

Title	Discrete-space continuous-time models of marine mammal exposure to Navy sonar
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Publication date	2021-10-15
Original Citation	Jones-Todd, C. M., Pirotta, E., Durban, J. W., Claridge, D. E., Baird, R. W., Falcone, E. A., Schorr, G. S., Watwood, S. and Thomas, L. (2021), 'Discrete-space continuous-time models of marine mammal exposure to Navy sonar', Ecological Applications. doi: 10.1002/eap.2475
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1002/eap.2475
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Download date	2025-05-10 00:03:08
Item downloaded from	https://hdl.handle.net/10468/12112



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Data Availability Statement

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- Code and example data are available in the R package mmre (Jones-Todd,
- ³ 2021), see https://doi.org/10.5281/zenodo.4876540 and Appendix S3. Raw
- ⁴ Argos whale tracking data are available from the Dryad Digital Repository, https:
- 5 //doi.org/10.5061/dryad.dr7sqv9zb (Jones-Todd et al., 2021). The sonar
- ⁶ data supporting this research are not accessible to the public, but are available
- ⁷ from the Naval Undersea Warfare Center. To gain access please contact the Naval
- 8 Undersea Warfare Center Division directly, https://www.navsea.navy.mil/
- 9 Home/Warfare-Centers/NUWC-Newport/Contact-Us/.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u>. Please cite this article as doi: 10.1002/EAP.2475

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Discrete-space continuous-time models of marine mammal exposure to Navy sonar

Running head: Marine mammal exposure to Navy sonar

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Article for publication in Ecological Applications

Abstract

Assessing the patterns of wildlife attendance to specific areas is relevant across 31 many fundamental and applied ecological studies, particularly when animals are 32 at risk of being exposed to stressors within or outside the boundaries of those 33 areas. Marine mammals are increasingly being exposed to human activities that 34 may cause behavioral and physiological changes, including military exercises us-35 ing active sonars. Assessment of the population-level consequences of anthro-36 pogenic disturbance requires robust and efficient tools to quantify the levels of 37 aggregate exposure for individuals in a population over biologically relevant time 38 frames. We propose a discrete-space, continuous-time approach to estimate in-39 dividual transition rates across the boundaries of an area of interest, informed by 40 telemetry data collected with uncertainty. The approach allows inferring the effect 41 of stressors on transition rates, the progressive return to baseline movement pat-42 terns, and any difference among individuals. We apply the modeling framework to 43 telemetry data from Blainville's beaked whale (Mesoplodon densirostris) tagged 44 in the Bahamas at the Atlantic Undersea Test and Evaluation Center (AUTEC), 45 an area used by the U.S. Navy for fleet readiness training. We show that transi-46 tion rates changed as a result of exposure to sonar exercises in the area, reflecting 47 an avoidance response. Our approach supports the assessment of the aggregate 48 exposure of individuals to sonar and the resulting population-level consequences. 49 The approach has potential applications across many applied and fundamental 50 problems where telemetry data are used to characterize animal occurrence within 51 specific areas. 52

- ⁵³ *Keywords:* Aggregate exposure; area attendance; beaked whales;
- ⁵⁴ individual-level random effects; sonar disturbance; Template Model Builder;
- 55 transition probability

1. Introduction

As a result of the expansion of human activities, individuals from wildlife 57 populations are increasingly being exposed to a variety of anthropogenic stimuli 58 (Halpern et al., 2008; Sanderson et al., 2002; Díaz et al., 2019). Some human 59 activities can have non-lethal effects on exposed individuals, causing deviations 60 in their natural patterns of behavior and physiology (Pirotta et al., 2018a; Frid and 61 Dill, 2002). Current European Union (European Habitats Directive 92/43/EEC) 62 and United States (Endangered Species Act, 16 U.S.C. §§ 1531 et seq.; Marine 63 Mammal Protection Act, 16 U.S.C. §§ 1361 et seq.) legislation provides the basis 64 for an assessment of the population-level consequences of these behavioral and 65 physiological changes. Understanding where, when, and how often animals come 66 into contact with human activities is the first step towards this assessment. In 67 particular, quantifying population consequences requires an evaluation of 1) the 68 proportion of the population that is exposed and 2) the aggregate exposure of 69 each individual (i.e., the total duration and intensity of exposure to the stressor of 70 interest during a biologically-meaningful period (Pirotta et al., 2018a)). Various 71 factors influence the patterns of exposure of individuals in space and time. For 72 example, a population's movement patterns (Pirotta et al., 2018b; Jones et al., 73 2017), the size of individual home ranges and the motivation underlying the use 74 of the area of interest (e.g., whether the area contains foraging patches or is used 75 solely for transit) (Hückstädt et al., 2020) will all contribute to determine if each 76 individual in a population is exposed at all and, if so, its aggregate exposure. 77

Many marine organisms rely on the use of sound for important life-history

functions (e.g., communication and prey finding) (Montgomery and Radford, 2017). 79 In recent decades, extensive work on the population consequences of disturbance 80 has thus been motivated by growing concerns on the effects of increasing anthro-81 pogenic noise pollution in the ocean (Popper and Hawkins, 2016), particularly 82 on marine mammals (National Research Council, 2005; Nowacek et al., 2007). 83 Among the various sources of noise, cetacean populations may be affected by 84 military operations using active sonar (Southall et al., 2016). Dedicated experi-85 ments and opportunistic exposure studies have shown that animals can respond to 86 active sonars by changing their horizontal movement and diving behavior, leading 87 to interruption of foraging activity, habitat displacement and, potentially, changes 88 in their physiology (Tyack et al., 2011; Southall et al., 2016; Falcone et al., 2017; 89 DeRuiter et al., 2017; Harris et al., 2018; Joyce et al., 2020). As such, current 90 environmental impact statements conducted in the areas used for naval training 91 activities (hereafter 'ranges') require an assessment of the number of individuals 92 that respond to sonar exercises; this number can be estimated from the probabil-93 ity of an individual getting exposed to the noise source, and the probability of 94 responding when exposed to a certain noise level (Harris et al., 2018). 95

A suite of individual-based animal movement models has been developed to estimate the number of individuals that are exposed and respond over the duration of a single navy exercise (e.g., Frankel et al. (2002); Donovan et al. (2017); Houser (2006); U.S. Department of the Navy (2018)). However, these models are not suitable for the estimation of individuals' exposure to sonar over time and across multiple exercises, because their predictions become increasingly un-

realistic when simulating movements for more than a few days, with individuals 102 tending to diffuse away from the range area (Donovan et al., 2017). Moreover, 103 simulating fine-scale animal movements over a long time period is computation-104 ally intensive, and unnecessary when the animals are outside the area of interest. 105 To overcome these difficulties, most existing models treat each day independently 106 and do not tally the number of times individuals are exposed over longer peri-107 ods, even though predictions of population-level effects may change drastically 108 depending on the level of aggregate exposure (Donovan et al., 2017; Pirotta et al., 109 2018a). An alternative method is required to characterize the long-term patterns 110 of individual occurrence in the target area and the effect of exposure and response 111 to disturbance on these patterns. Such a method would then form the basis for 112 a detailed quantification of the number of times each individual is exposed when 113 inside the area and thus susceptible to respond to disturbance. In order to capture 114 the various aspects of the ecology of a population that could influence usage of 115 the area, the method should be informed using empirical movement data collected 116 from individuals in the population over a comparable time scale. Modern satellite 117 telemetry technologies allow us to track marine mammal movements for long pe-118 riods, and could therefore be used to characterize the attendance to specific areas 119 of interest. However, they are often associated with substantial spatial error in 120 animal relocations (Costa et al., 2010). 121

