Conservation Biology

Contributed Paper

Predicting the Spatial Distribution of a Seabird Community to Identify Priority Conservation Areas in the Timor Sea

JENNIFER L. LAVERS,* ¶ MARK G. R. MILLER,† MICHAEL J. CARTER,‡ GEORGE SWANN,§ AND ROHAN H. CLARKE*

*School of Biological Sciences, Monash University, Building 17, Clayton, Victoria 3800, Australia
†BirdLife International, Wellbrooke Court, Girton Road, Cambridge CB3 0NA, United Kingdom
‡30 Canadian Bay Road, Mount Eliza, Victoria 3930, Australia
§Kimberley Birdwatching, P.O. Box 220, Broome, Western Australia 6725, Australia

Abstract: *Understanding spatial and temporal variability in the distribution of species is fundamental to the conservation of marine and terrestrial ecosystems. To support strategic decision making aimed at sustainable management of the oceans, such as the establishment of protected areas for marine wildlife, we identified areas predicted to support multispecies seabird aggregations in the Timor Sea. We developed species distribution models for 21 seabird species based on at-sea survey observations from 2000–2013 and oceanographic variables (e.g., bathymetry). We applied 4 statistical modeling techniques and combined the results into an ensemble model with robust performance. The ensemble model predicted the probability of seabird occurrence in areas where few or no surveys had been conducted and demonstrated 3 areas of high seabird richness that varied little between seasons. These were located within 150 km of Adele Island, Ashmore Reef, and the Lacepede Islands, 3 of the largest aggregations of breeding seabirds in Australia. Although these breeding islands were foci for high species richness, model performance was greatest for 3 nonbreeding migratory species that would have been overlooked had regional monitoring been restricted to islands. Our results indicate many seabird hotspots in the Timor Sea occur outside existing reserves (e.g., Ashmore Reef Marine Reserve), where shipping, fisheries, and offshore development likely pose a threat to resident and migratory populations. Our results highlight the need to expand marine spatial planning efforts to ensure biodiversity assets are appropriately represented in marine reserves. Correspondingly, our results support the designation of at least 4 new important bird areas, for example, surrounding Adele Island and Ashmore Reef.*

Keywords: at-sea observations, important bird area, oceanography, species distribution model

Pronostico de la Distribución Espacial de una Comunidad de Aves Marinas para Identificar Áreas Prioritarias de Conservación en el Mar de Timor

Resumen: *Entender la variabilidad espacial y temporal en la distribución de especies es fundamental para la conservación de los ecosistemas marinos y terrestres. Para apoyar la toma estratégica de decisiones enfocada en el manejo sustentable de los océanos, como el establecimiento de áreas protegidas para la vida silvestre marina, identificamos áreas pronosticadas como soporte para la agregación de múltiples especies de aves marinas en el Mar de Timor. Desarrollamos modelos de distribución de especies para 21 especies de aves marinas basándonos en censos realizados en el mar de 2000 a 2013 y variables oceanográficas (p. ej.: batimetría). Aplicamos 4 técnicas de modelado estadístico y combinamos los resultados en un modelo ensamblado con desempeño robusto. El modelo ensamblado pronosticó la probabilidad de la ocurrencia de aves marinas en áreas donde se han llevado a cabo pocos o ningún censo y demostró 3 áreas de riqueza alta*

¶*email jennifer.lavers@monash.edu*
Paper submitted October 24, 2013; revised manuscript accepted February 26, 2014.

DOI: 10.1111/cobi.12324

de aves marinas que variaron poco entre temporadas. Éstas se ubicaron dentro de 150 Km de la isla Adele, el Arrecife Ashmore y las islas Lacepede, tres de las agregaciones más grandes de aves marinas reproductoras en Australia. Aunque estas islas de reproducción fueron centros para una riqueza alta de especies, el desempeño del modelo fue mayor para 3 especies migratorias no reproductivas que habrían sido ignoradas si el monitoreo regional se hubiera restringido a las islas. Nuestros resultados indican que muchos sitios de importancia para aves marinas en el Mar de Timor ocurren fuera de las reservas existentes (p. ej.: la Reserva Marina del Arrecife Ashmore), donde las embarcaciones, las pesquerías y el desarrollo litoral probablemente sean una amenaza para las poblaciones residentes y migratorias. Nuestros resultados resaltan la necesidad de expandir los esfuerzos de planeación espacial marina para asegurar que los valores de biodiversidad estén correctamente representados en las reservas marinas. Proporcionalmente, nuestros resultados apoyan la designación de por lo menos 4 nuevas áreas de importancia para aves, por ejemplo, alrededor de la isla Adele y el Arrecife Ashmore.

Palabras Clave: Áreas de importancia para aves, modelo de distribución de especies, observaciones en el mar, oceanografía

Introduction

Understanding spatial and temporal variability in the distribution of fauna is fundamental to the management of ecosystems. While gathering such information has proven challenging in the dynamic marine environment, increasing pressure from a wide range of anthropogenic factors including fisheries (Anderson et al. 2011), pollution (Lavers et al. 2013), and offshore development (DERT 2010) highlights the importance of improving our understanding of how to effectively protect marine resources. For seabirds, foraging grounds and distant nonbreeding areas are often poorly defined and receive little or no protection (Lascelles et al. 2012; Thaxter et al. 2012). Because anthropogenic at-sea mortality has been linked to the decline of seabird populations (Lewison et al. 2004), marine areas used by seabirds during both breeding and migration require enhanced protection (Louzao et al. 2006).

The designation of important bird areas (IBAs) has been a key tool used to identify the most important areas where management is needed to alleviate these pressures (Halpern 2003). IBAs are increasingly recognized as a key component of an ecosystem-based approach to managing the marine environment (Browman & Stergiou 2004), particularly when designated in areas of high species abundance or diversity. Productive areas can be associated with static (e.g., shelf break) and dynamic (e.g., frontal system) features and, over different scales, reliably aggregate marine top predators (e.g., seabirds), which makes these areas ideal candidates for conservation (Nur et al. 2011; Cama et al. 2012). For example, protected areas that encompass critical habitat or minimize area-specific threats reduce overall mortality of whales and other marine vertebrates (Hooker & Gerber 2004; Game et al. 2009).

