


CONTRIBUTED PAPERS

Incorporating multidimensional behavior into a risk management tool for a critically endangered and migratory species

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Abstract

Conservation of migratory species exhibiting wide-ranging and multidimensional behaviors is challenged by management efforts that only utilize horizontal movements or produce static spatial–temporal products. For the deep-diving, critically endangered eastern Pacific leatherback turtle, tools that predict where turtles have high risks of fisheries interactions are urgently needed to prevent further population decline. We incorporated horizontal–vertical movement model results with spatial–temporal kernel density estimates and threat data (gear-specific fishing) to develop monthly maps of spatial risk. Specifically, we applied multistate hidden Markov models to a biotelemetry data set ($n = 28$ leatherback tracks, 2004–2007). Tracks with dive information were used to characterize turtle behavior as belonging to 1 of 3 states (transiting, residential with mixed diving, and residential with deep diving). Recent fishing effort data from Global Fishing Watch were integrated with predicted behaviors and monthly space-use estimates to create maps of relative risk of turtle–fisheries interactions. Drifting (pelagic) longline fishing gear had the highest average monthly fishing effort in the study region, and risk indices showed this gear to also have the greatest potential for high-risk interactions with turtles in a residential, deep-diving behavioral state. Monthly relative risk surfaces for all gears and behaviors were added to South Pacific TurtleWatch (SPTW) (<https://www.upwell.org/sptw>), a dynamic management tool for this leatherback population. These modifications will refine SPTW's capability to provide important predictions of potential high-risk bycatch areas for turtles undertaking specific behaviors. Our results demonstrate how multidimensional movement data, spatial–temporal density estimates, and threat data can be used to create a unique conservation tool. These methods serve as a framework for incorporating behavior into similar tools for other aquatic, aerial, and terrestrial taxa with multidimensional movement behaviors.

KEYWORDS

biotelemetry, ecological risk management, hidden Markov models, leatherback turtle, migratory species, multidimensional behavior

Incorporación del comportamiento multidimensional a una herramienta de gestión de riesgos para una especie migratoria en peligro crítico

Resumen: La conservación de especies migratorias con comportamientos amplios y multidimensionales se enfrenta a los esfuerzos de gestión que sólo utilizan

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movimientos horizontales o que producen resultados espaciotemporales estáticos. La tortuga laúd, una especie de las profundidades en peligro crítico, necesita con urgencia herramientas que pronostiquen los lugares en donde las tortugas tienen mayor riesgo de interactuar con las pesquerías para prevenir una mayor declinación poblacional. Incorporamos los resultados de un modelo de movimiento horizontal-vertical a las estimaciones de la densidad del núcleo espaciotemporal y de los datos de amenaza (equipo de pesca específico) para desarrollar mapas mensuales del riesgo espacial. De manera más concreta, aplicamos modelos ocultos multiestado de Markov a un conjunto de datos de biotelemetría ($n=28$ rastros de tortugas laúd, 2004-2007). Usamos los rastros con información de inmersión para caracterizar el comportamiento de las tortugas como uno de tres estados: en tránsito, inmersión mixta o por residencia e inmersión profunda o por residencia. Integramos los datos recientes del esfuerzo de pesca tomados de Global Fishing Watch a los comportamientos pronosticados y las estimaciones del uso mensual del espacio para crear mapas del riesgo relativo de las interacciones tortuga-pesquería. La pesca con palangre de deriva (pelágica) tuvo el promedio mensual más alto de esfuerzo de pesca en la región de estudio. Los índices de riesgo indicaron que este equipo también tiene el potencial más elevado de interacciones de alto riesgo con las tortugas en estado residencial o de inmersión profunda. Añadimos los comportamientos y las superficies de riesgo relativo mensuales a South Pacific Turtle Watch (SPTW) (<https://www.upwell.org/sptw>), una herramienta dinámica para la gestión de esta población de laúdes. Estos cambios pulirán la capacidad de SPTW para proporcionar predicciones importantes de las áreas con potencial alto de riesgo de pesca accesoria para las tortugas con comportamientos específicos. Nuestros resultados demuestran cómo los datos de movimiento multidimensional, las estimaciones de densidad espaciotemporal y los datos de amenaza pueden ser usados para crear una herramienta única de conservación. Estos métodos sirven como marco para incorporar el comportamiento a herramientas similares para otros taxones acuáticos, aéreos y terrestres con comportamientos multidimensionales.

PALABRAS CLAVE

biotelemetría, comportamiento multidimensional, especie migratoria, gestión de riesgos ecológicos, modelos ocultos de Markov, tortuga laúd

【摘要】

对表现出大范围、多维行为的洄游物种的保护面临着仅利用水平运动或仅产生静态时空产物的管理工作的挑战。对于深潜的、极度濒危的东太平洋棱皮龟来说,迫切需要能够预测海龟面临高风险渔业相互影响位点的工具,以防止其进一步发生种群下降。本研究将水平-垂直运动模型的结果与空间-时间核密度估计及威胁数据(特定渔具的捕捞)结合起来,获得了每月空间风险地图。具体来说,我们将多态隐马尔可夫模型应用于生物遥测数据集(28条棱皮龟轨迹,2004-2007年),并用带有潜水信息的轨迹来描述海龟3种状态的行为(经过、栖息及混合潜水、栖息及深潜)。我们还结合了来自全球渔业观察中最近捕捞量的数据与预测的行为和每月空间使用估计,创建了海龟与渔业相互影响的相对风险地图。在我们的研究区域,漂流的(中上层)延绳钓渔具月平均捕捞量最高,风险指数显示这种渔具与海龟在栖息及深潜行为状态下发生高风险相互影响的可能性也最大。我们将所有类型的渔具和行为的每月相对风险数据添加到了南太平洋海龟观察网站上(SPTW)(<https://www.upwell.org/sptw>),这是一个针对该地区棱皮龟种群的动态管理工具。这些改进将提高SPTW为特定行为的海龟提供潜在的高风险兼捕区重要预测的能力。我们的结果展示了如何运用多维运动数据、时空密度估计和威胁数据开发一个独特的保护工具。这些方法可作为一个框架来将行为纳入其他具有多维运动行为的水生、飞行和陆生类群的类似工具中。【翻译:胡怡思;审校:聂永刚】

关键词: 隐马尔可夫模型, 多维行为, 生态风险管理, 生物遥测, 洄游物种, 棱皮龟

INTRODUCTION

For animals that traverse long distances between habitats, conservation efforts relying on fixed management measures, such as static spatial area closures, are often ineffective because of spatial and temporal mismatches with animals' behavior and habitat use (Bolger et al., 2008; Bull et al., 2013; Meisinger et al., 2018; Runge et al., 2014). Successfully conserving a migratory species depends not only on alleviating harm in the habitats where they face significant threat, but also on understanding their movement ecology (Fraser et al., 2018; Westley et al., 2018). Furthermore, conservation involving animals with vertical dimensions to their behavior (e.g., flying, arboreal, diving) can be improved through the application of predictive models of threat risk in relation to vertical behaviors.