In this study, we develop a discrete-space, continuous-time analytical approach to monitor the occurrence of animals in an area of interest and their transition rates across the boundaries of that area, informed by telemetry data collected with un-

certainty. Our goal is to be able to estimate the aggregate exposure and response to 125 sonar of individuals in a population over biologically relevant time periods. The 126 approach allows for differences in movement patterns among individuals. Im-127 portantly, the potential repulsive effect that the activity under analysis has on the 128 animals and the progressive decay of such effect over time can also be quantified 129 (Tyack et al., 2011; Moretti et al., 2014). While the approach is motivated by and 130 applied to case studies involving the exposure of cetaceans to disturbance from ac-131 tive sonar operations on U.S. Navy ranges, it is widely applicable to other contexts 132 and types of stressors. The method would also be useful in situations where the 133 estimation of the movements in and out of an area is of interest, irrespective of the 134 presence of anthropogenic stressors (e.g., to monitor the attendance of individuals 135 to a protected area). 136

137 2. Materials and Methods

¹³⁸ 2.1. Telemetry data and exposure information

We use satellite telemetry data from seven Blainville's beaked whales (*Mesoplodon densirostris*) tagged between 2009 and 2015 within or near the Atlantic Undersea Test and Evaluation Center (AUTEC), in the Bahamas (Fig. 1). This region is regularly used by the U.S. Navy to carry out military exercises with active sonar. Tagging was carried out in advance of large-scale exercises (Submarine Command Courses) to monitor resulting changes in the animals' movement behavior.

Data collection techniques are described in detail in Joyce et al. (2020). An-146 imals were fitted with Wildlife Computers SPLASH transmitters (n = 2, Mk-10; 147 Wildlife Computers Inc., Redmond, WA, USA) and SPOT model tags (n = 5,148 AM-S240A-C; Wildlife Computers Inc.) in the Low Impact Minimally Percu-140 taneous External-electronics Transmitter (LIMPET) configuration; see Appendix 150 S1: Table S1. Tags were attached on or near the dorsal fin from distances of 5-25 151 m using a crossbow or black powder gun (Joyce et al., 2020; Tyack et al., 2011). 152 Location estimates of tagged whales were provided by the Argos system based on 153 the Kalman filtering method (Lopez et al., 2013). Tags were scheduled to transmit 154 up to 700 times during 12–18 hours of each day, timed to coincide with passes of 155 satellites from the Argos satellite system. 156

Information on the use of mid-frequency active sonars (MFAS) at AUTEC 157 was available from records in the U.S. Navy's internal Sonar Positional Reporting 158 System (SPORTS) database (including, but not limited to, the Submarine Com-159 mand Courses analyzed in Joyce et al. (2020)). While SPORTS data are known 160 to suffer from transcription errors and incomplete records, they offered the best 161 available source of sonar information. Specifically, we extracted bouts of high-162 power (hull-mounted, surface-ship) and mid-power (helicopter-deployed) MFAS 163 use (sensu Falcone et al. (2017)) during tag deployment periods, and calculated 164 the number of days since exposure to a sonar event for each individual relocation. 165 The outline of the hydrophone array at AUTEC was used as the range boundary, 166 and, for simplicity, animals were considered exposed when occurring within this 167 area during sonar activity. 168

In addition to tracks of *M. densirostris* from AUTEC, we applied our modeling approach to four other cetacean species with varying movement behavior and ecology, occurring over two different U.S. Navy ranges, the Hawai'i Range Complex (HRC) and the Southern California Range Complex (SOCAL). Details of these additional case studies and the challenges they present for estimating the effects of sonar exposure are described in Appendix S2.

175 2.2. Overview of modeling approach

We model movement probability in to and out of a region encompassing a Navy range where sonar exercises take place, and how this probability is influenced by the use of sonar on the range. The models presented below are implemented in the mmre R package; see https://github.com/cmjt/mmre and Appendix S3 for further details and examples.

Our modeling approach consisted of three interconnected steps. First, raw 181 tracking data were filtered for obvious mistakes in animal relocation, identified by 182 unrealistic horizontal displacement. While subsequent models can accommodate 183 uncertainty in satellite-derived locations of the animals, aberrant observations can 184 negatively affect model performance (Patterson et al., 2010). We therefore filtered 185 recorded Argos locations using the R package argosfilter (Freitas, 2012), so 186 that highly unlikely observations (i.e., those implying a horizontal displacement 187 greater than 15 m/s) were removed. Second, filtered tracks were adjusted for 188 Argos location uncertainty using a continuous-time correlated random walk state-189 space model, which returned estimated tracks based on the underlying movement 190

¹⁹¹ model (Section 2.3). Finally, estimated tracks were analyzed using a discrete-¹⁹² space continuous-time Markov model that quantified the transition rates across ¹⁹³ range boundaries and the effect of exposure to sonar disturbance on animal move-¹⁹⁴ ment patterns (Section 2.4).

Our approach is conceptually comparable to the continuous-time Markov chain 195 model proposed by Hanks et al. (2015). The authors discretize space into a grid, 196 and use tracking data to model residence time in each occupied cell and transitions 197 to neighboring cells in a Generalized Linear Modelling framework. Recently, a 198 discrete-space continuous-time model has been developed to analyse whale div-199 ing behavior from time series of binned depth observations (Hewitt et al., 2021). 200 Here, we reduce gridded space to two larger areas: on and off a Navy range. Oc-201 currence within each area is used to determine the known states of an individual at 202 the observation times, which are then analyzed in a multi-state modeling frame-203 work in continuous time to infer instantaneous transition rates (Jackson, 2011). 204 Our aim is to assess the patterns of attendance to an area of interest (as a function 205 of exposure to a stressor), as opposed to the role of environmental variables on 206 individuals' movement decisions. Similarly to Hooten et al. (2016) and Buder-207 man et al. (2018), we extend the model to include individual random effects on 208 the transition rates, thus making the model hierarchical. Because individual Argos 209 locations are provided with error, we first impute the tracks using a continuous-210 time correlated random walk (Johnson et al., 2008; Albertsen et al., 2015), as in 211 Hanks et al. (2015). In line with their work, we also propose multiple imputation 212 to fully propagate the uncertainty associated with estimated tracks to the results of 213

the Markov model (Section 2.4). In contrast with the formulation of Hanks et al. (2015) or Jackson (2011), our approach is fitted using Template Model Builder (TMB) (Kristensen et al., 2016), which implements automatic differentiation and applied Laplace approximation to complex random-effect models.

218 2.3. Continuous-time correlated random walk

Due to the uncertainty associated with Argos locations, individual tracks were estimated using the continuous-time correlated random walk model (CTCRW) described in Johnson et al. (2008) and Albertsen et al. (2015) using the R package argosTrack (Albertsen, 2017).

In brief, the CTCRW model is a state-space model (SSM) with measurement 223 equation given by $y_{ct} = \mu_{ct} + \epsilon_{ct}$ where y_{ct} is the *c*th coordinate (*c* = 1 (longitude), 224 2 (latitude)) of the observed location of an animal at time t (t = 1, 2, ..., n) with 225 measurement error term ϵ_{ct} . As in Albertsen et al. (2015) the joint distribution of 226 ϵ_{1t} and ϵ_{2t} is a bivariate *t*-distribution. The term μ_{ct} is then the "true" *c*th coor-227 dinate location of the animal at time t. This location process, μ_{ct} , is obtained by 228 integrating over the assumed instantaneous velocity of the animal at time t. This 229 velocity is assumed to follow an Orstein-Uhlenbeck (OU) process (see Albertsen 230 et al. (2015) for further details). 231

232 2.4. Discrete-space continuous-time Markov model

²³³ Continuous-time Markov models describe how an individual transitions be-²³⁴ tween states in continuous time. Given that an individual is in state S(t) at time ²³⁵ *t*, the transition intensity, $q_{rs}(t, z(t))$, represents the immediate hazard of moving

from one state *r* to another state *s*, and may be dependent on the time *t* of the process as well as some time-varying covariate z(t). These transition intensities can be written as

$$q_{rs}(t, \mathbf{z}(t)) = \lim_{\delta t \to 0} \mathbb{P}(S(t + \delta t) = s | S(t) = r) / \delta t$$
(1)

and form a square matrix **Q** with elements q_{rs} where $q_{rr} = -\sum_{s \neq r} q_{rs}$ (i.e., the rows of **Q** sum to zero) and $q_{rs} \ge 0$ for $r \ne s$.