The Browse Basin in the Timor Sea between northwestern Australia and the island of Timor encompasses both shelf (depth <200 m) and pelagic regions (>200 m) and is characterized by the warm, oligotrophic waters from the Indonesian Throughflow (Gordon 2005). Despite low levels of ocean productivity, the region supports exceptional numbers of breeding and nonbreeding seabirds (Clarke et al. 2011). Comparatively low levels of resource extraction (e.g., fisheries) and small human population size have led to the region being recognized as one of the least human-affected areas in the world (Halpern et al. 2008). The resilience of the basin, or ability to restore its structure following disturbance (natural or human induced), is therefore assumed to be relatively high (Harrison 1979). Maintaining the resistance of intact ecosystems, rather than attempting to recover degraded ones, is widely regarded as the most pragmatic and cost-effective approach to managing natural resources (Scheffer et al. 2001).

Evidence suggests communities within protected marine areas often exhibit higher species diversity and are more robust to disturbance than unprotected areas (Gaston et al. 2008). Within the basin, reserves have been established at Ashmore Reef and Cartier Island that form part of Australia's North-west Commonwealth Marine Reserves Network (hereafter North-west Network) (Director of National Parks 2013). However, the designation of protected sites has been largely driven by sociopolitical imperatives rather than ecological considerations (McNeill 1994). As a result, the ability of the North-west Network to protect marine biodiversity from emerging anthropogenic threats in the Browse Basin (e.g., offshore oil development; Commonwealth of Australia 2007) is uncertain.

The identification of candidate sites for the protection of marine species can be challenging because the distribution of individuals is often highly dynamic and temporal and spatial trends are not always known (Game et al. 2010). Nevertheless, when compared with some marine species (e.g., cetaceans), seabirds are one of the better candidate groups, particularly with the development of global databases (e.g., www.seabirdtracking.org) and their capacity to function as bio-indicators and umbrella species (Zacharias & Roff 2001). Modern techniques for identifying important at-sea areas associated with breeding colonies (e.g., feeding areas) often include biotelemetry, at-sea surveys, and colony radii extensions (Grecian et al. 2012; Thaxter et al. 2012). Limitations such as low sample size and representation for biotelemetry studies (e.g., only large species that breed locally), the inability to infer colony origin for at-sea survey data, and population estimates that are mostly restricted to breeding species (e.g. seabird island surveys) mean data from a variety of sources should be integrated to effectively guide IBA planning (Louzao et al. 2009; Lascelles et al. 2012).

Species distribution modeling (SDM) is an increasingly used technique in marine ecology that allows multiple data sets from a variety of sources (e.g., breeding island and at-sea surveys) to be statistically related to oceanographic variables thought to influence species' distributions. Such an approach allows the prediction of species distributions in unsurveyed areas and facilitates the identification of priority conservation areas (Nur et al. 2011; Ballard et al. 2012). Inclusion of both locally breeding species and nonbreeding migrants in at-sea survey data sets is especially valuable because the complete seabird assemblage underpins hotspot predictions. Where longitudinal sampling has occurred, the ability to incorporate interseasonal and interannual variation further drives model robustness and dynamism (Nur et al. 2011; Oppel et al. 2012).

We used oceanographic variables to develop species distribution models for 21 seabirds representing both local breeding and nonbreeding migrant species. At-sea survey data collected over 14 years, capturing both interseasonal and interannual variation, was combined with knowledge of regional breeding status and population estimates from local seabird islands to predict the distribution of an entire seabird community through the identification of species richness hotspots within the Browse Basin and for large areas of the adjacent Timor Sea, where little or no survey data are available, and to develop candidate IBAs to assess effectiveness of existing reserves for conserving biodiversity in the region.

Methods

At-Sea Surveys and Data Processing

The at-sea data for 21 seabird species (Table 1) were compiled from charter vessels conducting transect-based bird surveys in the Browse Basin from Broome to Ashmore Reef Commonwealth Marine Reserve between 12° and 18°S and 120 and 123°E in Western Australia (Supporting Information). At-sea surveys were conducted on average for 10 d from 20 September to 17 November 2000 to 2013 (excluding 2002; dry season) and 12 to 29 April 2010 to 2013 (wet season). Survey effort was relatively consistent between and within years. Recording occurred during daylight hours (approximately 12 h/d) weather permitting. Due to the inherently low abundance of seabirds in oligotrophic waters, all birds that could be identified to species level were recorded from the bow on both sides of the vessel as outlined by Tasker et al. (1984; Method II). Vessel speed averaged 8–9 knots, and observers were stationed 2–3 m above the sea surface. Lead observers were consistent across years, and records were made by 2 observers working simultaneously, which provided a high degree of confidence in the data. During 2000–2008, vessel position was recorded hourly with a GPS. Seabirds recorded within each 1-h period were assigned the midpoint for that hourly transect. From 2009 onwards, coordinates were recorded for each individual seabird observation with dedicated software on a GPS equipped personal digital assistant.

To provide the most informative models, we kept wet and dry season data sets separate with the aim to create species-specific predictive maps for each season. Survey route (observations) for each unique season-year combination was plotted, and results of species presence and absence were aggregated into a spatial grid at a 4-km scale (matching that of the environmental variables). For each survey route, a species was designated as present in grid cells if one or more birds were detected and absent in grid cells from remaining records on the survey if the species was not detected. Because survey routes frequently overlapped (occupied the same 4-km grid cells) over multiple years of sampling, species could be both present and absent in the same cell at different times.

Environmental Variables

To model seabird occurrence, we used a number of physical and environmental variables that are either known, or suspected, to be correlated with seabird distribution and abundance (Nur et al. 2011; Oppel et al. 2012). Static variables (bathymetric depth, seabed slope, minimum distance to land, and minimum distance to island) were derived from the Australian bathymetry and topography grid (Geoscience Australia 2009) as rasters with a 4-km cell size. For species that were breeding during each season, we calculated minimum distance to colony rasters to capture the central location where foraging occurs; this location constrains breeding seabirds. Dynamic oceanographic data, sea surface temperature (SST), and chlorophyll a concentration (CHL), were downloaded as monthly averages for years 2000–2013 from Terra MODIS satellite imagery via the OceanColor data portal (http://oceancolor.gsfc.nasa.gov). In total, 192 oceanographic images at 4 km resolution were converted to rasters and clipped to the extent of the study area.

