



Applying global criteria to tracking data to define important areas for marine conservation

B. G. Lascelles^{1*}, P. R. Taylor², M. G. R. Miller³, M. P. Dias¹, S. Opper², L. Torres⁴, A. Hedd⁵, M. Le Corre⁶, R. A. Phillips⁷, S. A. Shaffer⁸, H. Weimerskirch⁹ and C. Small²

¹BirdLife International, Cambridge, UK, ²RSPB Centre for Conservation Science, The Lodge, Sandy, UK, ³James Cook University, Cairns, Qld, Australia, ⁴Department of Fisheries and Wildlife, Marine Mammal Institute, Oregon State University, Newport, OR, USA, ⁵Memorial University, St John's, NF, Canada, ⁶University of Reunion, Saint Denis, Réunion, ⁷British Antarctic Survey, Cambridge, UK, ⁸Department of Biological Sciences, San Jose State University, San Jose, CA, USA, ⁹Centre d'Etudes Biologiques de Chizé, Villiers-en-Bois, France

ABSTRACT

Aim Enhanced management of areas important for marine biodiversity are now obligations under a range of international treaties. Tracking data provide unparalleled information on the distribution of marine taxa, but there are no agreed guidelines that ensure these data are used consistently to identify biodiversity hotspots and inform marine management decisions. Here, we develop methods to standardize the analysis of tracking data to identify sites of conservation importance at global and regional scales.

Location We applied these methods to the largest available compilation of sea-bird tracking data, covering 60 species, collected from 55 deployment locations ranging from the poles to the tropics.

Methods Key developments include a test for pseudo-replication to assess the independence of two groups of tracking data, an objective approach to define species-specific smoothing parameters (h values) for kernel density estimation based on area-restricted search behaviour, and an analysis to determine whether sites identified from tracked individuals are also representative for the wider population.

Results This analysis delineated priority sites for marine conservation for 52 of the 60 species assessed. We compiled 252 data groupings and defined 1052 polygons, between them meeting Important Bird and Biodiversity Area criteria over 1500 times. Other results showed 13% of data groups were inadequate for site definition and 10% showed some level of pseudo-replication. Between 25 and 50 trips were needed within a data group for data to be considered at least partially representative of the respective population.

Main conclusions Our approach provides a consistent framework for using animal tracking data to delineate areas of global conservation importance, allowing greater integration into marine spatial planning and policy. The approaches we describe are exemplified for pelagic seabirds, but are applicable to a range of taxonomic groups. Covering 4.3% of the oceans, the sites identified would benefit from enhanced protection to better safeguard the threatened species populations they contain.

Keywords

Important Bird and Biodiversity Areas, kernel analysis, marine protected areas, seabirds, site-based conservation, tracking data.

*Correspondence: B. G. Lascelles, BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, UK.
E-mail: ben.lascelles@birdlife.org

INTRODUCTION

Many migratory marine species travel across jurisdictional boundaries and into the High Seas, such that conventional

at-sea survey techniques are impractical at these large spatial scales. Developments in animal tracking techniques have revolutionized our understanding of the at-sea distributions, movements, ecology and activity patterns of marine species,

with the availability of small, affordable devices that greatly increase the number of species studied in recent decades (Gillespie, 2001; Tomkiewicz *et al.*, 2010). To date, devices have been attached to seabirds (Burger & Shaffer, 2008), seals (McConnell *et al.*, 1992), fish (Block *et al.*, 1998), turtles (Fossette *et al.*, 2007), whales (Bailey *et al.*, 2009) and even jellyfish (Honda *et al.*, 2009).

The utility of tracking as a tool to inform marine conservation planning is well-documented, facilitating detailed investigations of the spatial overlap of species and their threats, such as fisheries and marine developments (BirdLife International 2004; Tuck *et al.*, 2011). Enhanced spatial conservation measures to protect species and habitats in marine systems are now obligatory under a number of international treaties and policy instruments. Consequently there is widespread interest in using tracking data to identify biodiversity hotspots, particularly to define candidate sites for formal protection and other forms of management (Block *et al.*, 2011; Lascelles *et al.*, 2012). However, there is little consistency in how tracking data are analysed to identify areas of biological significance and thus how they can be used to inform marine management decisions.

Here, we demonstrate how the analysis of tracking data from a group of wide-ranging top predators can be used in combination with objective site selection criteria to delineate areas of global significance for biodiversity. We use seabirds to demonstrate our approaches because they must return to land to breed, and are therefore much easier to study than other wide-ranging marine taxa. Moreover, seabirds are top predators that utilize resources across broad oceanic regions making them good indicator species, (Caro & O'Doherty, 1999; Branton & Richardson, 2010) and information on their distributions can therefore provide surrogates for biodiversity hotspots in marine spatial planning (Zacharias & Roff, 2001; Aslan *et al.*, 2015). Processing and analysis of tracking data is complex, and previous efforts have typically developed species- and study-specific methods (Burger & Shaffer, 2008). The methods presented here therefore fulfil the urgent need for a consistent, comparable and repeatable approach to site identification.

