

Testing the transferability of track-based habitat models for sound marine spatial planning

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Abstract

Aim: Species distribution models (SDMs) are statistical tools aiming at mapping and predicting species distributions across landscapes. Data acquisition being limited in space and time, SDM are commonly used to predict species distribution in unsampled areas or years, with the expectation that modelled habitat–species relationships will hold across spatial or temporal contexts (i.e., model transferability). This key aspect of habitat modelling has major implications for spatial management, yet it has received limited attention, especially in the dynamic marine realm. Our aims were to test geographical and temporal habitat model transferability and to make recommendations for future population-scale habitat modelling.

Location: Two contrasted regions of the North Western Mediterranean Sea: the cold and productive waters of the Gulf of Lion, and the warm and oligotrophic waters of Corsica.

Methods: We GPS-tracked 189 Scopoli's shearwaters, *Calonectris diomedea*, at four breeding sites during the chick-rearing period in 2011 and 2012 (418 foraging trips), and analysed their fine-scale foraging behaviour. We then built colony-specific habitat models (GAMMs) to test SDM geographical and temporal transferability and investigated the effect of extrinsic (environmental extrapolation) and intrinsic (trip characteristics) factors on transferability.

Results: Scopoli's shearwaters from our four study sites had comparable foraging strategies (as assessed from trip characteristics and isotopic diet tracers). Despite such similarities, SDMs revealed colony-specific habitat associations. Geographical and temporal model transferability was better within than between regions.

Main conclusions: Crucially, our study illustrates how habitat–species relationships can vary between colonies located <200 km apart, and underlines the effect of spatio-temporal extrapolation in habitat modelling. We therefore warn that defining adequate spatial scales for model predictions is critical to sound marine spatial planning and conservation.

KEYWORDS

biologging, central-place foragers, extrapolation, habitat modelling, seabirds, transferability

1 | INTRODUCTION

Species distribution models (SDM) are increasingly used to track range shifts or delimit species core habitats for purposes of conservation planning or ecosystem management (Guisan et al., 2013; Robinson et al., 2011). SDMs correlate records of species occurrence, habitat-use or density with environmental data in geographic space to predict species distribution over a given spatial scale and time (Guisan & Zimmermann, 2000). One of the key aspects of these models is their ability to predict species distributions in unsampled areas or time periods (i.e., hind- or forecasting). Correlative SDMs have commonly considered stationarity, that is that model parameter estimates remained constant through space and time (Dormann et al., 2012). However, there is growing evidence that species-environment relationships can vary in space and time (Broennimann et al., 2007; Randin et al., 2006) and thus potentially impair model predictions at unsampled areas/times (Redfern et al., 2017; Torres et al., 2015). The ability of a model calibrated in one context to make accurate predictions in a different context is termed generality or transferability (Phillips, 2008; Vaughan & Ormerod, 2005). While SDM transferability has received much attention in terrestrial studies (Araujo, Pearson, Thuiller, & Erhard, 2005; Bonthoux, Balent, Augiron, Baudry, & Bretagnolle, 2017; Duque-Lazo, van Gils, Groen, & Navarro-Cerrillo, 2016; McAlpine et al., 2008; Randin et al., 2006), it has been largely overlooked in the marine environment (Sequeira, Bouchet, Yates, Mengersen, & Caley, 2018; but see Mannocci, Roberts, Miller, & Halpin, 2017; Mannocci et al., 2018), notably in tracking studies. Specifically, recent work highlighted the lack of transferability of ocean-specific SDMs and advocated enhanced testing of transferability conditions across ecologically relevant scales (i.e., the bounding-box where predictions are estimated and mapped, Torres et al., 2015; Paton & Matthiopoulos, 2016; Redfern et al., 2017).

Limited SDM transferability may stem from i) differences in the range and/or combinations of environmental predictors between the calibrated and generalization datasets (i.e., extrapolation), ii) incorrect identification of relevant processes/explanatory variables or iii) species-specific features such as phenotypic plasticity, ecotypes, competition, history of exploitation or local biotic interactions (McPherson & Jetz, 2007; Randin et al., 2006). For example, terrestrial bird studies showed that SDM geographical transferability was higher for specialist and resident species than for generalists and long-distance migrants (Bonthoux et al., 2017; McPherson & Jetz, 2007). Studies conducted in the marine pelagic environment also highlighted poor regional transferability of SDMs in two highly mobile and migratory marine taxa (e.g., seabird, Torres et al., 2015 and whale, Redfern et al., 2017). Mannocci et al. (2018) suggested assessing the environmental representativeness of a set of potential survey designs to help ensure model-based predictions are derived with limited extrapolation for the study region.

Seabird populations are typically organized in meta-populations with several breeding colonies dispersed across a large geographical range (Friesen et al. 2007). During the breeding season, seabirds are

central place foragers (Orians & Pearson, 1979), commuting regularly from their breeding grounds on land to their foraging grounds at sea. A limited number of studies undertook multi-colony tracking of central place foragers to model large-scale foraging distribution (Arthur et al., 2017; Wakefield et al., 2011), and it remains challenging and often impracticable for ethical and logistical reasons to track a representative number of individuals at each known breeding location. It is thus essential to better understand processes which influence SDM transferability and assess the spatial scale at which predictions can be safely attempted.

In this study, we tested SDM geographical and temporal transferability using a large telemetry dataset collected on Scopoli's shearwater, *Calonectris diomedea* (Sangster et al., 2012), a migratory seabird endemic to the Mediterranean Sea. Birds were tracked using GPS loggers during the breeding season in two consecutive years at four breeding sites (i.e., colonies) in the Western Mediterranean Sea. Scopoli's shearwaters breed on >40 Mediterranean islands (Anselme & Durand, 2012) located in highly dynamic and heterogeneous oceanographic contexts ("seascapes" *sensu* Louzao, Pinaud et al., 2011). Several studies conducted in Spain (Arcos et al., 2012; Louzao, et al., 2009; Louzao, Navarro, et al., 2011), Italy (Cecere et al., 2015) and France (Lambert et al., 2017) suggested this species to be generalist in its habitat and diet (Ramos, González-Solis, & Ruiz, 2009; Sarà, 1993). We therefore tested geographic SDM transferability across four study sites located in two contrasted oceanographic contexts: two colonies in the "cold" and highly productive waters of the Gulf of Lion and the two others in the warm and oligotrophic waters of Corsica Island (France). Furthermore, the second year of our tracking experiment was warmer (+1–1.5°C across all sites) than the first year, offering an opportunity to test temporal model transferability.

We applied a habitat selectivity approach based on foraging locations to build colony-specific foraging habitat models while controlling for the effects of unequal habitat accessibility caused by the central-place foraging.

We hypothesized that the heterogeneous seascapes of the NW Mediterranean Sea and generalist habits of Scopoli's shearwater would result in poor geographical transferability of colony-specific habitat models. We expected lower transferability between colonies located in distinct regions (Gulf of Lion vs. Corsica) than colonies located within the same region. We explored the extrinsic (environmental extrapolation) and intrinsic (trip characteristics, diving behaviour, trophic level, activity budget) factors potentially involved in the lack of model transferability. Novel conditions leading to extrapolation can be characterized in two ways: (i) for a given individual variable, values may be outside the range sampled during training (i.e., univariate extrapolation), and (ii) portions of the environmental space may be within the range of individual variables, but represent new combinations of predictors (i.e., combinational extrapolation) (Zurell, Elith, & Schröder, 2012; Owens et al. 2013). We expected lower model transferability when environmental extrapolation was high and when seabirds showed high intra- and inter-colony variability in their foraging strategies (i.e., generalist species).

