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Influence of device accuracy and choice of algorithm for species distribution modelling of seabirds: A case study using black-browed albatrosses

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Abstract

Species distribution models (SDM) based on tracking data from different devices are used increasingly to explain and predict seabird distributions. However, different tracking methods provide different data resolutions, ranging from <10m to >100km. To better understand the implications of this variation, we modeled the potential distribution of black-browed albatrosses *Thalassarche melanophris* from South Georgia that were simultaneously equipped with a Platform Terminal Transmitter (PTT) (high resolution) and a Global Location Sensor (GLS) logger (coarse resolution), and measured the overlap of the respective potential distribution for a total of nine different SDM algorithms. We found slightly better model fits for the PTT than for GLS data (AUC values 0.958±0.048 vs. 0.95±0.05) across all algorithms. The overlaps of the predicted distributions were higher between device types for the same algorithm, than among algorithms for either device type. Uncertainty arising from coarse-resolution location data is therefore lower than that associated with the modeling technique. Consequently, the choice of an appropriate algorithm appears to be more important than device type when applying SDMs to seabird tracking data. Despite their low accuracy, GLS data appear to be effective for analyzing the habitat preferences and distribution patterns of pelagic species.

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Introduction

Species distribution models (SDM) have emerged as a central tool in modern ecological research, but suffer from several sources of uncertainty (Franklin et al. 2009, Peterson et al. 2011). The latter include a bias in presence records (Fourcade et al. 2013, Syfert et al. 2013, Niami et al. 2014), the choice of appropriate environmental predictors (Rödder and Lötters 2010, Sheppard 2013), variation in habitat preference among study populations or regions (Torres et al. 2015, Wakefield et al. 2011), or the performance of different algorithms under certain conditions (Heikkinen et al. 2006, Hernandez et al. 2006, Reiss et al. 2011). An understanding of the role and relative importance of these different factors is useful not only when building and interpreting SDMs, but may allow these issues to be accounted for in improved study design.

For marine species, the availability of presence-only records is of particular concern, as most available datasets are from tracking devices deployed on relatively few individuals (usually 10s). This is particularly true for pelagic seabirds that range over large areas where there is usually limited at-sea observer coverage. Regardless, tracking studies in recent decades have resulted in enormous gains in knowledge of the distribution (Phillips et al. 2005, Masello et al. 2010), migration patterns (Pütz et al. 2006, Rayner et al. 2012, Quillfeldt et al. 2015), and feeding behavior of seabirds (Weimerskirch et al. 1993, Kotzerka et al. 2010). Together with the availability of digital marine environmental layers, often obtained using satellite remote-sensing (e.g., Bio-ORACLE, Tyberghein et al. 2012), these occurrence data are increasingly used in SDMs (e.g., Engler et al. this issue). However, each device type delivers occurrence information of different quality in terms of spatial and temporal resolution. While the temporal aspect is more straightforward, and can be dealt with to some extent by subsampling or interpolation, poor spatial resolution might seriously impact model results (Dambach and Rödder 2011), especially as the resolution of the tracking data

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may be much lower than that of the environmental data used to characterize the potential distribution.

Three main tracking devices are used frequently to study animal movement: satellite transmitters (Platform Terminal Transmitters, PTTs), Global Positioning System (GPS) loggers, and light level geolocators (Global Location Sensor or GLS loggers). PTTs have been used on seabirds since 1990 (Jouventin and Weimerskirch 1990), and until the last decade were relatively heavy devices suitable only for larger species. PTTs provide data at a resolution of 250-1500m, depending on satellite coverage and filtering (Douglas et al. 2012), and have the advantage in comparison to GPS and GLS loggers, that these are transmitted via the ARGOS satellite network, making animal recapture unnecessary. In contrast, GPS devices record data internally, birds need to be recaptured, or the data transferred via a radio link to a nearby ground station (although these devices are more expensive), and those that provide frequent fixes (< 15-30 mins.) for several weeks remain too heavy for many small seabirds (terns, storm petrels etc.); however, the spatial resolution is very high (< 10m). In contrast, GLS are very lightweight and hence suitable for deploying on seabirds of < 200g, but the data resolution is coarse, at 150-200km (Phillips et al. 2004, Pollet et al. 2014, Quillfeldt et al. 2015).