Seabird distribution typically displays a lag response to indicators of primary productivity (Louzao et al. 2009; Oppel et al. 2012). Consequently, SST and CHL values were averaged over each month and the 2 months

Table 1. Browse Basin seabird breeding islands, maximum population,[a] and maximum number of birds recorded at sea 2000–2013 that were included in the at-sea species distribution model.

Breeding status and common name	Scientific name	IUCN[b]	Ashmore Reef[c]	Cartier Reef[c]	Breeding island: Scott Reef	Breeding island: Adele Island[c]	Browse Island[c]	Lacepede Islands[d]	Max. count at sea
Breeding in the basin									
Brown Booby	*Sula leucogaster*	LC	14,686[a]	17[i]		4,329[a]	7[i]	36,000[a]	6,614
Masked Booby	*Sula dactylatra*	LC	126[a]			169[a]		<10[a]	23
Red-footed Booby	*Sula sula*	LC	360[a]			9[a]			31
Lesser Frigatebird	*Fregata ariel*	LC	4,742[a]	1[i]		6,390[a]	4[i]	2,000[a]	70
Black Noddy	*Anous minutus*	LC	1,471[a]			2,459[a]			286
Common Noddy	*Anous stolidus*	LC	62,227[a]	2[i]		15,964[a]	6[i]	20,000[a]	10,412
Wedge-tailed Shearwater	*Puffinus pacificus*	LC	80[ae]	1[f]			1[f]	X[i]	138
Bridled Tern	*Onychoprion anaethetus*	LC	377[a]	1[i]			2[i]	4,000[a]	2,287
Sooty Tern	*Onychoprion fuscatus*	LC	40,000[a]	20[i]			4[i]		684
Crested Tern	*Thalasseus bergii*	LC	5,937[a]	322[a]	X[j]	1,620[a]	7,225	600[a]	509
Roseate Tern[g]	*Sterna dougallii*	LC	68[a]						14,456
Not breeding in the basin									
Bulwer's Petrel	*Bulweria bulwerii*	LC	1	1[f]					441
Jouanin's Petrel	*Bulweria fallax*	NT							4
Tahiti Petrel	*Pseudobulweria rostrata*	NT							46
Hutton's Shearwater	*Puffinus huttoni*	EN							594
Streaked Shearwater	*Calonectris leucomelas*	LC	1[f]						214
Matsudaira's Storm-petrel	*Oceanodroma matsudairae*	DD							91
Swinhoe's Storm-petrel	*Oceanodroma monorhis*	NT							58
Wilson's Storm-petrel	*Oceanites oceanicus*	LC	1						65
Common Tern	*Sterna hirundo*	LC	7	2		215		50	2,005
Roseate Tern[g]	*Sterna dougallii*	LC	450			414		33,000	14,456
White-winged Black Tern	*Chlidonias leucopterus*	LC	8	3		552		X[h]	317

[a]*Adult birds, confirmed breeding.*
[b]*International Union for Conservation of Nature (IUCN) status: DD, data deficient; EN, endangered; LC, least concern; NT, near threatened.*
[c]*R. Clarke, unpublished data.*
[d]*Breeding population as of 2008 (BirdLife International 2013c).*
[e]*Forty burrows, occupancy not recorded.*
[f]*Bird found dead.*
[g]*Small numbers of Roseate Terns breed in the basin, and large numbers visit from elsewhere (see text).*
[h]*Present in small numbers.*
[i]*Adult birds recorded over land; breeding numbers not confirmed.*
[j]*May breed.*

preceding this to incorporate time lags in energy flow between remotely sensed phenomena (e.g., CHL blooms and higher tropic level organisms that constitute seabird prey [Wakefield et al. 2009]).

Model Construction and Data Exploration

Different statistical models built on the same input data predict different distributions, despite sharing similar predictive performance (Oppel et al. 2012). A credible solution is to use an ensemble of statistical models and combine their predictions, to provide more robust results (Araújo & New 2007; Oppel et al. 2012; Comte & Grenouillet 2013). We chose 4 widely used statistical models: generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT; Elith et al. 2008), and maximum entropy (MaxEnt; Merow et al. 2013). The inclusion of year as a categorical environmental variable was modeled as a random effect by using mixed forms of GLM and GAM. All models were constructed using R 2.15.2 with the following packages: lme4, mgcv, gamm4,gbm, and dismo, which interfaces with MaxEnt version 3.3.3e (standalone Java software; Phillips & Dudík 2008). Ensemble predictions were calculated from the 4 models with a weighted average. Weights were assigned to each model based on its predictive performance, measured by the area under the receiver-operated characteristic curve (AUC; Comte & Grenouillet 2013).

We used a multipanel scatter plot and Pearson correlation coefficients to examine collinearity in environmental variables in both seasonal data sets; we removed variables with a correlation >0.7 from input to modeling (Supporting Information). In both wet and dry season data sets, minimum distance to land showed over-threshold correlation with CHL and with 4 species-specific minimum distance to colony layers; consequently it was excluded from further analyses. Using data with significant spatial autocorrelation for SDMs can lead to invalid parameter estimates and inaccurate predictions (Dormann et al. 2007). We checked each species for spatial autocorrelation by calculating Moran's I values for the residuals of GLM, GAM, and BRT over 1:60 nearest neighboring 4×4 km grid cells with spdep package in R. Moran's I values range from -1 (perfect dispersion) to $+1$ (perfect correlation); values around zero indicate a random spatial pattern.

Model Evaluation

In each seasonal data set, species data were randomly divided into training (70%) and testing (30%) data sets. We distributed presences and absences to both data sets in proportions consistent with that of the pre-split data. We could not use spatial separation of wet or dry season data sets into static training and testing areas as per Oppel et al. (2012) because the multiple species distributions meant that static areas could not capture enough presence points for each species. To test predictive performance, we calculated the AUC value of each species' ensemble model for training and test data sets. To generate more robust AUC values, for each species we repeated data splitting to test and train data sets and the modeling process 10 times (limited by computational constraints) to give AUC values.