Here, the state at observation time *t* is determined by where the animal is located, i.e., μ_{ct} (see Section 2.3). We consider only two states (i.e., $r, s = \{1, 2\}$) where state 1 = off-range (i.e., outside the area used by the Navy for military operations) and state 2 = on-range (i.e., inside this area, see Fig. 1).

²⁴⁵ The equation of our model is given by

$$\log(q_{k,rs}(\mathbf{z}_k(t))) = (\beta_{0,rs} + u_{k,rs}) + \beta_{1,rs}\exp(-\beta_{2,rs}\mathbf{z}_k(t)) + \eta,$$
(2)

where $\beta_{0,rs}$ is the intercept term, representing baseline transition rates (on the log scale), and $u_{k,rs}$ indicates the individual-level random effects (for individual k =1, ..., 7) on the transition rates. Each $u_k = \{u_{k,rs}, u_{k,sr}\}$ follows a zero-mean bivariate Gaussian distribution (between states *r* and *s*) with 2 × 2 variance covariance matrix diag(σ_u^2, σ_u^2). The time-varying covariate is given by

$$z_k(t) \begin{cases} = 0 & \text{during exposure} \\ > 0 & \text{otherwise} \end{cases}$$

and represents the number of days since an individual was exposed to a sonar event. The Gaussian random error term is represented by η .

Here, $\beta_{1,rs}$ represents the change in transition rate, on the log scale, during 253 exposure (i.e., $z_k(t) = 0$ thus $\exp(-\beta_{2,rs}z_k(t)) = 1$). We constrain $\beta_{2,rs} \ge 0$ for 254 all $r \neq s$; by doing so, as the number of days since an individual was exposed to 255 sonar, $z_k(t)$, increases, transition rates decay exponentially towards their baseline 256 values, $\beta_{0,rs}$ (on the log scale). Therefore, $\beta_{2,rs}$ for $r \neq s$ can be thought of as the 257 lessening effect of sonar exposure on the transition rates after the termination of 258 sonar. It should be noted that, whilst we were limited by sample size in our case, 259 individual differences in the animals' response to sonar could also be investigated, 260 e.g., by including a random effect on the $\beta_{1,rs}$ and $\beta_{2,rs}$ parameters. Parameter es-261 timates are obtained via minimization of the negative log-likelihood, $-\log(L(\mathbf{Q}))$; 262 see Appendix S4 for details. 263

We use a likelihood ratio test (LRT) and Akaike Information Criterion (AIC) 264 to compare the full model in Equation (2) with two reduced versions: (a) a null 265 model that only includes baseline transition rates, and (b) a model with individual 266 random effects (but no effect of exposure). We refer to the full model as (c). 267 The test statistic for the LRT, $\lambda_{LR} = -2(\log(L(\mathbf{Q})_0) - \log(\mathbf{L}(\mathbf{Q})_A))$ (i.e., twice the 268 difference between the log-likelihoods of the reduced, subscript 0, and alternative, 269 subscript A, models), follows a χ^2 distribution with degrees of freedom equal to 270 the difference in the number of estimated parameters in each model. We quantify 271 the number of random-effect parameters as 14 + 1 = 15 (i.e., $2 \times 7 = 14$ for the 272 individual-level random effect means-twice the number of individuals-and 1 273

for the bivariate Gaussian variances, fixed to be equal). We calculate the number of parameters in each model as the sum of the random-effect and the fixed-effect parameters. Using AIC for models that include random effects depends on the intended level of inference and should be carried out with caution as the penalty is not obvious (Bolker et al., 2009; Vaida and Blanchard, 2005). Here, we are interested in population-level inference and therefore follow the recommendation of Vaida and Blanchard (2005) to use the marginal AIC for model comparison.

We used a multiple imputation procedure to show how the uncertainty associ-281 ated with the Argos tracks could be propagated to the Markov model (Buderman 282 et al., 2018; Scharf et al., 2017, 2016; Hanks et al., 2015). For each of the seven 283 individuals, a total of 100 tracks were imputed using the estimated bivariate t-284 distribution of measurement error from the CTCRW model, fitted to the Argos 285 tracks (see Section 2.3). We fitted the model given by Equation (2) to the 100 286 imputed datasets (each containing one potential track per individual), and calcu-287 lated the pooled point estimate and variance of each parameter as in McClintock 288 (2017). 289

290 2.5. Simulation

To assess the performance of the proposed model, we used the estimated parameter values from the fitted model (Equation 2) to simulate new datasets. Specifically, we simulated the states of individuals at each observed time using the fitted transition probabilities. This was done 500 times for each individual. We refitted the model to the 500 simulated datasets, and calculated root mean squared errors for each parameter, as well as the % errors for $\beta_{1,12}$, $\beta_{1,21}$, $\beta_{2,12}$, and $\beta_{2,21}$ (that is, the parameters relating to the sonar effect).

298 2.6. Goodness of fit

To assess the goodness of fit of the Markov model, we took a similar approach 299 to Aguirre-Hernández and Farewell (2002). Specifically, we partitioned obser-300 vations from each individual by time and covariate value (time since exposure), 301 and compared the observed number of transitions, o, to the number of transi-302 tions expected under the fitted model, e. Bins were created by splitting the data 303 into quantiles, [0%-25%), [25%-50%), [50%-75%), and [75%-100%], based on 304 observation times and covariate values (using estimated transition rates as rec-305 ommended by Aguirre-Hernández and Farewell (2002)). The expected number 306 of transitions in each time and covariate bin were calculated as the sum of the 307 estimated probabilities classified in that category. 308

We carried out a Pearson-type goodness-of-fit test similar to that proposed by 309 Aguirre-Hernández and Farewell (2002) using the test statistic $T = \sum_{uhk} \frac{(o_{uhk} - e_{uhk})^2}{e_{uhk}}$, 310 where *u* represented the number of levels defined by the quantiles of the observa-311 tion times, h represented the groupings due to the covariate, and k was the individ-312 ual whale. We assumed a chi-squared distribution for this test statistic and used 313 both a liberal and a conservative number of degrees of freedom; these were calcu-314 lated as 1) the minimum number of independent bins $(7 \times 4 \times 3 \times 2 = k \times u \times h \times n_{states})$, 315 and 2) the minimum number of independent bins minus the number of estimated 316 parameters, $n_p = 21$, respectively. 317

318 3. Results

Following the first two steps of our analytical approach, we obtained esti-319 mated tracks for the seven Blainville's beaked whales (Fig. 1). Note that, whilst 320 all adult individuals remained in proximity of the Navy range, the only tagged 321 subadult engaged in a wide-ranging trip across the region. The discrete-space 322 continuous-time Markov model was then used to estimate the transition rates 323 across the AUTEC range boundaries (Table 1). Differences in baseline transi-324 tion rates among individuals were captured by the inclusion of individual-level 325 random effects; Figs 2 and 3 show that there was noteworthy variation among 326 whales. Appendix S1: Fig. S2 shows the estimated individual-level random ef-327 fects. 328

³²⁹ Comparing models (b) and (a), $\lambda_{LR} = 27.22$ and, under $\lambda_{LR} \sim \chi_{15}^2$, $\mathbb{P}(\lambda_{LR} > 27.22) = 0.02$, suggesting that the individual-level random effects should be re-³³¹ tained. Comparing models (c) and (a), $\lambda_{LR} = 41.56$ and, under $\lambda_{LR} \sim \chi_{19}^2$, ³³² $\mathbb{P}(\lambda_{LR} > 41.56) = 0.006$, suggesting that the decaying effect of exposure should ³³³ be retained in the model. Using the marginal AIC (Vaida and Blanchard, 2005) ³³⁴ also confirmed the results of the LRT (Table 1).