Although a considerable number of studies have applied SDMs to the low resolution data provided by GLS (Quillfeldt et al. 2015, Torres et al. 2015), there has been no assessment of the accuracy of the modeled potential distributions relative to those provided by devices of much higher spatial resolution such as PTT or GPS. If the parameterization of models built using GLS data is poor, this would have particular implications for small seabird species that are typically tracked with these lightweight loggers (Pollet et al. 2014, Quillfeldt et al. 2015, Rayner et al. 2012).

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To better understand the effects of spatial resolution, we modeled the potential distribution of black-browed albatrosses *Thalassarche melanophris* from South Georgia that were equipped simultaneously with PTT and GLS devices, and measured the overlap of the respective potential distribution for a total of nine different SDM algorithms. The use of both devices on the same individuals provides the unbiased datasets that are essential for such a comparison. By using different SDM approaches, we compared the possible device-specific *vs.* algorithm-specific uncertainty. We specifically tested whether the higher spatial resolution of PTT data would lead to better model fit (higher AUC), and whether overlaps of potential distributions between PTT and GLS-based models were higher than overlaps among SDM algorithms.

Methods

We used GLS and PTT data from black-browed albatrosses tracked from South Georgia during chick-rearing in January-March 2002 (see Phillips et al. 2004 for details, Fig. 1). In brief, each of 12 individuals was equipped with a GLS and a PTT for 50-60 days, providing a total of 797 and 8497 locations, respectively. To allow for unbiased model comparisons, we subsampled each dataset to obtain the same number of records evenly distributed across individuals. Since there were fewer GLS locations, we used these as the reference to select the corresponding PTT data for each individual. As the minimum number of GLS locations for an individual was 47, we adopted the conservative approach of randomly selecting 25 records per individual (total 300 for all 12 birds) for each device type, which to some extent also accounts for the spatial autocorrelation. For the modeling, we used environmental information from the Bio-ORACLE dataset (Tyberghein et al. 2012). We pre-selected seven predictors that should reflect the relevant conditions for pelagic seabirds. These where: (1) minimum and (2) maximum chlorophyll concentrations, (3) minimum cloud cover, (4) pH, (5) salinity, (6) minimum

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and (7) maximum sea surface temperature. In addition, we used (8) bathymetry information from the ETOPO1 dataset, which integrates land topography and ocean bathymetry, and reflects the height of the Antarctic ice sheets (Amante and Eakins 2009). As recommended by Tyberghein et al. (2012) we excluded environmental data south of 70°S to avoid potential errors in remote-sensing data associated with extensive cloud cover in high latitude regions. In addition, the northern boundary was set at 20°S. However, a circum-Antarctic perspective was maintained by including the full longitudinal extent, given the circumpolar breeding and foraging distribution of the black-browed albatross (Wakefield et al. 2011).

For modeling, we used a total of nine different SDM algorithms as implemented in the BIOMOD2 R package (based on BIOMOD, Thuiller et al. 2009) as well as MAXENT 3.3.3k (Phillips et al. 2006, Phillips and Dudík 2008). The former included: generalized linear models (GLM), generalized boosted models (GBM), random forests (RF), classification tree analysis (CTA), multivariate adaptive regression splines (MARS), artificial neural networks (ANN), flexible discriminant analysis (FDA), and rectilinear envelopes similar to BIOCLIM (SRE; see Thuiller et al. 2009 for details). We generated 10,000 random background records across the whole study extent. In order to minimize projection bias, we used the *randomPoints* function in R's DISMO package (Hijmans et al. 2016) that allows for a latitudinal correction since the environmental layers are not in a planar coordinate system (Hijmans et al. 2016). Each algorithm was run 100 times for each device type, with 70% of presence records randomly chosen for model training per iteration. All other model settings were left at default mode. Model quality was evaluated using AUC classification. To cut off low suitability values, we selected the maximum sum of sensitivity and specificity thresholds among all algorithms as performed in BIOMOD2 (D. Georges pers. comm.). This was necessary as low suitability

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values add considerable noise in overlap measures and lead to overestimation; consequently, they should be omitted (Rödder and Engler 2011).

