utility of

the hierarchical Bayes approach by comparing day-to-night ratio estimates with those obtained from a conventional, *ad hoc* analysis of travel rates and with those obtained from a non-hierarchical state–space analysis.

Materials and methods

DATA

The data consist of movement pathways of 14 leatherback turtles that were captured, equipped with Argos satellite transmitters and released off the coast of Nova Scotia, Canada (see Fig. 1 for examples) (James *et al.* 2005c). More pathways exist, but we have chosen the largest subset of all the tagged turtles that had similar Argos transmitters and tag settings (James *et al.* 2005c). At the time of capture, individuals were measured, sexed and equipped with an Argos satellite tag, a passive integrated transponder (PIT) and flipper tags. Those with a curved carapace length greater than 145 cm were assumed to be sexually mature adults (following Eckert 2002a). Individuals below this size threshold are difficult to sex reliably and were therefore classed as juvenile. Evidence of breeding by males was inferred from Argos data indicating residency in waters adjacent to nesting beaches (James *et al.* 2005a). Evidence of breeding by females was obtained from re-observations of flipper tags and/or PITs on nesting turtles. We use this information on sex and breeding status to make inferences about their influence on travel rate patterns.

We focus our analyses on three predominant phases of the migratory cycle: phase A, northern foraging phase (Fig. 1, red segment); phase B, southward migration (Fig. 1, blue segment); and phase C, northward migration (Fig. 1, black segment). Phase A is preceded by a period of high travel rates (James *et al.* 2005b); we discarded observations from this period. The division between phases A and B was also determined on the basis of travel rates; James *et al.* (2005b) show that the onset of southward migration is characterized by a sharp, transient increase in travel rate. To identify the spatio-temporal position of this phenomenon we fitted a simple state–space model described in Jonsen *et al.* (2005) to each of the 14 pathways and calculated travel rates from the resulting state estimates. Because of the anomalous nature of this peak in travel rate, we chose to remove observations associated with it from our analyses; therefore, the start of the peak defines the end of phase A and the end of the peak defines the start of phase B. We define the end of phase B at 21°N, below which movement patterns are confounded with the onset of foraging and/or reproductive behaviours associated with tropical waters (e.g. James *et al.* 2005a). The start of phase C is defined as the point beyond which movements in tropical waters show a consistent northward bias. We define the end of this phase at the point where movements clearly show an initiation of foraging behaviour in northern waters. However, several tags transmitted intermittently during this phase, so the

