

Appendix A. Comparison of two behavioral-switch models for identifying two movement states in a loggerhead movement trajectory.

The models of Morales et al. (2004) and Jonsen et al. (2005) both allow locations within a movement trajectory to be characterized as belonging to one of two (or more) behavioral states. Under both multi-state models, the complete movement path is assumed to come from a mixture of two behavioral processes, with each process being described by a different set of parameters that must be estimated from the data.

In our models based on methods by Morales et al. (2004), the two behavioral processes are distinguished by differences in their mean movement rates ( $\mu_b$ ) and in their variance of turn angles ( $\omega_b$ ). These parameter estimates thus enabled us to easily characterize segments of a turtle's trajectory as "fast and straight" (large  $\mu_b$  and large  $\omega_b$ ) vs. "slow and tortuous" (small  $\mu_b$  and small  $\omega_b$ ), for example. These qualifications facilitated a cautious biological interpretation of these two states as intensive searching or foraging within resource patches and extensive or exploratory searching between resource patches, respectively. Similar rate/angle based interpretations of search behavior have been applied in many other movement-modeling frameworks (e.g., Fauchald and Tveraa 2003, 2006, Jonsen et al. 2005, Royer et al. 2005, Bailey and Thompson 2006). Importantly, if either rate *or* turn angle distribution does not differ substantially between two behavioral states, the states may still be distinguished by differences in the other parameter (e.g., fast vs. slow or straight vs. tortuous).

In the behavioral-switch model by Jonsen et al. (2005), the two behavioral processes are distinguished by differences in their mean turn angles ( $\theta_b$ ) and in the extent to which successive movements are correlated ( $\gamma_b$ ), i.e., how similar are the movement distances *and* directions from location to location. For simplicity, and because we would not expect a particular behavior to be

associated with a particular “handedness”, we will assume that mean turn angle is zero for both states. Thus, estimates of  $\gamma_b$  are used to characterize different portions of a trajectory as “more” or “less strongly correlated movement”. Straight-line or directional movement will consist of more similar successive turn angles – centered near zero – than will tortuous movement (Turchin 1998, Zollner and Lima 1999, Jonsen et al. 2005). However,  $\gamma_b$  does not reflect differences in movement rate between two behavioral types, only differences in the similarity (correlation) of successive movement lengths. Thus, two states – one with consistently short steps and one with consistently long steps – could be indistinguishable on the basis of  $\gamma_b$ , if distances and turn angles are similarly correlated, or if differences in these attributes between the two states are masked by process error described in the covariance matrix  $\Sigma$ . This, we believe, was problematic for using the Jonsen model to distinguish behavioral states in our system, because juvenile loggerhead tracks in the Mediterranean are very “noisy” and behavioral states seemed to differ primarily with respect to their rates, and less so with respect to turn angle distribution (Fig. 6, 9) or correlation between successive step lengths. We further illustrate the problem in two ways:

First, we used the methods of Jonsen et al. (2005) to simulate animal trajectories for 200 time steps that were based on only a single behavioral process (generated from a single behavioral state). Parameters for the simulations were set similar to values estimated for real data (see Appendix 2). We found that many trajectories, even though generated by this single autocorrelative process, contained a mix of sections reminiscent of foraging-type (intensive search) movements, connected by sections that looked like exploratory (extensive search) movements (Figure A1.1). These paths appeared superficially similar to some of our loggerhead paths (Figs. 1, 2), and they exemplify how movement paths composed of multiple biological processes might be described by a single correlated walk model under this framework.