Predicted Species Distributions

Because the spatial predictions of species distributions were intended to inform conservation and identify potential overlap with anthropogenic marine activities it was important to use only high-quality models. Only those models with an AUC $\geq$0.7 for prediction of test data were retained to provide spatial predictions for the wider Timor Sea (Fielding & Bell 1997). To generate species richness maps that show the overlap between the predicted distributions of multiple species, we set a threshold for each predictive map (scaled 0–1) into binary presence or absence. We used the minimum distance to the top-left corner in ROC plot (MinROCdist) approach to find the most appropriate presence-absence threshold for each species (Liu et al. 2005). Species presence-absence maps were summed within families (e.g., Sulidae) and across all species to generate richness maps, where higher richness values occur when more species are predicted to be present.

Existing Reserves and Candidate IBAs

To qualify as a marine IBA, candidate sites had to meet one or more of the BirdLife global IBA criteria: sites known or thought to hold on a regular basis at least 1% of the global population of a seabird species (A4ii), 20,000 individuals or 10,000 pairs of one or more species (A4iii), or significant numbers of a globally threatened species (A1; BirdLife International 2010).

Ashmore Reef, Adele Island, and the Lacepede Islands are currently recognized as terrestrial IBAs (BirdLife International 2013*a*, 2013*b*, 2013*c*) because they support 3–9% of the world's breeding population of Brown Booby (*Sula leucogaster*) and Lesser Frigatebird (*Fregata ariel*) (Table 1). The regular presence of up to 33,000 nonresident Roseate Terns (*Sterna dougallii*) also triggers terrestrial IBA listing for the Lacepede Islands (Table 1; BirdLife International 2013*c*). Ashmore Reef is also listed as a Commonwealth Marine Reserve and Ramsar wetland of international importance (Director of National Parks 2013; Ramsar Convention Bureau 2013).

Using information on the number of breeding pairs on each island (Table 1), we assessed which species might have sufficient populations or threatened status to trigger marine IBA criteria. For breeding species, the maximum species-specific foraging range (200 km for Brown Booby and Common Noddy [*Anous stolidus*]; unpublished tracking data; BirdLife International 2013*d*) was used as a radius from the colony to clip the extent of the ensemble model prediction. The ensemble model predictive values within this extent were normalized between 1 and 0, and the colony population was applied to the surface, creating a bird density prediction. We simplistically assumed that all birds from the colony stayed within this foraging radius. To trigger IBA criteria A4ii or A4iii, polygons of increasing size were fitted to the density surface; from highest to lowest densities, the polygons incrementally increased in area until they contained a large enough predicted population. For nonbreeding species, a population estimate could not be reliably determined, so only IBA criteria A1 could be tested. Ensemble model predictions classified as presence or absence (with MinROCdist), predicted the extent of species occurrence and provided an IBA boundary for globally threatened species.

Results

At-Sea Surveys

A total of 91,999 seabirds were recorded in 5775 at-sea encounters during 96 transect surveys (16 voyages)

Table 2. Area under the receiver-operated characteristic curve (AUC) values and range averaged over all seabird species for different statistical approaches to models of predicted at-sea distribution in wet (April) and dry seasons (September–November) 2000–2013.*

Model	Wet AUC	Wet AUC range	Dry AUC	Dry AUC range
Ensemble	0.79	0.40	0.78	0.33
BRT	0.80	0.41	0.78	0.33
GAM	0.74	0.42	0.72	0.36
GLM	0.73	0.44	0.71	0.35
MaxEnt	0.76	0.43	0.75	0.35

**The AUC values reported for prediction to testing data (independent 30% of data set—see Model Evaluation).*

covering 15,438 km from October 2000 to April 2013 (mean [SD] = 5.99 [8.51] individuals/km^2; Supporting Information). Roseate Tern (32.7%, $n = 30{,}113$) was the most numerically abundant species, followed by Common Noddy (27.3%, $n = 25{,}150$) and Brown Booby (16.8%, $n = 15{,}503$). Brown Booby, Masked Booby (*S. dactylatra*), Bulwer's Petrel (*Bulweria bulwerii*), Common Tern (*Sterna hirundo*), Crested Tern (*Thalasseus bergii*), Sooty Tern (*Onychoprion fuscatus*), Common Noddy, and Wedge-tailed Shearwater (*Puffinus pacificus*) were present during all voyages and accounted for 63.1% of the records. Of the 10 most abundant species, the Roseate Tern population in the Browse Basin was numerically dominated by visitors from breeding populations on coastal islands in the adjacent Kimberley region to the east and possibly the more distant Pilbara region to the southwest (G.S., M.J.C., and R.H.C., personal observation). Three other species (Streaked Shearwater [*Calonectris leucomelas*], Wilson's Storm-petrel [*Oceanites oceanicus*], and Bulwer's Petrel) are nonbreeding migrants to the Timor Sea.

Performance of Distribution Models

We found little evidence of spatial autocorrelation between environmental covariates; most species had low positive values (wet season: Moran's I range −0.01 to 0.14; dry season: Moran's I range −0.03 to 0.11). Almost all species displayed higher levels of spatial autocorrelation at <10 nearest neighbor cells (distances < 40 km) than at >10 nearest neighbor cells; spatial autocorrelation gradually decreased to 60 nearest neighbors.

The different statistical modeling approaches we used performed similarly in both seasons. Averaged over all species, GLMs had the poorest performance, followed by GAMs, MaxEnt, and BRT, respectively (Table 2). The high performing BRT models contributed significantly to the overall ensemble model. The ensemble model performance was excellent for most species in both seasons; all AUC was > 0.8 for predictions from training data, and most AUC was > 0.75 for predictions from testing data (Tables 3 & 4). In the dry season, 18 species were successfully modeled (Table 3), and in the wet season, 12 species were successfully modeled (Table 4). Lesser Frigatebird and Masked Booby in both seasons and Wedge-tailed Shearwater in the wet season had AUC predictions from testing data of <0.7 and were not considered further. Predictions from training data yielded AUC values that were higher on average by 0.08 (dry season) and 0.06 (wet season) than predictions from testing data.