We estimated the overlap of potential distributions using Schoener's *D* (Renkonen 1938, Kohn and Riggs 1982), a metric that is often used to measure the overlap of two probability distributions in geographic space, as recommended by Rödder and Engler (2011). Geographic overlaps were performed in two ways: (1) between data from each device type, separately for each algorithm, and (2) for all algorithms, grouped by device type. Except for the Maxent models, all analyses were conducted in R 3.3.0 (R Core Team 2016). We produced the maps in this work using the OPENSTREETMAP package v. 0.3.3 (Fellows 2016) using the 'nps' tile server for the background map.

Results

Model quality was high for all algorithms, with average test AUC values ranging from 0.842 (SRE for GLS data) to 0.992 (RF for PTT data, Table 1). Overall, AUC values were slightly higher for the PTT data (mean: 0.958, sd: 0.048), than for the GLS data (mean: 0.950, sd: 0.050) across all algorithms (t-test: t = -3.0, df = 1594.7, p = 0.003). The overlaps of the predicted distributions were higher between device types for the same algorithm than among algorithms for each device type (PTT: t = 4.1, df = 12.3, p = 0.001; GLS: t = 2.9, df = 11.3, p = 0.014; Fig. 2). Of the nine algorithms, the lowest overlaps between predicted distributions from each device type were in the outputs from SRE and CTA (*D* = 0.429 and 0.529 respectively; Fig. 3). In contrast, the highest overlap was for MARS (*D* = 0.832), followed by ANN (*D* = 0.752), FDA (*D* = 0.727), and GBM (*D* = 0.724). According to the classification of Rödder and Engler (2011), the overlaps for SRE and CTA were 'moderate', and for all other algorithms except MARS were 'high'; the overlap for MARS was in the top category of 'very high'. For the device-specific comparisons among algorithms, average overlaps largely fell into the

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‘moderate’ overlap category, with the exceptions of SRE, which was ‘low’ for PTT data (*D* = 0.357), and GBM , which was ‘high’ for GLS data (*D* = 0.607) (Fig. 3).

A closer visual inspection of the spatial overlap of predictions for each algorithm based on data from each type of device confirms this general pattern revealed by Schoener’s *D.* In addition the visual comparison indicates the regions where both predictions overlap, and where they diverge (Fig. 4). These regions can be roughly split into a core area (i.e. the waters around South Georgia, where the occurrence records originate) and the extrapolations elsewhere. In the core area, predictions from most algorithms, except CTA, show a high amount of overlap, albeit with a tendency for the GLS-based predictions to extend farther north than those from PTT data (Fig. 4). Across the algorithms, the predicted distributions were very similar in their extent within the core area, with the exception of SRE. Apparently suitable areas beyond this core area were subject to greater uncertainty, both between device types and among algorithms (Fig. 4).

Discussion

Studying at-sea distributions of seabirds relies largely on tracking devices that provide locations at different spatial and temporal resolution (Phillips et al. 2008, Wakefield et al. 2009). In this study we test the level of uncertainty introduced into species distribution models by using data from two different tracking devices (PTT and GLS) recording at different resolutions. We found an effect of device type (accuracy), but this was slight compared with the uncertainty in the predictions associated with the use of different modeling algorithms. This has some important consequences for the design of SDM studies.

Although lightweight GPS loggers have recently become available, these are expensive and provide relatively few fixes; hence, most tracking data available for small pelagic seabirds has come from deployment of GLS loggers (Pollet et al. 2014,