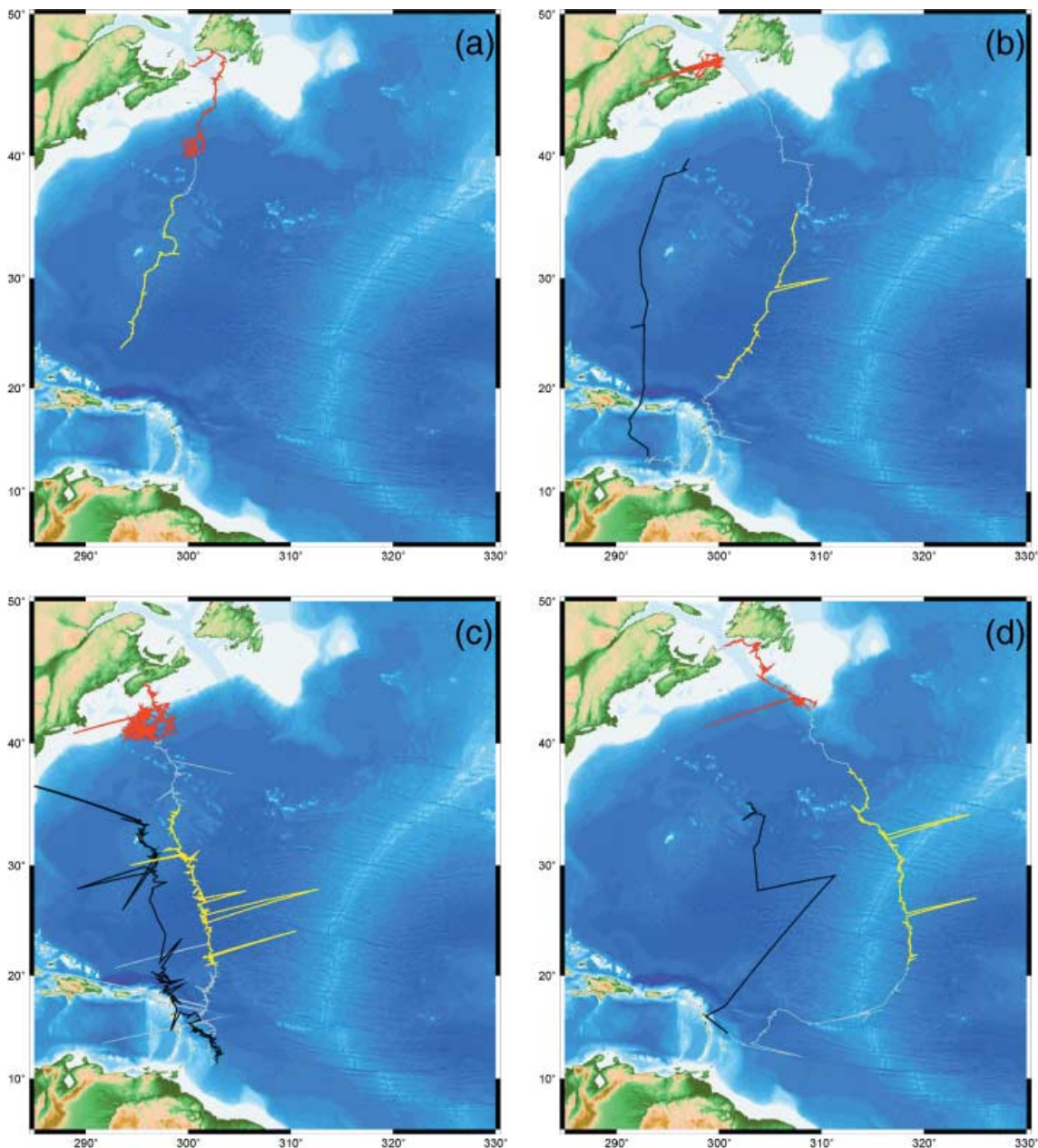


Fig. 1. Maps illustrating four representative leatherback turtle pathways. The segments of the pathways used in our analysis correspond to: (1) northern foraging (red); (2) southward migration (yellow); (3) northward migration (blue). The remainder of the pathways are displayed in white. Note for display purposes, the non-migratory portions of pathways have been smoothed to remove some extreme observations. The tracks in panels (a–d) are those of turtles E, G, K and L, respectively, from Figs 3–5. Note the northward migratory phase was not observed for turtle E in panel (a).

actual endpoint was the position of the last observation. In seven cases, we have no observations on the northward migratory phase. To estimate day vs. night travel rates, we first determined whether each observed position corresponded to day or night periods as defined by local sunrise and sunset times. This calculation can be made easily, as Argos provides the date and time associated with each observed position.

ESTIMATING TRAVEL RATES

To quantify travel rates during day and night periods, we fitted a two-dimensional random-walk-with-drift

model to the position data. Written in state–space form (see Jonsen *et al.* 2003; for further background details), the process model for turtle *j* is:

$$\mathbf{x}_{t,j} = \mathbf{x}_{t-1,j} + \boldsymbol{\alpha}_{p(t),j} + \boldsymbol{\eta}_j \tag{eqn 1}$$

where the time step *t* represents the transition from a day-time period to a night-time period, and so on. The state $\mathbf{x}_{t,j}$ is the position at time *t* and $\boldsymbol{\alpha}_{p(t),j}$ is the drift term with subscript *p(t)* denoting the period (day = 1 or night = 2) at time *t*. The random variable $\boldsymbol{\eta}_j$ represents the process variability. We assume that the process variability is constant between day and night and that

it is Gaussian and uncorrelated through time, e.g. $\boldsymbol{\eta}_j \sim N(0, \boldsymbol{\sigma}_j^2)$. The unobserved states $\mathbf{x}_{i,j}$ and the parameters $\boldsymbol{\alpha}_{p(t),j}$ and $\boldsymbol{\eta}_j$ are all two-dimensional vectors representing the longitudinal and latitudinal directions (hence the bold notation). Note that $\boldsymbol{\alpha}_{p(t),j}$ is scaled to account both for differences in duration of the day and night periods and for the earth's curvature. We account for differences in duration of day and night periods as follows; $\boldsymbol{\alpha}'_{p(t),j} = \boldsymbol{\alpha}''_{p(t),j} h_{p,j}$, where $h_{p(t),j}$ is the duration (in hours) of the day or night period. We also scale $\boldsymbol{\sigma}_j$ in this manner. We account for the earth's curvature by rescaling the longitudinal element of $\boldsymbol{\alpha}_{p(t),j}$ so that:

$$\boldsymbol{\alpha}_{p(t),j,1} = \boldsymbol{\alpha}'_{p(t),j,1} \frac{1}{\cos(\mathbf{x}_{t-1,j,2} \pi/180)}, \tag{eqn 2}$$

where $\boldsymbol{\alpha}_{p(t),j,1}$ is the longitudinal travel rate in period $p(t)$ for turtle j and $\mathbf{x}_{t-1,j,2}$ is the estimated latitude at time $t - 1$ for turtle j . Thus $\boldsymbol{\alpha}_{p(t),j}$ represents the mean travel rate during day or night periods and $\boldsymbol{\sigma}_j$ represents the stochasticity in travel rate.

Of prime interest is the ratio of day-to-night travel rates δ . We derive this value on the log-scale as $\delta_j = \log r_{1,j} - \log r_{2,j}$, where $r_{p(t),j} = |\boldsymbol{\alpha}_{p(t),j}|$.

This approach requires the assumption that the earth is globally spherical, provided by eqn 4, but locally flat. Here we define local as the typical distance travelled during a day or night period. Note that $r_{p(t),j}$ is an estimate of travel rate in period $p(t)$ over the entire pathway of turtle j . However, if one is interested in estimating day and night travel rates on a day-to-day basis one could fit a correlated random walk state-space model (e.g. Jonsen *et al.* 2005) with a shorter time step and then calculate travel rates for different periods of the day from the state estimates.