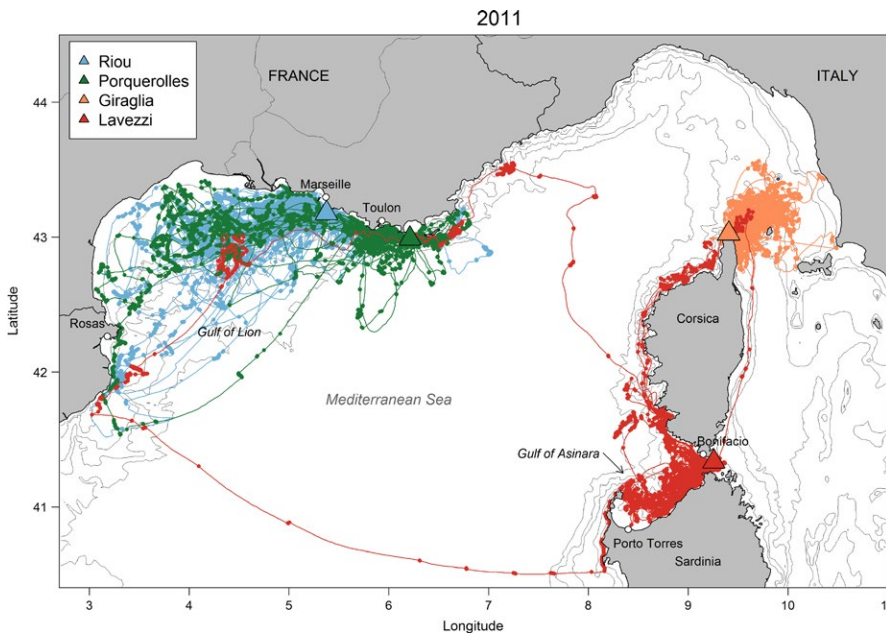


FIGURE 1 Map of 203 Scopoli's shearwaters foraging trips during the chick-rearing period (August 2011) at the four study colonies in the NW Mediterranean Sea. Lines represent tracks and dots represent foraging locations as estimated by state-space models and dive recorders [Colour figure can be viewed at wileyonlinelibrary.com]

Finally, because the Gulf of Lion is more productive and temporally dynamic than Corsica waters, we expected lower foraging effort and temporal transferability of habitat models for colonies located in the Gulf of Lion than for Corsica colonies.

We discussed the implications of our results in the context of spatial planning. It is indeed crucial for managers and environmental policy-makers to understand to what extent results obtained in one region can inform decisions in another, and adapt sampling schemes accordingly (Mannocci et al., 2018; McAlpine et al., 2008).

2 | METHODS

2.1 | Species ecology and study sites

Scopoli's shearwaters are long-lived pelagic seabirds nesting in burrows where they lay a single egg in June and raise their chick from July to October. Both parents feed the chick and alternate foraging trips at sea. Our telemetric study was carried out between the 15th of July and 15th September in 2011 and the 1st and 31st of August in 2012 during the chick-rearing period. We tracked shearwaters simultaneously on four colonies: two were located in the Gulf of Lion (Riou Is. offshore Marseille, and Porquerolles Is. offshore Hyères) and two were located on Corsica Is. (Giraglia Is. and Lavezzi Is., respectively, at the northern and southern tip of Corsica, Figure 1). The two largest colonies were located on Riou and Lavezzi Is. with ~350–400 breeding pairs each while Porquerolles and Giraglia Is. host ~180 pairs and ~30 breeding pairs, respectively (Anselme & Durand, 2012).

The Gulf of Lion is one of the most productive areas of the Mediterranean Sea (Figure 2); it is characterized by a large continental shelf, multiple canyons, large run-off from the Rhône river, high frontal and eddy activity and local upwelling driven by wind regimes (Durrieu de Madron et al., 2011). In contrast, Corsica Is. is

surrounded by warm and stable oligotrophic waters and more contrasted seafloor topography (Figure 2).

2.2 | Logger equipment

Logger deployments were approved by the boards of the "Conservatoire d'Espaces Naturels de Provence-Alpes-Côte d'Azur," the "Réserve Naturelle Nationale de l'archipel de Riou," the "Parc National de Port Cros" and the "Réserve Naturelle des Bouches de Bonifacio." Bird instrumentation was performed under personal animal experimentation permits #A34-369 (D. Grémillet) and #A34-505 (C. Péron) delivered by the French "Direction Départementale de la Protection des Populations." The same protocol was applied at the four study sites simultaneously by 8 fieldworkers (2 fieldworkers/colony).

All necessary precautions were taken to minimize handling stress: breeding adults were caught at night in their burrows, birds were kept in the dark and handling was performed silently in <10 min. Each bird was equipped with a GPS logger (Perthold Engineering LLC; 47 × 30 × 13 mm, 20 g), and most of the birds (90% in 2011 and 77% in 2012) were simultaneously equipped with Temperature-Depth-Recorders (TDR, G5, CEFAS Technologies, Lowestoft, UK; 2.7 g; 30 mm length, 7 mm diameter, Table 1). The combined mass of GPS and TDR represented 3.5% of the average birds' body mass (mean body mass = 618 ± 62 g). GPS loggers were attached to back feathers with black Tesa® tape, and TDRs were either taped to the underside of central rectrices or attached to a Darvic ring on the leg. GPS loggers recorded geographic location every 2–3 min (accuracy of 5–10 m). TDR recorded hydrostatic pressure every 2 s (accuracy of 0.2 m). We equipped 1–3 birds per day or every second day, which resulted in a very comprehensive coverage of the chick-rearing period (Supporting information Figure S1). GPS were recovered after 2 or 3 foraging trips to reduce potential detrimental effect on breeding success. Thirteen individuals (7%) either lost their logger or were

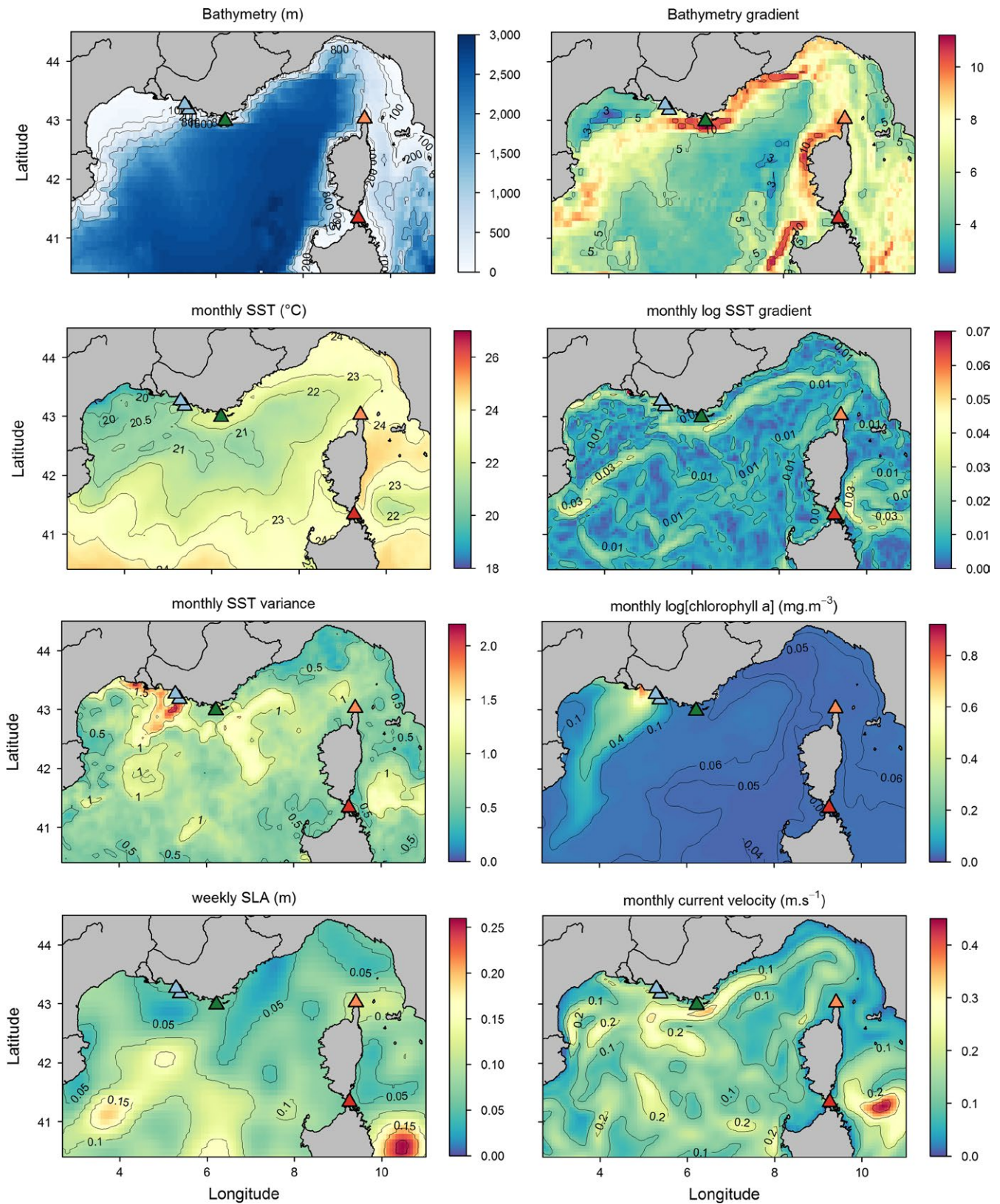


FIGURE 2 Maps of the oceanographic parameters estimated on the 15th of August 2011 in the NW Mediterranean Sea. Weekly and monthly composites correspond to averaged values of the daily maps of the 7 or 30 previous days. The triangles represent the colony locations (Marseille Is. in blue, Porquerolles Is. in green, Lavezzi Is. in red and Giraglia Is. in orange) [Colour figure can be viewed at wileyonlinelibrary.com]

