

Climate oscillation and alien species invasion influences oceanic seabird distribution

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Abstract

Aim: We aim to document the extent to which climate oscillation and rat infestation on islands affect the distribution of seabirds at sea. **Location:** The Chagos Archipelago, British Indian Ocean Territory, Central Indian Ocean **Methods:** At sea observations of seabirds ($n = 425$) were collected from 2012 to 2017 during the breeding season. We used generalized additive models to identify relationships between dominant seabird families (Laridae, Sulidae, and Procellariidae), geomorphology, oceanographic variability, and climate oscillation. We built boosted regression trees to quantify the effects of proximity to both rat-free and rat-infested islands on seabird distribution, identifying breaking point thresholds in distribution. **Results:** We identified oceanic hotspots and common geomorphic and oceanographic drivers for all seabird families. We documented positive relationships between Sulidae and Procellariidae abundance and the Indian Ocean Dipole, as represented by the Dipole Mode Index. The abundance of Laridae and Sulidae declined abruptly with greater distance to island. Both families aggregated more densely (1.08 and 1.25 times higher respectively) and in greater proximity (distribution thresholds at 16 and 44 km closer to islands, respectively) next to rat-free island compared with to rat-infested islands. In contrast, Procellariidae increased in abundance with greater distance to islands, plateauing at 83 km and were not significantly influenced by rat presence on nearby islands. We identified areas of increased abundance at sea under a scenario where rats are eradicated from infested islands with subsequent seabird recolonization. **Main conclusions:** Climate oscillations may cause shifts in seabird distribution, possibly through changes in regional productivity and prey distribution. Invasive species eradications and subsequent island recolonization can lead to predictable distribution gains and increased competition. Our analysis predicting range extension after successful eradications enables anticipatory threat-mitigation in these areas, minimising competition between colonies and thereby maximising the risk of success and the conservation impact of eradication programmes.

1. INTRODUCTION

Seabirds encompasses all avian species that depend on marine ecosystems for feeding and breeding (Votier & Sherley, 2017), and are usually considered top predators in marine ecosystems (Estes, Crooks & Holt, 2001; Ballance, Pitman & Fiedler, 2006). Some families such as the Sulidae, Procellariidae, complete their life cycle primarily at sea and feed predominantly on pelagic forage species (e.g. anchovies, flying fish, euphausiids), consuming over 7% of the ocean's productivity (70 million tonnes/year, Votier & Sherley, 2017; Brooke, 2004). Physiologically, seabirds have unique traits such as salt glands to excrete excess salt from seawater, wing designs for long-distance travel, and modified vision to help locate prey below water (Votier & Sherley,

2017). Seabirds occupy all marine ecosystems and play important ecological roles in ecosystem function such as linking ocean and terrestrial ecosystems via predation and nutrient cycling (Loder III, Ganning & Love, 1996; Schmidt, Dennison, Moss & Stewart, 2004; Fukami et al., 2006; Graham et al., 2018).

Seabird distribution at sea is closely linked to oceanographic conditions (e.g. sea surface temperature, chlorophyll-a) and geomorphic characteristic (e.g. slope, depth), reflective of their foraging strategies and the distribution of their prey (Fox et al., 2017; Mannocci, Catalogna, et al., 2014; Mannocci, Laran, et al., 2014; Maxwell & Morgan, 2013; Hyrenbach, Veit, Weimerskirch, Metzl, & Hunt Jr, 2007; Vilchis, Balance & Fiedler, 2006). Their important ecological role linking both terrestrial and oceanic trophic web makes seabirds sensitive indicators of long-term and large-scale changes in environmental conditions and human activities (Piatt, Sydeman & Wiese, 2007; Einoder, 2009). Human threats include entanglement in fishing gear at sea, overexploitation of seabird prey via fisheries, climate change, water pollution, energy production and invasive mammal species (Croxall et al., 2012). A recent assessment revealed that 69.7% of global seabird populations, including the families Laridae, Sulidae and Procellariidae, are declining (Paleczny, Hammill, Karpouzi, and Pauly 2015). A listing of seabirds according to the IUCN Red List criteria ranked 9% of species from these families as Endangered, 6% as Critically Endangered, and 1% as Extinct (IUCN, 2019).