ROBUST METHODS

A feature common to Argos and other types of remotely sensed tracking data is that locations are observed irregularly through time. In order to link the process model (eqn 1) to the observations we need a method to 'regularize' the data because the state transitions are assumed to occur over regular time intervals. We let i be an index for the locations observed during each day or night period, i.e. $i = (0, 1, 2, \dots, n_{i,j})$, where $n_{i,j}$ is the number of locations observed during the time interval between t and $t + 1$ for turtle j . Our observation equation is given by:

$$\mathbf{y}_{i,t,j} = \mathbf{x}_{i,t,j} + \boldsymbol{\epsilon}_{i,t,j} \tag{eqn 3}$$

where $\mathbf{y}_{i,t,j}$ are the locations observed during the day or night period t and $\boldsymbol{\epsilon}_{i,t,j}$ is a random variable representing the estimation error associated with a location's quality class. This formulation allows for the possibility of having multiple observation equations for each transition equation. A particular challenge for analysing many kinds of movement data is the need to deal with extreme observations (Fig. 2, see anomalous, large deviations in tracks) in an objective fashion. Extreme observations can be removed a priori by filtering on a maximum travel rate (e.g. McConnell, Chambers & Fedak 1992). This approach can lead to loss of information because the filters remove suspect observations; more importantly, it does not deal with biologically plausible but none the less erroneous observations. Fortunately, the Argos satellite system classifies each location into one of six quality classes and we can use this information to account for uncertainty in all the observations without

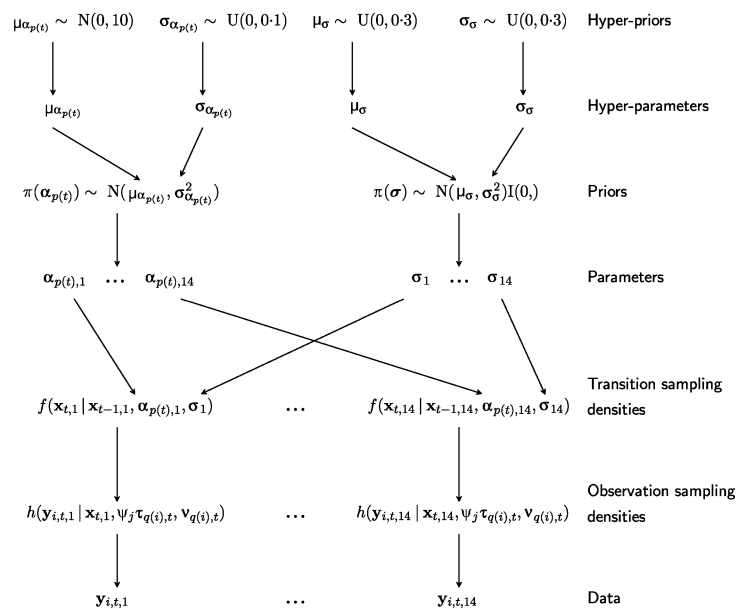


Fig. 2. Hierarchical structure of the state-space model for estimation of day-time travel rate $\boldsymbol{\alpha}_{p(t),j}$, the log ratio of day-to-night travel rates δ_j , and the process variability $\boldsymbol{\sigma}$. Note that \mathbf{x}_i are the unobservable states and \mathbf{y}_i are the data. The notation $I(0,)$ in the prior for $\boldsymbol{\sigma}$ denotes the constraint $\boldsymbol{\sigma} > 0$, i.e. a half-normal distribution. The transition and observations sampling densities are sampled from $t = 1, \dots, T_j$, where T_j is the maximum number of time steps for the i th individual. We do not show the ψ_s to simplify the figure.

resorting to a priori filtering methods (Jonsen *et al.* 2005). Jonsen *et al.* (2005) show that Argos location errors are non-Gaussian and that a t -distribution provides a far better fit to the location errors. The t -distribution is robust because it has the effect of making extreme values less unlikely, thereby ensuring that outliers do not have undue influence. We therefore choose to use t -distributions to model the estimation error in eqn 3. That is, for estimation errors in latitude or longitude of quality class q ($q = 1, \dots, 6$, see below) we let $\mathbf{e}_{q(i),i,j} \sim t(0, \boldsymbol{\tau}_{q(i),i,j}, \mathbf{v}_{q(i),i,j})$, where $\boldsymbol{\tau}_{q(i),i,j}$ is the scale parameter and $\mathbf{v}_{q(i),i,j}$ is the degrees of freedom. Rather than estimate the parameters of the 12 t -distributions within the state-space model, we make use of an independent data set (Vincent *et al.* 2002) to obtain maximum likelihood estimates for each of the six Argos error classes in the two directions (see Jonsen *et al.* 2005, Appendix A). This allows us to fix the parameters of each estimation error distribution within the state-space model, thereby reducing the total number of parameters to be estimated. Because we limited our analysis to individuals with similar tags and settings, one could assume that the estimation errors are constant among tags. However, there may be variability in performance even among identically configured transmitters of the same model type. Therefore, we include a scaling factor ψ_j that adjusts the scale of the estimation error $\boldsymbol{\tau}$ up or down for individual transmitters:

$$\mathbf{y}_{i,t,j} = \mathbf{x}_{i,t,j} + t(0, \psi_j \boldsymbol{\tau}_{q(i),i,t}, \mathbf{v}_{q(i),i,t}). \quad \text{eqn 4}$$

Note that ψ_j scales each of the $\boldsymbol{\tau}$ s identically. We examine two alternate assumptions; first, that $\psi_j = 1$ for all transmitters, and secondly, that ψ_j differs between latitude and longitude (see 'Alternate models', below).

HIERARCHICAL BAYES ANALYSIS

Thus far we have described a framework that allows state-space models to be fitted to individual pathways but without an explicit method for combining results to infer among-individual variation in travel rates. Such variation implies an underlying, biologically meaningful distribution of travel rates. We incorporate this idea formally into our analysis by formulating a model where the parameters $\boldsymbol{\alpha}_{p(i)}$ and $\boldsymbol{\sigma}$ have a hierarchical structure. Our state-space approach is fully Bayesian, consequently it is straightforward to specify the hierarchical structure by placing hyper-priors on the priors of the model parameters (Fig. 2).