Table 3. Performance of the seabird distribution ensemble model with the test and training data for the Browse Basin during the dry season, September–November 2000–2012.*

Species	Test AUC (SD)	Training AUC (SD)
Roseate Tern	0.90 (0.04)	0.93 (0.02)
Bulwer's Petrel	0.89 (0.02)	0.92 (0.01)
Hutton's Shearwater	0.89 (0.03	0.95 (0.01)
Common Noddy	0.87 (0.02)	0.91 (0.01)
Tahiti Petrel	0.87 (0.02)	0.93 (0.01)
Red-footed Booby	0.85 (0.06)	0.92 (0.03)
Matsudaira's Storm-petrel	0.84 (0.03)	0.93 (0.01)
Crested Tern	0.84 (0.03)	0.89 (0.02)
Swinhoe's Storm-petrel	0.81 (0.04)	0.91 (0.02)
Brown Booby	0.80 (0.02)	0.85 (0.01)
Sooty Tern	0.79 (0.03)	0.87 (0.01)
Common Tern	0.78 (0.04)	0.85 (0.02)
Bridled Tern	0.77 (0.03)	0.84 (0.02)
Jouanin's Petrel	0.77 (0.07)	0.91 (0.03)
White-winged Black Tern	0.76 (0.06)	0.82 (0.04)
Wilson's Storm-petrel	0.75 (0.03)	0.86 (0.02)
Streaked Shearwater	0.72 (0.06)	0.83 (0.03)
Wedge-tailed Shearwater	0.71 (0.06)	0.89 (0.02)

**Assessed using area under the receiver-operated characteristic curve (AUC) values.*

Table 4. Performance of the seabird distribution ensemble model (combined output from several methods used to predict seabird spatial distribution) with the test and training data for the Browse Basin during the wet season, April 2010–2013.*

Species	Test AUC (SD)	Training AUC (SD)
Black Noddy	0.98 (0.01)	0.99 (0.00)
Bulwer's Petrel	0.90 (0.02)	0.92 (0.01)
Roseate Tern	0.90 (0.04)	0.93 (0.02)
Common Noddy	0.86 (0.02)	0.91 (0.01)
Red-footed Booby	0.84 (0.07)	0.93 (0.03)
Crested Tern	0.82 (0.04)	0.90 (0.02)
Brown Booby	0.82 (0.02)	0.84 (0.01)
Sooty Tern	0.80 (0.03)	0.87 (0.01)
Common Tern	0.77 (0.04)	0.84 (0.02)
Bridled Tern	0.76 (0.03)	0.84 (0.02)
Wilson's Storm-petrel	0.76 (0.03)	0.87 (0.02)
Streaked Shearwater	0.75 (0.06)	0.82 (0.03)

**Assessed using area under the receiver-operated characteristic curve (AUC) values.*

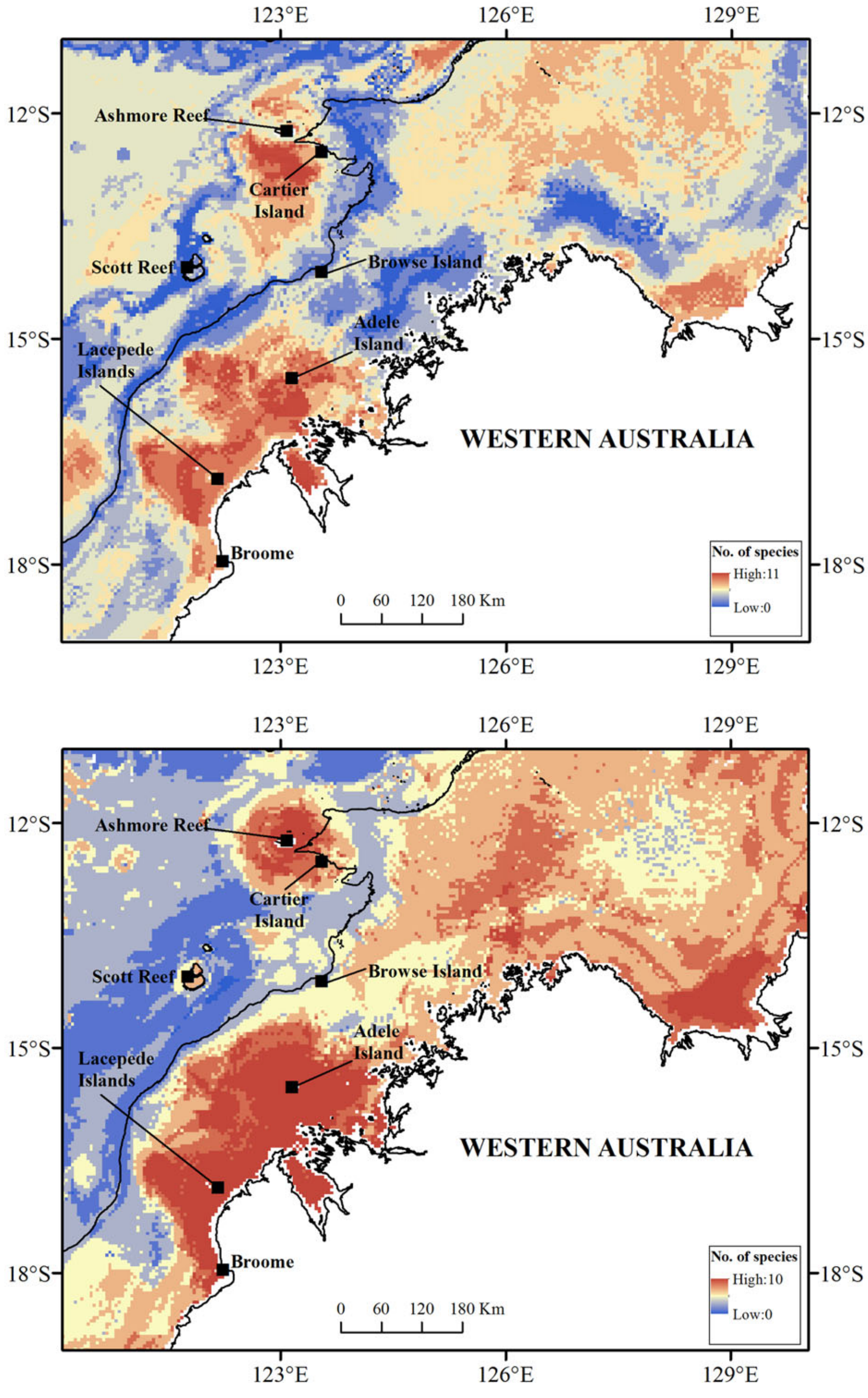

Figure 1. Predicted species richness of the Browse Basin seabird community (top) September–November 2000–2012 (dry season) (see Table 3 for species list) and (bottom) April 2010–2013 (wet season) (see Table 4 for species list) based on the ensemble model (combined output from several methods used to predict seabird spatial distribution) . Ocean depths >200 m indicated by the black contour line.