Second, we fit state-space switching-models (no covariates) from both frameworks (Morales et al. 2004, Jonsen et al. 2005) to one of our more visually interpretable turtle trajectories. We fit the track by itself (i.e., parameters estimated from this turtle's data only), and by using a hierarchical model (i.e., parameters estimated from model containing all turtle data). In the non-hierarchical setting, both frameworks assigned a large majority of points to a single behavioral state, and in a superficially similar way. Under the Morales framework, most points were assigned to the intensive-search state (state 1; average movement rate = 22 km/day,  $\omega_1 = 0.47$ ), with a small stretch of 7 consecutive locations assigned to the exploratory state (state 2; average movement = 76 km/day,  $\omega_1 = 0.66$ ; Figure A1.2, bottom panel). Under the framework of Jonsen et al., most points were assigned to a state (state 1) characterized by a moderate degree of autocorrelation ( $\gamma = 0.53$ ) and mean turn angle near zero ( $\theta = 0.14$  radians; Figure A1.2, top panel). Thirteen consecutive locations were assigned to the other state (state 2), including the seven points assigned to state 2 in the Morales model. These 13 locations were characterized by weak autocorrelation ( $\gamma = 0.18$ ) and a turn angle  $\theta = 0.59$  radians. We found it difficult to interpret the states distinguished by the Jonsen method. Neither state appeared consistently slower or more tortuous. State 2 included a mix of slow and fast segments, compared to only slow segments in state 1, but if state 2 is to be considered the extensive-search or exploratory state, we would expect it to have a higher value for  $\gamma$  and lower value for  $\theta$ , when in fact the opposite was true. Thus, as with the simulation exercise above, it appeared that different movement types (based on rates and turn-angle distributions), were not well distinguished by their autocorrelative attributes for this turtle.

Under the hierarchical version of both model frameworks, the movement states were again more interpretable to us when using the methods of Morales et al. (2004). Based on this model, state 1 was still the intensive-search state, but the average movement rates for the two

states were more similar (10 km/day vs. 28 km/day) than in the non-hierarchical model, and tortuosity of state 1 was much greater ( $\omega_1 = 0.21$ ,  $\omega_2 = 0.57$ ) in the hierarchical model. Thus, state 1 for this turtle was characterized by discrete clusters of ~10-15 successive locations within a small area (Figure A1.3, bottom panel). Using methods based on Jonsen et al. (2005), the trajectory for this turtle was divided into two segments; the first 22 points were state 2, and the remaining 132 points were state 1. As with the non-hierarchical Jonsen model, it was difficult to interpret these two segments biologically, as both contained short tortuous regions. The state-2 segment visually appeared to reflect faster movement overall (Figure A1.3, top panel), but rate or distance is not a diagnostic or output for this model, and average turn angles were similar for these states ( $\theta_1 = 0.20$ ,  $\theta_2 = 0.21$ ). And although state 2 appeared more directed, it was again state 1 – which contained the tight clusters of probable foraging movements – that was actually the more strongly autocorrelated state ( $\gamma_1 = 0.65$ ,  $\gamma_2 = 0.21$ ). This contrasts sharply with results obtained for hooded seals by Jonsen et al. [2005]), in which the faster more directed state was the more strongly correlated one

In summary, for both non-hierarchical and hierarchical models fit to our Mediterranean loggerhead dataset, we found behavioral types distinguished by the Morales method to be more biologically interpretable than those distinguished by Jonsen methods. For the trajectory used in this example, behavioral types appeared to be best distinguished by differences in rates and turn-angle variance, yet the Jonsen model did not capture these differences in its assignment of behavioral types. In the Jonsen model, the more strongly correlated movement state is expected to depict longer straighter, more directed movements, characteristic of migratory routes or corridors between foraging areas, whereas the less correlated movement state should depict intensive searching within foraging areas. This approach seems to work well for animal trajectories that reflect such discrete behaviors, such as seal and leatherback examples used in

previous analyses (e.g., Jonsen et al. 2005, 2006). However, for animals with “messy” movement pathways that do not consist of discrete “use” and “non-use” areas, but rather seem to consist of higher-use areas connected by wandering, non-directed search pathways, a rate and turn-angle variance approach may be more useful for identifying states with subtle behavioral signatures.