Dynamic management (DM), whereby risk assessment and mitigation interventions are based on data and models that generate real- (or near real-) time predictions (Bull et al., 2013; Hobday & Hartog, 2014; Lewison et al., 2015), has become popular for migratory species conservation. Dynamic management has been applied to a variety of taxa, including blue whales (Hazen et al., 2017), sharks and tuna (White et al., 2019), sea turtles (Degenford et al., 2021), shorebirds (Johnston et al., 2020), and manatees (Udell et al., 2019). However, DM approaches often rely on horizontal species distribution or presence/presence-absence-based models to predict habitat use. These approaches do not include multidimensional movement models, which allow for understanding where a target species is with respect to threats and the motivation (why, how, when, and where) of their movement with respect to those threats (Allen & Singh, 2016; Nathan et al., 2008).

Hidden Markov models (HMMs) encompass a suite of statistical models for time-series data that can be applied to movement tracks for inference on behaviors without direct detection (as is often the case with long-distance migrants). These models describe 2 stochastic processes: an observed, state-dependent process of telemetry data and accompanying metrics (e.g., locational positions, speeds, or turning angles between successive locations) and a hidden process consisting of N -discrete, unobservable states or behaviors that ultimately result in observed telemetry metrics (Patterson et al., 2009). Application of HMMs has progressed rapidly, with recent developments allowing for more complex movement models in multiple dimensions (Adam et al., 2019; Connors et al., 2021; DeRuiter et al., 2017; Leos-Barajas et al., 2017).

These HMMs can be paired with DM approaches to create integrative conservation tools, expanding beyond static conservation methods. For example, Bedriñana-Romano et al. (2021) paired a species distribution model (SDM) for blue whales (*Balaenoptera musculus*) with a fast-fitting movement model and marine vessel traffic data to determine significant areas of overlap. This comprehensive approach can be adapted for other DM tools lacking multidimensional movement in risk predictions. The TurtleWatch approach has been used to mitigate Hawaiian pelagic longline fisheries interactions with loggerhead (*Caretta caretta*) and leatherback (*Dermodochelys coriacea*) turtles (Howell et al., 2008, 2015). It has been modified to incorporate multiple envi-

ronmental predictors and has been applied in other areas to predict residence time of critically endangered eastern Pacific (EP) leatherbacks (Hoover et al., 2019) across their range in the entire southeastern Pacific (South Pacific Turtlewatch [SPTW] [upwell.org/sptw]) (Degenford et al., 2021; Hoover et al., 2019; Liang et al., 2023). The cryptic, highly migratory, and deep diving nature of leatherbacks has created challenges for understanding their movement ecology and protecting them from the most acute threats at sea. EP leatherbacks, more than other leatherback populations, likely spend extensive amounts of time searching for food at depth in the oligotrophic South Pacific (SP) Gyre (Bailey, Benson, et al., 2012; Bailey, Fossette, et al., 2012; Schick et al., 2013; Shillinger et al., 2011). Therefore, previous movement models using only horizontal movement metrics have likely underrepresented the numbers and locations of foraging and residential behaviors.

We extended SPTW to determine risk of interaction of turtles with different fishing gears during their migration and foraging in international waters, using multidimensional EP leatherback tracking data and publically-available commercial fishing effort data. Our approach builds on the methods of similar studies (Bedriñana-Romano et al., 2021; Roe et al., 2014), which allowed us to estimate risk by combining layers on gear-specific fishing effort, spatial intensities of notable movement behaviors, and kernel density estimates of overall population space use. Ours is a novel modification, incorporating both horizontal and vertical movement data to infer behavior. We developed a fast-fitting and simple multidimensional HMM easily adapted to future studies on other taxa. Additionally, we employed a multidimensional approach to estimate space use of our population over time, applying the product kernel estimator algorithm to the movement tracks to estimate monthly utilization distributions (UDs) (Keating & Cherry, 2009). We demonstrated these techniques with a biotelemetry data set from Shillinger et al. (2008), proposing a DM framework for integrating movement, multidimensional behavior, and threat data to determine risk. This novel approach can be applied to a wide range of urgent conservation issues for sea turtles and other migrating species in dynamic risk environments.

METHODS

Data sets and processing

Biotelemetry data were from 28 postnesting, migratory adult female leatherbacks from the EP population in Playa Grande, Costa Rica (Shillinger et al., 2008; Appendix S1). Individuals were tagged while nesting in January and February of each year (2004, 2005, 2007). Sea Mammal Research Unit Satellite Relay Data Logger tags transmitted surface locations via the ARGOS satellite system. These provided additional pressure-sensor dive information (e.g., total dive duration, maximum dive depth, and dive profiles, including intermediate depth and duration points), with dives categorized as vertical movements when depth reached was >10 and <1500 m. Each track was processed to obtain daily locations with current-corrected persistence velocities (Copernicus Marine Service

[<https://marine.copernicus.eu/>]), total dive counts, and counts of deep versus shallow dive types (D1, deep; D2, shallow [Barbour et al, 2023]) (version 4.2.0 [R Core Team, 2022]) (further processing details in Appendix S2).

Behavioral intensity and hidden Markov movement models

To predict behavioral and multidimensional states of movement, we developed an HMM that consisted of 3 hidden, discrete states of vertical (diving) and horizontal (surface) movement for each time series (individual movement tracks): a transiting behavior state (S1, shallow dives, fast and directed horizontal movement) and 2 different residential behavior states (S2, mixture of dive depths, slower and less directed horizontal movement; S3, deep dives, intermediate speeds, and partially directed horizontal movement). Three states were used because a previous model that had only 2 behavior states and horizontal data made it difficult to discern foraging and residential behavior (Bailey, Fossette, et al., 2012). Each behavior also had relevance for fisheries interaction. Slow, more tortuous movements can result in longer residence times and increased area usage that increase the risk of interaction with fishing vessels in the same area; dive depths can increase the risk if turtles are diving at the same depth and area as fishing gear. Each state was defined by a unique set of values for mean daily move persistence velocity (horizontal movement, the tendency of turtles to persist in a given direction, obtained by multiplying daily swimming speeds by the cosine of the turning angles), mean daily number of dives, and daily proportion of D1 (deeper) and D2 (shallower) (Barbour et al, 2023) dives. The HMMs were fit with a Markov chain Monte Carlo algorithm and were implemented using the Bayesian programming language Stan and its R interface, rstan (Stan Development Team, 2022). Details on the HMM specification and fitting are in Appendix S3.