Information regarding oceanographic drivers of seabird distribution in the Indian Ocean (IO) is limited. Hyrenbach et al. (2007) explored drivers of seabird distribution in the southern IO, identifying the influence of sea surface temperature (SST) and proximity to sub-Antarctic Islands. Mannocci, Laran, et al. (2014), found that seabird distribution in the Southwest IO was closely related to persistent oceanographic conditions, and that time-averaged values over the long term (> 7 years) were more predictive of distribution than those averaged over the short-term (1 week). Since both studies relied on seabird distribution data derived from a single snapshot in time, drivers of year-to-year variability in seabird distribution remain unclear. Multiyear studies could provide managers with useful information about the influence of inter-annual climate oscillations such as El Niño Southern Oscillation (ENSO; Sprogis, Christiansen, Wandres, & Bejder, 2018), and the IO Dipole (Saji, Goswami, Vinayachandran & Yamagata, 1999).

Interannual and climate variability in the tropical IO is to a large degree characterised by oscillations in SST gradient between the eastern and western basin, referred to as the IO Dipole (Saji et al., 1999). This gradient is represented by the Dipole Mode Index, where a positive or negative index value reflects a positive or negative IO Dipole respectively. Although the influence of climate oscillations and seabird dynamics has been well studied (reviewed in Oro, 2014), few studies have yet identified linkages between seabird ecology and the Dipole (Tryjanowski, Stenseth & Matysioková, 2013; Rivalan, Barbraud, Inchausti & Weimerskirch, 2010), due in part to its relatively recent discovery (Ashok, Guan & Yamagata, 2003).

Island invasion by rodents, such as the ship rat *Rattus rattus*, is one of the greatest threats to seabird populations (King, 1985, Jones et al., 2008). Seabirds need islands to rest and to breed and prefer to do both with limited disturbance (King, 1985). Rats successfully invade islands by quickly adapting to new habitats, in part because of their omnivorous diet. Rats prey on both chicks and adults and can cause both population declines and extirpation (Fleet, 1972; King, 1985; Major, Jones, Charette & Diamond, 2007). At the seabird species level, the impact of rat infestation depends upon a combination of factors, such as food availability, breeding strategy, body weight and life history. For example, small seabirds nesting in burrows are particularly vulnerable to rat predation (Woodward, 1972; Jones et al., 2008). Rat eradication programmes are considered a major component of successful island restoration and seabird population recovery (Hutton, Parkes, & Sinclair, 2007; Towns et al., 2009; Russell & Holmes, 2015; Le Corre et al., 2012).

The IO has 27 archipelagos that are considered hotspots of marine biodiversity (Danckwerts et al., 2014; Le Corre et al., 2012), most of which are particularly important to seabirds (Le Corre & Jaquemet, 2005). In the central IO, the Chagos Archipelago comprises 55 tropical islands, encompassed within the British Indian Ocean Territory (BIOT), which was designated a no-take marine protected area in 2010. The majority of the archipelago has been closed to human activities since 1971, and is therefore relatively undisturbed (Everaarts et al., 1999; Readman et al., 2013; Sheppard & Sheppard, 2019). The archipelago is considered of great importance for seabird conservation, harbouring eighteen species of resident breeders, and ten designated

and two proposed ‘Important Birds Areas’ (Hilton & Cuthbert, 2010; McGowan, Broderick & Godley, 2008; Carr, 2006). Historical coconut plantations, dating to the turn of the 18th century, led to infestations of ship rats and other invasive mammals (i.e. feral cats *Felis catus* ; Wenban-Smith & Carter, 2016) on 26 of the 55 islands (95.3% of the island area), negatively affecting the seabird populations (Harper, Carr & Pitman, 2019; Harper & Bunbury, 2015; Hilton & Cuthbert, 2010). Graham et al. (2018) found that seabird densities on rat-free islands were up to 760 times greater than on infested islands, leading to nutrients subsidies and increased productivity and function on adjacent coral reefs. Notably, these subsidised reefs may recover faster following coral bleaching (Benkwitt, Wilson & Graham, 2019). Rat eradication has therefore been designated a priority target within the conservation framework of the draft BIOT management plan (BIOT management conservation framework in prep. 2019). Rats were successfully eradicated from Île Vache Marine in 2017 (Harper et al., 2019).