Site	Colony size (breeding pairs)	Year	No. birds	No. trips	No. P1 feathers
Riou Is.	300–350	2011	26	62	20
		2012	19	51	17
Porquerolles Is.	100–180	2011	15	34	15
		2012	13	40	19
Giraglia Is.	38–40	2011	30	63	22
		2012	29	61	12
Lavezzi Is.	300–400	2011	24	44	19
		2012	33	63	19
Total	738–870	2011	95	203	76
		2012	94	215	67

TABLE 1 Summary of GPS tracking and feather sampling on Scopoli's shearwaters in August 2011 and 2012

not recaptured during the study period. When testing the effect of bird instrumentation on shearwater breeding success at Riou Is., we found no carry-over effects of loggers on breeding performances (Authier, Péron, Mante, Vidal, & Grémillet, 2013).

2.3 | Behavioural inference

GPS tracks were inspected visually to separate each individual trip and remove locations recorded on land. They were re-interpolated at a constant time interval (2 or 3 min). We used a state-space model (SSM) adapted from Morales, Haydon, Frair, Holsinger, and Fryxell (2004) to infer discrete behavioural modes from step length and turning angles (see Péron et al., 2013, for details on the method). We hypothesized three “hidden” behavioural modes: resting (small turning angle variance, small step length), foraging (large turning angle variance, intermediate step length) and travelling (small turning angle variance, large step length).

Diving times were extracted from pressure records by using an automatic procedure which defined a dive as a depth difference of >2 m between two records at 2-s interval. We choose this 2-m threshold because pressure data were noisy and our 2-s sampling regime was insufficient to identify shallow dives (Cianchetti-Benedetti, Catoni, Kato, Massa, & Quillfeldt, 2017). We matched diving times with GPS locations to define diving locations. Eighty percent of the diving locations were classified as “foraging” by SSM while the remaining were classified as resting (12%) or travelling (8%). We attributed the behavioural state “foraging” for all diving locations to correct for misclassification. All analyses were performed in R version 3.3.1 (R CoreTeam, 2016).

2.4 | Foraging habitat modelling

2.4.1 | Modelling approach

We modelled the environmental characteristics of the locations where birds from each colony were recorded to be foraging (utilized habitat) relative to the areas that they could potentially have used to forage (habitat use-availability analysis). The central-place foraging

imposed during the breeding season means that the accessibility of points in space is not equal (Orians & Pearson, 1979). Accordingly and following the approach of Raymond et al. (2015), for each individual bird, 10 trips were simulated from the same deployment location (Supporting information Figures S3 and S5), using a first-order vector autoregressive model fitted to the observed tracks. These simulated tracks indicated where the animals could potentially have travelled if they did not have any preference in terms of environmental conditions, while still respecting the constraints on their trip duration and travel characteristic (start and end locations, speed and turning angles). Presences corresponded to foraging locations estimated by SSM and dive data on the observed tracks and pseudo-absences corresponded to locations estimated as foraging from the 10 pseudo-tracks. We inferred pseudo-foraging locations using threshold values of foraging speed and turning angle calculated on observed real tracks of each individual. The ratio between the number of foraging locations over the total number of locations was kept constant for each trip to preserve information on foraging intensity and help the interpretation of coefficients (especially the intercept) in regression models. For example, if an individual foraged in 30 of 100 GPS locations, 70 locations classified as “foraging” were extracted on its pseudo-track to generate pseudo-absences. Foraging locations within 2 km from breeding colonies were removed because they may be associated to other social behaviours in the proximity of the colony. We also removed trips with range <15 km ($n = 24$ trips) because their spatial extent was insufficient to capture environmental preferences. To ensure inter-annual comparisons, we only kept the tracks recorded from the 1st to the 31st August in each year (Supporting information Figure S1). To allow for non-linear relationships between foraging probability and the environment, we used a mixed generalized additive model (GAMM) regression framework with a binomial (Bernouilli) distribution and logit link using the R package mgcv (Wood, 2004). The response variable took the value 1 if the location was from an observed foraging location, or 0 for a simulated foraging location on the pseudo-tracks (following Raymond et al., 2015). Bird identity was included as a random intercept term to account for the hierarchical structure of the data (Bolker et al., 2009).

2.4.2 | Environmental predictors

Environmental variables were collated at each location (foraging and pseudo-foraging) in both years. We considered seven environmental parameters and their derivatives (gradient, variance). Although sea-bird foraging distributions are unlikely to be directly influenced by bathymetry and others variables considered in our analyses, these variables influence birds indirectly by acting upon other biotic factors such as prey availability (Torres, Read, & Halpin, 2008) or others inter-specific interactions (Wakefield, Phillips, & Matthiopoulos, 2009).

Bathymetry (BAT) and seafloor slope (SLOPE) were included as they are known to structure marine ecosystems (Giannoulaki, Machias, Koutsikopoulos, & Somarakis, 2006). Sea Surface Temperatures (SST), SST gradient (GSST) and monthly variability in SST (VarSST) were calculated and included in the model as proxies of water masses structure and stability, which are good proxies of ectothermic prey and productive areas associated with upwelling of cold, nutrient-rich waters (Durrieu de Madron et al., 2011). Bathymetry slope and SST gradients were estimated using the function *terrain()* in the R package raster (Hijmans, 2014). Effects of Sea Level Anomalies (SLA) and current velocities (VEL) were included to account for meso-scale dynamic features affecting the distribution of primary productivity and low trophic levels subjected to advection. Chlorophyll a concentration (CHLA) was included as a proxy of primary productivity. We used CHLA predictions from the biogeochemical modeling tool (Ecological Mechanistic and Modular Model, ECO3M) (Baklouti, Diaz, Pinazo, Faure, & Quéguiner, 2006) to overcome the limit of imperfect spatial coverage of satellite data. The source, resolution and units of oceanographic variables were summarized in Supporting information Table S1. All environmental variables were re-interpolated on a $0.05^\circ \times 0.05^\circ$ grid, and dynamic oceanographic predictors were considered at three temporal resolutions: daily, weekly and monthly because we did not have *a priori* assumptions about the temporal scale at which these predictors influenced bird behaviour (Scales et al., 2016). Weekly and monthly values were calculated by averaging daily values over the 7 or 28 days prior to each sampled day.

2.4.3 | Model selection

For each study site, we implemented a selection procedure which tested models with at least one and up to four covariates, excluding all combinations of correlated covariates (correlation higher than 0.7 in absolute value and variance inflation factor, VIF, higher than 5). The different temporal resolutions of each covariate (daily, weekly, monthly) were never included in the same model. Environmental covariates were standardized to zero mean and unit variance. The maximum degree of freedom for smoothers was constrained to four to prevent over-fitting and limit extrapolation (Lambert et al., 2017). Model selection was based on Akaike criteria (AIC, Akaike, 1974). Once the “best” model (lowest AIC) was selected for each colony, the contribution of each explanatory variable to the model was

plotted (GAM response curve) with all other variables held at their average values.

2.4.4 | Model predictions

We used GAMMs calibrated on the 2011 data to predict and map the foraging probability in a geographic area centred on the calibration zone of each colony. As the focus of our study was to test model transferability and thus suitable habitat regardless of accessibility, we did not control for accessibility during model prediction. Input data were gridded oceanographic variables ($0.05^\circ \times 0.05^\circ$) corresponding to the predictors retained in the models. Daily prediction maps were produced for August 2011 and then averaged to provide monthly prediction.