Seabird Richness Hotspots and Proposed IBAs

The predicted hotspots based on seabird richness summed over all species were relatively consistent between seasons. An offshore area of high seabird diversity located within 150 km of Ashmore Reef was a particularly well-defined hotspot, especially during the dry season (Fig. 1). Two hotspots were identified northeast of Broome in relatively shallow (<200 m) coastal waters surrounding Adele and the Lacepede Islands (Fig. 1). The boundaries of all 3 sites extended approximately 150 km beyond currently recognized reserve boundaries and are therefore proposed as candidate marine IBAs in the Browse Basin (Fig. 2). These sites variously met marine IBA criteria based on the presence of breeding species (Brown Booby, A4ii and A4iii; Common Noddy,

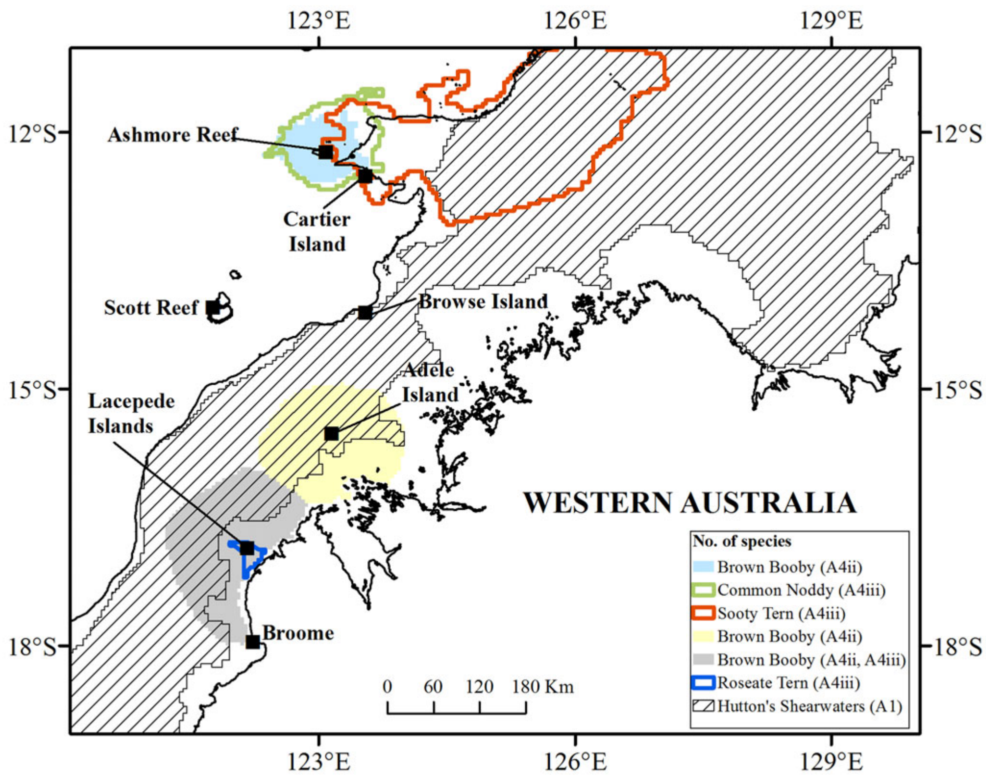

*Figure 2. Proposed marine important bird areas (IBAs) based on the predicted distribution of migratory Hutton's Shearwater (*Puffinus huttoni*) and Roseate Tern (*Sterna dougallii*) and the known breeding population of Brown Booby (*Sula leucogaster*) and Common Noddy (*Anous stolidus*) on Ashmore Reef, Adele Island, and the Lacepede Islands during the dry season (September–November). Criteria for IBA designation: site known or thought to hold on a regular basis 1% of the global population of a seabird species (A4ii), 20,000 individuals or 10,000 pairs of one or more species (A4iii), site regularly holds substantial numbers of a globally threatened species (A1) (BirdLife International 2010). Ocean depths >200 m indicated by the black contour line.*

A4iii; Roseate Tern, A4iii; Sooty Tern, A4iii) and the presence of the endangered, nonbreeding migrant Hutton's Shearwater (*Puffinus huttoni*, A1) (Fig. 2).

Discussion

We combined at-sea observations of seabirds gathered over 14 years with data on the physical and biological features of the marine environment to predict the distribution of seabird communities in the Browse Basin and broader Timor Sea region. Our focus was not on the fine-scale habitat preferences of individual seabird species, but rather on the identification of species richness hotspots at an appropriate scale to guide managers in the delineation of candidate sites for marine protection (Halpern 2003; McGowan et al. 2013). Because seabird ecology and life history varies across taxa, hotspots predicted for one species may not be the same as those predicted for other species (Nur et al. 2011; McGowan et al. 2013). In contrast, our results are broadly transferrable within the Timor Sea region because seabird hotspots were identified with data drawn from 4 seabird families (Procellariidae, Hydrobatidae, Sternidae, and Sulidae), which captures variation driven by contrasting wet and dry seasons.

Important Areas for Conservation in the Browse Basin

The performance of different species distribution models affects the identification of marine hotspots; therefore, a combined or ensemble approach has been advocated (Jones-Farrand et al. 2011; Oppel et al. 2012). In our study, the ensemble model provided the most robust method for predicting seabird hotspots based on patterns derived over large temporal and spatial scales (Table 2); the distribution of up to 18 species was successfully modeled, depending on the season (Tables 3 and 4). Overall, model performance was best for 3 migratory species (Bulwer's Petrel, Hutton's Shearwater, and Roseate Tern; AUC > 0.87; Table 3). This result highlights one of the core strengths of at-sea data: the inclusion of nonbreeding migrant species when assessing the importance of an area to marine wildlife conservation.

The model identified 3 main areas of high seabird species richness in the Browse Basin. The first, an area surrounding Ashmore Reef and to the southwest, referred to as the Ashmore Platform (Fairbridge 1953), was predicted to occur in the same area during both the wet and dry seasons (Fig. 1). Three of the 4 threatened species recorded in the basin were also predicted to occur in this area during the dry season (Supporting Information). Additional, independent evidence of the importance and validity of this area is provided by recent tracking of boobies, Red-tailed Tropicbirds (*Phaethon rubricauda*), and Lesser Frigatebirds breeding on Ashmore Reef (J.L.L. and R.H.C., unpublished data).