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Quillfeldt et al. 2015, Rayner et al. 2013). In our analysis, the SDMs based on GLS data had nearly as high AUC values as those based on PTT data, suggesting that accuracy of the tracking data has little impact. Possible explanations are the relatively coarse resolution of the environmental data, the lack of habitat specificity or presence of fine-scale habitat features in the foraging range of this species (but see Wakefield et al. 2011, Catry et al. 2013). Regardless, it appears that little variability is added when the precision of the occurrence data is low, which contrasts with SDMs applied to species in terrestrial habitats (McPherson et al. 2006, Graham et al. 2008, Fernandez et al. 2009, Moudrý and Šimová 2012, Beck et al. 2014). In our case study this variability is attributable largely to latitudinal uncertainty in the GLS data, which is generally larger than longitudinal uncertainty (Ekstron 2004, Fudickar et al. 2012). This uncertainty results in records further north than the real distribution (based on PTT data), and for this reason, there is a systematic over-prediction in these regions. Nevertheless, the algorithm-specific errors, especially those related to extrapolation, are much larger; hence if data from several device types were available for a given species, these could be combined, depending on the algorithm used, provided that the contribution for each individual was balanced or the data were weighted appropriately (see Methods).

Our study also has consequences for the choice of SDM approaches. As this is a single case study, caution is required before making specific recommendations about which algorithm to favor over others, as the algorithms that performed well here may not do so in other areas or under other circumstances (see also Leigh et al. 2015). However, it appeared that SRE performed least well. It has been suggested that the use of multiple SDMs, which vary in complexity, data requirements and statistical mechanisms is a more robust way to assess species distributions (Scales et al. 2016). Oppel et al. (2012) compared the performance of five modelling techniques (GLM, GAM, RF, GBA, and Maxent) applied to the distribution of Balearic shearwaters

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Puffinus mauretanicus, and concluded that none provided superior predictions in all performance criteria. This was in line with the conclusions from other comparative studies (Segurado and Araújo, 2004; Syphard and Franklin, 2009). As the predicted distributions obtained by different SDM techniques are affected by a number of factors, the overall prediction can be improved by combining them in an ensemble (Araújo and New, 2007, Jones-Farrand et al., 2011, Scales et al. 2016). This approach has also been applied to at-sea survey observations (rather than tracking data) for a seabird community in the Timor Sea in order to define feeding hotspots (Lavers et al. 2014).

Although the results from most SDM algorithms used here were good, the results have implications for the construction of ensemble models, and the comparison of results from different studies. There were statistical differences among approaches (also see Buisson et al. 2010, Scales et al. 2016), suggesting that there is value in identifying and potentially discarding under-performing algorithms. In addition, when ensemble model selection entirely relies on the AUC metric (which has been criticized; Lobo et al. 2008, Jiménez-Valverde 2011), then the additional spatial error introduced by device type may have a greater effect due to the inclusion of models sensitive to this error but yielding a high AUC. We therefore recommend adopting a careful study design and algorithm selection process. Finally, if different SDM approaches predict similar distributions, ensemble models may not always be needed, although a comparison is still useful in order to test for the robustness of the results (Qiao et al. 2015, Scales et al. 2016, this study).

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Table Legend

Table 1: Model performance and thresholds of nine different Species Distribution Model algorithms modeled for data from Platform Terminal Transmitter (PTT) and Global Location Sensor (GLS) devices respectively, deployed on black-browed albatrosses at South Georgia.

Algorithm	PTT			GLS		
	mean AUC	sd	threshold	mean AUC	sd	threshold
GLM	0.948	0.034	570.260	0.943	0.038	582.925
GBM	0.989	0.005	306.730	0.985	0.004	273.600
RF	0.992	0.005	84.620	0.986	0.006	109.200
CTA	0.945	0.020	634.115	0.924	0.028	522.125
MARS	0.984	0.006	550.690	0.98	0.007	517.840
ANN	0.987	0.005	455.750	0.982	0.006	425.720
FDA	0.968	0.011	323.155	0.962	0.011	380.505
SRE	0.849	0.025	500.000	0.842	0.025	500.000
MAXENT	0.978	0.005	0.095	0.976	0.004	0.156