Here, we expand on previous work done in the IO (i.e. Mannocci, Laran, et al., 2014; Hyrenbach et al., 2007) by using a multiyear seabird survey (from 2012 to 2017) within the BIOT marine reserve to identify drivers of distribution. We first seek to identify the influence of geomorphic and oceanographic variables in determining seabird distribution, in order to reveal ocean habitat hotspots and explore possible linkages with climate oscillation. Then, recognising that seabird are dependent on island and vulnerable to rat infestation, we determine the effect of rat infestations on seabird distribution at sea. Finally, we predict seabird distribution under an archipelago-wide, rat eradication scenario, identifying currently under-utilised habitats, and possible factors relevant for identifying island restoration priorities.

2. METHODS

2.1 Study Area

The Chagos Archipelago is located in the central IO at 6° S and 72° E at the southern limit of the Chagos-Laccadive ridge, and is over 1,500 km from the nearest continental land mass (Carr, 2012). Fifty-five islands are clustered within the atolls of Diego Garcia, Peros Banhos, Salomon, Egmont, and on the Great Chagos Bank (Figure 1a) and constitute combined approximately 60 km² of land area. The territory encompasses approximately 60,000 km² of shallow photic reefs, and 580,000 km² of primarily oceanic habitat, with a maximum depth over 6,000 meters (Carr, 2011; Dumbraveanu & Sheppard, 1999). The climate is tropical, characterised by oceanic conditions and the seasonal reversal monsoon (Sheppard, 1999). Situated in the inter-tropical convergence zone (ITCZ), the archipelago has moderate winds generally from the north-west (October to April) and the south-east (May to September). Sea surface temperature has an approximately bimodal distribution with maxima in December–January and March–April with a yearly mean of 28°C (Pfeiffer, Dullo, Zinke & Garbe-Schönberg, 2009).

2.2 Seabird observations

In order to identify the influence of oceanographic conditions and island rat infestation on seabird distribution, we conducted a multiyear survey of the archipelago of seabirds at sea. The survey was conducted from 2012 to 2017, between November and April, to overlap with the moderate phase of the monsoon. This period generally coincides with peak breeding activity in the Chagos Archipelago (Carr, et al., 2019; Carr, 2011; Carr, 2015). During the months of sampling, the BIOT marine reserve and the IO experienced two seasons of modestly positive IO Dipole (during 2012 and 2013), which was followed by three neutral IO Dipole events (2014–2016) and by one very positive event (2017; NOAA Earth System Research Laboratory [NOAA ESRL], 2017). Seabird count samples (n = 425) were conducted from a marine vessel during six expeditions. Three different sample types were generated: Transect counts (n = 329) were generated during vessel transit, by adapting the method of Tasker, Jones, Dixon & Blaker, (1984). Each transect count had a duration of 30 minutes, during which the vessel typically steamed at 12 knots and travelled c.11 km. Aggregation counts were generated opportunistically during any seabird feeding aggregation (n =

87). The birds within the aggregations were counted until all birds had been counted (median duration 60 min; Letessier et al., 2016). Finally, point counts ($n = 9$) were generated when the vessel was stationary (nominal count duration 30 min). All samples were generated within a 180° arc forward of the ship, out to approximately 300 meters (Table 1, Figure 1, Appendix S1). All seabird observations were conducted by Pete Carr, a co-author of this manuscript and an expert on seabirds within the Archipelago (e.g. Carr, 2011; Carr, 2012; Carr, 2015). This consistency in observer eliminates a potential source of bias. Observations were predominantly made in proximity to the islands and the shallow reefs (Figure 1b-1g).