Using the model given by Equation (2), we detected a change in transition rates following exposure to sonar activities (Table 1). The estimated $\hat{\beta}_1 = \{\hat{\beta}_{1,12}, \hat{\beta}_{1,21}\}^T$ parameters represent the effect on the log rate of transition off–on and on–off the range, respectively, during the time an individual was exposed to sonar. During exposure (i.e., z(t) = 0 in Equation (2)), transitions onto the range (off–on) decreased $(\hat{\beta}_{1,12} = -0.60)$ and transitions off the range (on–off) increased $(\hat{\beta}_{1,21} = 1.75)$. The

increase in on-off transitions during sonar exposure is illustrated in Fig. 3, where
 sonar activity is indicated by vertical grey lines.

The $\hat{\beta}_2 = {\{\hat{\beta}_{2,12}, \hat{\beta}_{2,21}\}}^T = {\{0.78, 0.85\}}$ parameters describe the exponential decay to the baseline transition rates off–on range and on–off range, respectively. Figs 2 and 3 illustrate this exponential decay for each individual; the effect of sonar exposure on the transition rates was estimated to end approximately 3 days after the activity ended (i.e., when transition probabilities returned to their baseline values).

Refitting the Markov model to 500 simulated datasets, generated using the estimates in Table 1, suggested that the model was able to retrieve the values of the parameters with limited bias. The root mean squared error (RMSE) and bias for each parameter in the simulation study are given in Appendix S1: Table S6, while the % errors for the parameters relating to sonar effect are shown in Appendix S1: Fig. S4.

The multiple imputation procedure allowed us to successfully propagate the uncertainty in the telemetry tracks across all modeling steps. A subset of 20 imputed tracks obtained using the parameter values from the fitted CTCRW model is shown in Appendix S1: Fig. S3 for 3 individuals. Uncertainty in the exact locations of the individuals had little effect on the estimated transition rates, as suggested by the parameter values averaged across the 100 fitted models (Table 2 and Appendix S1: Fig. S4).

The comparison of observed transitions, o, with those expected, e, for each individual k (see Section 2.6) suggested that the goodness-of-fit of the Markov model was satisfactory (Appendix S1: Fig. S4c. The Pearson-type test returned a test statistic T = 168.44; under $T \sim \chi^2_{147} \mathbb{P}(T > 168.44) = 0.109$ and under $T \sim \chi^2_{168} \mathbb{P}(T > 168.44) = 0.476$, i.e., we have no evidence to suggest that observed frequencies in each bin are significantly different from those estimated by our model.

369 4. Discussion

We developed a modeling approach that quantifies the rates at which animals 370 move across the boundaries of a discrete area of interest. The model can therefore 371 be used to describe patterns of attendance to that area. Individual differences in 372 movement and ranging behavior, which may lead to heterogeneity in area use, are 373 explicitly evaluated. By fitting a movement model to the raw telemetry tracks, un-374 certainty in animal relocations can also be accounted for. Moreover, because the 375 Markovian component is formulated in continuous time, the approach does not 376 require observations regularly sampled in time. These features are important, be-377 cause wildlife telemetry often involves irregular relocations with substantial mea-378 surement error (Patterson et al., 2017). Crucially, the method we propose can be 379 used to investigate the repulsive (or attractive) effect of a given stressor or activity, 380 operating either within or outside the target area and affecting the propensity of 381 an individual to cross the boundaries in either direction. Our simulation exercise 382 showed that the model performs well at estimating transition rates and any change 383 associated with exposure to disturbance. 384



We used a CTCRW model to account for uncertainty in animal relocations (Al-

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bertsen et al., 2015; Johnson et al., 2008). Alternative movement models could 386 be fitted, depending on the sampling frequency and degree of measurement er-387 ror in the telemetry data (Patterson et al., 2017). Irrespective of the underlying 388 movement model, we showed how a multiple imputation procedure can be used 389 to propagate any such uncertainty (Buderman et al., 2018; Scharf et al., 2017, 390 2016; Hanks et al., 2015). Our results suggest that location error does not alter the 391 conclusions here, probably due to the size of the target area in relation to the esti-392 mated uncertainty. In situations where the area of interest is smaller, particularly 393 with respect to the measurement error associated with telemetry locations, occur-394 rence inside the area (i.e., an animal's state) could become uncertain, warranting 395 the extension of the approach to a hidden Markov model (Langrock et al., 2012). 396

In this study, we applied the proposed approach to a specific management 397 problem: the assessment of the effects of exposure to military sonar operations 398 within navy ranges on the movement behavior of cetaceans, and the resulting 399 attendance of individuals to these range areas (Bernaldo de Quirós et al., 2019; 400 Southall et al., 2016; Nowacek et al., 2007). When fitted to tracking data from 401 Blainville's beaked whales tagged on or near the AUTEC U.S. Navy range in 402 the Bahamas, the model detected a change in the animals' movements following 403 exposure. Individual whales that were on the range at the time of exposure showed 404 an increased tendency of leaving the range, while individuals that were outside the 405 range area had a lower propensity to move onto the range, overall indicating an 406 avoidance response to sonar. This effect was found to last for approximately three 407 days after the end of the exposure, during which the transition rates progressively 408

⁴⁰⁹ returned to their baseline values.

The implications of these results are twofold. First, they contribute to the 410 increasing body of evidence suggesting that military sonar operations can cause 411 changes in the behavior of exposed beaked whales (Harris et al., 2018; Falcone 412 et al., 2017; Tyack et al., 2011; Bernaldo de Quirós et al., 2019; Wensveen et al., 413 2019; De Ruiter et al., 2013; Stimpert et al., 2014; Manzano-Roth et al., 2016). 414 Dedicated experimental studies, as well as observational studies, have shown that 415 these species modify their horizontal movement and diving pattern when exposed 416 to simulated or real sonar in this and other areas (Tyack et al., 2011; McCarthy 417 et al., 2011). In particular, passive acoustic monitoring of whale echolocation 418 clicks has previously suggested that Blainville's beaked whale detections decline 419 within the range area in AUTEC during sonar exercises, returning to baseline 420 levels after approximately three days. Using the same telemetry data we have 42 analyzed here, and focusing only on the effects of large-scale exercises (Subma-422 rine Command Courses), a recent study has provided further indication that this 423 indeed corresponds to animals moving out of the range, rather than cessation of 424 acoustic vocalizations (Joyce et al., 2020). With the proposed approach, we were 425 able to quantify this tendency in terms of individual transition rates, and show that 426 avoidance emerges in response to all sonar exercises occurring on the range. It has 427 been suggested that human disturbance is perceived by wildlife as a form of pre-428 dation risk, and, as such, can elicit comparable reactions, for example attempts to 429 move away from the stressor (Frid and Dill, 2002). A similar response could also 430 arise indirectly if beaked whale prey became less available due to sonar activity 431

(e.g., through displacement or changes in patch characteristics). We detected this
behavioral change despite the regular exposure of this population to sonar disturbance in the range area, which poses interesting questions on the role of tolerance,
habituation, and availability of alternative habitat (Harris et al., 2018).

Secondly, our model can support the assessment of an individual's aggregate 436 exposure to a stressor (that is, the total duration and intensity of exposure), which 437 is required to evaluate the consequences of disturbance on individual fitness and, 438 ultimately, population dynamics (Pirotta et al., 2018a). In particular, the model 439 estimates the patterns of occurrence of an individual in the area where the stressor 440 operates, which can then be combined with approaches that simulate fine-scale 441 movements. To date, these simulations have incurred the problem that, as time 442 progresses, simulated individuals tend to drift away from the target area (Frankel 443 et al., 2002; Donovan et al., 2017; Houser, 2006), leading to unrealistic movement 444 patterns and thus compromising the ability to estimate aggregate exposure over 445 time scales that are biologically relevant (e.g., one year). The results of our model 446 can inform realistic simulations of the occurrence in the area where an individual 447 is potentially exposed, and ignore the behavior when outside such area (although 448 this may require adjusting the range boundaries to account for noise propagation 449 and potential exposure outside the instrumented area (Joyce et al., 2020), simi-450 larly to the other case studies in Appendix S2). In practice, the estimated transi-451 tion probabilities could be used to simulate the daily presence or absence of an 452 individual inside the area where it is susceptible to exposure; when present, finer-453 scale approaches could be used to model its interactions with the stressor inside 454

the area. In some cases (e.g., when animals do not show high residency levels),
this will also save substantial computation time, which is important when many
scenarios of disturbance need to be simulated efficiently for large populations.