Globally consistent assessments for Important Bird and Biodiversity Areas

The Important Bird and Biodiversity Area (IBA) Programme, established by BirdLife International, uses objective and transparent criteria to define sites of key conservation importance at global and regional scales (Fishpool & Evans, 2001). Terrestrial sites have been identified using these criteria in over 120 countries, helping guide land-based conservation for over 30 years. More recently the same broad principles have been applied in the marine environment (BirdLife International 2009a), and seabird tracking data have been used in a number of national (e.g. Ramirez *et al.*, 2008; Arcos *et al.*, 2009; Delord *et al.*, 2014) and international (e.g. in Areas Beyond National Jurisdiction, BirdLife International 2009a) projects to define IBAs and inform spatial manage-

ment, such as the designation of Marine Protected Areas (MPAs). The IBA criteria and thresholds align closely with those used in several marine policy agreements, such as the European Union's Birds Directive (BirdLife International 2010), the Ramsar Convention (Lynch-Stewart, 2008) and the Convention on Biological Diversity (BirdLife International 2009a).

To qualify as an IBA, a site must hold a 'regular presence' of a 'threshold number of birds (e.g. $\geq 1\%$ of global or biogeographic population)'. For globally threatened species with very small populations (i.e. Critically Endangered or Endangered according to IUCN) regular presence alone may be enough to warrant designation; however, for other species, abundance thresholds must also be met. IBA criteria are readily applicable to most threatened and congregatory species during different life history stages and can be used to identify areas such as breeding colonies, feeding areas around colonies, non-breeding congregations, migratory bottlenecks and pelagic feeding aggregations (Osieck, 2004). While it is relatively easy to assess seabird breeding colonies against IBA criteria, it is more difficult to locate areas of aggregation at sea and determine if they warrant designation. Vessel-based observations cannot adequately describe the at-sea distributions of most seabirds; tracking data have therefore proved vital in filling this data gap, allowing us to understand where important areas occur and when these are being used by different species and life history stages.

Here, we present a method to derive proposed IBAs (areas representative at the population level) from raw locations of individuals tracked using a variety of tracking devices. Our approach objectively defines the spatial scale at which seabirds interact with their marine environment, and then proceeds to critically assess whether the number of tracked individuals is sufficient for population-level inference. We use changes in track characteristics (speed or sinuosity) and density of fixes (locations) to qualify areas as candidate IBAs, and estimate the overall number of individuals that use those areas based on colony sizes and how representative the tracked birds are of their respective populations.

The approaches we describe are exemplified for pelagic seabirds, but can be used with tracking data from a range of taxonomic groups. Seabird tracking data are available via several online data portals, including the *Tracking Ocean Wanderers* database (BirdLife International 2004; www.seabirdtracking.org), which is the repository of the data from the 60 species included in our analysis. This large global dataset covers multiple species and life history stages and thus provided a unique opportunity to develop and test consistent methodologies with direct applications to policy.

METHODS

Data preparation

This analysis included data from the three most commonly used tracking devices for vertebrates: Platform Terminal

Transmitters (PTT), Global Positioning Systems (GPS) and Geolocators (GLS loggers). Our methods were applied to raw data consisting of the location (latitude and longitude) provided by the tracking device at each date and time, and a unique identifier for the individual bird. We standardized datasets to allow ready combination and comparison where needed (Appendix S1).

Most seabirds exhibit changing space-use patterns during different life history stages and sometimes between years (e.g. BirdLife International 2004; Riotte-Lambert & Weimerskirch, 2013). Additionally, examples of spatial segregation in foraging areas of separate populations of the same species are becoming more widespread (Gremillet *et al.*, 2004; Wakefield *et al.*, 2013). To account for this variation, we split data into homogenous 'data groups', pooling data from all years and classifying them into unique combinations of species, colony and life history stage (Table 1). This procedure ensures that any spatial aggregation patterns exhibited by a species during a given life history stage are captured and not diluted by inclusion of data from other life history stages with potentially very different distributions. All analyses described hereafter are undertaken at the level of the individual data group with data projected into Lambert Equal-Area Azimuthal customized to each data group (Appendix S1).

When breeding, seabirds are central-place foragers that return to their colonies for parental duties, and tracking data from breeding adults often include multiple foraging trips from the same individuals. To maximize the use of available data we considered each trip by an individual as an independent sample, (Fig. 1) as using only the first foraging trip made by an individual for subsequent analysis is likely to under-estimate the size of the home range at the population level (Soanes *et al.*, 2013). Foraging trips were defined as any occasion where a tracked individual travelled a minimum specified time and distance from the colony, which varied

between species and life history stages (BirdLife International 2004).