2.3 Oceanic habitat modelling

2.3.1 Response variables

In order to model the oceanic distribution of seabirds, we selected the most frequent and abundant seabird families in the BIOT marine protected area as our response variables. This comparatively high-level taxonomic classification allowed us to generate more statistical power by increasing our counts. This grouping approach requires the assumption that taxonomically similar species have similar ecological requirements, in relation to habitat-use or energetic needs (Mannocci, Catalogna, et al., 2014; Mannocci, Laran, et al., 2014). The oceanic seabird distributions were modelled based on geomorphic and oceanographic variables using Generalised Additive Models (GAM; Wood, 2006), accounting for the different sampling types (Appendix S2). The GAMs were fitted using individual family count per sample (a proxy for abundance) as the response variables, against all possible combination of four of six variables (depth, slope, year, sea level anomalies [SLA], sea surface temperature [SST] and chlorophyll-a concentration [CHL]). We avoided highly correlated variables (Spearman coefficient, $r > 0.60$ and < -0.60) in the same model, following Mannocci, Laran, et al. (2014) and retained the models with the lowest generalised cross-validation score (GVC). We used the explained deviance to evaluate the explanatory power of the models. GAMs were fitted using the *mgcv* package in R (R Development Core Team 2017 version R version 3.3.3) that determines the degrees of freedom for each smoother internally when fitting the model (Wood, 2006). Splines were limited to three knots in order to maintain ecological sense and to avoid overfitting (Mannocci, Laran et al., 2014).

2.3.2 GAM Predictions

Spatial predictions in unsampled areas were limited to the convex hull defined by the BIOT marine reserve and restricted by the range values of the variables used to build each model. This ensured that predictions were only made in areas with similar environmental conditions. Using this approach, we avoided extrapolating beyond the range of the model, whilst generating meaningful predictions beyond our sampled area (Yates et al., 2018). Whenever [year] was retained, we rendered predictions set at the last year of sampling, in 2017. Uncertainty for each model was derived from the Bayesian covariance matrix of model coefficients (Wood, 2006). We rendered predictions and modelled uncertainty on a 0.4×0.4 decimal degree resolved grid. This resolution is considered a reasonable trade-off in order to capture distribution for species with uncertain range sizes (Seo, Thorne, Hannah, & Thuiller, 2008).

2.4 Modelling the effect of rat infestation

We hypothesise that seabird distribution is sensitive to rat-infestation on islands and that this sensitivity restricts seabird distributions in the water adjacent to infested islands. We modelled the effect of rat infestation on seabird distribution at sea using Boosted Regression Trees (BRT). BRT are considered an advanced form of regression (Friedman, Hastie & Tibshirani, 2000) that use boosting to combine and adapt large numbers of relatively simple tree models, enabling performance optimization (Elith, Leathwick & Hastie, 2008). A pair of BRT models were fitted each for the Laridae, Sulidae and Procellariidae families (Appendix S3). The models were fitted using the set of variables selected by the GAMs. In addition, the first model of the pair was built with the additional inclusion of the variable ‘distance to the closest rat-free islands (km)’. This model was considered to represent bird distribution at its theorised maximum abundance, in

the absence of any rat effect. The second BRT was built the additional inclusion of the variable ‘distance to the closest rat-infested islands (km)’. For each BRT we also included a nearest island area variable (in m²), to account for the potential effect of landmass availability. To reduce variability, we used transect counts samples only. BRTs were fitted following the methodology and adapting the code in Elith et al. (2008) and the *gbm* package in R (R Development Core Team 2017 version R version 3.3.3). The BRT models were fitted using a trade-off between learning rate and numbers of trees (Elith et al., 2008; D’agata et al., 2014).

We identified thresholds (break-point) to which seabird distribution is influenced by the distance to rat-free or rat-infested islands, using a Davies’ test. To find significant differences between families and whether the island was rat-free and rat-infested islands, break-points (BP) were determined with the 95% confidence intervals (CI). To determine the net gain in seabird abundance following a scenario of an archipelago wide rat eradication programme, we subtracted the difference of the predictions resulting from the rat-infested models from the predictions of the rat-free models. The predictions were mapped only where the nearest island was rat-infested since we assume that no new islands will be infested, showing net gain and net lost in seabird distribution.

3. RESULTS

3.1 Seabird sightings

In total, 15,063 seabirds were observed during the six expeditions between 2012 and 2017 (Figure 2) across all samples. Seven families were recorded: Laridae (noddies and terns), Sulidae (boobies), Procellariidae (shearwaters and petrels), Phaethontidae (tropicbirds), Fregatidae (frigatebird), Hydrobatidae (northern storm-petrels) and Oceanitidae (southern storm-petrels). Observations were dominated by the Laridae (8,817 individuals), Sulidae (5,057 individuals) and Procellariidae (872 individuals). These families were retained for further distribution modelling (Figure 2). For the Laridae, Sulidae, and Procellariidae, individuals per sample was highest in 2013 (33.1 ind. per sample), 2017 (24 per sample, and 2012 (16.3 ind. per samples), respectively and lowest in 2015 (16 ind. per sample), 2014 (3.2 ind. per sample) and 2013 (no ind.), respectively.