Several R packages have recently been developed to quickly and easily fit HMMs to time-series movement data (e.g., moveHMM [Michelot et al., 2016] and momentuHMM [McClintock & Michelot, 2018]). However, these packages have little room for user parameter modification and can result in problems with convergence, identifiability, and biologically meaningful inference (Auger-Méthé et al., 2016). Modifying the structure of our HMM requires the user to have a reasonable understanding of HMMs, Bayesian methods, and the coding software used (e.g., R, Stan). However, example code and data to replicate methods and similar results are available on GitHub (https://github.com/barb3800/ExampleFilesandCode_Barbour_etal). Therein, we highlight where users can modify model parameters and input data, perform essential checks for convergence problems, and determine optimal model structures through model selection and comparison.

Behavioral intensity and surface creation

To create behavioral intensity spatial surfaces used in an overlap analysis, each unique HMM behavioral state prediction was aggregated across individuals into a 1° resolution grid for the study area by summing each behavioral state in each grid cell for all tracks combined. This resolution captured a suitable number of positions, which were on average 28 km apart. The product was 3 spatial layers of behavioral intensity (**B**) in our study region, 1 for each movement state (*s*), with each being a matrix of size $m \times n$ (see also Appendix S4):

$$\mathbf{B}^{(s)} = \begin{bmatrix} b_{11}^{(s)} & \cdots & b_{1n}^{(s)} \\ \vdots & \ddots & \vdots \\ b_{m1}^{(s)} & \cdots & b_{mn}^{(s)} \end{bmatrix}. \quad (1)$$

Monthly kernel density estimates

To effectively estimate the probability density function (UD) in time and space, we used the product kernel estimator algorithm, developed by Keating and Cherry (2009), on the regularized location data. The R package adehabitatHR and its kernelkbase function (Calenge, 2006) were used for these purposes.

To create a leatherback probability density distribution at the same temporal scale as the currently existing SPTW tool, monthly UD surfaces were estimated for each turtle. A smoothing parameter (*b*) must be specified to determine these UD surfaces. This value is somewhat subjective (Keating & Cherry, 2009), and we chose an *b* of 3° for the spatial dimension (*X*, *Y*) and 30 days for the third dimension, time. This was based on an initial exploration of values for *b* that yielded a sufficiently heterogeneous surface and an understanding of the resolution of our data, with respect to our goal of estimating monthly surfaces.

To obtain population-level monthly UD surfaces, monthly UD surfaces were averaged across individuals. Following a migratory corridor into lower latitudes, these turtles have high regional densities in the months following their release from the nesting beach in Playa Grande, Costa Rica (Shillinger et al., 2008). To prevent these track sections from biasing other monthly UD surface results and to aid in visualizations of UD surfaces for each month independent of other months, values for each monthly UD surface were normalized between 0 and 1.

Each UD surface was estimated on an $m \times n$ -sized grid equivalent to that of the 3 behavioral state intensity layers. This grid was converted to a matrix format, resulting in a final product of 12 UD surface layers (**U**), 1 for each unique month (*t*).

$$\mathbf{U}^{(t)} = \begin{bmatrix} u_{11}^{(t)} & \cdots & u_{1n}^{(t)} \\ \vdots & \ddots & \vdots \\ u_{m1}^{(t)} & \cdots & u_{mn}^{(t)} \end{bmatrix}. \quad (2)$$

Monthly fishing effort

To create layers of monthly fishing effort, we utilized open-source data from Global Fishing Watch (GFW), an online database that provides high-resolution (1/100th°) global data sets on fishing effort across different gear types (Global Fishing Watch Inc. [<https://globalfishingwatch.org/>]).

Data for vessels included location and gear type. Fishing effort is reported with automatic identification system devices deployed on industrial fishing vessels (6–146 m) and measured in hours fishing in a grid cell (Kroodsmas et al., 2018). Average fishing effort (2018–2020) was used to best capture recent high fishing effort, aggregated to the same spatial resolution as the behavior and UD layers.

To match SPTW’s monthly temporal resolution already produced for EP leatherbacks, fishing effort was further separated by month (t). To assess gear-specific interactions, fishing effort was categorized by gear type (g), of which there were 8 unique categories (drifting longline, fishing, purse seines, pole and line, set gillnets, set longlines, squid jigger, trawlers, and tuna purse seines). Each gear-specific and monthly fishing effort raster was converted into an $m \times n$ matrix (\mathbf{F}).

$$\mathbf{F}^{(t,g)} = \begin{bmatrix} f_{11}^{(t,g)} & \dots & f_{1n}^{(t,g)} \\ \vdots & \ddots & \vdots \\ f_{m1}^{(t,g)} & \dots & f_{mn}^{(t,g)} \end{bmatrix}. \quad (3)$$

Relative risk of interaction

To determine the relative risk of gear-specific bycatch in multiple dimensions, we applied an overlap analysis. This consisted of using elementwise multiplication of the individual turtle behavior matrices (\mathbf{B}), monthly fishing effort surfaces for each gear (\mathbf{F}), and monthly UD estimates (\mathbf{U}). A higher empirical overlap or risk of interaction would occur when a particular cell had more of a particular behavior, a higher effort for a particular gear type, a higher population density, or any combination of the 3.

All matrix layers were first scaled to have the same nonzero, positive range (values 1–5). Elementwise cell multiplication (Appendix S4) was used to find the resulting monthly overlap matrices (\mathbf{O}) between fishing effort, UD estimates, and turtle behavioral states. This resulted in 324 initial overlap matrices (one for each unique combination of month, fishing gears, and behavioral state) (Equation 4). To create a matrix of relative risk (\mathbf{R}) (Equation 5), the value of each cell in the initial overlap matrix, \mathbf{O} , was divided by the sum of all cells within \mathbf{O} , representing the proper weight of each cell in the matrix. Each final matrix, \mathbf{R} , was then visualized as part of a monthly heat map of relative risk of interaction and incorporated into SPTW online monthly maps.

$$\mathbf{O}^{(t,s,g)} = \begin{bmatrix} f_{11}^{(t,g)} b_{11}^{(s)} u_{11}^{(t)} & \dots & f_{1n}^{(t,g)} b_{1n}^{(s)} u_{1n}^{(t)} \\ \vdots & \ddots & \vdots \\ f_{m1}^{(t,g)} b_{m1}^{(s)} u_{m1}^{(t)} & \dots & f_{mn}^{(t,g)} b_{mn}^{(s)} u_{mn}^{(t)} \end{bmatrix}, \quad (4)$$

$$\mathbf{R}^{(t,s,g)} = \frac{1}{\sum_{i=1}^m \sum_{j=1}^n f_{ij}^{(s,g)} b_{ij}^{(s)} u_{ij}^{(t)}} \mathbf{O}^{(t,s,g)}. \quad (5)$$

To create a temporal index of high relative risk of interaction, values within the 75th to 100th quantiles for each final matrix, \mathbf{R} , were extracted and summed across each unique combination of variables (behavioral state, month, gears), providing a quantitative table of the relative risk of significant overlap.