Test for site fidelity

Datasets including multiple trips from a single bird may show pseudo-replication (i.e. if individuals show site fidelity) and bias results (Giuggioli & Bartumeus, 2010; Auge *et al.*, 2013). We designed a test for pseudo-replication that compared the similarity of foraging locations of a single tracked bird with those of the rest of the data group. This test selected all trips for an individual that had completed more than one, identified the 50% kernel utilization distribution (UD, see below) for each trip, and calculated the Hausdorff distance between these areas, to quantify proximity (Munkres, 2000). For each individual, distances between core foraging ranges were calculated between every combination of its trips, and then compared to a data group reference distribution. To calculate the reference distribution we randomly selected the same number of trips from each tracked individual, and calculated the Hausdorff distance for core foraging ranges between individuals. The within individual distances were then compared against the population-level distances using a Mann–Whitney *U*-test. This examined whether the null hypothesis – that the proximity of core areas from a single individual is similar to the proximity of core areas between different individuals of the same population and life history stage – could be rejected, in which case there was some indication of site-fidelity and thus pseudo-replication. This process was repeated 100 times to account for possible bias in the random sample, and the mean p-value calculated.

We used an extremely conservative $\alpha = 0.25$ to ensure that no data indicating pseudo-replication were used in subsequent analyses. If pseudo-replication was detected a single trip was randomly selected from each individual for use in further analyses; otherwise, all data were retained.

Table 1 Description of seabird life history stages included within this analysis and the number of data groups assessed within each.

Life history stages	Description	No. data groups
Breeding	Covering the entire breeding period. Used when it was not possible to define more detailed life-history stages	39
Pre-egg	The period prior to breeding during which adults may visit the colony, copulate and spend time at-sea feeding in preparation for egg production and incubation	7
Incubation	The period when adults are alternating incubation of eggs and undertaking maintenance trips to sea	43
Brood-guard*	The period when adults are feeding small chicks. Adults alternate staying with the chick to brood or guard it against predators while the other forages at sea	38
Post-guard	The period when adults are feeding large chicks. The chick is generally left alone during this time with both adults feeding at sea	44
Fledging	Young birds leaving the colony for the first time	3
Immature†	Young birds which are not yet old enough to breed. For many seabirds this period can last several years	13
Non-breeding	Adult birds outside of the breeding season during which time they do not need to return to the colony	61
Sabbatical	Adult birds with breeding experience that have skipped breeding that season	4

*Includes *sulid* data groups classed as chick-rearing.

†Includes all data groups classed as juveniles.

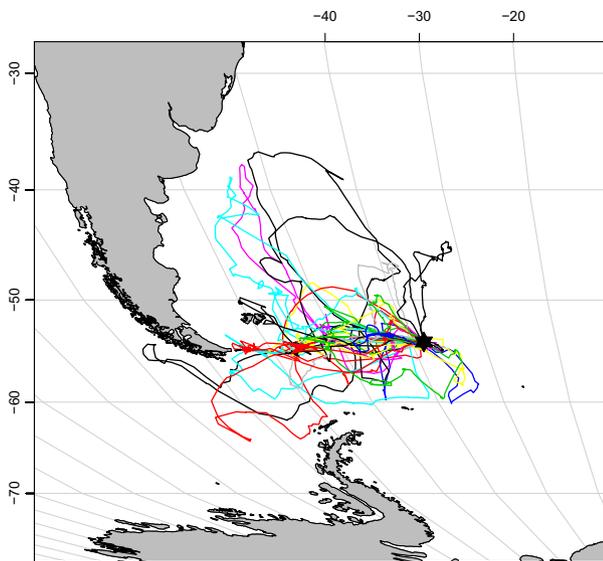


Figure 1 Individual foraging trips (each trip coloured differently) of Wandering Albatross during the incubation period at Bird Island, South Georgia. We defined a trip as any occasion where a tracked individual travelled for > 25 km from the colony for > 12 h, giving us a sample size of 27 trips.

Defining core-use areas and scales of interaction with the marine environment

We used kernel density estimation (KDE), a measure of the probability of occurrence, to define important areas for six reasons; (1) KDE is ideally suited for assessing regularity of use and determining whether the number of individuals using a site exceeds selection thresholds; (2) core areas identified by KDE are less influenced by outliers (Hemson *et al.*, 2005); (3) comparative studies have found that KDE omitted fewest key areas of interest (BirdLife International 2009b, Tancell *et al.*, 2013); (4) KDE is used widely in the seabird tracking literature, thus facilitating comparison and integration of results obtained in this and other studies, (5) KDE is one of the more straightforward techniques for analysis of distributions; (6) the outputs of KDE are generally well-understood by non-scientists within policy arenas.