3.2 Predictive Modelling

3.2.1 Oceanic drivers of distribution

Total deviance explained for each GAM was 33.7% for Laridae, 46.3% for Sulidae and 21.2% for Procellariidae. Seabed depth explained 42.90% and 33.64% deviance in the distribution of Laridae and Sulidae respectively (Figure 3a and 3e). The only other geomorphometric variable that was important for Sulidae distribution was slope (28.68%, Figure 3f). In terms of oceanographic variables, sea level anomaly influenced the Procellariidae (Figure 3c, 3g and 3i), explaining 31.24% of the deviance. Sea surface temperature and chlorophyll-a were important variables for Laridae (13.11% and 42.60%) and for Procellariidae (24.31% and 23.97%, Figure 3b, 3d, 3h and 3j) but not the Sulidae.

Sulidae and Procellariidae showed high yearly variability (28.68 and 20.47% deviance respectively) consistently decreasing in abundance from 2012 to 2015, an increasing from 2015 to 2017 (Figure 4).

3.2.2 Spatial Predictions within the Chagos Archipelago

Spatial model predictions for Laridae and Sulidae distribution revealed a strong seabed depth signature (Figure 5a, b, d, and e), while Procellariidae distribution was more uniform with higher abundance levels near land and towards the northwest of the Archipelago (Figure 5c and f). Laridae abundance was pronounced over shallow seabeds (< 1000 m) in proximity to islands and atolls (Figure 5a, d). Sulidae abundance was more pronounced in pelagic and deeper areas (Figure 5b, e), and in areas with intermediate slope (c. 15°,

Figure 5b). Both Laridae and Sulidae distribution was pronounced along the Lakshadweep-Maldives-Chagos ridge. Model prediction uncertainty was spatially and family specific (Appendix S2).

3.2.3 Response to rat presence

Rat-free BRT models explained more deviance (Sulidae [?] 71%, Laridae [?] 37%, and Procellariidae [?] 20%) than rat-infested models (Sulidae [?] 59%, Laridae [?] 31%, and Procellariidae [?] 12%). Distance to a rat-free or rat-infested island was important for Laridae and Sulidae (39.3 - 48.5%, 32.5 - 36.1% respectively) compared with the Procellariidae (0- 14.6 %). Deviance explained by Distance to a rat-free island was consistently higher than that by Distance to rat-infested island (Laridae [?] 48%, Sulidae [?] 36%, and Procellariidae [?] 15%). Conversely, deviance explained by the area of the nearest island was higher in the rat-infested models (Laridae [?] 8%, Sulidae [?] 11%, and Procellariidae [?] 5%; Figure 6a - 6g).

All seabird families were sensitive to the proximity to rat-free islands, as revealed by broken stick regressions (Figure 6g - 6i). Breaking points (BP) indicated the threshold to which the nearest island, whether infested or not, influenced the distribution of seabirds. Thresholds BP in the effect of islands were apparent for all families. The BP for Laridae was at 47.5 km for rat-free islands [CI 44.8, 50.2] and at 63.6 km for rat-infested islands [CI 59.1, 67.9]. The BP for Sulidae was at 16.51 km [CI 11.9, 21.1] for rat-free islands and 60.54 km for rat-infested islands [CI 54.0, 67.3]. No effect of rat presence on nearby islands was detected for the Procellariidae family, as the BP showed no significant difference in the CI between rat-free island (BP 82.9 km [CI 82.9, 96.4]) and rat-infested islands (BP 73.5 km [CI 68.6, 78.4]). Threshold breaking points are reported in Appendix S3 (Table S3).

The presence of rats on nearby islands reduced the abundance of all seabird families (Figure 7a - 7f). This pattern was more pronounced for Laridae (Figure 7b and 7e). Following rat eradication all seabird families increased in abundance (Figure 7). The gain was most pronounced near larger islands (Figure 7g - 7l). This was particularly pronounced for Laridae (Figure 7 k). Gains for Procellariidae were minor and uniformly distributed (Figure 7l).