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Figure Legends

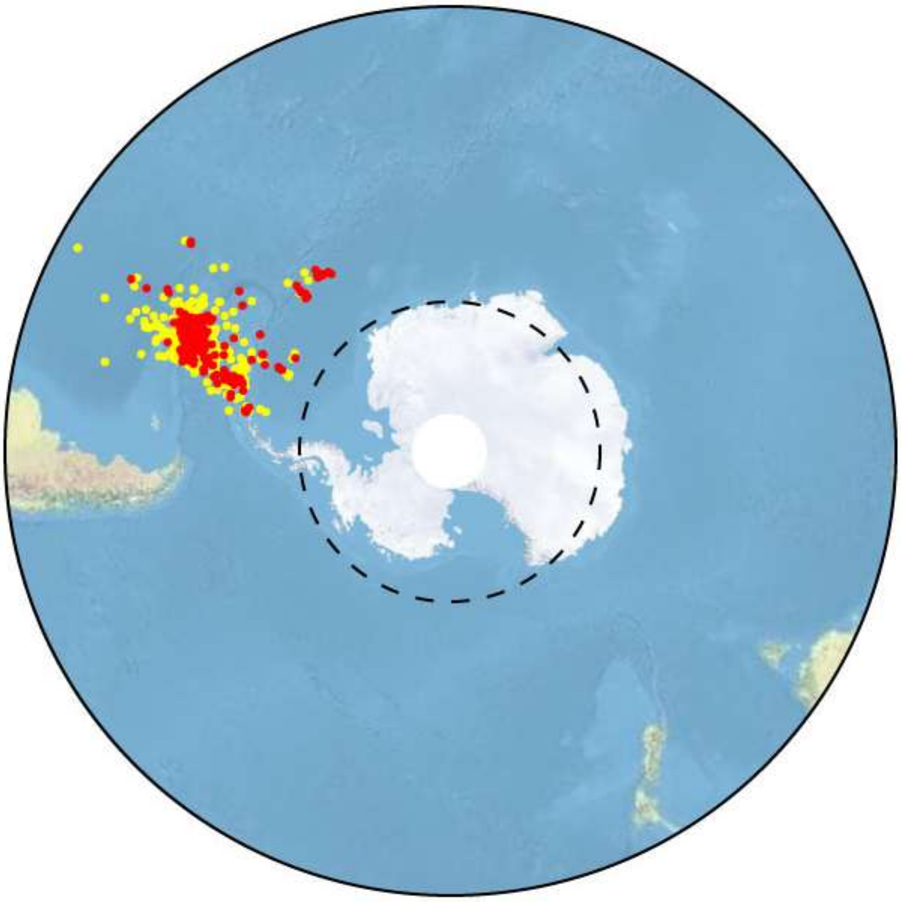

Fig. 1: Map of the study area surrounding Antarctica between 35°S and 85°S in a South Polar stereographic projection. The dashed line corresponds to the southern limit of our predictions, at 70°S (see Methods and Fig. 4 for details). The points indicate the tracking data from black-browed albatrosses breeding on South Georgia used in this study (PTT and GLS locations in red and yellow, respectively).

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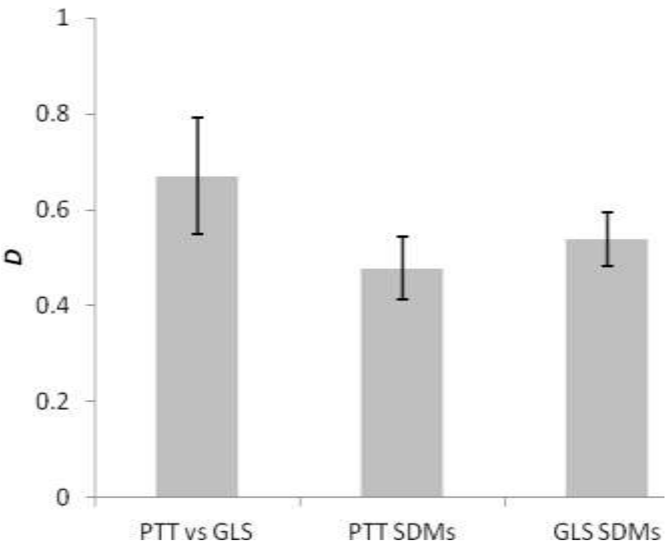

Fig.2.: Differences in geographic overlap (average Schoener's *D* ± sd) of potential distributions modeled for data from two tracking devices - Platform Terminal Transmitters (PTT) and Global Location Sensor (GLS) loggers - of different spatial resolutions deployed on black-browed albatrosses at South Georgia, according to nine Spatial Distribution Model (SDM) algorithms. Overlaps were higher between device types (PTT vs. GLS) for each algorithm, than among algorithms for each device type (PTT SDMs and GLS SDMs).