We estimated kernel UD for every individual trip and, following previous studies, defined the 50% isopleth as the ‘core-use area’ for each trip (Fig. 2) (Ramirez *et al.*, 2008; Arcos *et al.*, 2009; Soanes *et al.*, 2013). To assess regularity of use we overlapped the 50% UD of each trip onto a $0.01 \times 0.01^\circ$ grid projected into a customized Lambert Equal-Area Azimuthal projection, and assumed that a grid cell was in the core area of an individual trip if it intersected the 50% UD. To identify core-use areas where multiple trips co-occurred, we summarized how often each $0.01 \times 0.01^\circ$ cell was included in a core-use area of individual trips (Fig. 3).

To estimate density, KDE assumes an area of influence around each point (the smoothing factor h). The results of KDE are extremely sensitive to this value, which must be defined *a priori*. However, despite considerable debate

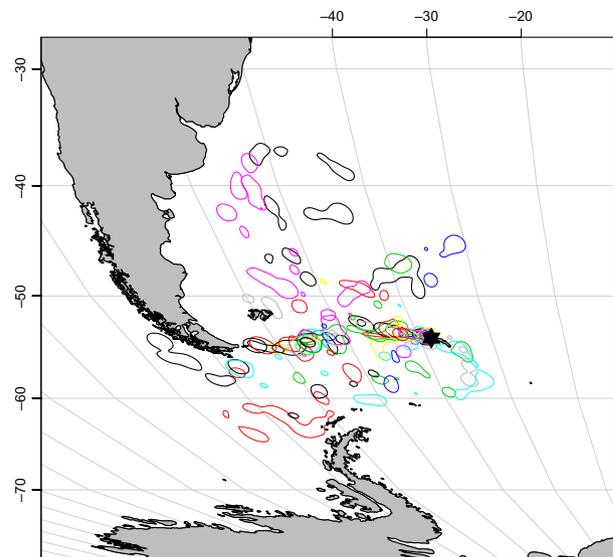


Figure 2 Identification of ‘core-use areas’ for each trip (coloured as Fig. 1) from the 50% kernel density utilization distributions. The kernel smoothing factor (h value) was based on the result of the area-restricted search assessment in Fig. 4.

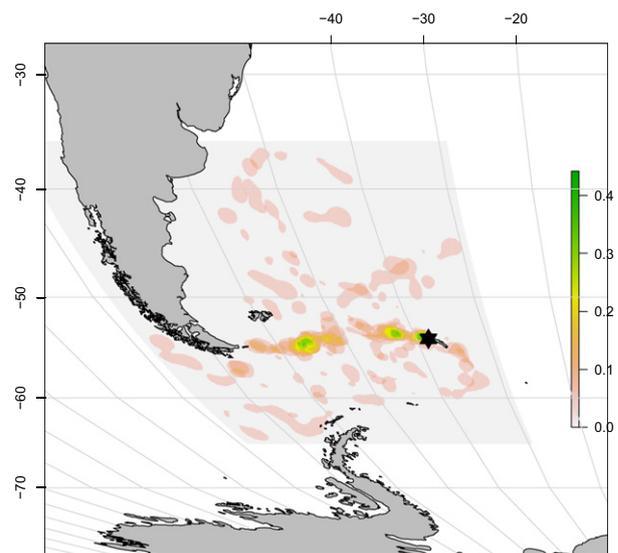


Figure 3 Count surface showing the frequency of inclusion of 0.01 degree grid cells in individual 50% utilization distribution isopleths. The colour scale indicates the proportion of foraging trips with a core-use area in a given grid cell and thus indicates the important areas at the population level.

(Worton, 1989; Wand & Jones, 1995), there is no consensus and values are frequently set arbitrarily. To assign smoothing factors to GPS and PTT data in a justifiable and consistent way, we employ a novel approach based on area-restricted search behaviour (ARS – e.g. Weimerskirch *et al.*, 2007), assessed via First Passage Time (FPT) analysis, to determine the spatial scales individuals interact with different aspects of the environment (Suryan *et al.*, 2006). We used the average ARS exhibited across all trips within a data group (Fig. 4) to define the h value – see Appendix S1. For GLS data, we used

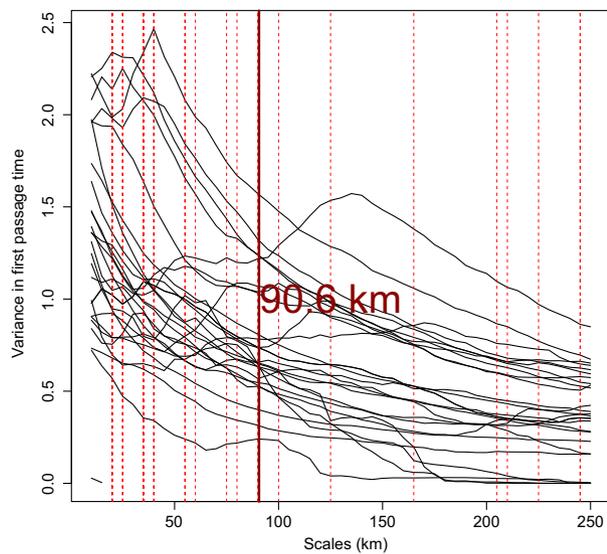


Figure 4 Characterizing the Area Restricted Search patterns of the data group. Each black line shows the log variance in First Passage Time at each scale for an individual foraging trip, dotted red lines show the peak scales for each individual foraging trip [i.e. the area-restricted search (ARS) scale], assessed from 10 to 250 km at 5 km intervals, solid red line shows the average ARS scale for the data group which was then used as kernel smoothing factor (h values) for home range estimation.