4. DISCUSSION

Through our observations at sea in the Chagos Archipelago we have identified spatio-temporal trends in seabird distribution. Our multiyear survey spanned a broad range of environmental conditions and has enabled us to identify geomorphic and oceanographic conditions driving seabird distribution, including a possible association between regional abundance and the IO Dipole oscillation. Accounting for unbalanced sampling effort, we have identified seabird hotspots within the BIOT MPA, complementing previous investigations in the southwest and southern IO (Mannocci, Laran, et al., 2014; Hyrenbach et al., 2007). We have modelled the spatially explicit impact of islands with and without rats on seabird distribution, and have identified areas of net increase in abundance under an archipelago-wide rat eradication scenario. Information on seabird hotspots, sensitivity to climate oscillation, and how eradication can result in distribution shifts has critical implications for tropical seabird conservation and for island restoration strategies.

4.1 Drivers of seabird distribution within the Chagos Archipelago

The distribution of the Laridae, dominated by the brown noddy, was strongly related to depth and chlorophyll-a, with modelled abundance concentrated around islands, and over shallow water (<100 m). Laridae in the Chagos Archipelago have previously been observed to be mostly lagoonal foragers (Carr, pers. comm), consistent with their modelled distribution here. Our results are also consistent with previous observations of the brown noddy and lesser noddy leaving and returning to islands during the same day in the breeding season, suggesting they are not long-distance or multiday foragers (Surman, Nicholson, & Ayling, 2017; Jaquemet, Le Corre, & Weimerskirch, 2004). In line with theoretical expectations due to their

small size (Harper & Bunbury, 2015), the Laridae were the group most sensitive to rats, resulting in elevated abundance near rat-free islands.

The Sulidae showed a primarily oceanic distribution, with pronounced hotspots east of the Diego Garcia and west of the Peros Banhos atolls, and along the Lakshadweep-Maldives-Chagos ridge. Sulidae distribution has traditionally been thought to be positively associated with areas of high productivity and elevated chl-a concentration (Ballance, Pitman, & Reilly, 1997; Jaquemet, Le Corre, Marsac, Potier, & Weimerskirch, 2005; Weimerskirch, Le Corre, Jaquemet, & Marsac, 2005). In contrast, Mendez et al. (2017) identified a negative correlation between red-footed boobies and chl-a. Mendez et al. (2017) collected data on the foraging behaviour of red-footed boobies using tracking devices in five colonies along the equator (Galapagos Islands, Mozambique Channel, New Caledonia and the IO) permitting a more robust understanding of factors that determines distribution. They concluded that across the pantropical range of the red-footed booby, distribution is closely driven by intra and interspecific competition for prey. As chl-a concentration was not prognostic here, our results were consistent with Mendez et al. (2017). Sulidae were sensitive to rats although less so than Laridae, aggregating in greater abundance near rat-free islands.

Procellariidae were evenly distributed across the BIOT marine protected area, preferring warmer ($>30^{\circ}\text{C}$), and less productive waters ($<0.20\text{ mg. m}^{-3}\text{ chl-a}$). Our observations were consistent with those of Mannocci, Laran, et al. (2014) in the western IO, reporting greater number of shearwater in warmer waters ($>29.5^{\circ}\text{C}$) and lower number in productive areas ($>0.37\text{ mg m}^{-3}$). The Procellariidae were the group the least sensitive to island proximity and, in contrast to the Laridae and Sulidae, appeared to increase in abundance with distance from islands. A potential reason for this is that Procellariidae typically have a wider foraging range from nesting colonies (i.e. 480 km; King 1974) than both Sulidae (i.e. 67.5 km; Young et al. 2010) and Laridae (i.e. 80 km; Harrison & Stone-Burner, 1981; King, 1974). Procellariidae return to burrows only at night; that their distribution appears independent from islands may be due to a predominantly scattered and remote distribution during the day (Dias, Alho, Granadeiro & Catry, 2015). Although we found no significant effect of rat presence on Procellariidae distribution, many Procellariidae species are particularly vulnerable to invasive land predators (Smith, Polhemus, & Vaderwerf, 2002), because they nest in ground burrows (i.e. shearwaters). The pelagic behaviour and large foraging range of this family (up to 3500 km in the Seychelles; Catry, Ramos, Le Corre & Phillips, 2009), which our sampling range could have failed to capture, may mask any distribution shift related to rat presence.