Figure A1.1. Simulated movement paths based on the process equation of Jonsen et al. (2005), with a single behavioral state (mean turn angle  $\theta = 0$ , correlation parameter  $\gamma = 0.4$ , covariance matrix parameters:  $\sigma_x^2 = 0.06$ ,  $\sigma_y^2 = 0.03$ ,  $\rho = 0.07$ ). Ovals indicate portions of the trajectories that seem to reflect “foraging” areas, indicated by shorter or more tortuous movements.

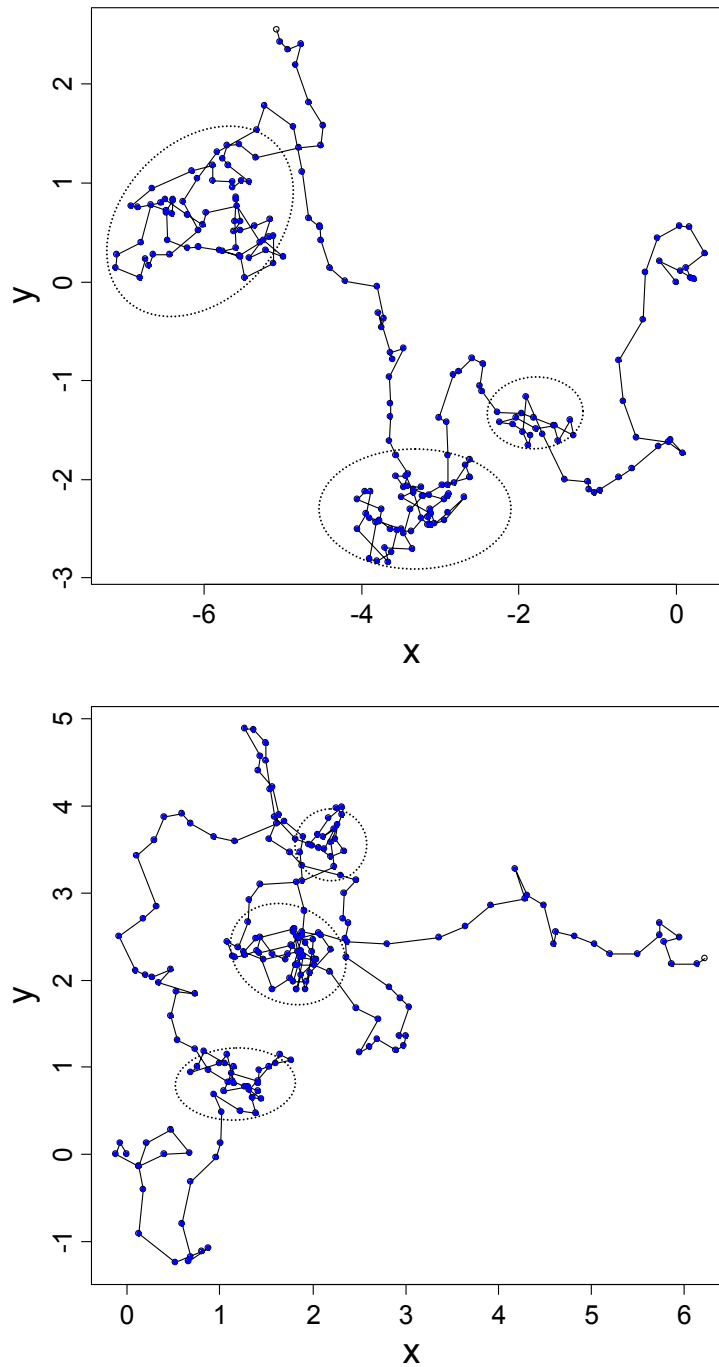


Figure A1.2. Estimated behavioral states of a single loggerhead turtle, from state-space models based on methods of Jonsen et al. (2005; top) and Morales et al. (2004; bottom), fit to Argos satellite tag data from that individual. Estimated locations in both graphs are based on methods of Jonsen et al.

