Quantifying Habitat Accessibility in Marine Species Distribution Models

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Abstract

Species distribution models (SDMs) inform scientists and resource managers where species of interest are located and which environmental parameters characterize their habitat. Consequently, they are important tools in marine spatial planning and other conservation efforts. Though these models include measures of habitat suitability, there is no standard method for incorporating habitat accessibility. This is especially a concern for highly mobile species, such as seabirds and other marine predators. The energy landscape conceptual model quantifies the cost of transport across heterogeneous landscapes and its inclusion in the SDM process may quantify habitat accessibility. This paper outlines a modeling approach to implement energy landscapes in a SDM and proposes a pilot study using seabirds and wind as a model system. It further suggests two experiments to test increases in model predictive power and transferability. Considering the mobility of many marine predators, the combination of SDMs and energy landscapes could become a valuable conservation tool.
Introduction

Species distribution models (SDMs) are an essential tool in biogeography and conservation, used to create predictive maps of a species’ range as a function of its environment (Franklin 2009). However, SDMs are less accurate for highly mobile species, especially when the most ecologically relevant environmental variables are difficult to measure (Robinson et al. 2011, Eskildsen et al. 2013, Torres et al. 2015). These two factors, mobility and environmental measurement, are common concerns in the marine environment. Pelagic species frequently traverse thousands of kilometers across open-ocean environments that are particularly challenging to monitor (Weimerskirch et al. 2000, Ballance 2007). Because marine protected areas and other types of marine spatial planning rely on accurate SDMs, improving model quality is an important conservation goal (Ardron et al. 2008, Scales et al. 2014, Pérez-Jorge et al. 2015).

This paper hypothesizes that SDMs’ reliance on measures of habitat suitability over accessibility limits their effectiveness. The following section demonstrates this constraint is most pronounced for highly mobile species, which often violate assumptions of species-habitat equilibrium (Eskildsen et al. 2013). The energy landscape conceptual model, which applies movement ecology principles to heterogeneous environments, may provide a solution to the issue of accessibility in SDMs (Wilson et al. 2011, Shepard et al. 2013). Thus, I propose (1) an energy
landscape method for SDMs and (2) an experiment to test the model in a seabird-wind model system.

**Species Distribution Models**

Though there are diverse approaches to developing SDMs, a few principles hold universally. One consequence of these principles is that SDMs consider a habitat’s suitability (such as presence of prey or breeding sites) but not its accessibility. When selecting between multiple suitable habitats, animals experience selective pressure to minimize energy costs, for example avoiding steep slopes or flying with tailwinds (Wilson et al. 2011, Shepard et al. 2013). Thus, SDMs may be confounded when locations with equal intrinsic value (suitability) are differentially utilized due to extrinsic factors (accessibility). This section explains the components of SDMs, why they model suitability and not accessibility, and the consequences of excluding this important habitat characteristic.

**Developing Species Distribution Models**

Though there are diverse implementations, SDMs frequently share four components: (1) sightings of individuals, (2) maps of environmental variables, (3) a response function that links sightings and the environment to describe a niche, and (4) a map of the predicted distributions based on suitable habitat (Figure 1, Franklin 2009).
There are two complementary methods for collecting sightings. In one strategy, observations come from traversing transects (sampling paths) and counting individuals along the route. This provides two important benefits: in addition to presence observers can also record density (e.g. flock size) and absence. But transects are logistically difficult in the marine environment as research cruises require large crews and budgets (Ballance 2007). The alternative, telemetry, tracks an individual remotely using radio or satellites. Rather than record all the individuals at a location, telemetry
records all the locations visited by an individual. This only provides presence, not absence nor density, and it has some statistical biases (Aarts et al. 2008). But despite these issues, telemetry has become widespread for its relative logistical ease and higher resolution. In addition to location, telemetry can also provide estimates of behavioral state (e.g. commuting, foraging, or resting) and may track animals to locations a transect study might miss (Weimerskirch et al. 2008, Louzao et al. 2012). Both methods have their advantages and disadvantages that must be accounted for in model design.