We assume the $\boldsymbol{\alpha}_{p(i),j}$ s come from Gaussian prior distributions with mean $\boldsymbol{\mu}_{\text{cap}(i)}$ and variance $\boldsymbol{\sigma}_{\text{cap}(i)}^2$. Following Gelman (2005), we use a half-normal prior distribution centred on 0 for the process variability, $\boldsymbol{\sigma}_j$, with mean $\boldsymbol{\mu}_{\boldsymbol{\sigma}}$ and variance $\boldsymbol{\sigma}_{\boldsymbol{\sigma}}^2$. Parameter values for the hyper-priors were chosen initially to yield extremely broad distributions and then systematically changed to yield narrower (but still vague) distributions. The results were consistent across all hyper-prior parameter values examined.

IMPLEMENTATION

We use the freely available software WinBUGS (version 1.4.1, Spiegelhalter *et al.* 2004) to implement the robust hierarchical state-space model. The software uses Markov chain Monte Carlo (MCMC) methods to estimate the joint posterior distribution of the model parameters. A total of 35 000 samples were generated in each of two chains; the first 20 000 were discarded as a 'burn-in' and every fifth sample thereafter was retained to reduce autocorrelation, yielding 6000 samples from the joint posterior. By deriving δ within the WinBUGS model, we obtain marginal posterior distributions for δ_j , μ_{δ} and the Bayes predictive distribution for δ . The model code is included in Appendix S1. Estimates obtained from the marginal posterior distributions of the δ_j s (denoted $\hat{\delta}_j$) are the key parameters of interest and are presented as raindrop plots (Barrowman & Myers 2003). We also present the absolute day and night travel rates $r_{p(i),j}$. Similar plots for the process variability $\boldsymbol{\sigma}_j$ are presented in Appendix S2. These plots convey information about the shape of the posterior distributions that conventional point estimates with credible intervals cannot (see Barrowman & Myers 2003 for interpretation of raindrop shapes). In addition, we present the hierarchical Bayes means (with 95% credible intervals) $\hat{\mu}_{\delta}$ and \hat{r}_p as well as the corresponding Bayes predictive distributions. The Bayes predictive distributions summarize the information about model parameters for an unobserved data set, given the priors, the model structure and the observed data (Efron 1996; Carlin & Louis 2000).

COMPARATIVE ANALYSES

Focusing on the southward migratory segment of the pathways, we illustrate the advantage of taking a hierarchical approach to state-space estimation by comparing estimates with those from two alternative analyses. First we take a conventional approach to calculate the ratio of day-to night-time travel rates from the original data. We use a method similar to that of Luschi *et al.* (1998), who calculated day- and night-time travel rates of migrating green sea turtles (*Chelonia mydas*). We first use the travel rate filter of McConnell *et al.* (1992) to remove any locations that infer rates exceeding 5 km h⁻¹ (James *et al.* 2005c). We then calculate the travel rates (log-scale) between locations within any given day or night period and present the mean ratio with 95% confidence intervals. Secondly, we fitted the state-space model described earlier in a non-hierarchical fashion to the 14 turtle data sets. That is, we fitted the state-space model separately to each of the individual turtle tracks. For both the conventional and non-hierarchical state-space analyses, we conduct a random effects meta-analysis (e.g. Barrowman *et al.* 2003) to combine the individual estimates of the log ratio of day- to night-time travel rates.

ALTERNATE MODELS

Our focus is on testing the hypothesis of diel variation in travel rates, therefore we are interested primarily in determining how well we have estimated the μ_{δ} . We assess the robustness of $\hat{\mu}_{\delta}$ to alternative model parameterizations by fitting five additional models; four models are identical to the default model except for a single parameter and the fifth model is a one-dimensional analogue of the default model (Appendix S2).

Results

The hierarchical mean of the log ratio of day–night travel rates, $\hat{\mu}_{\delta}$, indicates no difference while the turtles are foraging in northern waters (Fig. 3a), significantly faster daytime rates on the southward migration (Fig. 3b) and equivocal evidence for slightly faster daytime rates on the northward migration (Fig. 3c).

FORAGING IN NORTHERN WATERS

There is considerable uncertainty in the $\hat{\delta}_j$ and $\hat{\mu}_{\delta}$ for the northern foraging phase (Fig. 3a), suggesting greater variability in behaviour exhibited by the turtles than in

the other two phases. This is not surprising, because the turtles are predominantly foraging and travelling between foraging sites while in northern waters. The $\hat{\mu}_{\delta}$ appears to be influenced by a single $\hat{\delta}_j$ estimate suggesting substantially higher night- vs. daytime travel rates (Fig. 3a, turtle M). However, this individual initiated its southward migration about 1 week after tagging, providing few data for estimation of δ_j during this phase. Along with female M, two others (F and H) nested immediately following their southward migration and had higher travel rates than any other individuals (Fig. 4a). These three turtles were tagged ≥ 1 week later in the northern foraging phase than other turtles and initiated their southward migration shortly after tagging.

SOUTHWARD MIGRATION

During the southward migration all but three turtles had higher travel rates during the day (Fig. 3b, turtles C, H and M). There is no clear evidence for differences in the day-to-night ratios between the sexes or between individuals that bred immediately following their southward migration and those that did not. However, individuals that did breed had nominally higher travel rates during at least the daytime than individuals that did not breed (Fig. 4b).