RESULTS

Behavioral intensity and hidden Markov movement models

The HMMs converged for each individual, for a total of 28 successful models. The 3 hidden states were distinct with respect to the means and standard deviations of their state-dependent parameters (Table 1; Figure 1a), indicating that the HMM successfully identified 3 distinct behavioral states for the parameters of daily move persistence velocity (high persistence velocity: high speeds, low turning angles; low persistence velocity: low speeds, high turning angles) and daily proportion of deep dives.

Population-level inferences were obtained by examining the distribution of horizontal and vertical movement variables for each predicted behavioral state. On average, turtles spent 62% (SD 19) of their time in S1 behaviors (shallower dives, high move persistence velocities), 19% (10) in S2 behaviors (mixture of dive depths, low move persistence velocities), and 20% (14) in S3 behaviors (deeper dives, intermediate move persistence velocities) (Table 2). When in an S1 state, turtles had a mean dive count (over the entire study period) of 444 dives (332) versus 128 (120) and 209 (233) times, respectively, in S2 and S3 states. Turtles moved with an average move persistence velocity of 27.8 km/day (16.3) in an S1 state, versus 17.9 (15.1) and 22.0 (13.2) km/day in S2 and S3 states, respectively, (Table 2).

The behavioral states also showed strong latitudinal and temporal trends. The S1 behaviors were dominant around the equator, through the migratory corridor in latitudes north of the equator (Shillinger et al., 2008), and throughout the middle of the SP Gyre (15–35° S) (Figure 2a). The S2 and S3 behaviors peaked at low latitudes (~5°N), mid-latitudes south of the equator (5–20° S), and along the edges of the gyre into higher latitudes (20–30° S) (Figure 2a). Plotting the monthly proportion of each behavioral state indicated the highest proportions of S1 behaviors in December and February through April; S2 behaviors in May and January; and S3 behaviors in May and November (Figure 1b). Density histograms of behavioral states by month and latitude showed S2 and S3 behaviors had the largest peaks in mid-latitudes (5–20° S) from April to August (Figure 2b), with another March peak in areas north of the equator (0–10° N). The S1 behaviors had the largest peaks following departure from nesting beaches in latitudes north of the equator in February and March and in lower latitudes (~30° S) in

TABLE 1 Population-level parameter means and standard deviations for behavioral states (S1, S2, S3)^a of individually fit hidden Markov models for 28 individuals in the eastern Pacific leatherback population.

Parameter ^b	State 1 (SD)	State 2 (SD)	State 3 (SD)
μ	30 (9.9)	2.0 (1.3)	21 (8.4)
σ	8.9 (3.0)	5.9 (4.6)	4.8 (3.2)
P	0.16 (0.048)	0.68 (0.096)	0.84 (0.048)
λ	8.1 (4.8)	8.1 (4.8)	8.1 (4.8)

^aStates: S1, shallow dives, fast and directed horizontal movement; S2, mixture of dive depths, slower and less directed horizontal movement; S3, deep dives, intermediate speeds, and partially directed horizontal movement.

^bDescriptions: μ and σ (Cauchy distribution), move persistence; P (Poisson distribution), proportion of deep type dives; λ (Poisson distribution, a constant [Appendix S3]), mean number of dives per day.