Satellite remote sensing has transformed environmental monitoring, especially in marine settings (Longhurst 2010). Though satellite-borne sensors cannot match the breadth of in situ measurements (e.g. prey densities and water column properties) they do have advantages in ubiquity and cost. Landsat, Advanced Very High Resolution Radiometer, and other remote sensing systems have global coverage with visitation frequencies of days or weeks (Wang et al. 2010). These data are publicly available and are frequently used in both telemetry- and transect-based SDMs (Oppel et al. 2012, McGowan et al. 2013).

The response function links sighting and environmental data to describe the species’ niche. In most studies, SDMs derive this function from regression models that identify patterns in occurrence or abundance as a function of the environment (Franklin
More recent studies have drawn on machine learning and other branches of artificial intelligence to simulate complicated, non-linear relationships (Oppel et al. 2012). Both regression and machine learning fall under the category of correlative approaches: they identify patterns and leave processes open to interpretation. An alternative branch of SDMs model processes directly. These mechanistic, or process-based, models simulate ecological interactions directly to predict spatial distribution patterns (Kearney and Porter 2009, Robinson et al. 2011). As a new addition to the field, process-based models are still relatively uncommon but may provide new methods for testing hypotheses. It has also been suggested that process-based models are better equipped than correlative models to extrapolate predictions to novel conditions (e.g. under climate change scenarios or in new locations) because environmental parameters influence patterns more than processes, but this assertion has little evidence to date (Dormann et al. 2012).

Problems Modeling Habitat Accessibility

Niche-based response functions describe habitat suitability without considering accessibility. This methodology assumes a static relationship between population and environment (Franklin 2009). But movement of sufficient magnitude, as seen in seabirds and other marine predators, violates this assumption. Static models only account for intrinsic habitat parameters (suitability), not the factors influencing movement (accessibility).
Addressing the issue of mobility in SDMs remains generally unresolved. Some process-based models explicitly simulate movement, but these are rare and highly specialized. In one example, Merow et al. (2011) developed a mechanistic SDM that incorporated seed dispersal by birds to predict the spread of invasive plants. However, general methods for quantifying habitat accessibility are lacking. Movement ecology analyzes connections between an organism’s internal state, capacity for movement, and its environment (Nathan et al. 2008). Hybrid models that incorporate these principles into the standard SDM workflow may be applicable to a wider range of species.

Evidence for the Importance of Accessibility

Multiple studies have demonstrated an inverse relationship between SDM accuracy and species mobility, especially when predictions are extrapolated to new times or places (model transferability). One relevant study tested the ability of SDMs developed in an earlier time period to predict future distributions (Eskildsen et al. 2013). They developed a set of SDMs using alpine butterfly sightings in 1992-1999, then predicted changes in spatial distributions due to climate change in 2002-2009. After validating their predictions using observations from the latter period, researchers found an accuracy gradient across species mobility. Specifically, predictions were more accurate for the relatively immobile chestnut heath butterfly (Coenonympha glycerion) than for far-ranging black-veined white (Aporia crataegi) and peacock (Nymphalis io).
butterflies. This pattern has been further substantiated in other SDM research (Luoto et al. 2005, Pöyry et al. 2008).

Model transference to new locations has also confounded SDMs for mobile species. Torres et al. (2015) tested whether a grey petrel (*Procellaria cinerea*) SDM developed using data from the Antipodes and Kerguelen Islands’ populations could predict the distribution of a separate population on Marion Island. Grey petrels are highly mobile seabirds, with foraging ranges exceeding 1,000km (Rollinson et al. 2016). These three islands are distributed across a 10,000km swath of the Southern Ocean, providing a severe test of transferability. Though the model accurately predicted distributions around Antipodes and Kerguelen Islands, where the training data originated, it was less successful with the Marion Island sample. Per Torres et al. (p. 15), “Strong interpolation and weak extrapolation indicate that our models are able to describe the potential response of grey petrels to environmental variation, but the realized response of each grey petrel population to oceanographic conditions is context-dependent.” Both Torres et al. (2015) and Eskildsen et al. (2013) demonstrate that for mobile species, intrinsic measures of habitat suitability alone limit the transferability of models to new locations and times.