Constant competition over prey is expected to lead to a prey depredation zones around colonies, otherwise known as The Ashmole's Halo (Ashmole, 1963). The Halo is expected to vary as a function of colony proximity, size, and bird foraging range (Birt, Birt, Goulet, Cairns & Montevecchi, 1987). Within the Chagos Archipelago, many islands are less than 100 km apart and are clustered close together ($<20\text{ km}$ between islands) within atolls. The range to which both the abundant Laridae and Sulidae distribution radiates out from islands (i.e. 100.7 km and 176.0 km respectively), makes it therefore very likely that neighbouring colonies overlap in distribution and therefore compete (in line with Mendez et al. 2017), unless individuals from different colonies express different behaviour to minimise foraging overlap (Wakefield et al. 2013). The wide distribution range and lower abundance of the Procellariidae makes it likely that the competition pressure resulting from colony proximity is less pronounced than for the other families (Gaston, Ydenberg & Smith, 2007).

4.2 Implication for rat eradication programmes

Past eradication efforts in the Chagos Archipelago include a failed attempt on Eagle Island (Meier, 2006) and successful attempts on Iles Vache Marine, du Sel and Jacobin (Harper et al., 2019). The latter attempts focussed on small islands to test the feasibility of eradication and appropriate methodologies on a small scale. Island rodent eradication is increasingly recognized as a powerful strategy for the preservation and recovery of avian populations (Brooke, et al., 2018; Jones et al., 2016; Lavers, Wilcox, & Donlan, 2010). However, eradication is technically challenging and expensive (Warren, 2018), requiring the application of toxic rodenticide posing a risk to humans, livestock, pets, and wildlife (Pickrell, 2019; Van den Brink, Elliott,

Shore & Rattner, 2017). Eradication is more likely to fail in the tropics, with high mean annual temperatures and constant precipitation (Russell & Holmes, 2015), and in the presence of land crabs and coconut palms (Holmes, et al., 2015), making a programme in the Chagos Archipelago challenging. Eradication on the largest island of Diego Garcia is likely to be particularly complex and expensive as it is inhabited (Harper & Carr, 2015).

Our analysis has revealed that gains in seabird distribution at sea following eradication are spatially and family-specific, and that eradication on larger islands will yield greater distribution gain. This, combined with the presence of thresholds in distribution, suggests that prioritising remote islands (> 50 km from nearest bird colonies) will impose less spatial competition at sea to the recolonizing seabirds. From the perspective of our study, we propose that eradication should prioritise Ile Sud-Est and Ile Lubine in Egmont Islands, Ile du Coin and Ile Pierre in Peros Banhos Atoll, Ile Boddam in Salomon Islands and Eagle Island in the Great Chagos Bank, in order to minimise potential overlap in distribution, and therefore competition, between recovering colonies. We note that these recommendations are on the basis of factors explored in this study only and that there are multiple factors that dictate the feasibility, success and approach to rodent eradication. Our results here aim to be useful to feed into a far wider set of considerations, with the ultimate aim of eradicating rats from all islands in the archipelago, in order to achieve full conservation impact.

4.3 Influence of Climate Oscillation

Our multiyear time series enable us to test for distribution effect of climatic oscillations at the inter-annual scale. We observed similar abundance trends for Sulidae and Procellariidae during the six years of sampling, with both families decreasing initially, followed by an increase. The abundance of both families appeared therefore to closely match the strength of the Dipole Mode Index, with the Procellariidae doing so to a lesser degree. We detected no correspondence between seabird and the ENSO index. Our results are consistent with current understanding regarding the influence of the dipole of higher trophic levels in the Indian Ocean. For example, Kumar, Pillai & Ushadevi (2016), identified a positive association between IO tuna productivity and the Dipole Index. While in the southern IO, Albatross breeding-success has been correlated with the Dipole Index (Rivaland et al., 2010). While knowledge of mechanisms driving these patterns is at present limited, our results add to a fledgling body of research on the importance of the Dipole on IO megafauna.