Model results highlighted differences among individuals in transition rates and 458 presence on the range, which will result in heterogeneous levels of aggregate ex-450 posure within the population (Pirotta et al., 2018b; Jones et al., 2017). Differences 460 among individuals could be explained by sex (Stewart, 1997), age (Carter et al., 461 2020), life history stage (Pack et al., 2017; Ersts & Rosenbaum, 2003), body con-462 dition (Chaise et al., 2018), exposure history (Bejder et al., 2006) or social pref-463 erences (Ersts & Rosenbaum, 2003; Hauser et al., 2007). This information, when 464 available, could readily be incorporated into the model as fixed effects on the tran-465 sition rates. These differences are relevant because long-term effects on individual 466 vital rates tend to emerge from the chronic disruption of activity budget and the 467 impaired ability to acquire energy (Pirotta et al., 2018a). Therefore, characterizing 468 variation in exposure and identifying the proportion of the population with high 469 exposure level will ultimately contribute to the assessment of the population-level 470 consequences of disturbance resulting from human activities, an important target 471 for many regulatory frameworks (Pirotta et al., 2018a; National Research Council, 472 2005). 473

The application of the modeling approach to other case studies in different U.S. Navy ranges demonstrates some of the outstanding challenges associated with this analysis (see Appendix S2). The model might not be appropriate in situations where the animals rarely leave the target area, as shown for rough-toothed

dolphins Steno bredanensis in Hawai'i (Baird et al., 2019; Baird, 2016) and Cu-478 vier's beaked whales Ziphius cavirostris in southern California (Falcone et al., 479 2017). In the latter case, the short time-scale of documented behavioral responses 480 (Falcone et al., 2017) compared to the resolution of the telemetry data further 481 complicates the use of the model. In that region, the model could be more appro-482 priate for fin whales *Balaenoptera physalus*, which regularly transits in and out 483 of the area where sonar activities operate (Scales et al., 2017), but uncertainty on 484 the boundaries of such area also presents an issue. Access to reliable information 485 on the spatial and temporal patterns of sonar occurrence is critical for the pro-486 posed approach. The comparison of the SPORTS database with acoustic record-487 ings on Navy ranges has shown that the database is prone to transcription errors 488 and incomplete records (Falcone et al., 2017), which have likely contributed to 489 the problems encountered when fitting the model to the additional case studies. 490

Beyond the effects of disturbance resulting from military sonar operations on 491 cetacean species, our approach can be used to quantify the exposure to any activity 492 that occurs within a discrete area and has either an attractive or a repulsive effect 493 on exposed animals. Potential examples include attendance of marine predators 494 to fish farms (Callier et al., 2018), changes in use of windfarm areas by birds 495 (Pearce-Higgins et al., 2009), attractions to supplemental feeding sites for a range 496 of species (Corcoran et al., 2013), temporal variation in the use of refuges as 497 a function of anthropogenic risk in terrestrial ungulates (Visscher et al., 2017), 498 or elephant occurrence in areas with differential human-associated mortality risk 490 (Graham et al., 2009). More generally, it is often valuable to assess the probability 500

of occurrence within predefined regions, e.g., to evaluate the effectiveness of the
boundaries of a protected area for covering the occupancy of a sufficiently large
proportion of a population (Cabeza et al., 2004; Lea et al., 2016; Licona et al.,
2011), a common application of telemetry data (Hays et al., 2019). The transition
rates estimated in our model would inform decisions regarding such boundaries.

The approach can be easily extended to model additional states, that is, addi-506 tional discrete areas where individual patterns of occurrence are of interest. For 507 example, the model could be used to estimate the connectivity among multiple 508 protected areas, or the degree of usage of distinct portions of a population's range 509 (Webster et al., 2002; Espinoza et al., 2015). The effect of other covariates (e.g., 510 environmental characteristics) on the transitions among areas could be included to 511 elucidate the ecological or anthropogenic processes influencing these movement 512 patterns (Buderman et al., 2018; Hanks et al., 2015). 513

In conclusion, we introduced a versatile method to monitor animals' atten-514 dance to discrete areas in continuous time, and assess the effects of stressors or 515 attractors on the transition rates across these predefined boundaries. We used the 516 method to quantify the effect of sonar on the occurrence of a cetacean species 517 on a U.S. Navy range, and found changes in the propensity of moving in to and 518 out of this area as a result of exposure. These results will help to assess the ag-519 gregate exposure of individuals and any resulting population-level consequences. 520 However, we anticipate the model could have wide applications in both applied 521 and fundamental ecological studies that use telemetry data to characterize animal 522 movements. 523

⁵²⁵ CJT, EP and LT conceived the ideas and developed the methodology; RWB, ⁵²⁶ JD, EF, TJ, GS, and SW collected and obtained permissions for use of the data. ⁵²⁷ CJT and EP analyzed the data and led the writing of the manuscript. All authors ⁵²⁸ contributed critically to the drafts and gave final approval for publication.

529 6. Acknowledgments

This study was supported by Office of Naval Research (ONR) grant N00014-530 16-1-2858: "PCoD+: Developing widely-applicable models of the population 531 consequences of disturbance". We thank Ruth Joy, Rob Schick, John Harwood, 532 Cormac Booth, Leslie New, Dan Costa and Lisa Schwarz for useful discussions. 533 Tagging in AUTEC was conducted under Bahamas Marine Mammal Research 534 Permit #12A. issued by the Government of the Bahamas to the Bahamas Marine 535 Mammal Research Organization (BMMRO) under the regulatory framework of 536 the Bahamas Marine Mammal Protection Act (2005). Methods of deployment, 537 tag types, and sample sizes were preapproved by BMMRO's Institutional Animal 538 Care and Use Committee (IACUC) and by the U.S. Department of the Navy, Bu-539 reau of Medicine and Surgery Veterinary Affairs Office. Protocols were reviewed 540 annually by BMMRO's IACUC throughout the duration of the study. Funding 541 support for tagging was provided by the U.S. Navy's ONR and Living Marine 542 Resources (LMR) program, the Chief of Naval Operations' Energy and Environ-543 mental Readiness Division and the NOAA Fisheries Ocean Acoustics Program 544 (see Joyce et al. (2020) for details). We thank Charlotte Dunn, Leigh Hickmott, 545

Holly Fearnbach and the Marine Mammal Monitoring on Navy Ranges acoustic 546 team at the U.S. Naval Undersea Warfare Center for support during fieldwork. 547 Hawai'i tagging research was undertaken under NMFS Scientific Research Per-548 mits No. 731-1774 and 15330. Hawai'i field efforts were funded by the U.S. 540 Navy (Pacific Fleet, LMR) and the National Marine Fisheries Service (Pacific 550 Islands Fisheries Science Center). In SOCAL, tags were deployed under U.S. Na-551 tional Marine Fisheries Service permit numbers 540-1811 and 16111. All tags, 552 in Hawai'i and SOCAL, were deployed in accordance with the IACUC guide-553 lines for satellite tagging established by Cascadia Research Collective. Field ef-554 forts were supported by grants from the U.S. Navy's LMR and N45 programs. 555 The authors wish to acknowledge the use of New Zealand eScience Infrastruc-556 ture (NeSI) high performance computing facilities as part of this research. URL 557 https://www.nesi.org.nz. Finally, we thank the two anonymous reviewers 558 and editor for their helpful comments and suggestions, which were greatly appre-559 ciated. 560

561 **References**

Aguirre-Hernández, R. and Farewell, V. (2002). A Pearson-type goodness-of-fit
 test for stationary and time-continuous Markov regression models. *Statistics in Medicine*, 21(13): 1899–1911.