**Seabirds’ Energetic Windscapes**

Mobile species have the capacity to choose among multiple suitable habitats and save energy by choosing the most accessible (Stephens et al. 2007). In turn, these
choices have profound effects on species’ spatial distributions. This section reviews the energy landscape conceptual model, which applies movement ecology principles to analyze cost of transport in heterogeneous environments (Wilson et al. 2011, Shepard et al. 2013). Then it addresses seabirds specifically, with a discussion of wind’s impact on these organisms’ movement, energetics, and spatial distribution.

Energy Landscapes

The energetic cost of transport is not uniform across varied landscapes. For many terrestrial animals, variables such as slope and substrate (e.g. sand or brush) increase cost of transport, influencing route selection and distribution (Wall et al. 2006). The effect of wind on aerial movement is also well documented, with many species displaying situational preferences for tail- or crosswinds (Weimerskirch et al. 2005b, Adams and Flora 2010, Kranstauber et al. 2015, Vansteelandt et al. 2016).

The energy landscape approach calculates the cost of transport as a function of environmental parameters (Wilson et al. 2011, Shepard et al. 2013). For example, Wall et al. (2006) developed a cost function for African savannah elephants (Loxodonta africana) based on slope incline and Wilson et al. (2011)
estimated movement costs for imperial cormorants (*Phalacrocorax atriceps*) using flight distance from colony and dive depth. Shepard et al. (2013) suggested visualizing the cost of transport function across a landscape by mapping contours of locations with equal energy costs. These iso-energy polygons (IEPs) are analogous to isotherms or isobars in climatology and can aid in interpretation of movement paths (Figure 2). Applying this principle to SDMs affords the model a metric for differentiating the relative importance of habitat suitability and accessibility.

**Impacts of Wind on Seabird Movement**

Many seabirds are specially adapted to exploit wind power when covering long distances. Allometric models apply aerodynamic principles to predict energetic flight costs based on the size and shape of a bird’s body (Pennycuick 2008). Studies across several families of seabirds demonstrate they expend far less energy than allometric models predict, likely due to their ability to extract power from wind. Ballance (1995) found red-footed boobies (*Sula sula*) expend only one third of predicted energy costs in flight. These savings increase with wind power, as energy expenditure of northern fulmars (*Fulmarus glacialis*) dropped by almost 50% in 8m/s winds compared to 3m/s (Furness and Bryant 1996). In an extreme example, wandering albatrosses (*Diomedea exulans*) expend less energy flying than walking (Figure 3, Weimerskirch et al. 2000).
The energy savings from exploiting wind affect many movement parameters, including route selection and timing. When Pacific Ocean wind patterns change during El Niño and La Niña conditions, Laysan (Phoebastria immutabilis) and black-footed (P. nigripes) albatrosses shift their foraging ranges to follow the strongest winds (Thorne et al. 2016). Schreiber and Chovan (1986) found red-footed boobies and great frigatebirds (Fregata minor) roost in greater numbers in calmer conditions and leave to forage when winds increase.

Figure 3: Wandering albatross heart rate in various behavioral states. Reproduced from Weimerskirch et al. 2000.
Wind direction has a significant impact as well as wind strength. Many species display stereotypic preferences for tail- or crosswinds. On long, directed migratory flights sooty shearwaters (*Puffinus griseus*) favor quartering tailwinds whereas Hawaiian (*Pterodroma sandwichensis*) and grey-faced (*P. gouldi*) petrels forage in counterclockwise loops and therefore prefer tailwinds on the right side (Figure 4, Adams and Flora 2010).