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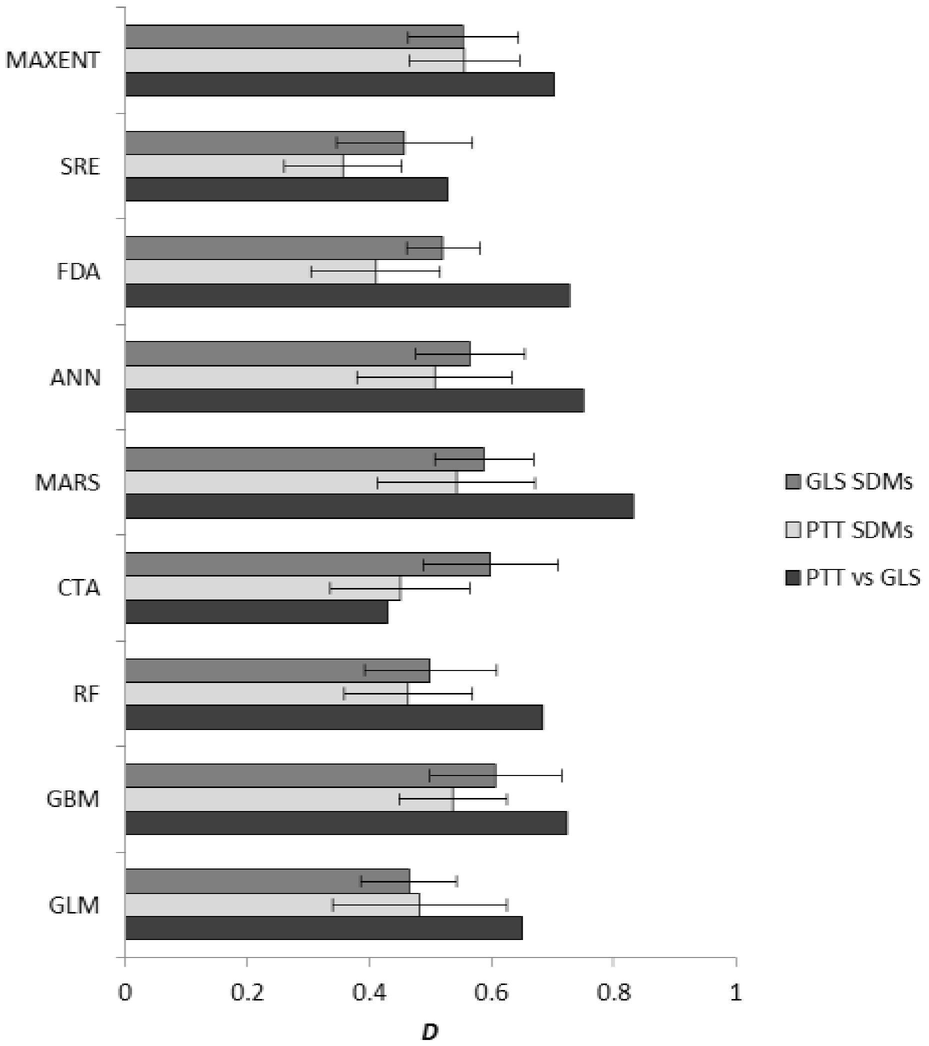

Fig.3. Comparison of geographic overlaps (average Schoener's *D* ± sd) for individual Spatial Distribution Model (SDM) algorithms fitted to data from Platform Terminal Transmitters (PTT) and Global Location Sensor (GLS) loggers deployed on black-browed albatrosses at South Georgia (GLS SDMs, dark grey; PTT SDMs, light grey), comparing overlap between device types for each algorithm (PTT vs. GLS, black).