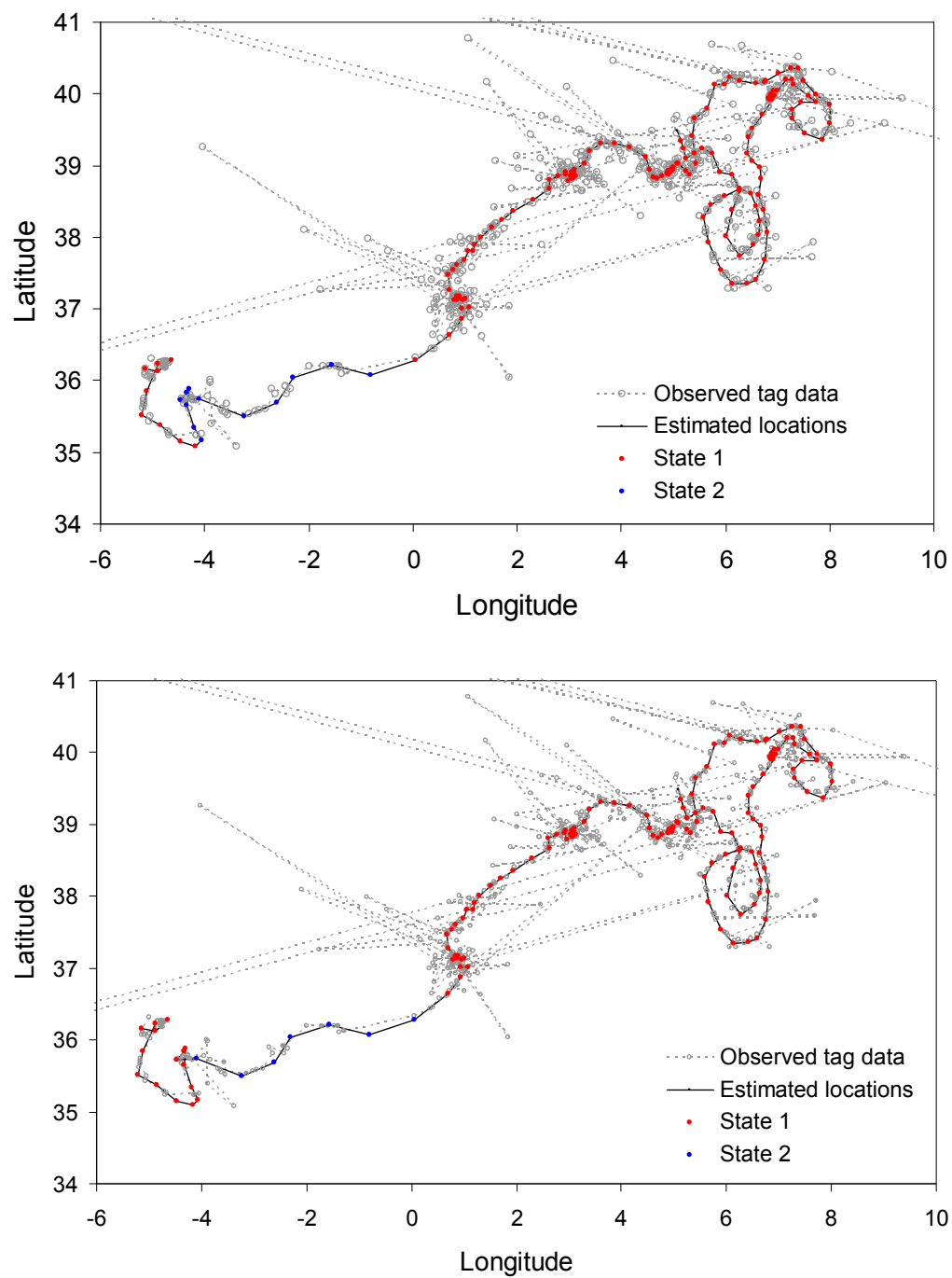