![Rose diagrams of winds experienced by three species. SOSH = sooty shearwater, HAPE = Hawaiian petrel, GFPE = Grey-faced petrel. Reproduced from Adams and Flora 2010.](image)

Energy savings are further modulated by behavioral state, with lower costs in transit than in active foraging. The discrepancy in cost between behaviors can be attributed to several factors. In some species, plunge diving in pursuit of prey results in a six-fold increase in energy output (Jodice et al. 2003). Furthermore, flight patterns change when predators engage in area-restricted search (ARS, searching for prey within a limited area), typified by sinuous paths with higher turning angles than more linear commuting flights (Fauchald and Tveraa 2003). Per optimal foraging theory,
sinuous flight is more expensive than linear and efficiency will be greatest during commuting (Pennycuick 1978). Amélineau et al. (2014) demonstrated this cost empirically for northern gannets (*Morus bassanus*). Birds experienced a higher proportion of headwinds when engaged in ARS and spent more energy in sinuous flight than linear even when controlling for wind (Figure 5).

![Figure 5](image)

*Figure 5: Overall dynamic body acceleration (ODBA) increases with headwinds and is overall higher during ARS (A) than when commuting (B). Reproduced from Amélineau et al. 2014.*

**Incorporating Energy Landscapes in SDMs**

Complementing SDMs’ use of environmental maps to quantify habitat suitability, energy landscapes may quantify habitat accessibility. For seabirds, an energy landscape – referred to hereafter as an energy windscape – requires three components: maps of wind strength and direction, a cost of flight metric, and telemetry to link the
two. This section covers (1) a model organism – the red-footed booby – for implementing energy windscapes, (2) how wind, flight costs, and telemetry combine to produce an energy windscape, and (3) a method for validating energy windscapes’ efficacy in SDMs.

Red-footed Boobies – a Model Organism

An effective model organism for implementing energy landscape SDMs should be strongly influenced by habitat accessibility. Furthermore, this organism should have relatively simple foraging habits to avoid interference from other variables. However, the organism must be sufficiently mobile to provide a rigorous test of SDM transferability.

Given these requirements, red-footed boobies are excellent candidates for an energy landscape model organism. Like other members of the sulidae family, red-footed boobies typically make single-day foraging trips (Weimerskirch et al. 2005b). This is a useful trait for a parsimonious model, as trip durations for other species are more variable. For example, other seabirds often coordinate short and long trips (bimodal foraging) between a pair of provisioning adults, which introduces a layer of complexity (Baduini and Hyrenbach 2003, Sommerfeld and Hennicke 2010) (but see Young et al. (2010) for occasional bimodal foraging in boobies). Furthermore, phenology (phases and timing of breeding) has a pronounced influence on the duration and distance of many seabirds’ foraging trips. Provisioning (chick-feeding)
Laysan and black-footed albatrosses dramatically expand their foraging range when chick brooding (parent with chick majority of time) ends and chick rearing (chick alone majority of time) begins (Hyrenbach et al. 2002). Red-footed boobies do exhibit some fluctuations in foraging strategy across the breeding cycle, but not nearly to the same extent (Mendez et al. 2016). Overall, red-footed booby foraging strategies provide a simplified system, facilitating creation of the energy windscape.

Despite the relative simplicity of their foraging behavior, red-footed boobies are a highly-mobile species. They forage up to 250km from land and juvenile birds may disperse to islands thousands of kilometers from their natal colony (Harrison 1990). Red-footed boobies are considered the most pelagic of all boobies and are found farthest from land. (Nelson 1978, p. 655) offers this description:

“The red-foot is the smallest booby ... long-winged ... and long-tailed ... with a light build and a graceful, more flexible and faster flight than other boobies, tending to skim and shear the waves and often gliding for long distances. Red-footed and white [masked] boobies [S. dactylatra] are met with further from land than any other booby.”