$h = 186$, which corresponds to the average error of the locations in kilometres (Phillips *et al.*, 2004).

Assessing representativeness

Generally only a fraction of a population is tracked; therefore the representativeness of such data needs to be evaluated if inferences are to be drawn at the population level (Lindberg & Walker, 2007). Small sample sizes may be insufficient to capture

the variability among individuals in space use (Lindberg & Walker, 2007) and debate continues over the appropriate sample size required to account for variability in behaviour and distribution of the wider population (Seaman *et al.*, 1999; Soanes *et al.*, 2013; Delord *et al.*, 2014). Therefore, the analysis of unrepresentative samples risks placing false emphasis on areas, particularly for species that show high variability in distribution within and between individuals or have broad habitat preferences (Delord *et al.*, 2014). In order to assess whether data were representative and allow inferences to be drawn about the spatial use patterns of a population, we examined how core area distribution (based on inclusion rather than spatial coverage) changes with increasing sample size (Fig. 5) – an approach similar to those applied to species discovery curves (Bebber *et al.* 2007) and chick growth rates (Schekkerman *et al.* 2003). We randomly selected individual trips iteratively, and compared the randomly selected (the ‘sampled’) with the unselected (the ‘un-sampled’) data. For each sample size, a 50% UD was calculated from the sampled data, using an average ARS scale to define the smoothing factor (Fig. 4). We then assessed what proportion of the unsampled data was located within this 50% UD. This ‘inclusion value’ is a metric indicating how well the sampled data explain the space use of individuals in the unsampled data (details in Appendix S1). These assessments allowed us to determine (1) whether a tracked sample was representative of the wider population, and (2) what correction factors should be used to assess the number of individuals using an area.

Defining sites at the population level

Important Bird and Biodiversity Area require not only evidence that areas are used regularly, but also that a certain proportion of a population is found there. It is therefore necessary to determine the number of individuals using a site. Such information cannot be estimated directly from

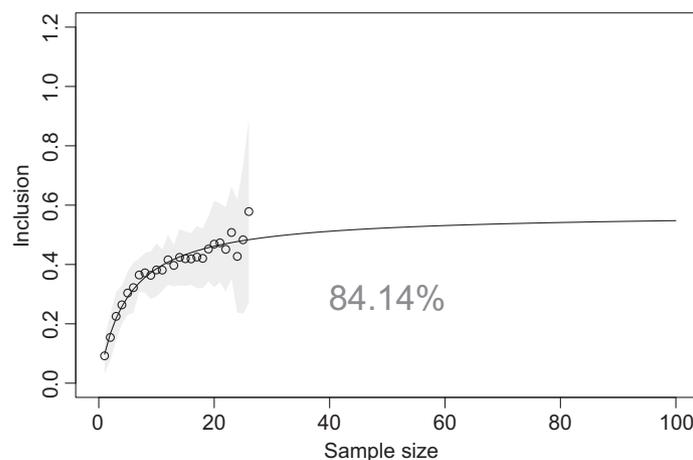


Figure 5 Assessing the representativeness of the data group to determine if population-level inference is possible. The graph indicates what proportion of out-of-sample locations were located within the 50% core-use areas estimated from sampled locations (Inclusion value) for 100 random draws of sample sizes from 1 to 26 trips. Grey bars indicate variability of inclusion value for 100 random data selections, and the solid line represents a nonlinear regression line. Inclusion rate (and thus representativeness of the tracking data set) is based on the estimated asymptote of the nonlinear regression.

tracking data unless the tracked sample is representative of the wider population. For those data groups that were considered to be representative (Table S3), we determined the number of individuals using each grid cell by multiplying the size of the overall population by the proportion of the tracked population which had a core-use area in this grid cell (Fig. 3). We use this assessment to assign correction factors to infer abundance estimates from the tracking data. These correction factors were set conservatively to reduce the probability of errors of commission.

RESULTS

Our global analysis assessed tracking data from 125 deployments at 55 locations, covering 60 species, collected over a 20 year period (1992–2012). Data were homogenized into 252 'data groups' (i.e. pooling data from all years and classifying them into unique combinations of species, colony and life history stage) which between them included over 8000 individual tracks made up of over 2 million data points. The species assessed included albatrosses (21 species; 140 data groups), shearwaters (11; 34), *Pterodroma* petrels (12; 27), giant-petrels (2; 18), *Procellaria* petrels (5; 17), sulids (5; 7), tropicbirds (2; 6) and frigatebirds (2;3).