2.4.5 | Model evaluation—internal cross-validation

Model predictive ability was assessed using the Brier score, a proper scoring rule defined as the mean squared difference between actual and predicted outcomes (Brier, 1950). This score has the advantage of capturing both discrimination and calibration aspects of model predictions. We performed internal 10-fold cross-validation based on randomly selected training and test datasets (created by a random selection of 75% and 25% of the 2011 data, respectively). The lower is the Brier score, the better are the predictions.

2.5 | Geographical and temporal transferability

The Brier score was also used to quantify (a) geographic transferability: the ability of colony-specific habitat model to predict foraging probability at others colonies in the same year (2011) and (b) temporal transferability, the ability of colony-specific habitat model fitted on 2011 tracking data to predict foraging probability at the same colony in 2012 (Supporting information Figure S4).

2.6 | Effect of environmental extrapolation on transferability

We investigated whether the percentage of environmental extrapolation was a potential indicator of poor model transferability. An extrapolation is a prediction made from a combination of environmental values that falls outside the multi-dimensional convex hull determined by the data used to calibrate a model (King & Zeng, 2007). Multi-dimensional convex hulls were assessed with the non-parametric Gower's distance on each calibration dataset (i.e., values of the four environmental covariates selected by AIC corresponding to foraging presence/absence GPS locations). The percentage of predictions that were extrapolations at others colonies (or year) was quantified using the function *whatif()* in the R package WhatIf (Stoll, King, & Zeng, 2014), which provides method to evaluate counterfactuals described in King and Zeng (2007). All analyses were performed in R version 3.3.1 (R Development Core Team, 2016).

2.7 | Foraging strategy

We investigated whether intrinsic factors such as site familiarity or plasticity in foraging strategy could affect habitat model transferability. Foraging strategy was characterized by foraging trip parameters and trophic level. We estimated foraging trip parameters (distance travelled, trip duration, range, travelling speed, number of dives, activity budget) from GPS tracks and dive recorders. When birds performed multiple trips, we kept the first trip to avoid pseudo-replication. Graphical comparisons were carried out with boxplots. We calculated daily activity budget (percentage of time spent in each behavioural state by 20-min bin) to compare at-sea behaviour between colonies. We used a bootstrap procedure using one random trip per bird to draw minimal and maximal envelopes.

Conventional dietary techniques such as stomach content analyses were not rated as ethical on Scopoli's shearwaters, we therefore used stable isotopic analyses (SIA) to assess their trophic status during the breeding season. $\delta^{15}\text{N}$ isotopic values reflect the trophic level while $\delta^{13}\text{C}$ values reflect carbon source characteristic

of inshore (higher $\delta^{13}\text{C}$) versus offshore feeding location (Hobson, Piatt, & Pitocchelli, 1994; Kelly, 2000).

In this species, the first primary feathers (P1) are moult in September (Ramos et al., 2009) which means that the feather samples collected in July or August 2011 and 2012 were representative of their diet during the previous summers (2010 and 2011, respectively). We sampled the tip (1–2 cm) of P1 on breeding adults handled during biotelemetry fieldwork. A total of 76 P1 were analysed for SIA in 2011 and 67 in 2012 (Table 1). Prior to stable isotope analyses, feathers were rinsed in a 2:1 chloroform:methanol solution, rinsed twice in a methanol solution, dried for 48 hr at 60°C and homogenized with scissors. Analyses were performed at the Institut Littoral Environnement et Sociétés (LIENSs, La Rochelle, France) on approx. 0.5 mg subsamples of material loaded into tin cups, using an elemental analyser (Thermo Fisher, Flash EA 1112) coupled in continuous flow mode to an isotope ratio mass spectrometer (Thermo Fisher, Delta V Advantage, Bremen, Germany). Stable isotope abundances were expressed in standard δ (‰): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or

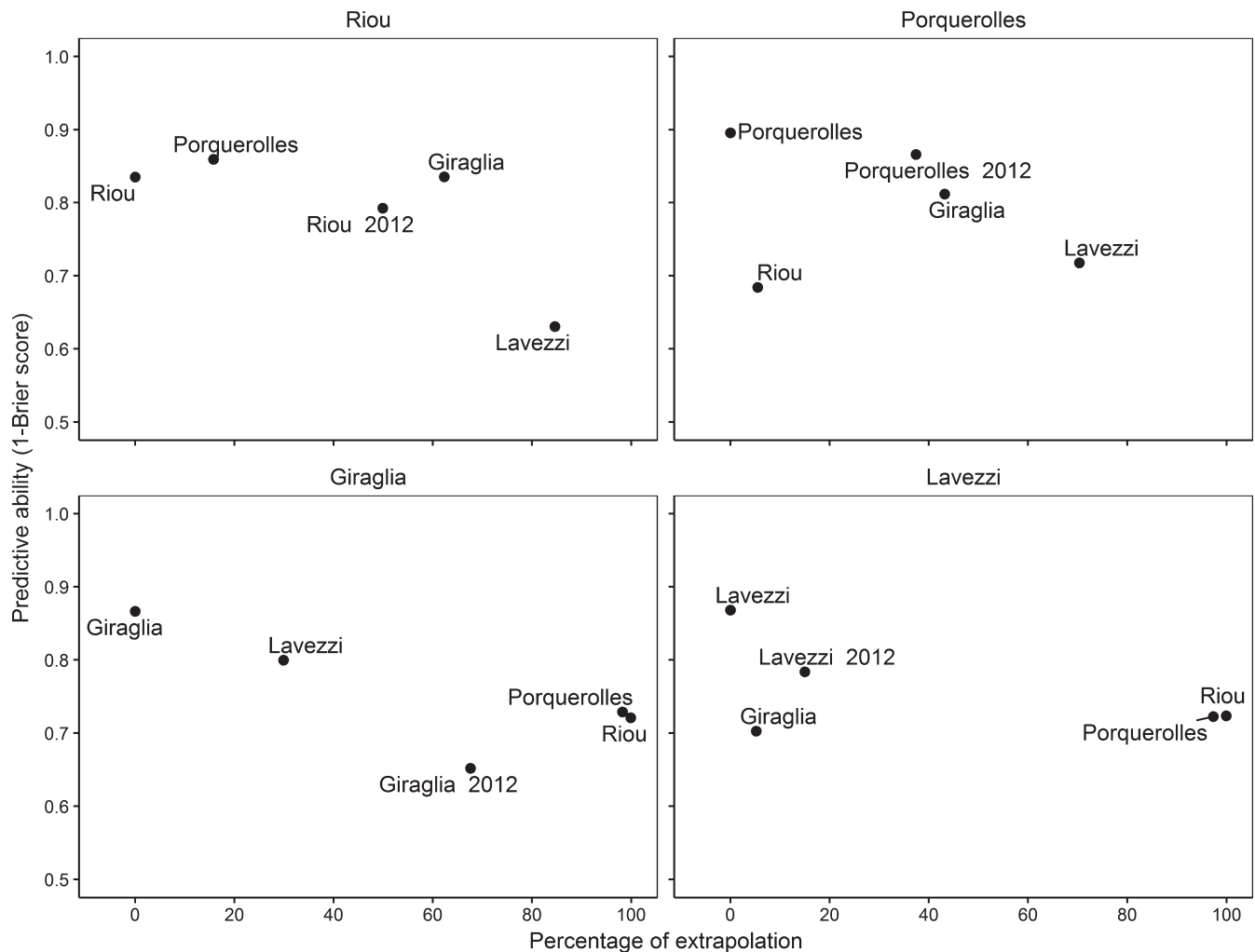


FIGURE 3 Effect of percentage of extrapolation between colonies or years on predictive ability of colony-specific models (the panel title indicates model calibration site). Predictive ability is represented as the complement of the Brier score (1-Brier score) to ease interpretation (i.e., the higher values correspond to the better prediction ability)

$^{15}\text{N}/^{14}\text{N}$. Standard values were Vienna-PeeDee Belemnite (VPDB) for C and atmospheric N_2 (air) for N.