- ⁵⁶⁵ Albertsen, C. M. (2017). argosTrack: Fit Movement Models to Argos Data for
 ⁵⁶⁶ Marine Animals. R package version 1.1.0.
- ⁵⁶⁷ Albertsen, C. M., Whoriskey, K., Yurkowski, D., Nielsen, A., and Mills, J. (2015).
 ⁵⁶⁸ Fast fitting of non-Gaussian state-space models to animal movement data via
 ⁵⁶⁹ Template Model Builder. *Ecology*, 96(10): 2598–2604.
- Baird, R. W. (2016). *The lives of Hawai'i's dolphins and whales: natural history and conservation*. University of Hawai'i Press, Honolulu, Hawai'i, 993–994.

Baird, R. W., Webster, D., Jarvis, S., Henderson, E., Watwood, S., Mahaffy,
S., Guenther, B., Lerma, C., Cornforth, A., Vanderzee, A., and Anderson, D.
(2019). Odontocete studies on the Pacific Missile Range Facility in August
2018: satellite-tagging, photo-identification, and passive acoustic monitoring.
Prepared for Commander, Pacific Fleet, under Contract No. N62470-15-D-8006
Task Order 6274218F0107 issued to HDR Inc., Honolulu, HI, 995–997.

Bejder, L., Samuels, A., Whitehead, H., and Gales, N. (2006). Interpreting shortterm behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour*, 72(5): 1149–1158.

Bernaldo de Quirós, Y., Fernandez, A., Baird, R., Brownell Jr, R., Aguilar de
Soto, N., Allen, D., Arbelo, M., Arregui, M., Costidis, A., Fahlman, A., et al.
(2019). Advances in research on the impacts of anti-submarine sonar on beaked
whales. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 286(1895): 20182533.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens,
M. H. H., and White, J. S. S (2009). Generalized linear mixed models: a
practical guide for ecology and evolution. *Trends in Ecology & Evolution*,
24(3): 127–135.

Buderman, F. E., Hooten, M. B., Alldredge, M. W., Hanks, E. M., and Ivan,
J. S. (2018). Time-varying predatory behavior is primary predictor of fine-scale
movement of wildland-urban cougars. *Movement Ecology*, 6(1): 22.

⁵⁹³ Cabeza, M., Araújo, M. B., Wilson, R. J., Thomas, C. D., Cowley, M. J. R.,
 ⁵⁹⁴ and Moilanen, A. (2004). Combining probabilities of occurrence with spatial
 ⁵⁹⁵ reserve design. *Journal of Applied Ecology*, 41(2): 252–262.

⁵⁹⁶ Callier, M. D., Byron, C. J., Bengtson, D. A., Cranford, P. J., Cross, S. F., Focken,
⁵⁹⁷ U., Jansen, H. M., Kamermans, P., Kiessling, A., Landry, T., et al. (2018).
⁵⁹⁸ Attraction and repulsion of mobile wild organisms to finfish and shellfish aqua⁵⁹⁹ culture: a review. *Reviews in Aquaculture*, 10(4): 924–949.

Carter, M. I., McClintock, B. T., Embling, C. B., Bennett, K. A., Thompson, D.,
 and Russell, D. J. (2020). From pup to predator: generalized hidden Markov

models reveal rapid development of movement strategies in a naíve long-lived
 vertebrate. *Oikos*, 129(5): 630–642.

⁶⁰⁴ Chaise, L. L., Prinet, I., Toscani, C., Gallon, S. L., Paterson, W., McCafferty, D. J.,
⁶⁰⁵ Thèry, M., Ancel, A. and Gilbert, C. (2018). Local weather and body condi⁶⁰⁶ tion influence habitat use and movements on land of molting female southern
⁶⁰⁷ elephant seals (*Mirounga leonina*). *Ecology and Evolution*, 8(12): 6081–6090.

⁶⁰⁸ Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman,
D. D., and Harvey, G. M. (2013). Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the
southern stingray, *Dasyatis americana*. *PLoS One*, 8(3): e59235.

⁶¹² Costa, D. P., Robinson, P. W., Arnould, J. P., Harrison, A. L., Simmons, S. E., Has⁶¹³ srick, J. L., Hoskins, A. J., Kirkman, S. P., Oosthuizen, H., Villegas-Amtmann,
⁶¹⁴ S., and Crocker, D. E. (2010). Accuracy of ARGOS locations of pinnipeds
⁶¹⁵ at-sea estimated using fastloc GPS. *PLoS One*, 5(1): e8677.

DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J.,
Friedlaender, A. S., and Southall, B. L. (2017) A multivariate mixed hidden
Markov model for blue whale behaviour and responses to sound exposure. *The Annals of Applied Statistics*, 11(1): 362–392.

⁶²⁰ De-Ruiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M., Sadykova, D.,

Falcone, E. A., Friedlaender, A. S., Joseph, J. E., Moretti, D., Schorr, G. S.,

623

et al. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, 9(4): 20130223.

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., et al. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)*, available at https://uwe-repository.worktribe.
 com/output/1493508

Donovan, C. R., Harris, C. M., Milazzo, L., Harwood, J., Marshall, L., and
Williams, R. (2017). A simulation approach to assessing environmental risk
of sound exposure to marine mammals. *Ecology and Evolution*, 7(7): 2101–
2111.

- Ersts, P. J., and Rosenbaum, H. C. (2003). Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground.
 Journal of Zoology, 260(4): 337–345.
- Espinoza, M., Lédée, E. J. I., Simpfendorfer, C. A., Tobin, A. J., and Heupel,
 M. R. (2015). Contrasting movements and connectivity of reef-associated
 sharks using acoustic telemetry: implications for management. *Ecological Applications*, 25(8): 2101–2118.

Falcone, E. A., Schorr, G. S., Watwood, S. L., De Ruiter, S. L., Zerbini, A. N.,

Andrews, R. D., Morrissey, R. P., and Moretti, D. J. (2017). Diving behaviour of
Cuvier's beaked whales exposed to two types of military sonar. *Royal Society Open Science*, 4: 170629.

Frankel, A. S., Ellison, W. T., and Buchanan, J. (2002). Application of the Acoustic Integration Model (AIM) to predict and minimize environmental impacts. *IEEE Journal of Oceanic Engineering*, 3: 1438–1443.

⁶⁴⁹ Freitas, C. (2012). *argosfilter: Argos locations filter*. R package version 0.63.

Frid, A. and Dill, L. M. (2002). Human-caused disturbance stimuli as a form of
 predation risk. *Conservation Ecology*, 6(1): 11.

- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., and Lee, P. C. (2009). The
 movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5): 445–455.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa,
 C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann,
 D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M.,
 Steneck, R., and Watson, R. (2008). A global map of human impact on marine
 ecosystems. *Science*, 319(5865): 948–52.

Hanks, E. M., Hooten, M. B., and Alldredge, M. W. (2015). Continuous-time
discrete-space models for animal movement. *The Annals of Applied Statistics*,
9(1): 145–165.

Harris, C. M., Thomas, L., Falcone, E. A., Hildebrand, J., Houser, D., Kvadsheim,
P. H., Lam, F.-P. A., Miller, P. J. O., Moretti, D. J., Read, A. J., Slabbekoorn,
H., Southall, B. L., Tyack, P. L., Wartzok, D., and Janik, V. M. (2018). Marine
mammals and sonar: dose-response studies, the risk-disturbance hypothesis and
the role of exposure context. *Journal of Applied Ecology*, 55(1): 396–404.