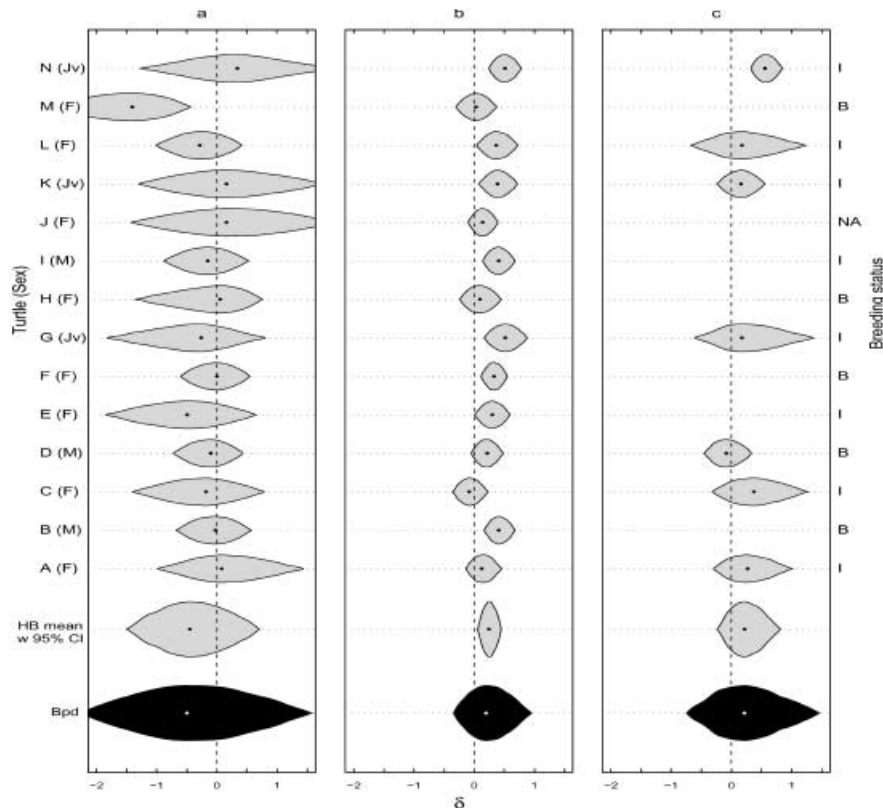


Fig. 3. Raindrop plots (Barrowman & Myers 2003) summarizing the 95% credible intervals of the posterior densities of $\hat{\delta}_j$, the log ratio of day-to-night travel rates of leatherback turtles during the predominant phases of their migratory cycle: (a) northern foraging, (b) southward migration and (c) northward migration. The sex and breeding status (where known) of each turtle are displayed on panels (a) and (c), respectively. The point within each raindrop indicates the posterior mode. The taller raindrops in the bottom two rows of the panels are hierarchical summaries, and are interpreted differently from the raindrops for the individual turtles. The ‘mean w 95% CI’ raindrops are the estimated hierarchical means $\hat{\mu}_{\delta}$ with 95% credible intervals. The raindrops for the Bayes predictive distributions (Bpd) are shaded in black to emphasize that they are different from the mean. These distributions summarize all the information available to predict δ_j for an unobserved turtle.

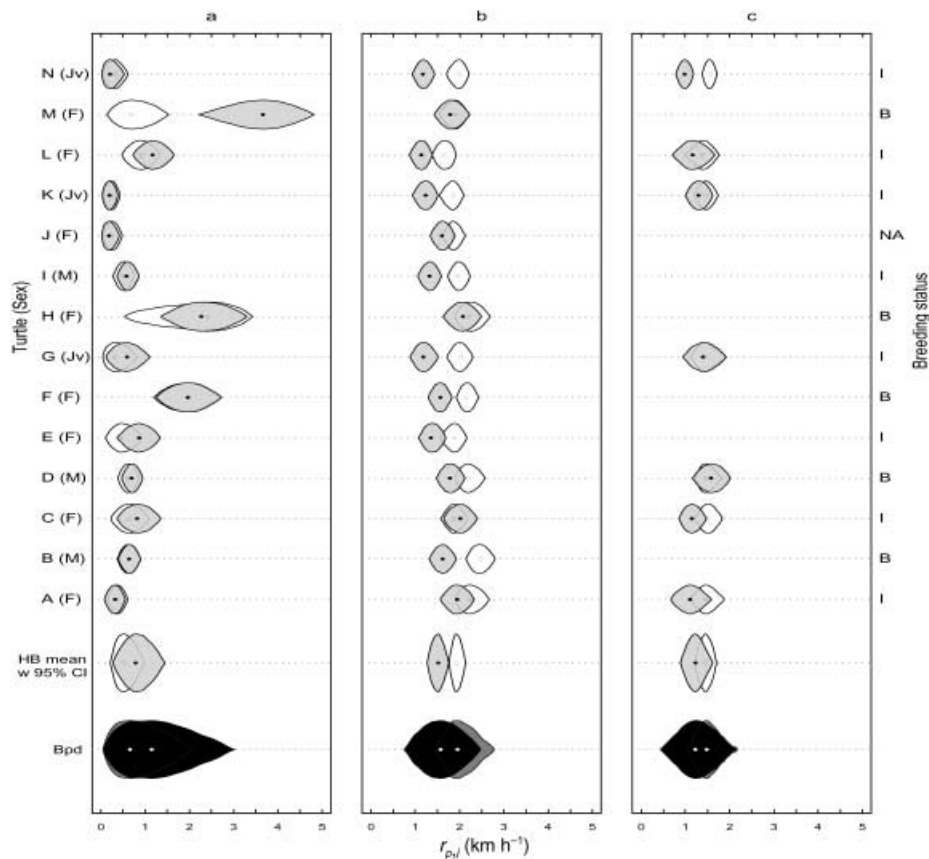


Fig. 4. Raindrop plots (Barrowman & Myers 2003) summarizing the 95% credible intervals of the posterior densities of $\widehat{r}_{p,j}$, the absolute day (white) and night (grey) travel rates of leatherback turtles during the predominant phases of their migratory cycle: (a) northern foraging (b) southward migration, and (c) northward migration. The sex and breeding status (where known) of each turtle are displayed on panels (a) and (c), respectively. The point within each raindrop indicates the posterior mode. The taller raindrops in the bottom two rows of the panels are hierarchical summaries, and are interpreted differently from the raindrops for the individual turtles. The ‘mean w 95% CI’ raindrops are the estimated hierarchical means $\widehat{\mu}_p$ with 95% credible intervals. The raindrops for the Bayes predictive distributions (Bpd) are shaded-in darker (day = grey, night = black) to emphasize that they are different from the mean. These distributions summarize all the information available to predict $r_{p,j}$ for an unobserved turtle.