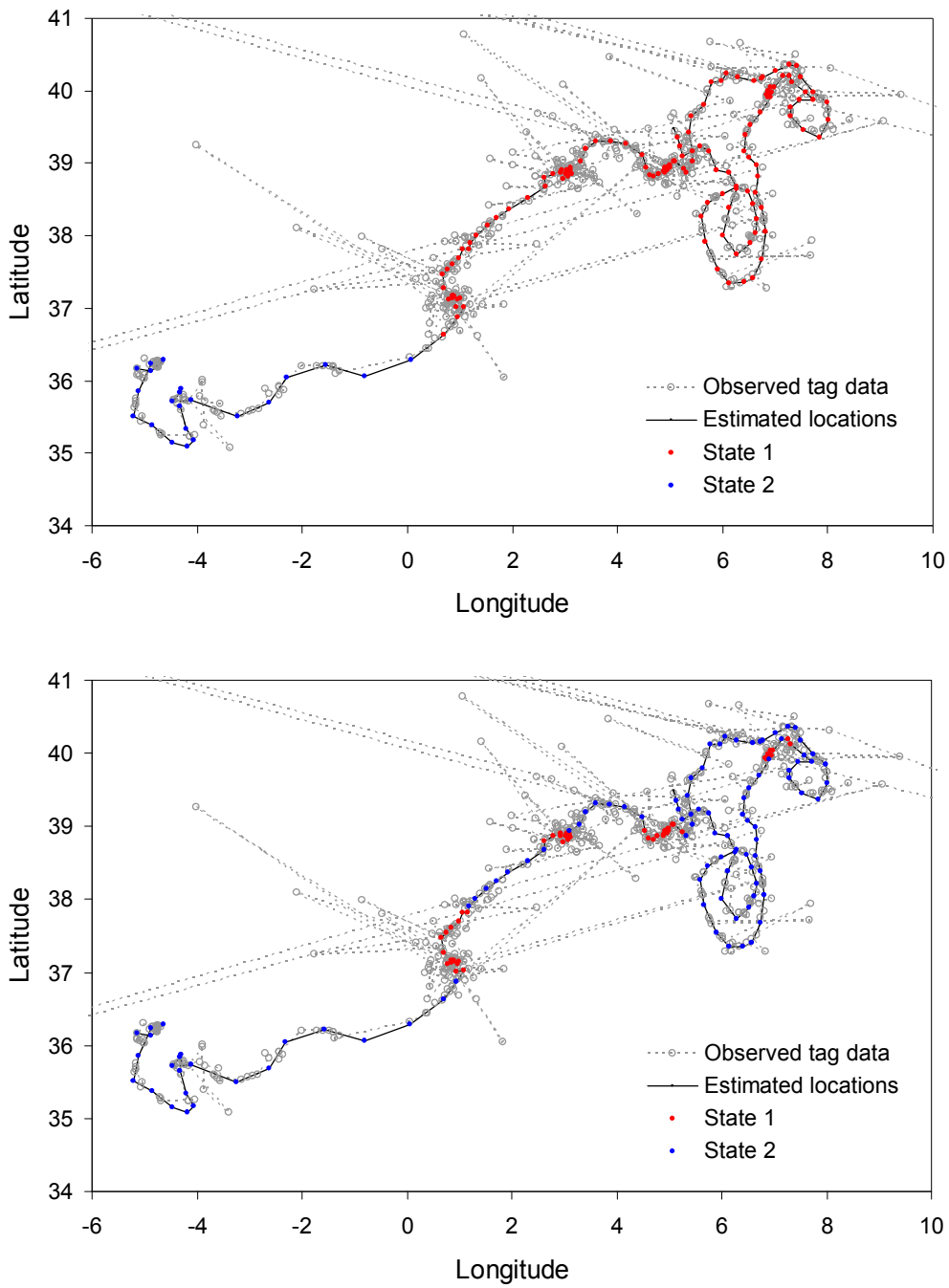