In total, 1052 polygons were defined for 52 of the 60 species included in the analysis, with between 1 and 36 polygons (mean 4.4) resulting for each data group (Fig. 6). These polygons were assessed against three IBA criteria, with A1 (regular presence of a threatened species) triggered 715 times, A4ii (areas holding $\geq 1\%$ of global population) triggered 687 times and A4iii (areas holding $\geq 10,000$ pairs seabirds) triggered 128 times (Appendix S2). Note that polygons can trigger more than one criterion. The resulting

polygons can be viewed in Fig. 6 and, along with other IBAs for seabirds, at www.birdlife.org/datazone/marine.

Some data groups (48; 19%) were inadequate for IBA assessment due to them either (1) not being representative enough of the wider population (i.e. $< 70\%$ representative – 22 data groups; 10%), (2) no polygons were defined during the analysis (15 data groups; 7%) due to wide habitat preferences or (3) where polygons resulting did not meet IBA criteria (11 data groups; 5%) because small source populations were tracked or the polygons held below threshold numbers.

Over 50% of the species ($n = 31$) assessed are listed by IUCN as globally threatened (i.e. Critically Endangered, Endangered or Vulnerable), with a further 10 species listed as Near Threatened and the remainder ($n = 19$) Least Concern (Table 2). The analysis of the 122 data groups (48% of total) for globally threatened species resulted in the definition of over 660 polygons (63% of total) with IBA criteria triggered 1191 times (77% of total).

While the analysis was undertaken on each data group individually, when looking across the entire dataset (i.e. results for all species, sites and life history stages combined) there was often overlap amongst the polygons defined (Fig. 6 insets). Dissolving the overlapping polygons highlighted 7.6% (c. 30 million km²) of the oceans as feeding areas for seabirds, with c. 18 million km² of this being found in Areas Beyond National Jurisdiction. When only looking at polygons that were shown to meet the IBA criteria and thresholds the area of the ocean highlighted reduced to 4.3% (c. 17 million km²).

Other outputs from the analysis showed that 10% of data groups included individuals that exhibited some level of site-fidelity. The number of trips within a data group ranged from 5 to 299 and ARS scales determined for PTT and GPS data groups ranged from 11 to 135 km (Table S2). The

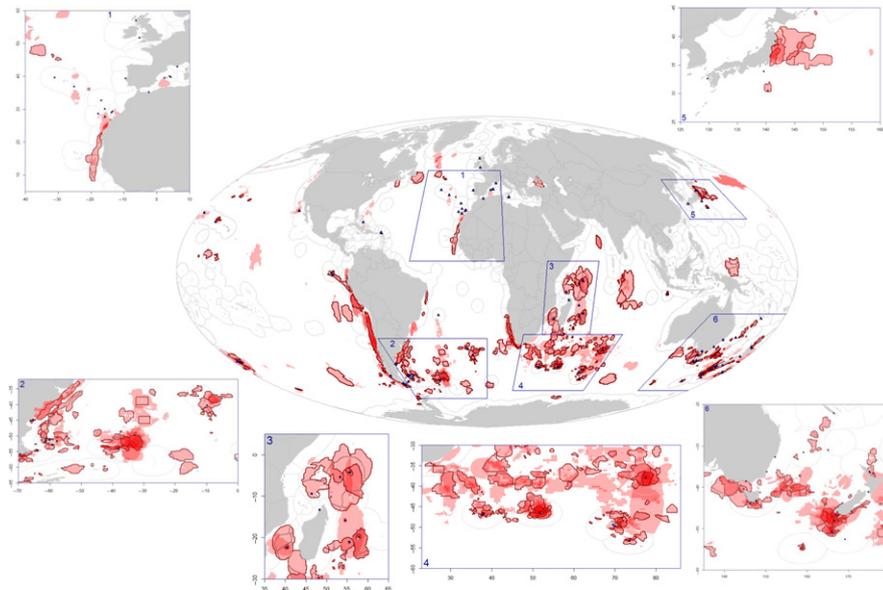


Figure 6 Polygons resulting from the analysis of all 252 data groups. Polygons are aggregated to show areas of overlap between data groups (darker areas), with insets providing further detail on those with greatest convergence. Also shown are the 55 deployment locations (blue stars) and Exclusive Economic Zones.

Table 2 IUCN Red List status of species included within the analysis, the number of data groups assessed and the polygons resulting along with the Important Bird and Biodiversity Area criteria triggered within these.