NORTHWARD MIGRATION

Although there is slight evidence for faster daytime travel rates during the northward migration (Fig. 3c), the ratio $\widehat{\mu}_\delta$ is less than that estimated from the southward migration and the credible interval contains 0 (Fig. 3b). This equivocal evidence is due most probably to a reduced number of pathways that could be analysed and to substantial segments of missing data in four of the seven pathways that were analysed (Fig. 3c, turtles A, C, G and L). The latter deficiency is supported by the relatively large and uncertain $\widehat{\sigma}_{i,j}$ ’s (Appendix S2). It is also possible that while on the northward migration the turtles engage in somewhat different behaviours than on the southward migration. Travel rates were similar but slightly slower overall to those estimated for the southward migration (Fig. 4c).

COMPARATIVE ANALYSES

The conventional analysis of migratory phase B suggests that one individual had travel rates that were significantly faster during the day (Fig. 5a). The random effects mean for the day-to-night ratios (0.03 ± 0.05 , 95% CI)

suggests that on average the turtles’ travel rates are slightly faster during the day. However, the random effects variance is undefined, suggesting no heterogeneity in the ratios. In several cases we cannot estimate the correct sign of the log-ratio of day-to-night travel rates [compare panels (a) and (c), Fig. 5]. The non-hierarchical state–space analysis indicates that there is indeed heterogeneity among the ratios and that several individuals clearly moved faster during the day than at night (Fig. 5b). The random effects mean and variance estimates confirm this, the former suggesting a much higher overall ratio (0.23 ± 0.12 , 95% CI) than that obtained from the *ad hoc* analysis. There was, however, a lack of convergence for the $\widehat{\delta}_i$ ’s for two pathways (Fig. 5b, turtles I and L). The hierarchical Bayes state–space analysis reveals a similar overall pattern to the nonhierarchical analysis, but note the reduced uncertainty in the individual estimates (Fig. 5c). The $\widehat{\mu}_\delta$ is similar to the random effects mean calculated from the non-hierarchical estimates ($\widehat{\mu}_\delta = 0.25$, $0.07–0.46$, 95% CI); however, the Bayes predictive distribution suggests that a slightly broader range of values are plausible for unobserved turtles than does the random effects distribution from Fig. 5(b). This latter difference is expected

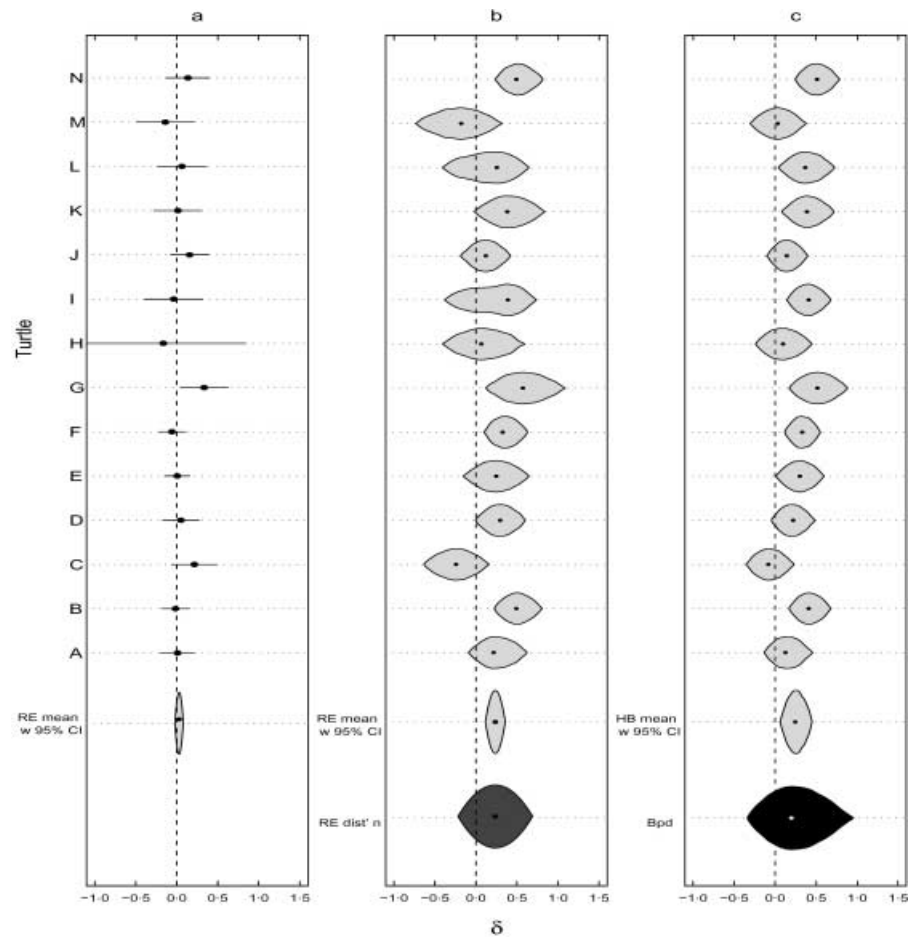


Fig. 5. Comparison of $\hat{\delta}_j$, the log ratio of day-to-night travel rates for (a) a conventional calculation of travel rates from *ad hoc* filtered data, (b) non-hierarchical state–space model estimates of δ_j and (c) hierarchical state–space model estimates of δ_j . The results presented are for the southward migratory segments only. The ratios presented in (a) are means with 95% confidence intervals, and those presented in (b) and (c) are posterior modes with 95% credible interval raindrops. Note there is no random effects variance presented in (a) because the estimate was 0.