3 | RESULTS

3.1 | Habitat modelling

We fitted colony-specific GAMMs to presence/pseudo-absence of foraging locations of 203 foraging trips performed by 95

individuals on four colonies in 2011 (Table 1). Oceanographic variables used as explanatory variables did not show multicollinearity (max VIF = 3.37 at Giraglia Is.). For each colony, the best model was selected with a $\Delta\text{AIC} > 20$ with the next best model (Supporting information Table S2). Models fitted on Porquerolles, Lavezzi and Giraglia tracking data had the best predictive ability with a mean Brier score of 0.10, 0.13 and 0.13, respectively (Figure 3). Model for Riou had lower but still reasonable predictive ability (mean Brier score of 0.16).

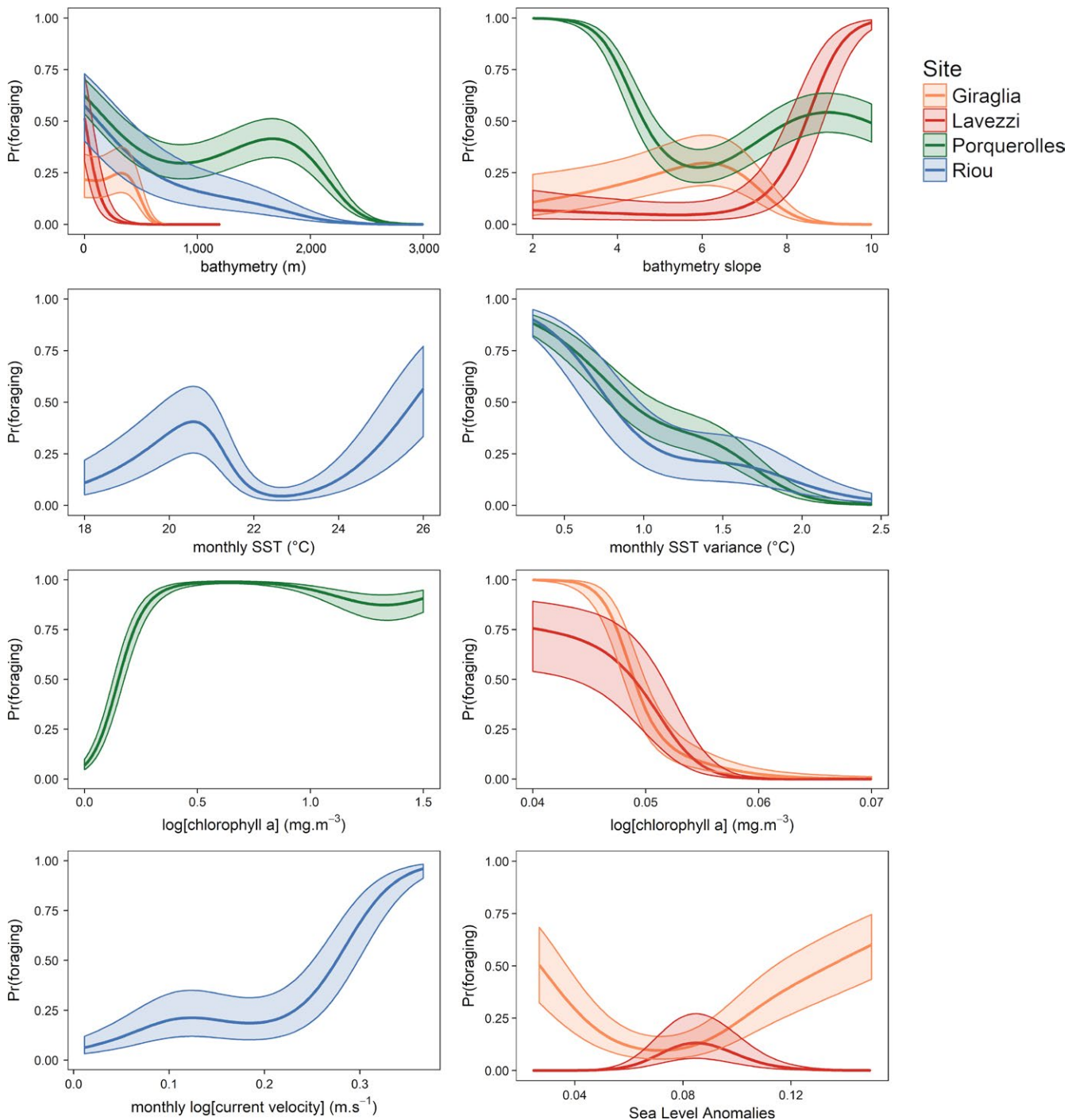


FIGURE 4 GAMMs response curves for the selected predictors of foraging probability [Colour figure can be viewed at wileyonlinelibrary.com]

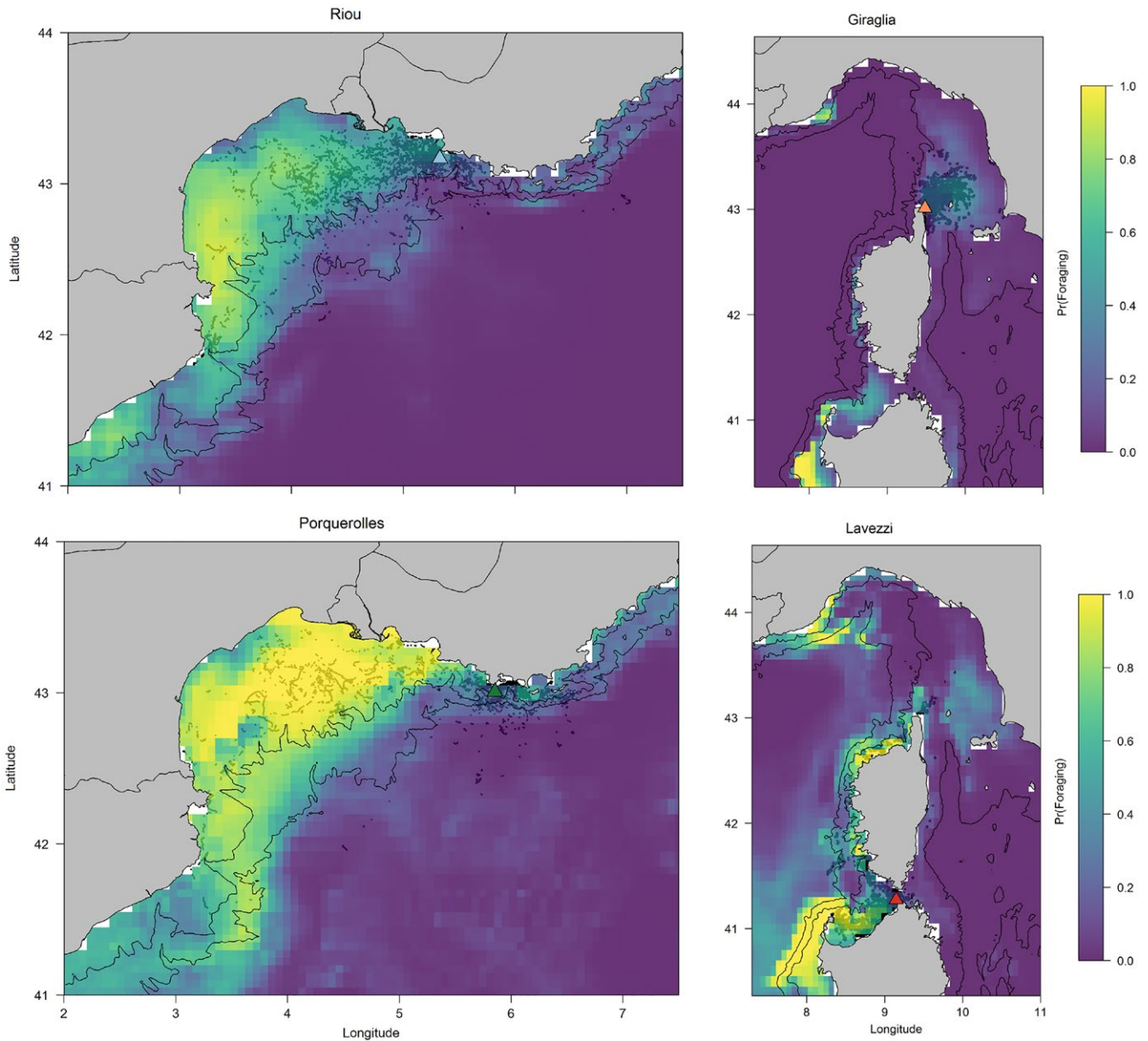


FIGURE 5 Prediction maps of foraging probability of Scopoli's shearwaters for each colony during the chick-rearing period in August 2011. Black dots represent foraging locations as estimated by state space models and dive recorders. Black lines are -600 and $-1,800$ m isobaths [Colour figure can be viewed at wileyonlinelibrary.com]

At each colony, the best model included four covariates but the combination of explanatory variables or the shape of the response curve varied between sites. Models of the two colonies located near the Gulf of Lion (Riou and Porquerolles) shared two variables (BAT and monthly SST variance) while models from the two colonies located in Corsica had the same covariates (BAT, SLOPE, SLA and CHLA).