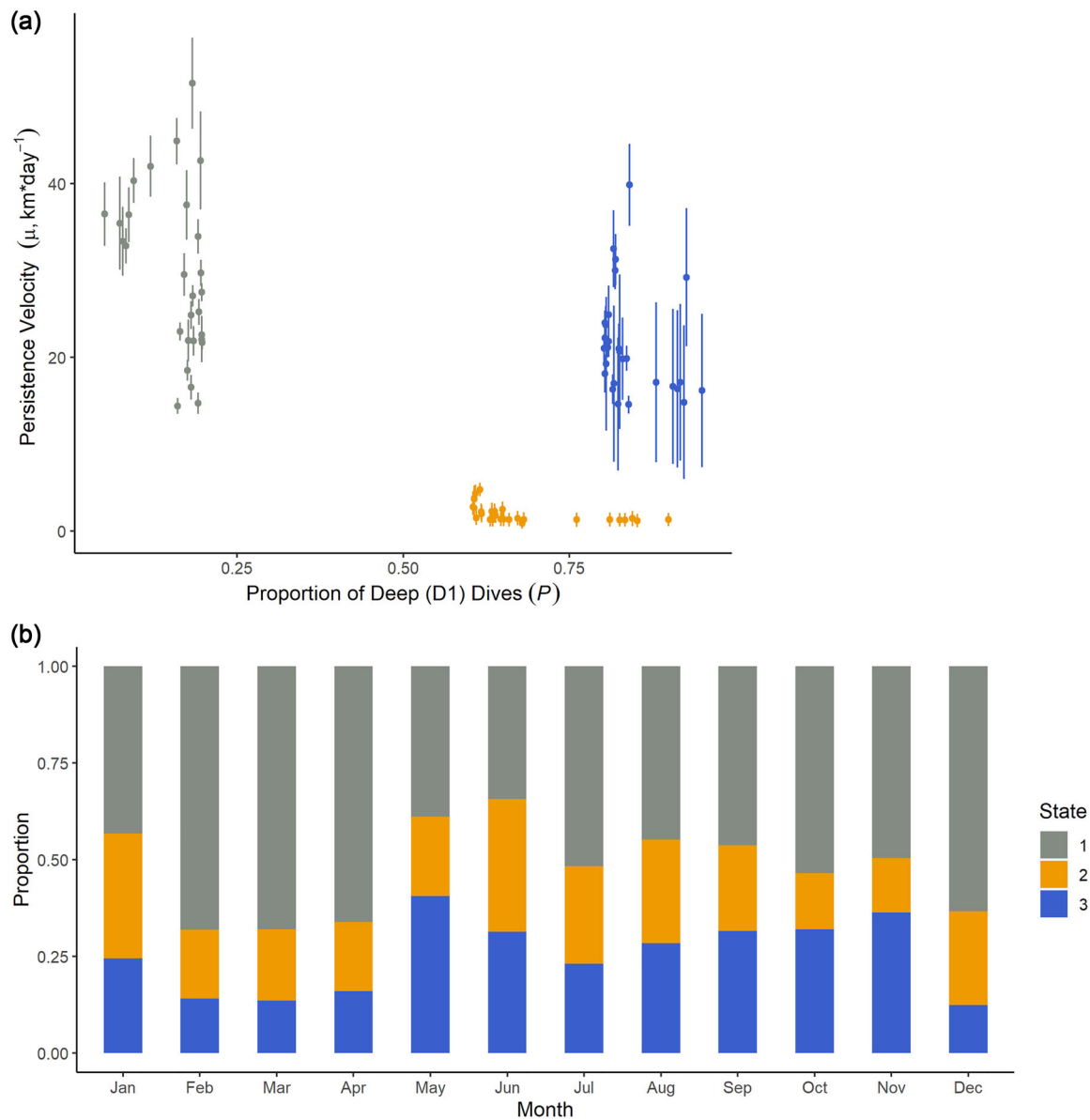


FIGURE 1 (a) For eastern Pacific leatherback turtles, individual means and standard deviations for hidden Markov model (HMM) parameters for move persistence velocity (μ) as a function of the parameters for the proportion of deep D1 (Barbour et al., 2023) dives (P) and (b) monthly proportions of HMM-derived behavioral states (S1, transiting behavior; S2, residential or foraging behavior; S3, deep diving and exploratory behavior) for 28 leatherback turtles in the eastern Pacific.

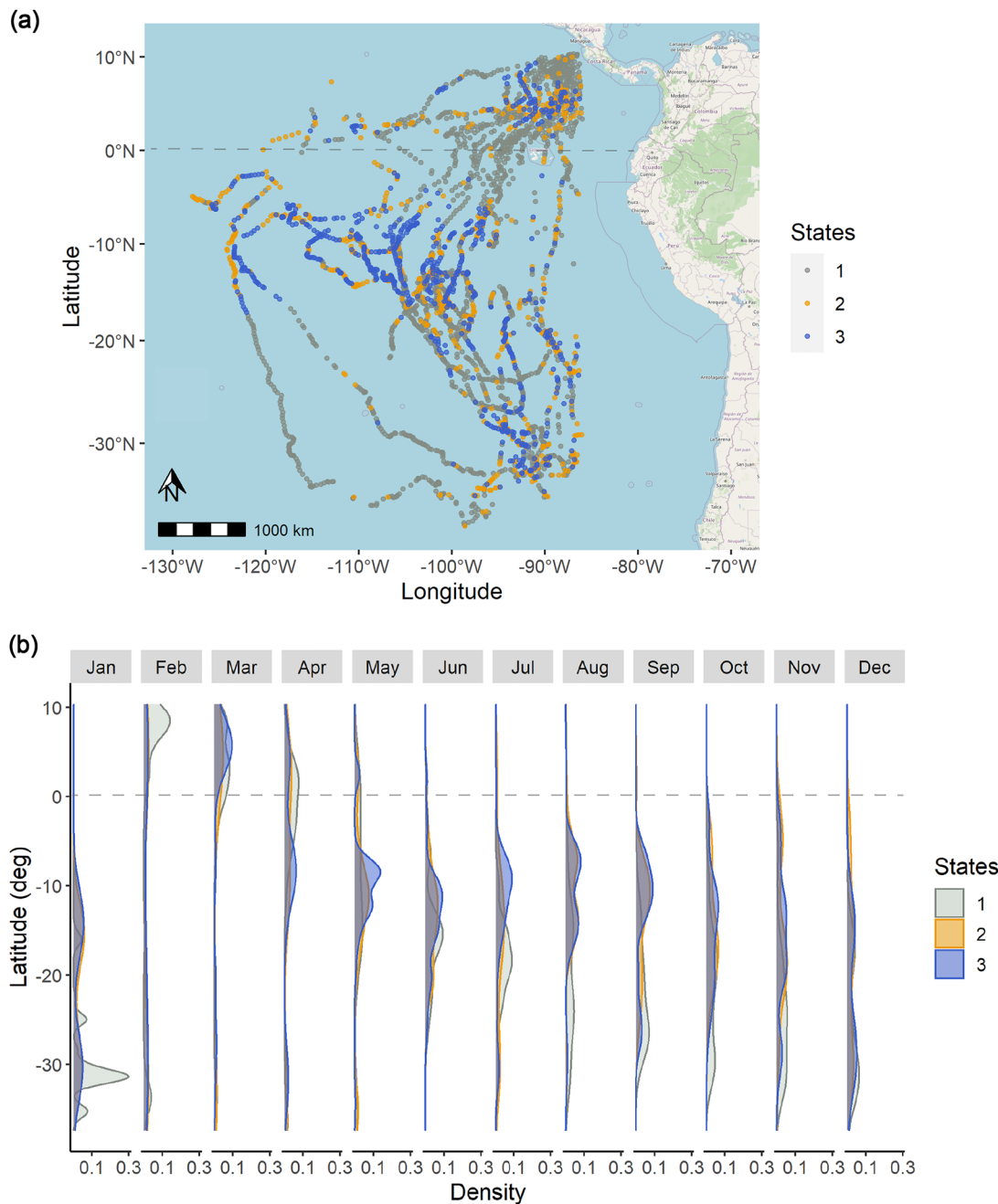


FIGURE 2 (a) Location and (b) monthly densities of hidden-Markov-model-derived behavioral states (S1, transiting behavior; S2, residential or foraging behavior; S3, deep diving or exploratory behavior) as a function of latitude for daily positions of 28 leatherback turtles in the eastern Pacific (gray dashed line, equator).

January (Figure 2b). For both latitude and month, S2 and S3 behaviors were mostly co-distributed with respect to patterns in the horizontal dimension.

Monthly kernel density estimates

Monthly UD estimates for leatherbacks in our region revealed variation in core-use areas over time (Appendix S5). Turtles initially had a single peak in their probability density surface during

February and March, due to their departure from the nesting beach and their following of a migration corridor into more southerly latitudes. Around April, they passed into their foraging region (south of 8.27° S) and began to radiate out into the SP Gyre, where multiple core-use areas emerged. Their distribution peaked near the Galapagos Islands (equator) in April and May; in the center of the gyre May through July; along the eastern edge of the gyre (~90°W) in May, June, and September; and near the southern edges of the gyre (30° S) in November and December.

TABLE 2 Vertical and horizontal movement variables for hidden Markov model–predicted behavioral states (S1, S2, S3) for daily locations of eastern Pacific leatherback turtles ($n = 28$).