IUCN status	No. Species	No. data groups	No. polygons resulting	No. polygons A1	No. polygons A4ii	No. polygons A4iii
CR	5	16	132	127	126	4
EN	9	36	212	195	136	17
VU	17	70	317	301	257	28
NT	10	72	257	92	109	50
LC	19	58	134	0	61	31
Total	60	252	1052	715	689	130

A1 = *Globally threatened species* – The site is known or thought regularly to hold significant numbers of a globally threatened species, or other species of global conservation concern. A4ii = *Congregations* – Site known or thought to hold, on a regular basis, > 1% of the global population of a congregatory seabird or terrestrial species. A4iii = *Congregations* – Site known or thought to hold, on a regular basis, > 20,000 waterbirds or > 10,000 pairs of seabirds of one or more species.

assessment of representativeness indicated that between 25 and 50 trips were generally needed for a data group to be considered at least partially representative (i.e. $\geq 70\%$) of the wider population (Table S3).

To demonstrate our approach, we provide an example using PTT data for the Wandering Albatross (*Diomedea exulans*), obtained during the incubation period at Bird Island, South Georgia (Appendix S3). We defined a trip as any occasion where a tracked individual travelled for > 25 km from the colony for > 12 h, providing a sample size of 27 trips (Fig. 1). We assessed interaction with the marine environment by exploring scales from 10 to 250 km at 5 km intervals, and our FPT analysis indicated ARS behaviour at a radius of 45.3 km (Fig. 4). We used this value as the kernel smoothing factor to estimate core-use areas for each trip (Fig. 2), and aggregated these to quantify the frequency of usage for 0.01 degree grid cells (Fig. 3). By sub-sampling 1 to 26 trips from the data set, we estimated that the tracked population represented 84.14% of the locations that would have been used by the entire population (Fig. 5), and the data were therefore suitable for population level inference. For each polygon that was used by > 12.5% of the tracked population, we then assessed whether abundance thresholds for IBA criteria were met by multiplying the size of the colony (2406 individuals) by the proportion of tracked birds using this polygon, and by the correction factor of 0.75 (Table S3). For example, one polygon was used by at least 15% of tracked birds and was therefore considered to be used by $2406 \times 0.15 \times 0.75 = 271$ birds. The four polygons identified (Fig. 7) were then assessed against IBA thresholds, with all four qualifying for the regular presence of a globally threatened species (Wandering Albatross is listed as Vulnerable by IUCN) and two polygons also qualifying by holding > 1% of the global population (> 241 individual Wandering Albatrosses).

DISCUSSION

Our approach provides a consistent framework to delineate areas of global conservation importance based on animal tracking data and internationally accepted criteria. It offers an objective yet pragmatic tool that uses a set of well-established

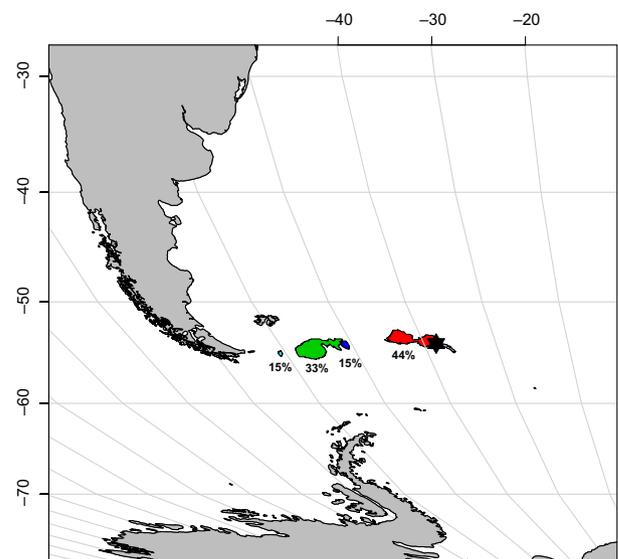


Figure 7 Resulting Important Bird and Biodiversity Area (IBAs) identified for the example data group, including the percentage of tracked birds occurring in each site. Population estimates for each polygon were determined by multiplying the number of birds breeding at Bird Island (2406 individuals), by the percentage of birds using a site and the appropriate correction factor determined from the representativeness analysis in Fig. 5 and Table S3 (in this case 0.75). Polygons were therefore shown to be holding the regular presence of a threatened species or > 1% of the global population (241 individuals), thus qualify as IBAs for this species.

statistical approaches for the analysis of tracking data. Although the approach is both ecologically and statistically sound, it is also flexible enough to account for variation between species, geographic distributions and tracking technologies; and provides intuitive outputs that can inform management processes. Such a tool should help convince policy makers of the utility of tracking data for identifying key marine areas for conservation. The approach described here can be adapted for other marine or terrestrial central-place foragers with known population sizes.

Our approach is robust and applicable to a wide range of species and scenarios, and minimizes the inclusion of arbitrary

trary threshold values. All thresholds and correction factors presented here are extremely conservative, supported by decades of seabird research, and based on the ecological characteristics of the species involved. We tested all thresholds and correction factors across multiple datasets to ensure that our approach avoids erroneous designation of sites that do not meet international criteria. Critically, our approach assesses objectively whether data are appropriate for population-level inference, and identifies important areas only when a species exhibited behaviour appropriate for site-based conservation approaches.