Identifying red-footed boobies’ habitat preferences has proven to be more difficult than for other seabird species, which may indicate that accessibility strongly influences their habitat selection. This difficulty may be an indirect effect of boobies’ single-day foraging trips. Despite being more pelagic than other boobies, red-footed boobies forage over smaller territories than many other seabirds in the same region. Laysan albatrosses and red-tailed tropicbirds (Phaethon rubricauda) both share colonies
with red-footed boobies throughout the Central Pacific, but Hawaiian red-tailed
tropicbirds have a foraging range of 475km and Laysan albatrosses range beyond
3,500km (Felis et al. 2015, Thorne et al. 2016). Their smaller range affords red-footed
boobies fewer habitat options, which may reduce specialization. In habitat suitability
models of Pacific seabirds, red-footed boobies display weaker affinities for sea-surface
temperature, sea-surface salinity, and other oceanographic variables than shearwaters
and petrels (Ballance et al. 2002, Vilchis et al. 2006). Qualitative analysis of red-footed
boobies foraging from Lehua Islet in the Main Hawaiian Islands further indicates that
this species chooses habitat by minimizing flight costs over intrinsic qualities such as
oceanographic variables (Czapanskiy et al. 2016). The role of habitat accessibility in
red-footed boobies’ spatial distribution makes them a suitable model organism to test
the energy landscape method.

Application of Dijkstra’s Algorithm

Shepard et al. (2013) suggested visualizing energy landscapes using iso-energy
polygons, but a grid of least-cost pathways may be more effective for SDMs. Kranstauber et al. (2015) applied Dijkstra’s algorithm to create a time-minimization
model for migration routes as a function of wind. Dijkstra’s algorithm calculates the
least-cost pathway between two points when cost of movement is non-uniform (Dijkstra
1959). By replacing flight times with energy costs, the same process may be used to
produce an energy windscape. The model developed by Kranstauber et al. gridded a
map of the world and superimposed layers of typical wind speeds and directions. Using ground speed equations from allometric models, they weighted step costs (i.e. time required to fly between adjacent grid cells) as a function of wind speed and direction. By applying Dijkstra’s algorithm, they calculated the least-cost routes between randomly selected migration endpoints (Figure 6). Their results provided evidence that flying along shortest-distance routes required more time than curving routes that optimize wind speed and direction. In a later field study, Vansteelandt et al. (2016) provided empirical evidence for the predicted routes, further supporting the use of this methodology.

Figure 6: Following Dijkstra's algorithm, recursive calculation of least-cost paths emanating from an origin weighted by wind speed. Reproduced from Kranstauber et al. 2015.
Rather than minimizing time, an energy windscape should calculate paths that minimize energy expenditure. The following sections review the methods physiologists use to measure energy expenditure in the field and suggest a modification to the methods in Kranstauber et al. (2015) to produce an energy windscape.

Flight Energy Costs and ODBA
Field energetic studies typically employ three methods: heart-rate monitors (HRMs), doubly-labeled water (DLW), or accelerometers. HRMs measure heart beats-per-minute and provide a high-resolution measure of energy expenditure. Weimerskirch et al. (2000) implanted these devices in wandering albatrosses to measure the energetic costs of different behaviors, such as walking, flying, and take-off. Though they provide high-resolution and highly accurate data, implanting HRMs requires surgery and is highly invasive. DLW uses water with a unique signature of hydrogen and oxygen isotopes (the “label”), which is injected into the study subject. As the animal expends energy, oxygen is lost in CO\textsubscript{2} through exhalation but hydrogen is retained. After a few hours or days, the researcher recaptures their subject and takes a blood sample. The difference in labeled hydrogen and oxygen may then be converted to overall energy expenditure (Shaffer 2011). DLW has the advantage of being less invasive than HRMs, but it integrates energy use over the entire study period, providing a lower-resolution metric.
The use of accelerometers (devices that measure changes in acceleration) to measure energy expenditure is a more recent development. Deployed on wildlife, accelerometers measure overall dynamic body acceleration (ODBA), which quantifies the mechanical work (i.e. movement) performed by the animal. Many processes other than movement require energy, such as digestion and thermoregulation, but movement is often responsible for much of the variance in energy expenditure, which makes ODBA an effective proxy for energy expenditure (Gleiss et al. 2011). In recent years, accelerometers and ODBA have been applied in numerous studies to quantify the links between energetics and behavior (Laich et al. 2011, Shamoun-Baranes et al. 2012, Bouten et al. 2013, Amélineau et al. 2014, Duriez et al. 2014). For more details on field measurements of flight costs, see Elliott (2016).