Predicted state	Mean percent time (SD)	Mean dive count (SD)	Mean move persistence velocity (absolute, km/day) (SD)	Mean proportion D1 dives	Mean proportion D2 dives	Median maximum dive depth (m)	Median time at depth (min)
S1	62 (19)	444 (332)	27.8 (16.3)	0.112	0.888	57	13.5
S2	19 (10)	128 (120)	17.9 (15.1)	0.411	0.589	92	12.8
S3	20 (14)	209 (233)	22.0 (13.2)	0.803	0.197	112	13.7

*Behavioral states defined in Table 1 footnote.

Monthly fishing effort

Throughout the study area, fishing effort distribution varied by month and by gear type (Appendices S6 & S7; also see globalfishingwatch.org/map). Of the 8 fishing gears, drifting longline and squid jigger gears had very high average monthly fishing effort relative to the others (Appendix S5). Average fishing effort for drifting longline gear peaked in September through December. Average fishing effort for tuna purse seines exhibited a smaller peak in October. In contrast, squid jigger gear exhibited reduced fishing effort in September through November but had bimodal peaks in January through February and July to August.

Aggregated across gears, total monthly fishing effort was quite variable spatially and monthly (Appendix S7). In February through March, effort had broader spatial distributions, with concentrations in latitudes south of the equator ($\sim 10\text{--}20^\circ$ S). Effort was focused around the equator in January and May through July. Effort occurred in hotspots slightly south of the equator ($\sim 5^\circ$ S) and toward the eastern edge of the SP Gyre in April and September through December.

Relative risk of interaction

We produced monthly relative risk of interaction maps between behavior states and fishing gears, where monthly predictions of relative risk were visualized for each gear and behavior combination. The full product is available online as an overlay on the SPTW interactive map (upwell.org/sptw). For brevity, we only provide resulting monthly maps of relative risk of interaction between drifting longline gear and leatherbacks performing deep-diving behaviors (behavior S3) (Figure 3). Other behaviors (S1, S2) are available for comparison in Appendix S8. Results showed temporal and spatial differences in relative risk for leatherbacks performing S3 behaviors, with peaks in latitudes north of the equator in February through March; in the center of the SP Gyre ($\sim 10\text{--}20^\circ$ S) in May through June and September through November; and along the eastern and southern edges of the gyre in June and November through December.

These results were further reflected in the developed indices representing high relative risk, which were summarized across the unique groupings of month, behavioral state, and fishing gear (Table 3). Drifting longline gear had the highest risk values with deep-diving leatherbacks in October through November and the lowest risk values in January. Across gears, the highest risk values were seen for turtles performing a mixture of dive types (D1, deeper; D2, shallower), with lower move persistence (S2) in March and May. For turtles performing transiting behaviors with shallower dives (S1), risk values peaked in March and July. Other notable high risk values were seen for set longline, and trawler gears with turtles displaying transiting (S1) behaviors in May. Gear totals across all months and behavioral states showed drifting longline gear had the highest total relative risk of interaction with leatherbacks, followed by set longline gear.

TABLE 3 Summary of relative risk index values for eastern Pacific leatherback turtle, showing risk of interaction for 9 fishing gears with hidden Markov model–inferred turtle behavioral states and for each month.^a

Month	Behavioral state ^b	Drifting longline	Fishing	Pole and line	Purse seine	Set gillnet	Set longline	Squid jigger	Trawlers	Tuna purse seine
January	S1	0.026	0.040	0.039	0.039	0.039	0.039	0.038	0.038	0.038
January	S2	0.057	0.069	0.071	0.071	0.071	0.071	0.067	0.068	0.067
January	S3	0.029	0.043	0.042	0.042	0.042	0.042	0.041	0.041	0.040
February	S1	0.056	0.051	0.056	0.056	0.056	0.056	0.052	0.058	0.056
February	S2	0.035	0.035	0.036	0.036	0.036	0.036	0.037	0.037	0.045
February	S3	0.052	0.051	0.054	0.054	0.054	0.054	0.052	0.054	0.060
March	S1	0.089	0.10 ^c	0.11 ^c	0.11 ^c	0.11 ^c	0.11 ^c	0.11 ^c	0.11 ^c	0.12 ^c
March	S2	0.10 ^c	0.11 ^c	0.12 ^c	0.11 ^c	0.11 ^c	0.12 ^c	0.11 ^c	0.11 ^c	0.12 ^c
March	S3	0.046	0.049	0.052	0.052	0.052	0.053	0.051	0.052	0.064
April	S1	0.065	0.08	0.075	0.076	0.081	0.077	0.074	0.074	0.088
April	S2	0.065	0.064	0.072	0.069	0.071	0.064	0.063	0.063	0.069
April	S3	0.042	0.050	0.053	0.051	0.054	0.046	0.047	0.045	0.049
May	S1	0.094	0.10 ^c	0.097	0.099	0.099	0.10 ^c	0.096	0.10	0.098
May	S2	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.13 ^c	0.11 ^c
May	S3	0.085	0.087	0.081	0.083	0.084	0.085	0.081	0.090	0.077
June	S1	0.047	0.048	0.049	0.047	0.047	0.049	0.049	0.047	0.043
June	S2	0.058	0.061	0.062	0.060	0.060	0.063	0.062	0.060	0.054
June	S3	0.078	0.080	0.080	0.079	0.080	0.082	0.081	0.080	0.078
July	S1	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c	0.12 ^c
July	S2	0.043	0.051	0.053	0.053	0.053	0.055	0.051	0.053	0.047
July	S3	0.041	0.047	0.047	0.047	0.049	0.047	0.047	0.049	0.045
August	S1	0.081	0.083	0.083	0.083	NA	0.084	0.083	0.083	0.075
August	S2	0.052	0.051	0.051	0.051	NA	0.055	0.051	0.051	0.051
August	S3	0.067	0.065	0.065	0.065	NA	0.065	0.065	0.065	0.066
September	S1	0.063	0.055	0.055	0.055	NA	0.055	0.055	NA	0.052
September	S2	0.067	0.038	0.039	0.039	NA	0.039	0.038	NA	0.035
September	S3	0.082	0.071	0.073	0.073	NA	0.073	0.073	NA	0.070
October	S1	0.12 ^c	0.084	0.078	0.078	NA	0.078	0.078	NA	0.073
October	S2	0.092	0.050	0.051	0.051	NA	0.051	0.053	NA	0.053
October	S3	0.11 ^c	0.046	0.046	0.046	NA	0.046	0.048	NA	0.045
November	S1	0.12 ^c	0.089	0.089	0.089	NA	0.090	0.089	NA	0.084

(Continues)

TABLE 3 (Continued)

Month	Behavioral state ^b	Drifting longline	Fishing	Pole and line	Purse seine	Set gillnet	Set longline	Squid jigger	Trawlers	Tuna purse seine
November	S2	0.10 ^c	0.059	0.059	0.059	NA	0.059	0.059	NA	0.051
November	S3	0.12 ^c	0.084	0.084	0.084	NA	0.084	0.084	NA	0.080
December	S1	0.072	0.069	0.074	NA	NA	0.074	0.069	NA	0.062
December	S2	0.048	0.054	0.059	NA	NA	0.059	0.054	NA	0.047
December	S3	0.048	0.052	0.053	NA	NA	0.053	0.052	NA	0.042
Totals		2.6	2.4	2.4	2.2	1.5	2.5	2.4	1.7	2.4

^aSome gears had months with no fishing data available (NA). All fishing data were sourced from Global Fishing Watch (Global Fishing Watch, Inc. [<https://globalfishingwatch.org/>]).