Bathymetry was the only covariate common to all colonies but response curves varied slightly between colonies (Figure 4). Foraging probability was higher in shallow waters at all colonies but depth limit varied from 200 to 800 m depending on colonies. Birds from Lavezzi Is. foraged preferentially in shallow waters (<200 m deep) compared to birds

from Porquerolles Is. that foraged both in shallow and deep waters (Figure 4). SLOPE was selected at three colonies but response curves differed (Figure 4); Birds from Lavezzi and Porquerolles foraged over steep slopes, although birds breeding at Porquerolles also selected flat continental shelf areas. Birds from the Riou and Porquerolles were similarly affected by monthly SST variance, foraging where variability in SST was the lowest.

Birds from Riou were influenced by SST and current velocity, with a higher probability of foraging in waters masses centred around 21°C or $>24^{\circ}\text{C}$, and strong surface currents (Figure 4). Birds from Porquerolles had higher foraging probability when CHLA concentration increases ($>0.2 \text{ mg}\cdot\text{m}^{-3}$), which contrasts with birds from Corsica, which were

negatively influenced by CHLA concentration, at much lower levels compared to the Gulf of Lion (Figure 4).

SLA (daily or weekly) was retained in the two models fitted in Corsica but response curves were opposite (Figure 4).

Prediction maps highlighted the importance of continental shelves as foraging areas for all colonies (Figure 5). Model predictions of Riou and Porquerolles agreed on the attractiveness of the Gulf of Lion (Figure 5), particularly in the Western part of the continental shelf and along canyons of the Spanish coastline (Figure 5). Predictions from Corsica models both highlighted foraging hotspots on the north coast of Corsica Is. around the Tuscany archipelago and along the NW coast of Sardinia

Is. (Figure 5). Maps of prediction standard errors showed higher uncertainties in Riou and Lavezzi (Supporting information Figure S7).

3.2 | Geographical transferability

Habitat models had better transferability (Figure 3) within region than between regions (Gulf of Lion *versus* Corsica). Models fitted at Riou had very good predictive ability on Porquerolles foraging probability but poor transferability to Corsica (Figure 3). The same applied to the Corsica colonies, except for the Giraglia which transfer well to Lavezzi (Figure 3).

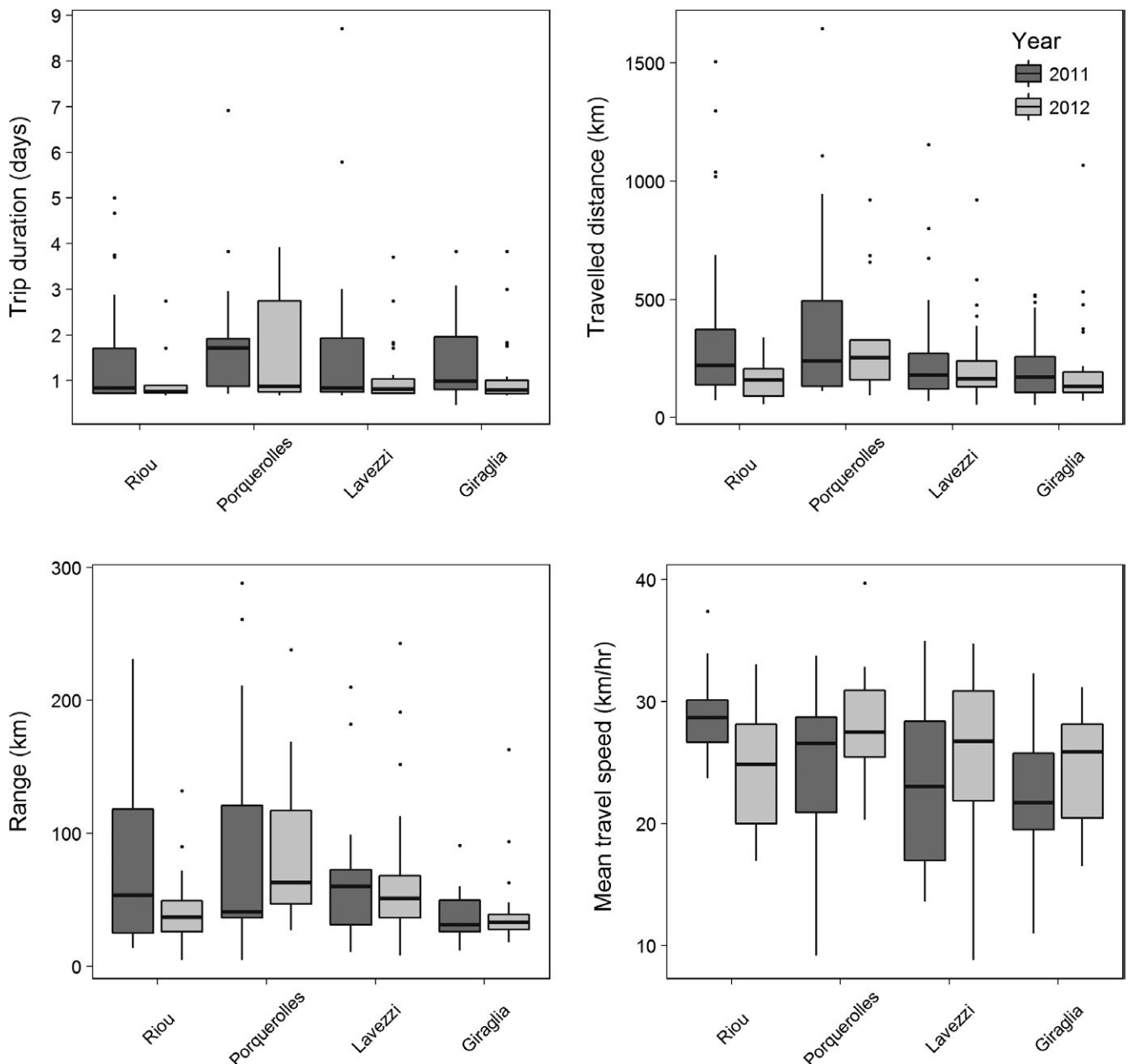


FIGURE 6 Inter-colony and inter-annual comparisons of foraging trip parameters during the chick-rearing period. Mean travel speed was calculated using travelling locations estimated by state-space models

3.3 | Temporal transferability

Despite warmer and less productive waters in 2012 compared to 2011 (Figure 2; Supporting information Figure S2), Brier scores indicated good temporal transferability of the model fitted on Porquerolles (0.13) and reasonable temporal transferability for the others colonies (0.21, 0.22 and 0.35 for Riou, Lavezzi and Giraglia, respectively; Figure 3). Prediction maps for 2012 mean foraging suitability models are shown in Supporting information Figure S8.

3.4 | Effect of environmental extrapolation on transferability

At each colony, model geographical transferability (i.e., predictive ability at different colonies) declined with the percentage of environmental extrapolation in the test dataset (Figure 3). As expected, the percentage of environmental extrapolation was lower within region than between regions and could explain why geographical transferability was sometimes poor between regions.

Temporal transferability was relatively good at Riou and Porquerolles despite high percentage of environmental extrapolation (49.9% and 37.4%, respectively), while it transferability was sometimes poor for the two Corsica colonies (Figure 3).

3.5 | Foraging strategy

Foraging trip parameters did not show striking differences between colonies and years (Figure 6). Most trips (86%) lasted 24-hr at all colonies, except at Porquerolles where most trips lasted 2 days in 2011. Travelled distance, range and travel speed were slightly higher and more variable in the Gulf of Lion than in Corsica in both years (except 2012 travel speed). Two-day trips were frequent (12%), and trips longer than 2 days were occasional (max 5–8 days).