Two additional areas of seabird richness were in shelf and coastal waters along the continental margin (<200 m water depth) surrounding Adele Island and the Lacepede Islands (Fig. 1). This pattern was largely driven by the presence of terns and noddies and was consistent across both seasons (Supporting Information). However, Procellariiforme richness was also predicted to be high in this region, particularly during the dry season (Supporting Information). This pattern was driven primarily by the 2 inshore species, Streaked and Hutton's Shearwaters (Supporting Information, Fig. 2). Seabirds are often found in association with frontal features and regions of elevated ocean productivity (Louzao et al. 2009). This likely explains the diversity of seabird species observed here and predicted to occur adjacent to the continental shelf (200 m bathymetric contour).

The seabird richness hotspots we identified extend at least 150 km beyond existing IBA and marine reserve boundaries, which currently include only the islands and surrounding waters to the 50 m bathymetric contour (BirdLife International 2013*b*; Director of National Parks 2013). For Brown Booby, 3 proposed marine IBA sites were identified for Ashmore Reef and Adele Island (IBA criteria: A4ii) and the Lacepede Islands (A4ii and A4iii). Two further sites were identified on Ashmore Reef for Common Noddy and Sooty Tern (A4iii [Table 1]) and for Roseate Tern roosting on the Lacepede Islands (A4iii [Table 1]). A proposed marine IBA was identified in shelf waters (<200 m depth) for nonbreeding, endangered Hutton's Shearwater because this species is regularly encountered during the dry season (IBA criteria A1 [Fig. 2]). Other nonbreeding species, Jouanin's Petrel (*Bulweria fallax*), Tahiti Petrel, and Swinhoe's Storm-petrel (*Oceanodroma monorhis*), have lower near threatened status and were not encountered frequently enough in surveys to meet A1 criteria. Lesser Frigatebird and Masked Booby could not be successfully modeled (AUC < 0.7), but they are likely to benefit from the proposed IBAs that encompass at least 50% of the species' foraging range in the basin (J.L.L. and R.H.C., unpublished data). Within the Browse Basin, the distribution of the Brown Booby captured important at-sea areas for many of the other seabird species (Fig. 2). As a result, the Brown Booby is likely to function as a reliable indicator species for future monitoring within the basin.

Seabird Conservation

The continental shelf off northwest Australia holds significant hydrocarbon reserves that overlap with many of the biodiversity values identified above (Clarke et al. 2011; Hayes 2012). The 2009 blowout at the Montara H1 well located 165 km east of Ashmore Reef resulted in a visible surface sheen of oil that covered approximately 36,400 km^2 (Borthwick 2010). Western Australia has experienced at least 12 other offshore spillage events (mean 496 L, SD 436 L; 1988–1991; May 1992), and small offloading spills (1,000–10,000 L) are predicted to occur once every 2–3 years (Commonwealth of Australia 2007). While the risk to seabirds and other wildlife posed by offshore development can extend over thousands of kilometers in the case of a large spill, marine species are not distributed evenly across the ocean. Therefore, using species distribution models to identify foraging hotspots for marine species, as we have done here, can provide the scientific justification for more effective protection for a disproportionately large number of species from offshore development, as well as other localized disturbances such as fishing activities and light pollution (Hooker et al. 1999; Burke et al. 2012). This protection could be in the form of appropriate zoning to limit or exclude key threatening processes. In instances where potential threats are already well established, such as production wells for oil and gas extraction, heightened preparedness for spill events in proximity to foraging hotspots is also appropriate.

Overall, the most effective reserve designs are ecologically driven, providing at least some protection for entire communities, particularly in relatively intact ecosystems (Halpern et al. 2008). In the marine context, however, there are few examples in which the distribution of a large number of marine species (i.e., a community) has been modeled, particularly over a large area and over a considerable period, to identify key areas for conservation (except see Nur et al. 2011; Ballard et al. 2012). The multispecies approach we used incorporates data on seabird habitat preferences over the past decade and provides the most robust assessment of where marine birds are likely to congregate. As such, our approach identifies spatially explicit areas that will benefit most from protection. Thus, our results contribute substantially to our ability to balance increasing resource demands and provide effective conservation in this relatively intact system.

Acknowledgments

A. Herrod provided logistical support and assistance in the field. The manuscript benefited from comments provided by D. Ainley, B. Lascelles, S. Oppel, and 2 anonymous reviewers.

Supporting Information

A description of our approach to addressing collinearity (Appendix S1), monthly survey effort (Appendix S2), a map showing the location of seabird observations (Appendix S3), and the predicted distribution of threatened seabirds (Appendix S4), terns and noddies (Appendix S5), and Procellariformes (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Anderson, O. R. J., C. J. Small, J. P. Croxall, E. K. Dunn, B. J. Sullivan, O. Yates, and A. Black. 2011. Global seabird bycatch in longline fisheries. Endangered Species Research **14:**91–106.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution **22:**42–47.

Ballard, G., D. Jongsomjit, S. D. Veloz, and D. G. Ainley. 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation **156:**72–82.

BirdLife International. 2010. Marine Important Bird Areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. Version 1.2. BirdLife International, Cambridge, United Kingdom.

BirdLife International. 2013*a*. Important Bird Areas factsheet: Adele Island. Birdlife International, Cambridge, United Kingdom. Available from http://www.birdlife.org(accessed September 2013).

BirdLife International. 2013*b*. Important Bird Areas factsheet: Ashmore Reef. International, Cambridge, United Kingdom. Available from http://www.birdlife.org(accessed September 2013).

BirdLife International. 2013*c*. Important Bird Areas factsheet: Lacepede Islands. International, Cambridge, United Kingdom. Available from http://www.birdlife.org(accessed September 2013).

BirdLife International. 2013*d*. Species factsheet: *Anous stolidus*. International, Cambridge, United Kingdom. Available from http://www.birdlife.org(accessed September 2013).

Borthwick, D. 2010. Report of the Montara Commission of inquiry. Department of Resources, Energy and Tourism, Canberra.

Browman, H. I., and K. I. Stergiou. 2004. Marine Protected Areas as a central element of ecosystem-based management: defining their location, size and number. Marine Ecology Progress Series **274:** 269–303.