^bDefinitions: S1, transient behavior; S2, residential or foraging behavior; S3, deep diving or exploratory behavior.

^cHigh values for each gear column (≥ 0.9).

DISCUSSION

Our results demonstrate how multidimensional movement data for a critically endangered and migratory species can be integrated with spatial–temporal data on overlapping threats to produce a risk management tool. This approach can be used by conservationists and managers to target areas on a chosen temporal (e.g., monthly) and spatial scale where species are performing behaviors that put them at risk for harmful interactions with threats. Additionally, we provide a method for creating a risk index that extends these predictions beyond illustrative maps of interactions, allowing for the level of overlap of a species performing particular behaviors to be quantified with respect to time and threat type. Our results provide a novel addition to the dynamic management tool for EP leatherbacks, SPTW (Hoover et al., 2019). We modeled this approach with anticipation of application to similar conservation studies on other taxa, especially those with cryptic, multidimensional behaviors that have challenged previous initiatives.

The product we produced with this analysis is immediately and urgently applicable. A recent population viability assessment (PVA) (Philip Miller, IUCN SSC Conservation Planning Specialist Group) indicated a high probability (>90%) of extirpation for the Costa Rica EP leatherback subpopulation (<45 years), with the Mexico subpopulation and the combined metapopulation facing extirpation in <55 years (Copsey et al., 2021). Another PVA (Laúd OPO Network, 2020) estimated EP leatherbacks will be extirpated by the year 2059 if bycatch is not significantly reduced. Our results highlight drifting (pelagic) longlines to have a high relative risk of interaction with EP leatherbacks while they are performing S2 (foraging, resting) and S3 (deep-diving, exploratory) behaviors in productive areas of the ocean gyre (Table 3; Figure 3). Given the low likelihood of another tagging data set of equivalent size ever being acquired for this population, the method we provide to produce dynamic risk maps will contribute to existing products for EP leatherbacks (e.g., SPTW) and may help slow their decline in concert with ongoing ex situ (e.g., head-starting) and in situ (e.g., nest protections) conservation efforts.

The results from our HMMs and monthly UD_s showed EP leatherbacks have multidimensional behaviors varying in space and time and latitudinal differences in monthly space use and identified behaviors (S1, S2, S3) consistent with past findings. Previous dynamic time warp clustering analyses showed that dives for turtles in this population can be classified into unique categories (D1 [deeper dives] or D2 [shallower dives]), each representing different vertical behaviors (Barbour et al., 2023). The S3 behavioral state identified by the HMMs likely represents the use of deep dives (D1) to shed excess heat gained from traveling through warm equatorial waters (Okuyama et al., 2021; Shillinger et al., 2010, 2011; Wallace & Jones, 2008) and prey search in the nutrient-poor SP Gyre, where zooplankton prey is dispersed at depth (Saba et al., 2008; Shillinger et al., 2011; Stromberg et al., 2009). The S2 behavioral state is likely more of a traditional foraging or residential state, where turtles are using

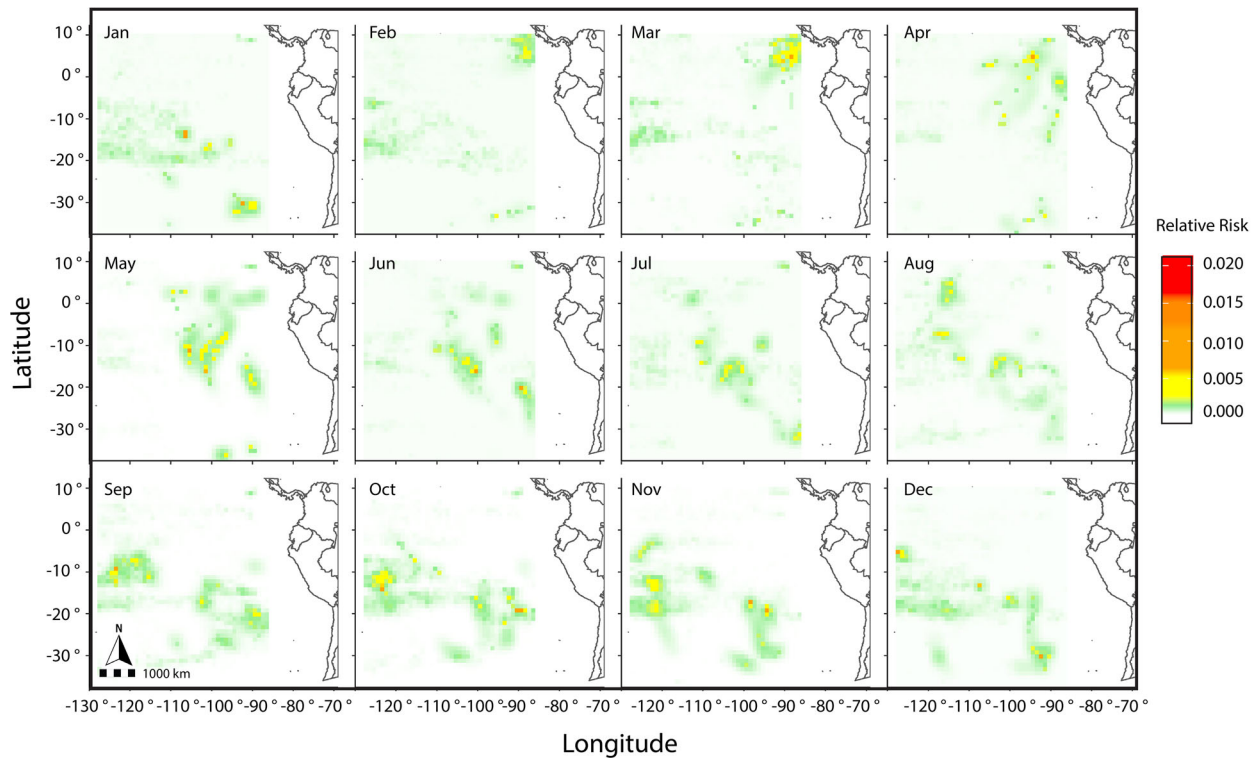


FIGURE 3 Example monthly areas of relative risk for eastern Pacific leatherbacks interacting with drifting longline gear while they are in a deep diving behavioral state (S3, deep diving and exploratory behavior). Relative risk is shown on a 1° resolution grid found through elementwise multiplication of monthly matrices of S3 behavioral intensities, drifting longline fishing effort, and utilization distributions. Maps are currently incorporated in the online tool, South Pacific TurtleWatch (upwell.org/sptw).