Nonetheless, there are plausible refinements to the analysis to account for additional variation. Most of the tracking data pertained to medium-sized to large procellariiform species, i.e., albatrosses and petrels (93% of data groups). Application of this methodology to smaller or less mobile marine species (e.g. penguins, terns, seals and otters) will require different definitions for the length of trips, and other species-specific amendments which are required as input parameters in the R code.

Further improvements may also be possible by additional rigorous tests of the various analytical components underlying our approach (Appendix S1). We encourage the scientific community to conduct sensitivity analyses of the various thresholds and approaches presented here to further validate and improve the analysis of tracking data to inform marine spatial planning.

For data groups that were inadequate for IBA assessment or where resulting polygons did not meet IBA criteria this was either due to the very small sample of tracked individuals, because the tracking was undertaken at a colony where the population size was already below the IBA threshold, or because at-sea distributions were too dispersed to show spatial aggregation.

Many of the resulting sites are located over productive waters associated with boundary currents, upwelling's, canyons, seamounts, river outflows and other oceanographic and bathymetric features which help to regulate food availability. Figure 6 shows a number of inset maps detailing particular areas of the world's oceans that are diverse in seabirds, holding large numbers of sites, species and individuals. These areas are priorities for conservation action, and require transnational collaborations, marine spatial planning and management regimes to be established at scales that are relevant to seabirds.

The total area of the IBAs identified during this analysis amounts to 4.3% of the world's oceans and with over 50% of the species assessed threatened with extinction, the network of sites are of key important for marine conservation efforts. Together these sites show where species can be most effectively conserved as a group and where potential threats may have population level impacts.

Seabird declines have been caused by ten primary pressures (Croxall *et al.*, 2012), with the exact pressures acting upon sites varying depending on the species present, the geography and the time of year. At sea these include: incidental bycatch (in longline, gillnet and trawl fisheries); pollution (oil spills,

marine debris); overfishing; energy production and mining. On land, invasive alien species, problematic native species (e.g. those that have become super abundant), human disturbance, infrastructural, commercial and residential development, hunting and trapping have driven declines. Climate change and severe weather affect seabirds on land and at sea. Future work could look to assess threats across the IBA network identified, to highlight species and sites where particular pressures are having greatest impact and thus most urgently need associated management responses.

Given their imperilled conservation status (Croxall *et al.*, 2012), many seabirds have been highlighted for special conservation status and action under a range of international, regional and national agreements and mechanisms (Lascelles *et al.*, 2012). Data collected via the IBA identification process (e.g. distribution, abundance, behaviour, seasonality and pressures) can be used to inform the design of effective management regimes for seabirds. Best practice management of any activity that may negatively impact seabirds occurring within IBAs should be undertaken. Depending on the species, the priority actions needed may involve formal and effective protection of the most important sites. For site protection to be effective, it should ensure that areas are large enough to capture critical behaviour (such as key breeding sites, the marine areas around them used for maintenance and more distant feeding and aggregation sites), consider temporal and spatial variations, and have adequate regulation to minimize effects of any pressures. Where national, regional and global networks of MPAs are being developed, inclusion of key seabird sites in those networks would contribute substantially to the necessary site protection and make a vital contribution to the conservation of seabirds (and other marine life found in these areas) by helping halt and reverse the declines many species have undergone in recent decades.

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DATA ACCESSIBILITY

A compilation of customized R scripts needed to undertake the analysis described here is available in Appendix S4, along

with a sample dataset in Appendix S3. The script package, and assistance with its use, can also be requested by emailing seabirds@birdlife.org. All tracking data assessed in this project is housed in the Tracking Ocean Wanderers database, and can be viewed and requested via www.seabirdtracking.org.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional details of the methods employed in this analysis, please use this in combination with that contained in the main text.

Appendix S2 Summary of data included within the analysis including the seabird species and their IUCN Red List status, the number of tracking data sets assessed and the owners of these data, and the number of IBAs resulting and the IBA criteria that have been met.

Appendix S3 Example of a complete script, with all the steps included.

Appendix S4 An example dataset included within the paper to illustrate analysis for the Wandering Albatross (*Diomedea exulans*) during the incubation period at Bird Island, South Georgia.

Appendix S5 Complete R script needed to undertake the analysis presented here.

BIOSKETCH

Ben Lascelles is Senior Marine Officer for the BirdLife International Marine Programme in Cambridge, UK. His research focuses on methods to define Important Bird and Biodiversity Areas (IBAs) for seabirds around the world. He also leads on the presentation of this information in a range of global and regional policy and management fora that can provide positive conservation outcomes for seabirds.

Author contributions: B.G.L. conceived the ideas, coordinated the delivery and led the writing. P.R.T., M.G.R.M., M.P.D and S.O. wrote the scripts, analysed the data and contributed to the text. L.T., A.H., M.L.C., R.A.P, S.A.S., H.W. and C.S. were appointed as a steering committee for the project to provide analytical advice and access to seabird tracking data.

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