Energy Windscape Construction

The energy-wind response function quantifies cost of transport in the energy windscape. Data must include three variables: (1) ODBA, (2) wind speed and direction, and (3) location data to link ODBA with wind. For example, a combination accelerometer/GPS tag and remotely-sensed wind data provides all three. Using these data, the energy-wind response function may be modeled by regressing ODBA against morphological and environmental parameters in a generalized linear model. I propose four independent variables: the bird’s mass \((m)\), groundspeed velocity \((v_g)\), wind speed \((v_w)\), and the relative angle between flight and wind \((\theta)\).
\[ ODBA = f(m, v_g, v_w, \theta) \]

Mass is easily measured in the field with spring-scales or other similar tools, groundspeed velocity can be estimated from GPS tracks with sufficient temporal resolution, and wind speed/direction may be measured from satellite scatterometry or numerical models (Adams and Flora 2010, Hitzl et al. 2014). Substituting the species’ mean mass and flight speed isolates the wind variables, yielding:

\[ ODBA = f(v_w, \theta) \cdot f'(m, v_g) \]

Where \( f' \) is a constant. This equation predicts ODBA (and by proxy, energy expenditure) based on wind conditions, providing the energy-wind response function.

As mentioned earlier, energy expenditure, in addition to being wind-dependent, is also mediated by behavior. Commuting birds spend less energy than those actively foraging, and birds resting on the water are not interacting with wind. Including foraging and resting behavior in the analysis will therefore likely confound the wind-response function. The residence in space and time (RST) algorithm differentiates behavioral states and can be used to isolate commuting data points from foraging or resting (Torres et al. in review). This algorithm should be applied before the regression analysis to subset the relevant data.

In modeling a central-place forager (one who leaves from and returns to its nest) like the red-footed booby, it is necessary to further modify the model from Kranstauber
et al. (2015). At relevant spatio-temporal scales, migrations are one-way trips. Foraging seabirds, though, return immediately to the colony after foraging and must optimize both the outbound and inbound trips. For example, red-footed boobies foraging in the Europa Channel choose routes with crosswinds, because the gains from flying with tailwinds are offset by the losses from struggling against headwinds. Therefore, the energy landscape model should sum Dijkstra’s algorithm in both the outbound and inbound directions to calculate roundtrip costs.

The Proposed Research

This research uses data from the U.S. Geological Survey (USGS) and University of Hawaii to test whether an energy landscape can improve SDM predictive power and transferability. USGS tracked breeding Hawaiian seabirds in the years 2013-2016, including three red-footed booby colonies (Figure 7). Birds at two of these colonies (Lehua and Marine Corps Base Hawaii, MCBH) were tracked with GPS alone, while individuals at the third colony (Kilauea Point) were tracked with both GPS and accelerometers. The Kilauea Point data may be combined with wind data from University of Hawaii’s Weather Research and Forecasting Model (WRF) to construct the energy windscape using the methods described above. This energy windscape can be integrated in an SDM to test whether it improves distribution predictions compared to a null model. Data from Lehua and MCBH represent independent datasets. Predicting
their distributions using the model from Kilauea Point tests whether energy windscapes improve model transferability (sensu Torres et al. 2015).