because the hierarchical Bayes model accounts for uncertainty at all levels of the hierarchical structure (Fig. 2), whereas the random effects meta-analysis does not.

ALTERNATE MODELS

Comparison of the $\hat{\mu}_\delta$ (Appendix S2) from the main and alternate models shows that the results are similar, except in comparison with model D ($\psi = 1$). This latter result indicates that variability in performance among transmitters is a critical feature influencing parameter estimation and must be treated explicitly in the model or by estimation from a more comprehensive independent data set (e.g. Jonsen *et al.* 2005) than is currently available to us. On balance, however, our results are robust to different model formulations.

Discussion

We have illustrated how information can be extracted from complex, noisy time-series data using robust hierarchical state–space methods. The methods are flexible

enough to deal with the complex features of the data and provide estimates that cannot be obtained by conventional, *ad hoc* approaches. We find compelling evidence for diel variation in travel rates during southward migrations of leatherbacks tagged in Canada, equivocal evidence for a similar pattern during the return, northward migration, and no evidence while the turtles are foraging in northern waters. Estimates of the day-to-night ratio in travel rates suggest that 11 of the 14 turtles analysed move southward faster during the day than at night. These results stand in stark contrast to those obtained from a conventional approach, suggesting essentially no difference. This is not surprising, given that such conventional approaches are reliant upon removal of suspect observations, do not use an underlying probability model for the remaining uncertainty in the data and do not typically account for temporal dependencies in the data (but see Hays *et al.* 2001b).

MODELLING APPROACH

The statistical analysis of remotely sensed movement data is complicated by the serial correlation and often

irregular timing of observations and by the non-constant and potentially non-Gaussian nature of estimation errors. A number of conventional approaches can be used for dealing with some of these complicating features of the data. These include removing observations that suggest a travel rate in excess of some predetermined maximum (e.g. McConnell *et al.* 1992) and reducing serial correlation by decreasing the resolution of the data (e.g. Turchin 1998). Unfortunately, most of these approaches lead to loss of information through removal of 'noisy' data and this can become a serious impediment when the data are comprised primarily of poor-quality observations (as is often the case for marine animals, e.g. Vincent *et al.* 2002). Remotely sensed data are expensive and time-consuming to collect, therefore it makes little sense to discard observations needlessly. Furthermore, upon using these conventional methods, we still require tools for reliably estimating parameters. We must account for the uncertainty in the data. Our comparative analyses show that estimation of relatively simple behaviours such as day vs. night travel rates can be misleading when uncertainty in the data is ignored. The robust hierarchical Bayes state-space approach that we advocate addresses all of these issues. The state-space model avoids the need to remove 'bad' observations by using a recursive procedure where predictions of the unobserved states are made via a process model and these predictions are refined by combining them with current observations via Bayes' rule (see Jonsen *et al.* 2003). This approach is typically most useful when the error distribution(s) of the data are estimated independently, as is the case here. The robust approach reduces the influence of extremely poor-quality observations on parameter estimation. By taking a hierarchical Bayes approach to modelling migratory travel rates we assume that individual animals exhibit some degree of similarity in their migratory behaviour; individual travel rates come from a common distribution. The hierarchical model is the formal representation of this assumption (Fig. 2), with the goal being to estimate not only the parameters for the individual data sets but also those at a higher level(s) in the model. There are two principle advantages of this approach over a non-hierarchical analysis. First, hierarchical models use information from all the data sets to estimate parameters at each of the levels in the hierarchy (Gelman *et al.* 2004) and this has the effect of reducing uncertainty in parameter estimates at the individual data set level (e.g. Barrowman *et al.* 2003). Secondly, hierarchical Bayes models allow quantification of all the uncertainty in the parameter estimates, i.e. at all levels of the hierarchy, via the Bayes predictive distribution (the induced prior, Efron 1996). The hierarchical Bayes approach provides a more faithful estimate of uncertainty in model parameters because, unlike frequentist hierarchical models, uncertainty is assumed to be present at all levels of the hierarchy. Consequently, the Bayes predictive distribution represents our best estimate of uncertainty in the parameter estimates. When the hierarchical Bayes

approach is combined with a state-space analysis, parameter uncertainty is reduced further by accounting simultaneously for estimation errors and variability in the modelled process. In future applications, we would like to use a model selection approach that allows us to distinguish among alternative models or hypotheses. Unfortunately, a Bayesian analogue of Akaike's information criterion (AIC), deviance information criterion (DIC; Spiegelhalter *et al.* 2002) does not work with robust models because the likelihood is not log-concave. This situation results in negative estimates of the effective number of parameters (p_D , Spiegelhalter *et al.* 2002) which is clearly invalid. Cross-validation methods could be used instead but these are of most benefit when the goal of the modelling exercise is prediction. Here our primary interest is reliable parameter estimation for the purposes of testing a simple hypothesis. Our approach is not to find the best model or subset of models, but rather to ensure that estimates of key parameters are robust both to data errors and reasonable differences in model formulation.