In August 2011, 90% of the birds dived at least once but only 60% of the trips included a 'deep' dive (>2 m). Birds from Lavezzi dived more frequently (5.3 ± 5.4 dive locations/1-day trip, $n = 17$ ind) than birds from the others colonies (Riou: 2.8 ± 2.8 dive locations/1-day trip, $n = 18$ ind; Porquerolles: 1.2 ± 1.7 dive

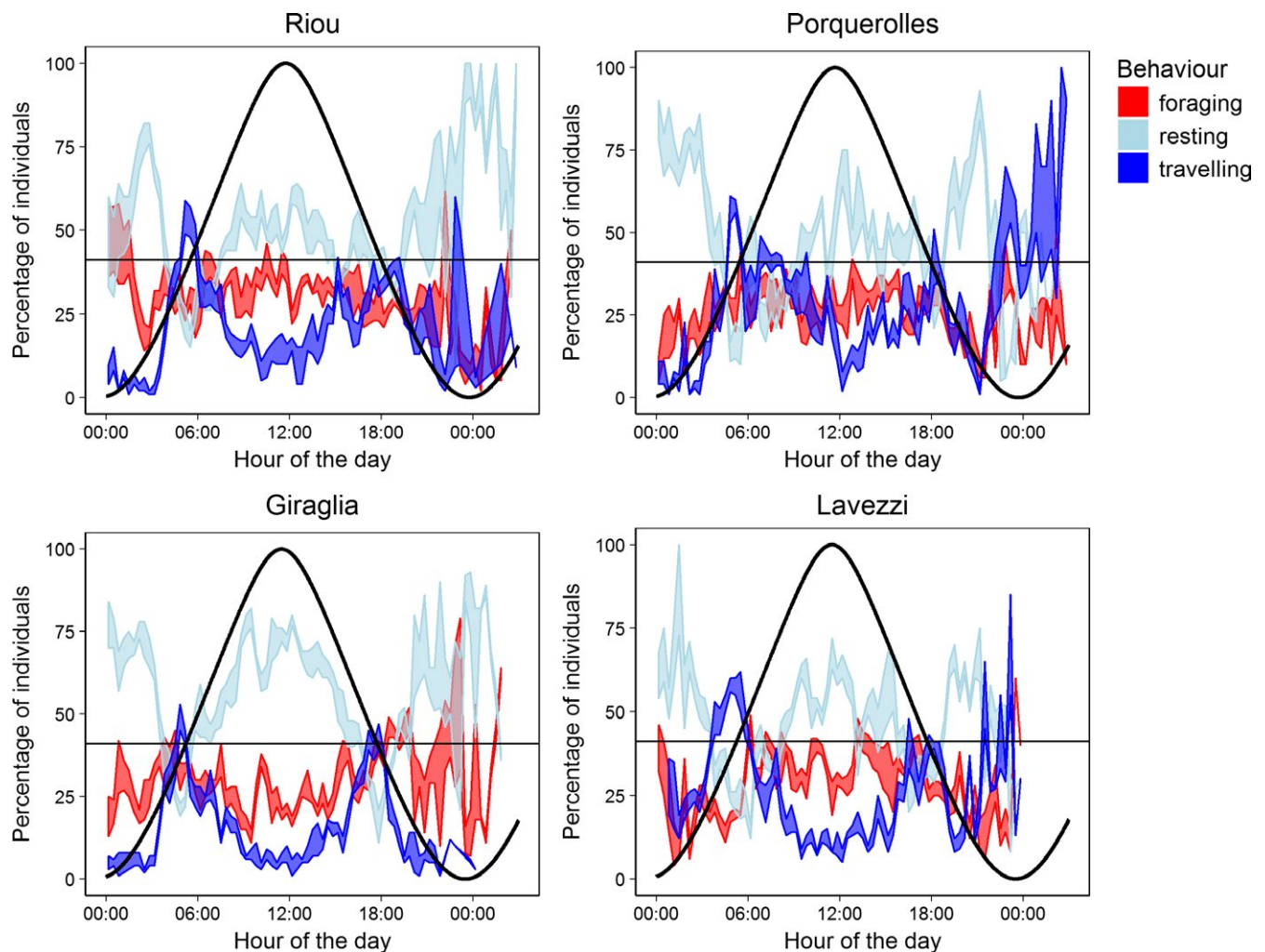


FIGURE 7 Daily activity patterns of Scopoli's shearwaters at the four study colonies during the chick-rearing period in 2011 (1-day trips only). The thick black line is the light intensity showing the day/night cycle with the horizontal black line corresponding to the astronomical dusk [Colour figure can be viewed at wileyonlinelibrary.com]

locations/1-day trip, $n = 10$ ind; Giraglia: 0.9 ± 1.4 dive locations/1-day trip, $n = 18$ ind).

Daily activity budgets showed similar patterns across colonies (Figure 7) and years (Supporting information Figure S6). Shearwaters mainly rested on the water at night and travelled at dawn and dusk. They spent between 25% and 30% of their time foraging during the day and a high proportion of time resting on the water (60%–75%), particularly at Giraglia (Figure 7).

Finally, stable isotope signatures revealed little inter-colony and inter-annual differences ($<1.5\%$) in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values during the chick-rearing period (Figure 8). Scopoli's shearwater $\delta^{15}\text{N}$ values ranged from 8.3‰ to 9.7‰, with slightly lower $\delta^{15}\text{N}$ values and C enrichment in 2012 compared to 2011 (except in Giraglia, Figure 8).

4 | DISCUSSION

Colony-specific habitat models revealed that shearwaters associate with different oceanographic variables to locate foraging areas. Geographical and temporal model transferability was better within than between regions or years, as expected given the marked differences in oceanographic conditions. Environmental extrapolation had a negative effect on model geographical transferability, while foraging trip characteristics were comparable between colonies. Testing of model transferability should complement procedures of model evaluation and help decide at which spatial scale predictions should be undertaken.

4.1 | Colony-specific oceanographic preferences

From one colony to another, habitat models differed either in the predictors retained in the models or in the shape of the response curve of a given predictor. As expected from previous work (Cecere, Gaibani, & Imperio, 2014; Cecere et al., 2015; Grémillet et al., 2014; Lambert et al., 2017; Louzao et al., 2009), bathymetry was a strong predictor of Scopoli's shearwater foraging grounds whatever the

region and its level of primary productivity. Within the continental shelf, the offshore foraging habitat of Scopoli's shearwaters was driven by dynamic oceanographic processes, which differed depending on colonies and regions, but often resulted from mesoscale activities forced by wind-driven local circulation (SLA, currents, water mass stratification) and bathymetry (Durrieu de Madron et al., 2011). In the Gulf of Lion, birds from Riou and Porquerolles foraged in well-stratified waters where monthly SST variability was the lowest, but other predictors differed (SST and current velocity for Riou and bathymetry gradient and CHLA for Porquerolles). In Corsica, the same set of four covariates was selected at both sites but the shape of their relationships differed for most covariates except for monthly CHLA, which negatively affected the foraging probability at both colonies. Colony-specific habitat preferences have already been observed in other seabird species (black-browed albatrosses *Thalassarche melanophris*, Wakefield et al. 2011; grey petrels *Procellaria cinerea*, Torres et al., 2015; black-legged kittiwakes *Rissa tridactyla*, Ponchon et al., 2017) but the potential drivers of such regionally dependent habitat associations are poorly understood.

4.2 | Higher geographical transferability within than between regions

As expected, model geographical transferability tended to be higher within than between regions. Poor between-region transferability could result from little overlap in environmental space (high extrapolation) between regions (e.g., Corsica waters are warmer and 10 times less productive than the Gulf of Lion).

Despite differences in habitat selection, transferability of suitability model was good for the two colonies located in the Gulf of Lion and predictions of foraging habitat suitability were relatively comparable. The high productivity of the Gulf of Lion may, together with small colony sizes at our study sites (~350 breeding pairs), result in low competition for food resources and explain the observed overlap in foraging areas. This situation contrasts with most colonial seabirds (Wakefield et al., 2013), including Scopoli's shearwaters, which typically show foraging segregation between relatively close colonies in other regions (Cecere et al., 2014; Genovart et al., 2018). In contrast, within-region transferability was poor for Corsica colonies although habitat models shared the same covariates. Despite a common specification, habitat models for the Corsica colonies were different in the shape of functional relationships between foraging and bathymetric slope and sea level anomaly. Shearwaters from Corsica colonies segregate in geographical space and select in fact different habitats in the shallow oligotrophic waters off Corsica ($<0.05 \text{ mg/m}^3$).