Hauser, D. D., Logsdon, M. G., Holmes, E. E., VanBlaricom, G. R., and Osborne,
R. W. (2007). Summer distribution patterns of southern resident killer whales *Orcinus orca*: core areas and spatial segregation of social groups. *Marine Ecol- ogy Progress Series*, 351: 301–310.

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael,
R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., et al. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, 34(5): 459–473.

Hewitt, J., Schick, R. S., and Gelfand, A. E. (2021). Continuous-Time
Discrete-State Modeling for Deep Whale Dives. *Journal of Agricul- tural, Biological and Environmental Statistics*, https://doi.org/10.1007/
\$13253-020-00422-2.

Houser, D. S. (2006). A method for modeling marine mammal movement and
behavior for environmental impact assessment. *IEEE Journal of Oceanic Engineering*, 31(1): 76–81.

Hooten, M. B., Buderman, F. E., Brost, B. M., Hanks, E. M., and Ivan, J. S.

(2016). Hierarchical animal movement models for population-level inference.
 Environmetrics, 27(6): 322–333.

Hückstädt, L. A., Schwarz, L. K., Friedlaender, A. S., Mate, B. R., Zerbini,
A. N., Kennedy, A., Robbins, J., Gales, N. J., and Costa, D. P. (2020). A
dynamic approach to estimate the probability of exposure of marine predators
to oil exploration seismic surveys over continental shelf waters. *Endangered Species Research*, 42: 185–199.

Jackson, C. H. (2011). Multi-State Models for Panel Data: The msm Package for
 R. *Journal of Statistical Software*, 38(8): 1–29.

Johnson, D. S., London, J. M., Lea, M.-A., and Durban, J. W. (2008). Continuous time correlated random walk model for animal telemetry data. *Ecology*, 89(5):
 1208–1215.

Jones, E. L., Hastie, G. D., Smout, S., Onoufriou, J., Merchant, N. D., Brookes,
K. L., and Thompson, D. (2017). Seals and shipping: quantifying population
risk and individual exposure to vessel noise. *Journal of Applied Ecology*, 54(6):
1930–1940.

Jones-Todd, C. M. (2021). cmjt/mmre: Release for accepted manuscript. *Zenodo*. https://doi.org/10.5281/zenodo.4876540.

Jones-Todd, C. M., Pirotta, E., Durban, J., Claridge, D., Baird, R., Falcone, E., Schorr, G., Watwood, S., and Thomas, L. (2021). Discrete-space continuous-

time models of marine mammal exposure to Navy sonar (Version 3) [Data set].
 Dryad, https://doi.org/10.5061/DRYAD.DR7SQV9ZB

Joyce, T. W., Durban, J. W., Claridge, D. E., Dunn, C. A., Hickmott, L. S., Fearn bach, H., Dolan, K., and Moretti, D. (2020). Behavioral responses of satellite
 tracked Blainville's beaked whales (*Mesoplodon densirostris*) to mid-frequency
 active sonar. *Marine Mammal Science*, 36(1): 29–46.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. (2016). TMB:
Automatic differentiation and Laplace approximation. *Journal of Statistical Software*, 70(5): 1–21.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., and Morales,
J. M. (2012). Flexible and practical modeling of animal telemetry data: hidden
Markov models and extensions. *Ecology*, 93(11): 2336–2342.

Lea, J. S. E., Humphries, N. E., von Brandis, R. G., Clarke, C. R., and Sims, D. W.
(2016). Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 283(1834): 20160717.

Licona, M., McCleery, R., Collier, B., Brightsmith, D. J., and Lopez, R. (2011).
 Using ungulate occurrence to evaluate community-based conservation within a
 biosphere reserve model. *Animal Conservation*, 14(2): 206–214.

Lopez, R., Malardé, J.-P., Royer, F., and Gaspar, P. (2013). Improving argos

doppler location using multiple-model Kalman filtering. IEEE Transactions on 724 Geoscience and Remote Sensing, 52(8): 4744–4755.

Manzano-Roth, R., Henderson, E. E., Martin, S. W., Martin, C., and Matsuyama, 726 B. M. (2016). Impacts of U.S. Navy training events on Blainville's beaked 727 whale (Mesoplodon densirostris) foraging dives in Hawaiian waters. Aquatic 728 Mammals, 42(4): 507. 729

McCarthy, E., Moretti, D., Thomas, L., DiMarzio, N., Morrissey, R., Jarvis, S., 730 Ward, J., Izzi, A., and Dilley, A. (2011). Changes in spatial and temporal dis-731 tribution and vocal behavior of Blainville's beaked whales (Mesoplodon den-732 sirostris) during multiship exercises with mid-frequency sonar. Marine Mam-733 *mal Science*, 27(3): E206–E226. 734

McClintock, B. T. (2017) Incorporating Telemetry Error into Hidden Markov 735 Models of Animal Movement Using Multiple Imputation. JABES, 22(3): 249-736 269. 737

Montgomery, J. C. and Radford, C. A. (2017). Marine bioacoustics. Current 738 Biology, 27(11): R502–R507. 739

Moretti, D., Thomas, L., Marques, T., Harwood, J., Dilley, A., Neales, B., Shaf-740 fer, J., McCarthy, E., New, L., Jarvis, S., and Morrissey, R. (2014). A risk 741 function for behavioral disruption of Blainville's beaked whales (Mesoplodon 742 densirostris) from mid-frequency active sonar. PloS One, 9(1): e85064. 743

National Research Council (2005). *Marine mammal populations and ocean noise: determining when noise causes biologically significant effects*. The National
 Academies Press, Washington, DC.

⁷⁴⁷ Nowacek, D. P., Thorne, L. H., Johnston, D. W., and Tyack, P. L. (2007). Re⁷⁴⁸ sponses of cetaceans to anthropogenic noise. *Mammal Review*, 37(2):81–115.

Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., Waterman, J. O., Herman,
E. Y. K., Deakos, M. H., Hakala, S., and Lowe, C. (2017) Habitat preferences
by individual humpback whale mothers in the Hawaiian breeding grounds vary
with the age and size of their calves. *Animal Behaviour* 133: 131–144.

Patterson, T. A., McConnell, B. J., Fedak, M. A., Bravington, M. V., and Hindell,
 M. A. (2010). Using GPS data to evaluate the accuracy of state–space methods
 for correction of Argos satellite telemetry error. *Ecology*, 91(1): 273–285.

Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., and King,
R. (2017). Statistical modelling of individual animal movement: an overview
of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101(4): 399–438.

Pearce-Higgins, J. W., Stephen, L., Langston, R. H., Bainbridge, I. P., and Bull man, R. (2009). The distribution of breeding birds around upland wind farms.
 Journal of Applied Ecology, 46(6): 1323–1331.

Pirotta, E., Booth, C. G., Costa, D. P., Fleishman, E., Kraus, S. D., Lusseau, D.,
 Moretti, D., New, L. F., Schick, R. S., Schwarz, L. K., Simmons, S. E., Thomas,

766

767

L., Tyack, P. L., Weise, M. J., Wells, R. S., and Harwood, J. (2018a). Understanding the population consequences of disturbance. *Ecology and Evolution*, 8(19): 9934–9946.

Pirotta, E., New, L., and Marcoux, M. (2018b). Modelling beluga habitat use
and baseline exposure to shipping traffic to design effective protection against
prospective industrialization in the Canadian Arctic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(3): 713–722.

Popper, A. N. and Hawkins, A. (2016). *The effects of noise on aquatic life II*.
Springer, New York.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., and
Woolmer, G. (2002). The human footprint and the last of the wild: the human
footprint is a global map of human influence on the land surface, which suggests
that human beings are stewards of nature, whether we like it or not. *BioScience*,
52(10): 891–904.

Scales, K. L., Schorr, G. S., Hazen, E. L., Bograd, S. J., Miller, P. I., Andrews,
R. D., Zerbini, A. N., and Falcone, E. A. (2017). Should I stay or should I go?
Modelling year-round habitat suitability and drivers of residency for fin whales
in the California Current. *Diversity and Distributions*, 23(10): 1204–1215.