slower speeds and more tortuous movements to perform diurnal dives (deeper D1 dives during the day, shallower D2 dives at night) to forage on prey patches near more productive gyre areas (Bailey, Fossette, et al., 2012; Fernandez-Alamo & Farber-Lorda, 2006; Okuyama et al., 2021; Saba et al., 2008; Shillinger et al., 2011; Barbour et al., 2023).

The S1 behaviors were the shallowest (primarily D2 dives) and had the highest move persistence (fast and straight movements), corresponding to a transiting behavioral state. S1 behaviors had peaks north of the equator, where turtles are known to be migrating within a corridor into the SP Gyre (Shillinger et al., 2008), and peaks in southern latitudes (~20–35° S), corresponding to a couple of divergent tracks transiting through the oligotrophic gyre center (Figure 2a). The UD estimates of monthly population-level turtle space use reflected patterns seen in the HMMs, with hotspots near the Galapagos Islands (~5° N latitude), along the eastern (~90–100° W) and southern (south of 30° S) edges of the gyre, and in the region around 10° S latitude (Figure 2a; Appendix S5). These correspond to potential foraging areas, due to equatorial and island upwelling, frontal and convergence zones, and a shallower thermocline and nutricline compared to other gyre areas (Bailey, Fossette, et al., 2012; Fernandez-Alamo & Farber-Lorda, 2006; Saba et al., 2008).

Priority conservation areas were identified from the combination of monthly UD surfaces for each behavioral state (S1,

S2, S3) with fishing effort. Of the 8 fishing gears analyzed, drifting longlines and squid jiggers greatly surpassed other gear in their average monthly fishing effort in the region (Appendix S6). However, the overlap analysis with turtles showed leatherbacks are most at risk of interaction with drifting longlines because of spatial and temporal overlap (Table 3). The index of relative risk showed drifting or pelagic longline gear had the most high-value risk indices, especially where turtles are moving slower or diving deeper (S2 and S3 behaviors) (Table 3). For S2 behaviors, where turtles likely have higher residence times and increased area coverage due to lower move persistence velocities (e.g., foraging or residential behavior), risk of interaction with fishing gears may be increased when they overlap spatially and temporally with vessels similarly targeting productive fishing areas.

Risk may also be increased for turtles moving with intermediate move persistence velocities and diving at depth (behavior S3) in areas where fishing gear, such as deep drifting longlines, is deployed at similar depths (Table 3; Figure 3). Pelagic longlines pose a danger to leatherbacks at depth (Moore et al., 2009; Spotila et al., 2000; Wallace et al., 2010; Appendix S9), but previous risk models have not accounted for vertical behavior in their predictions of spatial–temporal overlap between leatherbacks and longlines (Roe et al., 2014).

Conservation efforts for this population can use our monthly surface maps and quantitative indices of risk to disseminate monthly products to managers and fishers. These can serve

as spatial–temporal predictions of the most beneficial fishing avoidance areas (Welch et al., 2019), with maps made available to users through an interactive online interface (upwell.org/sptw). Application can be further extended to identify which fishing gears could employ gear modifications to increase target prey catches while reducing bycatch (Sales et al., 2010; Watson et al., 2005).

Dynamic management methods have become increasingly useful and accessible for marine migratory species. Such species often utilize international waters outside the feasible scope of static management approaches, which are limited by national jurisdictions and physical boundaries. Dynamic management approaches, however, typically use presence–absence data of target species in relation to environmental covariates (Lewison et al., 2015; Maxwell et al., 2015) without integrating models of movement and/or multidimensional behaviors. Our application of HMMs to horizontal and vertical movement data allowed for a comprehensive understanding of space use over time. Although dynamic management approaches have primarily been developed for marine species, many terrestrial migratory species (e.g., elevational migrants, such as birds, bats, and ungulates [Hsiung et al., 2018]) demonstrate multidimensionality and temporal complexity to their spatial movements. These species could benefit from incorporating multidimensional, multistate movement models into conservation efforts, including the identification of priority conservation areas.

For species that migrate thousands of kilometers, the massive spatial scale of their movements, combined with individual variability in habitat use and behavior, can make highlighting priority conservation areas challenging. These challenges are further magnified for critically endangered species: rapidly shrinking populations inherently limit how many animals can be observed or tagged over time, potentially biasing understanding of recent habitat use and behavior. Our movement data are the largest tracking data set for the EP leatherback population. Therefore, we were limited to using biotelemetry data that did not overlap temporally with recent fishing effort data, and we assumed EP leatherbacks currently follow the same behavioral and spatial–temporal patterns at the time of data collection (2004–2007). This assumption is not implausible because previous research supports that turtles use a migratory corridor as they depart their nesting beaches for their foraging region in the SP Gyre (Shillinger et al., 2008), and it is hypothesized, based on round-trip migration data from other populations, that adults and subadults will return to foraging sites interannually with fidelity (James et al., 2005; Saba et al., 2008). However, future risk models for this population could be refined by additionally using simulations of migratory movements for multiple age classes (Gaspar et al., 2012), incorporating data for male turtles, and adding multidimensional abiotic data (Barbour et al., 2023).

Although our approach serves as a useful risk model of monthly interactions between turtle behavior and fishers in the SP, it could be further advanced by incorporating relationships with environmental or habitat covariates; creating higher resolution predictions of risk and behavior using higher resolution movement data; estimating population-level UDs while simul-

taneously accounting for autocorrelation and duration bias in movement tracks; and using abiotic and movement data at depth to create three-dimensional product maps of risk. We provide this product as an initial assessment of EP leatherback risk of interaction with key fisheries. Future modifications include updating monthly predictions with new fisheries effort data as it becomes available and modifying the model structure to address stakeholder (managers, nonprofit organizations, fishers) input and needs.

We present this holistic application of risk management for a critically endangered population of leatherback turtles, with the immediate goal of informing current conservation approaches. We provide a framework for integrative risk management that can be modified to benefit both aquatic and terrestrial species that demonstrate multidimensional and cryptic behaviors.

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SUPPORTING INFORMATION

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