Our results regarding geographic transferability agree with previous studies showing that habitat models with good fit to the training data may work well in adjacent habitats with similar characteristics, but fail when applied to more distant areas where environmental conditions and local processes are distinct (Redfern et al., 2017; Torres et al., 2015). They provide a good illustration of the trade-off

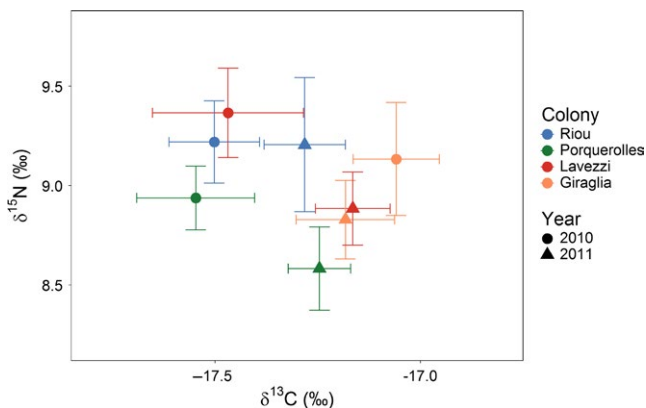


FIGURE 8 Stable isotopes signatures (mean \pm SD) of the primary feather of Scopoli's shearwater at the four study colonies in summer 2010 and 2011 [Colour figure can be viewed at wileyonlinelibrary.com]

between prediction and estimation bias described in Paton and Matthiopoulos (2016) when defining relevant scales in habitat modelling. Using the model fitted on Riou to predict foraging probability at a large spatial scale encompassing Corsica would have resulted in prediction bias, by ignoring the full range of animal responses to different environment composition (i.e., non-transferability, *sensu* Paton & Matthiopoulos, 2016). However, fitting one model to the entire tracking data (all sites included) would lead to estimation bias, because response curves would be averaged over a wide variety of habitat availabilities and compositions (i.e., homogenization, *sensu* Paton & Matthiopoulos, 2016).

A venue for future research is to investigate the use of hierarchical models to estimate an overall response curves together with colony-specific ones to model explicitly a colony-level variation in habitat preferences (Matthiopoulos, Hebblewhite, Aarts, & Fieberg, 2011).

4.3 | Higher temporal transferability in the Gulf of Lion than off Corsica

Contrary to our expectations, temporal model transferability was higher in colonies of the Gulf of Lion where oceanographic conditions varied the most within and between years (Figure 2; Supporting information Figure S2). Models fitted at the two Corsica colonies did not accurately predict foraging locations in 2012. Temporal transferability could probably be improved by fitting models to several years of tracking data, to incorporate the full range of animal responses at each colony. We may also have missed an important structuring variable in our models. For example, visual observations at Lavezzi Is. indicated shearwaters association with tunas or delphinids, which are present in the same habitats (Lambert et al., 2017; Pennino, Mérigot, Fonseca, Monni, & Rotta, 2017) and known to facilitate access to prey for seabirds (Veit & Harrison, 2017).

4.4 | Factors influencing model transferability

4.4.1 | Extrapolation and scale of predictions

As expected, model geographical transferability decreased with the level of environmental extrapolation in the test dataset. Results from our extrapolation analysis suggested three biologically relevant scales for model fitting and predictions: (a) the gulf of Lion and Provençal waters for the Provençal colonies, (b) the northern part of Corsica and the Tuscan archipelago for colonies located in this area and (c) south Corsica and north Sardinia for colonies located in Lavezzi and south Sardinia. In this study, we focused on colony-specific habitat models and extrapolation; another approach would be to adopt the generalized functional response approach proposed by Matthiopoulos et al. (2011) to account for regional availability of habitats within a single population model. This approach may be challenging on our large tracking dataset (>160,000 locations) but seems promising given the need for population-level predictions of habitat suitability.

The level of environmental extrapolation between 2011 and 2012 was high (30%–70%) at most sites but did not compromise models temporal transferability except at Giraglia. This result illustrates how a habitat model can produce accurate predictions while extrapolating, if it provides a good approximation of the true data-generating mechanism. In practice whether this is the case or not is unknown, but transferability may reflect how close the selected model is to the true data-generating mechanism. In contrast, the poor temporal transferability in Giraglia may indicate inter-annual changes in habitat associations that were not captured in the selected model or changes in what environmental proxies stand for in different contexts.

4.4.2 | Foraging strategies

We were expected poor geographical or temporal transferability to translate into different foraging strategies between colonies or years, particularly for generalist species (Bonthoux et al., 2017; Randin et al., 2006). However, isotope signatures, trip parameters and daily activity patterns did not reveal striking differences between years and colonies. Trip parameters and activity budgets suggested slightly lower foraging effort for birds breeding on Lavezzi and Giraglia (lower travelling speed, more resting, shortest travel distances) as compared to the Gulf of Lion. This result did not support our hypothesis of higher foraging effort or the onset of a dual foraging strategy (short and long trips) for colonies located in oligotrophic waters (Cecere et al., 2014). Unfortunately, our TDR data were too noisy to identify short-shallow dives (<2 m) which have been shown to represent half of Scopoli's shearwater dives in the Sicilian channel (Cianchetti-Benedetti et al., 2017). However, the low frequency of dives deeper than 2 m reported in our study suggested than Scopoli's shearwaters are mostly surface feeders in the region, with the exception of birds from Lavezzi where dives >2 m were more frequent.

The high intra-colony variability in isotope signatures was typical of a generalist species, but the inter-colony differences were too small to explain regional variations in diet. Nevertheless, shearwaters may feed on different prey items within the same trophic level, or feed on the same prey species but in different oceanographic contexts. Behavioural plasticity has been reported in other seabird species that have developed habitat-specific foraging strategies and exploited prey available locally in various oceanographic regimes (e.g., Gentoo penguins, *Pygoscelis papua*, Lescroël & Bost, 2005; black-browed albatrosses, *Thalassarche melanophris*, Wakefield et al., 2011; Australasian gannets, *Morus serrator*, Wells, Angel, & Arnould, 2016). Birds from Porquerolles Is. may feed at slightly lower trophic levels than the others, but differences in $\delta^{15}\text{N}$ were not substantial. $\delta^{15}\text{N}$ values and comparison with other studies in the region (Cardona, Martínez-Inigo, Mateo, & Gonzalez-Solis, 2015; Péron et al., 2013) suggested that Scopoli's shearwaters from all breeding sites fed predominantly on zooplankton or a mix of fish and zooplankton (Courbin et al., 2018), and potentially on squids or offals from fishing vessels. The

generalist feeding habits of Scopoli's shearwaters may be partially responsible for the lack of transferability, with shearwaters feeding opportunistically on the locally most abundant/accessible prey resources (Courbin et al., 2018).

4.5 | Conservation and modelling implications

Our work confirmed that habitat model transferability cannot be taken for granted and needs to be assessed (Zurell et al., 2012). Otherwise, misinformed conservation decisions (such as MPA delineation) can result from a casual use of habitat models with poor transferability.

In the Mediterranean Sea, our results can guide spatial planning for shearwaters conservation. First, we showed to managers that monitoring foraging parameters only does not necessarily give relevant information about habitat associations and model transferability. Second, we recommended to managers of the colonies located along the Gulf of Lion to pursue multi-year GPS tracking only at one colony (Riou Is.). Our rationale is that multi-year tracking will help refine shearwater habitat models, while making the reasonable assumption that birds from other Provençal colonies (e.g., Porquerolles Is.) will be represented given good regional model transferability. Models from the Gulf of Lion yet cannot be applied to predict foraging hotspots of the two Corsica colonies, which need to be modelled separately.

Future models aiming at predicting the foraging distribution of Scopoli's shearwaters at the scale of the entire Mediterranean Sea would need to use hierarchical models to explicitly model regional variations in habitat preferences and environmental extrapolation to define ecologically relevant regions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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