LEATHERBACK DIEL TRAVEL RATES

The diel differences in leatherback travel rates on the southward migration are consistent with diel differences in diving behaviour observed during the same migratory phase (James *et al.* in press). Migrating leatherbacks spend extended periods at depth at night, whereas more time is spent at or near the surface and dive durations are generally shorter during the day (James *et al.* in press). This pattern of diving may be indicative of foraging activity and is consistent both with that observed in tropical waters, both for gravid females (Eckert *et al.* 1989) and nesting females (Hays *et al.* 2004a), and with that observed in waters off South Africa (Sale *et al.* 2006). Additionally, the lack of diel travel rate patterns in northern waters shown here is consistent with diving patterns observed in the same region (James *et al.* in press). On their southward migration the turtles may be responding to the diel vertical migration of their gelatinous prey by foraging at night, when prey have ascended to depths where they can be most profitably exploited. In contrast, turtles migrating northward appear not to show as strong a diel pattern in travel rates, perhaps because they are foraging more often in response to increasing prey abundance as they near the northern foraging area (James *et al.* 2005b). However, we cannot examine these hypotheses in any detail because the behaviour, species composition and distribution of leatherback prey remains poorly understood. A complementary explanation for the diel differences in travel rate during southward migration may be related to the leatherback's ability to maintain a chosen course while travelling between foraging areas or between foraging and breeding areas. Leatherbacks may use both a solar and a geomagnetic compass (Lohmann & Lohmann 1996; Eckert 2002b). For other species, such as migratory songbirds (Wiltschko & Wiltschko 2005) and

Eastern red-spotted newts (*Notophthalmus viridescens*) (Phillips *et al.* 2001), a geomagnetic compass sense can be influenced by the wavelength and/or intensity of ambient light. This influence of light on the geomagnetic compass is mediated via the pineal gland in at least some reptiles and amphibians (Deutschlander, Phillips, & Borland 1999), and the conspicuous nature of this structure in leatherbacks (McDonald *et al.* 1996) does not rule out the possibility that it plays a similar role here. Alternatively, leatherbacks migrating southward may simply be choosing to rest at night due to the physiological demands of maintaining relatively high travel rates during the day, as was suggested for green turtles (Hays *et al.* 2001a). On the northward migration, where the diel pattern is less distinct, overall travel rates of leatherbacks are on average 0.5 km h⁻¹ slower than on the southward migration. However, resting seems an unlikely explanation for diel differences in leatherback travel rates, given that increased diving activity is observed during the night (James *et al.* in press). Regardless of the underlying mechanism(s) for diel differences in movement rate, there are potential conservation implications for this behaviour, as the leatherback migration routes analysed here traverse fishing areas. These include waters south-west of Bermuda and north and north-east of the Lesser Antilles where there is considerable effort by the US pelagic longline fleet (Witzell 1999). Further analysis of the spatial and temporal overlap of turtle movements and fishing effort, e.g. from fisheries targeting night-active species such as swordfish, is required to clarify how the diel behaviour of leatherbacks may put them at risk in these areas. Although we did not account formally for sex or breeding status in our hierarchical model, we do find some evidence that individuals have higher daytime travel rates while migrating south to mating and nesting sites than do individuals that did not breed following their southward migration. Although the evidence is not consistent in all cases, the result is interesting because little is known about how breeding condition may influence the migratory cycle of male or female sea turtles. We might expect turtles that breed in the year following foraging at high latitudes to both depart the foraging area earlier and to travel faster during southward migration than turtles in an interbreeding year. Male turtles arriving earlier in the breeding area will maximize their reproductive fitness (James *et al.* 2005a) and this may also be true for females.

Conclusions

We have demonstrated how the use of robust hierarchical state–space models can reveal features of the migratory behaviour of leatherback turtles that hitherto were obscured by biological and statistical complexities present in the remotely sensed data. This analysis leads to interesting hypotheses regarding the mechanistic basis of migratory behaviours and their broader conservation implications, which merit empirical examination. For example, recent advances in telemetry technology (e.g.

Wilson & Liebsch 2003; Hays *et al.* 2004c) could potentially be used to test the hypothesis that leatherbacks feed at night during migration. Furthermore, new sensors that measure travel speed (e.g. 9000X SRDL, SMRU, St Andrews, Scotland) can provide valuable information that can be incorporated formally into our state–space modelling approach, extending the types of analysis possible. The framework presented here enables researchers to: (1) infer underlying pattern from error prone, complex data without discarding suspect observations or otherwise reducing information; and (2) combine analyses of individual data sets in a single model, thereby improving estimation at the individual level by ‘borrowing strength’ from all the data and accounting for uncertainty at a number of hierarchical levels. Although we have focused on inferring movement behaviour, the framework is applicable to any form of temporally sampled data, including other types of behavioural data and population data of various types (e.g. Newman *et al.* 2006).

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>

Appendix S1. WinBUGS code for the default model.

Appendix S2. Alternate model: details and results.

Table S2.1. Summary of alternate models fit to evaluate the robustness of the key parameters $\hat{\mu}_s$ and $\hat{\delta}_j$

Table S2.2. Assessment of $\hat{\mu}_s$ sensitivity to alternate model structures for the three phases of the migratory cycle.

Appendix S3. Process variability plots from default model.

Fig. S3. Raindrop plots summarizing the 95% credible intervals of the posterior densities of $\hat{\sigma}_{\delta_j}$ (process variability) from the default model fit to (a) northern foraging, (b) southward migration, and (c) northward migration phases of the migratory cycle.