![Map of Kilauea Point tracking data](image)

**Figure 7: Red-footed booby colonies.**

**Test of Predictive Power**

The Kilauea Point tracking data includes both location and acceleration records, making it suitable for an energy windscape experiment. As detailed above, the energy windscape can be generated using the following steps:

1. Apply the RST algorithm to the GPS data to isolate commuting points.
2. Calculate ODBA along commuting routes.
3. Use a generalized linear model to regress ODBA against mass, groundspeed, wind speed, and relative wind direction.
4. Substitute species mean mass and flight speed to isolate wind variables and produce the energy-wind response function.

5. Input WRF wind data into the energy-wind response function to calculate round-trip flight costs within the study area using Dijkstra’s algorithm.

This process yields the energy windscape. It should be used as one environmental layer within the Kilauea Point red-footed booby SDM. Other ecologically relevant environmental variables that should be included are sea-surface temperature (SST), sea-surface chlorophyll density (chl a), and sea-level anomaly gradient (gSLA) (Ballance et al. 2006, Vilchis et al. 2006, Mendez et al. 2016). SST and chl a frequently correlate with seabird densities. High sea-level anomaly gradients indicate an oceanic front or eddy; these features concentrate prey and attract predators (Nel et al. 2001, Weimerskirch et al. 2005a). For comparison, a null model should also be developed using the same environmental variables (SST, chl a, gSLA) but substitute a distance-from-colony variable for the energy windscape (Figure 8). This null model assumes habitat accessibility decreases uniformly from the colony. Calculating Akaike’s information criterion (AIC) for both models determines if the energy windscape improved SDM predictive power (Burnham and Anderson 2002).

Test of Model Transferability

The model transferability test uses data from Lehua and MCBH to validate the model in independent conditions (Figure 8). Again, this test uses the energy-wind
response function and WRF wind data to produce energy windsapes, now for the areas surrounding Lehua and MCBH. It compares predicted red-footed booby distributions from both the energy windscape and null model SDMs against telemetry from the Lehua and MCBH colonies. Area under the curve and true skill statistics determine whether the energy windscape SDM improved model transferability (Fielding and Bell 1997, Allouche et al. 2006).

Figure 8: Flowchart of energy windscape predictive power and transferability tests.

**Conclusion**

SDMs attempt to answer two questions: why do we find organisms in certain places and where else might we find them? Current SDM methodology answers the first question by examining the species’ niche – the combination of environmental variables that characterize suitable habitat. But as mobility increases, so too does the
importance of those variables’ spatial configurations (e.g. a prey patch upwind versus crosswind of a colony). When SDMs don’t consider habitat accessibility, they are incompletely describing habitat for mobile species. In turn, this limits their ability to answer the second question. Predictions based on incomplete understanding are less accurate (Eskildsen et al. 2013, Torres et al. 2015).

This paper presents a solution that quantifies habitat accessibility by drawing on the energy landscape conceptual model. Mobile species benefit from minimizing energy expenditure when selecting habitats. Thus Shepard et al (2013) proposed using maps of variable transport costs in a heterogeneous environment to explain differential exploitation of equally suitable habitats. Consider the upwind and crosswind prey patches mentioned in the last paragraph. Furthermore, consider that these two patches occupy similar environmental conditions (e.g. surface temperature and chlorophyll density). To save energy, seabirds aggregate more at the crosswind prey patch than the upwind one. Using only habitat suitability measures, a SDM cannot meaningfully interpret this differential exploitation. But with an energy landscape, the model has a metric to weight differences in accessibility. Properly applied, this yields a more ecologically realistic model that may make better predictions, especially when transferred to novel conditions. This paper proposes an experiment, using data from tracked red-footed boobies, to validate this hypothesis.
SDMs are important tools in reserve planning and other conservation efforts that require an understanding of species’ spatial distribution (Robinson et al. 2011). Marine predators, such as seabirds, sharks, and whales, are frequent targets of these efforts (Coll et al. 2012). But these organisms cover vast territories, which can limit the effectiveness of SDMs. Improving SDM methodology for these highly mobile species should be an important goal for marine conservation.

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