Burke, C. M., W. A. Montevecchi, and F. K. Wiese. 2012. Inadequate environmental monitoring around offshore oil and gas platforms on the Grand Bank of Eastern Canada: Are risks to marine birds known? Journal of Environmental Management **104:**121–126.

Cama, A., R. Abellana, I. Christel, X. Ferrer, and D. R. Vieites. 2012. Living on predictability: modelling the density distribution of efficient foraging seabirds. Ecography **35:**912–921.

Clarke, R. H., M. J. Carter, G. Swann, and J. Thomson. 2011. The status of breeding seabirds and herons at Ashmore Reef, off the Kimberley coast, Australia. Journal of the Royal Society of Western Australia **94:**365–376.

Commonwealth of Australia. 2007. Petroleum and minerals industries in the northwest marine region. A report to the Department of the Environment, Water, Heritage, and the Arts. Document no. ENV-REP-07-0086 REV 0. IRC Global Risk Management, Perth.

Comte, L., and G. Grenouillet. 2013. Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. Diversity and Distributions **19:**996–1007.

DERT. 2010. Australia's offshore petroleum industry. Department of Resources, Energy, and Tourism, Canberra.

Director of National Parks. 2013. North-west Commonwealth Marine Reserves Network Management Plan 2014–24. Director of National Parks, Canberra.

Dormann, C., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography **30:**609–628.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology **77:**802–813.

Fairbridge, R. W. 1953. The Sahul Shelf, northern Australia: its structure and geological relationships. Journal of the Royal Society of Western Australia **37:**1–33.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24:**38–49.

Game, E. T., H. S. Grantham, A. J. Hobday, R. L. Pressey, A. T. Lombard, L. E. Beckley, K. Gjerde, R. Bustamante, H. P. Possingham, and A. J. Richardson. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology & Evolution **24:**360–369.

Game, E. T., H. S. Grantham, A. J. Hobday, R. L. Pressey, A. T. Lombard, L. E. Beckley, K. Gjerde, R. Bustamante, H. P. Possingham, and A. J. Richardson. 2010. Pelagic MPAs: the devil you know. Trends in Ecology & Evolution **25:**63–64.

Gaston, K. J., S. F. Jackson, L. Cantú-Salazar, and G. Cruz-Piñón. 2008. The ecological performance of protected areas. Annual Review of Ecology, Evolution, and Systematics **39:**93–113.

Gordon, A. L. 2005. Oceanography of the Indonesian Seas and their throughflow. Oceanography **18:**14–27.

Grecian, W. J., M. J. Witt, M. J. Attrill, S. Bearhop, B. J. Godley, D. Grémillet, K. C. Hamer, and S. C. Votier. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: an example using Northern Gannets breeding in the north east Atlantic. Biological Conservation **156:**43–52.

Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications **13:** S117–S137.

Halpern, B. S., et al. 2008. A global map of human impact on marine ecosystems. Science **319:**948–952.

Harrison, G. W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. The American Naturalist **113:**659–669.

Hayes, J. 2012. Operator competence and capacity—lessons from the Montara blowout. Safety Science **50:**563–574.

Hooker, S. K., and L. R. Gerber. 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. BioScience **54:**27–39.

Hooker, S. K., H. Whitehead, and S. Gowans. 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation Biology **13:** 592–602.

Jones-Farrand, D. T., T. M. Fearer, W. E. Thogmartin, F. R. T. Iii, M. D. Nelson, and J. M. Tirpak. 2011. Comparison of statistical and theoretical habitat models for conservation planning: the benefit of ensemble prediction. Ecological Applications **21:**2269–2282.

Lascelles, B. G., G. M. Langham, R. A. Ronconi, and J. B. Reid. 2012. From hotspots to site protection: identifying Marine Protected Areas for seabirds around the globe. Biological Conservation **156:**5–14.

Lavers, J. L., J. Hodgson, and R. H. Clarke. 2013. Prevalence and composition of marine debris in Brown Booby (*Sula leucogaster*) nests on Ashmore Reef. Marine Pollution Bulletin **77:** 320–324.

Lewison, R. L., L. B. Crowder, A. J. Read, and S. A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology & Evolution **19:**598–604.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography **28:**385–393.

Louzao, M., J. Bécares, B. Rodríguez, K. D. Hyrenbach, A. Ruiz, and J. M. Arcos. 2009. Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Marine Ecology Progress Series **391:**183–197.

Louzao, M., K. D. Hyrenbach, J. M. Arcos, P. Abelló, L. G. d. Sola, and D. Oro. 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. Ecological Applications **16:**1683–1695.

May, R. F. 1992. Marine conservation reserves, petroleum exploration and development, and oil spills in coastal waters of Western Australia. Marine Pollution Bulletin **25:**147–154.

McGowan, J., E. Hines, M. Elliott, J. Howar, A. Dransfield, N. Nur, and J. Jahncke. 2013. Using seabird habitat modeling to inform ocean zoning in central California's National Marine Sanctuaries. PLoS One **8:**e71406.

McNeill, S. E. 1994. The selection and design of marine protected areas: Australia as a case study. Biodiversity & Conservation **3:** 586–605.

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography **36:**1058–1069.

Nur, N., et al. 2011. Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. Ecological Applications **21:**2241–2257.

Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A. F. O'Connell, P. I. Miller, and M. Louzao. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biological Conservation **156:**94–104.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography **31:**161–175.

Ramsar Convention Bureau. 2013. Annotated list of wetlands of international importance: Australia. Ramsar Convention Bureau, Gland, Switzerland.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413:**591–596.

Tasker, M. L., P. H. Jones, T. Dixon, and B. F. Blake. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. The Auk **101:**567–577.

Thaxter, C. B., B. Lascelles, K. Sugar, A. S. C. P. Cook, S. Roos, M. Bolton, R. H. W. Langston, and N. H. K. Burton. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biological Conservation **156:**53–61.

Wakefield, E. D., R. A. Phillips, and J. Matthiopoulos. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Marine Ecology Progress Series **391:** 165–182.

Zacharias, M. A., and J. C. Roff. 2001. Use of focal species in marine conservation and management: a review and critique. Aquatic Conservation: Marine and Freshwater Ecosystems **11:**59–76.