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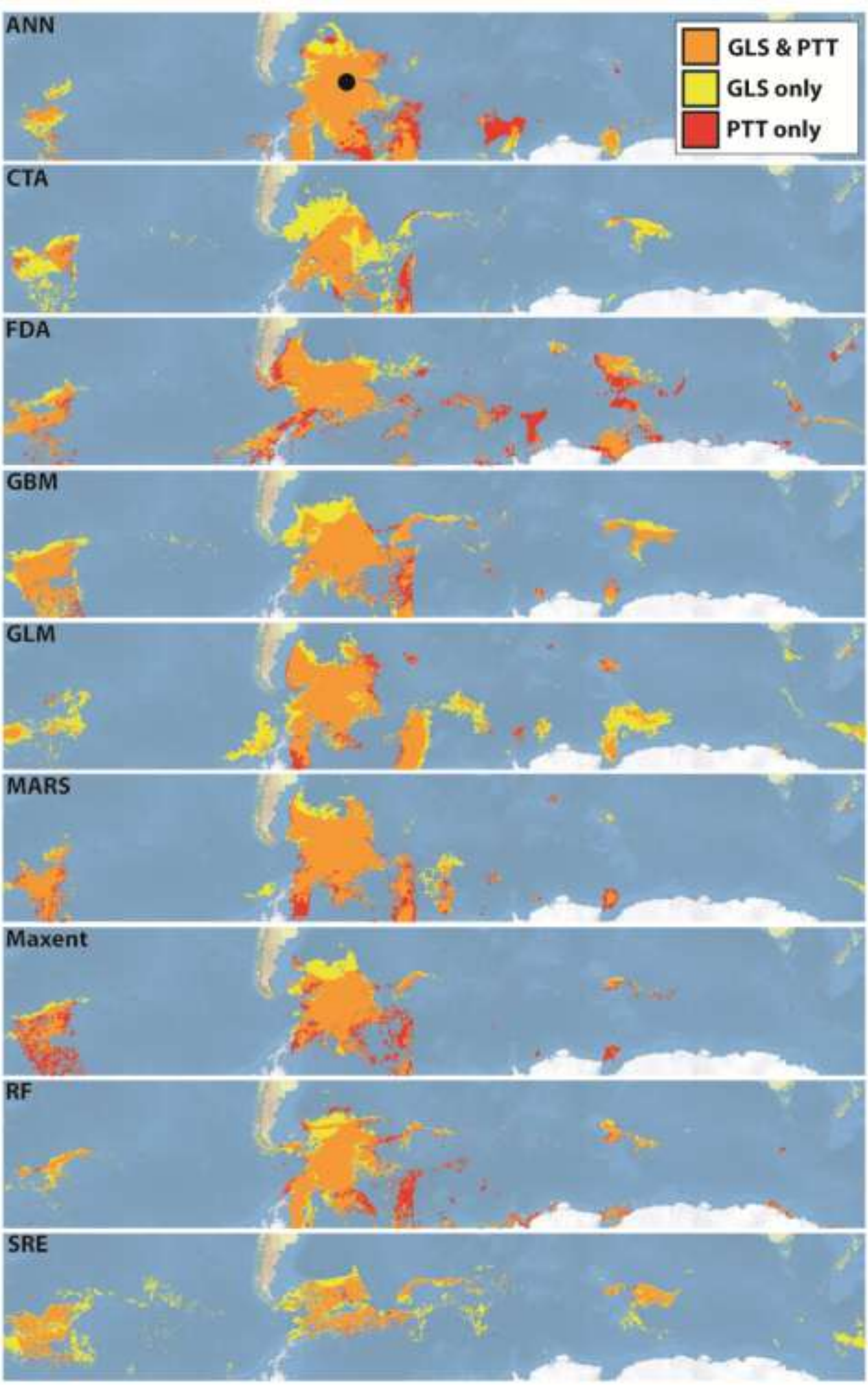

Fig. 4: Predicted distributions from tracked black-browed albatrosses breeding at South Georgia (black dot in top panel) using PTT (red) and GLS (yellow) data for nine different modeling algorithms. Overlapping predictions are highlighted in orange.

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