Figure A1.3. Estimated behavioral states of a single loggerhead turtle, from hierarchical state-space models based on methods of Jonsen et al. (2005; top) and Morales et al. (2004; bottom), fit to Argos satellite tag data from 15 turtles. Estimated locations in both graphs are based on methods of Jonsen et al.



Appendix B. Parameter estimates (2.5%, median, 97.5%) from stage-1 hierarchical Bayesian state-space model including 15 turtles, based on methods in Jonsen et al. (2005; also see Table 1). Sample sizes ( $N$ ) are the number of intervals (days) and total satellite-tag locations, for each turtle.  $\theta$  is the mean turn angle.  $\gamma$  is the correlation between movements.  $\psi$  indexes relative tag error (tags vary in quality). Covariance matrix ( $\Sigma$ ) median estimates:  $\Sigma_{1,1} = 0.06$ ,  $\Sigma_{1,2} = 0.003$ ,  $\Sigma_{2,2} = 0.03$ .

		$\theta$	$\gamma$	$\psi$	$N$
Hyper-parameter, $\mu$		(-0.91, 0.04, 0.89)	(0.31, 0.41, 0.52)	NA <sup>a</sup>	NA
Hyper-parameter, $\sigma$		(0.97, 1.41, 1.92)	(0.13, 0.19, 0.27) <sup>b</sup>	NA <sup>a</sup>	NA
Individual	1	(-0.59, -0.23, 0.10)	(0.17, 0.28, 0.38)	(0.22, 0.27, 0.34)	311, 541
Turtles	2	(-3.02, -2.23, 3.00)	(0.06, 0.35, 0.62)	(0.08, 0.12, 0.19)	19, 86
	3	(-0.19, 0.01, 0.25)	(0.37, 0.50, 0.63)	(0.07, 0.08, 0.09)	155, 660
	4	(-2.68, -1.79, 0.10)	(0.02, 0.10, 0.17)	(0.11, 0.13, 0.16)	138, 633
	8	(-0.80, -0.06, 0.90)	(0.04, 0.17, 0.31)	(0.63, 0.76, 0.94)	188, 498
	9	(-0.05, 0.40, 0.78)	(0.34, 0.59, 0.83)	(0.26, 0.65, 1.42)	7, 38
	10	(-2.43, 1.24, 2.84)	(0.05, 0.30, 0.68)	(0.16, 0.26, 0.42)	19, 81
	11	(-0.06, 0.11, 0.29)	(0.49, 0.60, 0.73)	(0.36, 0.53, 0.77)	110, 192
	12	(-0.22, 0.41, 1.02)	(0.06, 0.16, 0.27)	(0.44, 0.54, 0.65)	410, 728
	13	(-0.48, -0.24, 0.05)	(0.35, 0.49, 0.63)	(0.30, 0.37, 0.46)	200, 487
	14	(-0.24, 0.14, 0.52)	(0.29, 0.51, 0.73)	(0.07, 0.09, 0.10)	57, 359
	15	(0.07, 0.60, 1.15)	(0.15, 0.32, 0.49)	(0.15, 0.18, 0.24)	111, 691
	16	(-3.14, 2.55, 2.92)	(0.58, 0.68, 0.78)	(0.03, 0.04, 0.06)	46, 172
	17	(-1.02, -0.45, 0.11)	(0.22, 0.45, 0.66)	(0.11, 0.16, 0.24)	23, 89
	19	(2.01, 2.20, 2.36)	(0.47, 0.56, 0.66)	(0.04, 0.06, 0.08)	67, 216

<sup>a</sup>  $\psi$  was estimated as a fixed effect, so there is no hyper-distribution for this parameter.

<sup>b</sup> Population SD for  $\gamma$  was calculated from estimates of beta hyper-parameters  $r$  and  $s$ .