Scharf, H., Hooten, M. B., Fosdick, B. K., Johnson, D. S., London, J. M., and
Durban, J. W. (2016). Dynamic social networks based on movement. *The Annals of Applied Statistics*, 10(4): 2182–2202.

Scharf, H., Hooten, M. B., and Johnson, D. S. (2017). Imputation approaches for
 animal movement modeling. *Journal of Agricultural, Biological and Environ- mental Statistics*, 22(3): 335–352.

Southall, B. L., Nowacek, D. P., Miller, P. J., and Tyack, P. L. (2016). Exper imental field studies to measure behavioral responses of cetaceans to sonar.
 Endangered Species Research, 31(1): 293–315.

Stewart, B. S. (1997). Ontogeny of differential migration and sexual segregation
 in northern elephant seals. *Journal of Mammalogy*, 78(4): 1101–1116.

Stimpert, A. K., De Ruiter, S. L., Southall, B. L., Moretti, D. J., Falcone, E. A.,
Goldbogen, J. A., Friedlaender, A., Schorr, G. S., and Calambokidis, J. (2014).
Acoustic and foraging behavior of a Baird's beaked whale, *Berardius bairdii*,
exposed to simulated sonar. *Scientific Reports*, 4: 7031.

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E.,
Durban, J. W., Clark, C. W., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy,
E., Morrissey, R., Ward, J., and Boyd, I. L. (2011). Beaked whales respond to
simulated and actual navy sonar. *PLoS ONE*, 6(3): e17009.

U.S. Department of the Navy (2018). Quantifying acoustic impacts on marine
mammals and sea turtles: methods and analytical approach for phase iii training and testing. NUWC Division Newport, Space and naval Warfare Systems
Center Pacific, G2 Software Systems, and the National Marine Mammal Foundation. Newport, RI: Naval Undersea Warfare Center. Technical report.

Vaida, F., and Blanchard, S. (2005). Conditional Akaike information for mixedeffects models. *Biometrika*, 92(2): 351–370.

⁸⁰⁹ Visscher, D. R., Macleod, I., Vujnovic, K., Vujnovic, D., and Dewitt, P. D. (2017).
⁸¹⁰ Human risk induced behavioral shifts in refuge use by elk in an agricultural
⁸¹¹ matrix. *Wildlife Society Bulletin*, 41(1): 162–169.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., and Holmes, R. T. (2002).
Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, 17(2): 76–83.

Wensveen, P. J., Isojunno, S., Hansen, R. R., von Benda-Beckmann, A. M.,
Kleivane, L., van IJsselmuide, S., Lam, F.-P. A., Kvadsheim, P. H., De Ruiter,
S. L., Curé, C., and Narazaki, T. (2019). Northern bottlenose whales in a
pristine environment respond strongly to close and distant navy sonar signals. *Proceedings of the Royal Society of London. Series B: Biological Sciences*,
286(1899): 20182592.

821 Tables

model $[n_p]$	random/exposure	$P(t = 1)^*$	log-likelihood	AIC	$\hat{oldsymbol{eta}}_0$	$\hat{oldsymbol{eta}}_1$	$\hat{oldsymbol{eta}}_2$	time to fit (s)
(a) [2]	-/-	$\begin{bmatrix} 0.877 & 0.123 \\ 0.505 & 0.495 \end{bmatrix}$	-257.04	518.08	$\begin{bmatrix} -1.65 \ (0.18) \\ -0.23 \ (0.16) \end{bmatrix}$	-	-	0.664
(b) [17]	+/-	$\begin{bmatrix} 0.858 & 0.142 \\ 0.525 & 0.475 \end{bmatrix}$	-243.43	492.87	$\begin{bmatrix} -1.45 \ (0.40) \\ -0.14 \ (0.40) \end{bmatrix}$	-	-	251.8
(c) [21]	+/+	$\begin{bmatrix} 0.807 & 0.193 \\ 0.421 & 0.579 \end{bmatrix}$	-236.26	486.51	$\begin{bmatrix} -1.21 \ (0.48) \\ -0.43 \ (0.47) \end{bmatrix}$	$\begin{bmatrix} -0.60 \ (0.61) \\ 1.75 \ (0.56) \end{bmatrix}$	$\begin{bmatrix} 0.78 \ (1.01) \\ 0.85 \ (0.60) \end{bmatrix}$	925.7

Table 1: Table of estimated parameters, log-likelihood, and AIC values for the fitted models; standard errors are given in brackets. The first column gives the model name as discussed in Section 2.4 and the associated number of parameters, n_p . The second column indicates if the model includes individual random effects (random) or an exposure component (exposure). For example, +/+ indicates that a model includes both components. The baseline transition rates, on the log scale, are given by $\hat{\beta}_0 = \{\hat{\beta}_{0,12}, \hat{\beta}_{0,21}\}^T$. Where applicable, the changes in transition rate during exposure are given by $\hat{\beta}_1 = \{\hat{\beta}_{1,12}, \hat{\beta}_{1,21}\}^T$ and the decay parameters are given by $\hat{\beta}_2 = \{\hat{\beta}_{2,12}, \hat{\beta}_{2,21}\}^T$. The final column gives the time taken, in seconds, to fit each model using system.time() in R 4.0.2 on a laptop computer with a 2.5GHz processor. Here, * denotes that $\mathbf{P}(\mathbf{t} = \mathbf{1})$ is calculated at the baseline transition rate (i.e., ignoring any other effects, if there are any).

	P (t = 1)*	$\hat{oldsymbol{eta}}_0$	$\hat{oldsymbol{eta}}_1$	$\hat{oldsymbol{eta}}_2$
Est. (Var.)	$\begin{bmatrix} 0.801 & 0.199 \\ 0.416 & 0.584 \end{bmatrix}$	$\begin{bmatrix} -1.18 \ (0.41) \\ -0.44 \ (0.24) \end{bmatrix}$	$\begin{bmatrix} -0.61 \ (3.59) \\ 0.64 \ (8.92) \end{bmatrix}$	$\begin{bmatrix} 1.97 \ (0.59) \\ 0.98 \ (0.52) \end{bmatrix}$

Table 2: For each of the seven Blainville's beaked whales, 100 sets of CTCRW tracks were imputed and the fitted model given by Equation 2. The table shows the pooled point estimate (est.) and variance (Var.) of each parameter, calculated following McClintock (2017). As in Table 1, * denotes that P(t = 1) is calculated at the baseline transition rate.

Figure Legends

Figure 1: Estimated tracks of the seven Blainville's beaked whales (*Mesoplodon densirostris*), at the AUTEC range (shown by the light grey polygon), Bahamas. The bottom right plot shows the plotted region, for each individual, in relation to Florida, USA; the calculated raw transition probability matrix for sequential transitions across AUTEC range boundaries, averaged across individuals, is shown as an inset table. The raw ARGOS data can be seen in Appendix S1: Fig. S1.

Figure 2: Estimated transition probabilities for each of the seven Blainville's beaked whales as a function of days since exposure to sonar, calculated at one day since tagging (t = 1); the corresponding transition rate is given by Equation 2. In each plot, colors indicate different individuals; the top plot shows on–off transition probabilities and the bottom plot shows off—on transition probabilities. The grey shaded areas show the 95% confidence interval around the mean transition probabilities (dashed grey lines) as a function of days since exposure. The vertical line indicates three days since exposure.

Figure 3: Fitted on–off range transition probabilities, $p_{21}(t = 1)$, for each of the seven Blainville's beaked whales (derived from the corresponding transition rates given by Equation 2). In each plot, the vertical grey lines indicate the time of sonar events; the points represent the time of observed locations (in days) of each individual since tagging. The different horizontal asymptotes in each panel illustrate the differences in baseline transition rates among individuals.

826 Figures







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