Previous studies may give some clues to possible mechanisms why seabird abundance in the Chagos Archipelago is higher during positive Dipole events, although these must remain speculative. There is, for example, evidence that equatorial upwelling in the IO are more pronounced and that westerly winds decrease in intensity during positive Dipole events (Du & Zhang, 2015). In the Chagos Archipelago, it is possible that a drop in regional upwelling require seabirds to forage further afield, leading to a drop in regional abundance. This would be consistent with understanding regarding other climate oscillations such as ENSO, which is known to influence forage species productivity (Lehodey, Bertignac, Hampton, Lewis, & Picaut, 1997), with implications for the demography and foraging behaviour of higher trophic levels (Champagnon, Lebreton, Drummond & Anderson, 2018). For example, Sprogis et al. (2018), found that the common bottlenose dolphin (*Tursiops truncatus*) migrated offshore during strong ENSO years, possibly due to a lack of inshore prey. Use of telemetry and satellite tracking is currently being deployed on red-footed boobies in BIOT (Carr, pers. comm.), which will enable mechanisms to be explored in more detail. The greater sensitivity of Procellariidae to both oceanographic variables and to the Dipole suggests this family may be the most vulnerable to global environmental change.

Any linkage between the Dipole and mobile megafauna are likely mediated by multiple trophic links (Oro, 2014). As foragers commensal with subsurface predators, seabirds could be impacted by the Dipole both directly, for example, by a reduction in forage species abundance, and indirectly, by an increase in tuna abundance (Maxwell & Morgan, 2013; Kumar et al., 2016). It is beyond our scope to distinguish these processes here, however we are currently expanding our analysis of seabird distribution to include data on subsurface prey and predator abundance collected simultaneously to the seabird observations, using midwater baited videography (Letessier, Bouchet & Meeuwig, 2017; Letessier et al., 2019).

4.4 Concluding remarks

Seabird abundance and distribution at sea in BIOT is driven by geomorphology and oceanographic conditions. Our modelled distribution complements previous efforts elsewhere in the IO and our time-series has enabled us to identify potential interannual variability related to climate oscillation. Seabird populations are vulnerable to both climatic variability and interactions with human activities (Paleczny et al., 2015). Environmental variability is predicted to increase globally under climate change scenarios (Allen et al., 2014), and evidence suggest that global warming variability may decouple the Dipole from upwelling in the western IO (Watanabe, Watanabe, Yamazaki, Pfeiffer & Claereboudt, 2019). Identifying how inter-annual processes like the IO Dipole drives seabird distribution, where human activities are limited, is valuable for identifying long-term strategies for seabird protection.

To our knowledge, this is the first attempt at predicting the response of seabird distribution to a rat-eradication scenario. We have demonstrated areas of net gain in distribution and have predicted new hotspots at sea after a rat-eradication programme. There is considerable impetus for eradicating invasive species on islands (Brooke et al., 2018; Jones et al., 2016; Lavers et al., 2010). In addition to practical considerations such as cost and probability of success, eradication programmes should identify where eradication can have the greatest conservation impact and ecological footprint. We have successfully identified multiple factors that should influence conservation activities, which is particularly important for seabirds, whose niche extends beyond terrestrial breeding colonies.

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BIOSKETCH

Julian Perez-Correa is an ecologist interested in describing and modelling biodiversity patterns focused on birds.

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AUTHORS’ CONTRIBUTIONS

P.C. conducted the seabird observations. J.P.C. and T.B.L. conceive the ideas and led the analysis and writings, assisted by J.M., H.K., and P.C. All authors contributed to the ecological interpretation of the analysis.

DATA AVAILABILITY STATEMENT

R code and data used to conduct this research are available for public access in <https://github.com/juperez/SeabirdChagos>

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TABLE 1. Number of transects, aggregations and point counts samples made by month and year within the BIOT Marine Reserve.

Sampling Month	Transect	Aggregation	Point Count
November 2012	50	11	3
December 2012	40	9	3
February 2013	7	7	-
March 2013	3	-	-

Sampling Month	Transect	Aggregation	Point Count
March 2014	10	1	-
April 2014	5	1	1
January 2015	92	10	2
March 2015	1	6	-
April 2015	-	3	-
February 2016	109	31	-
April 2017	12	8	-

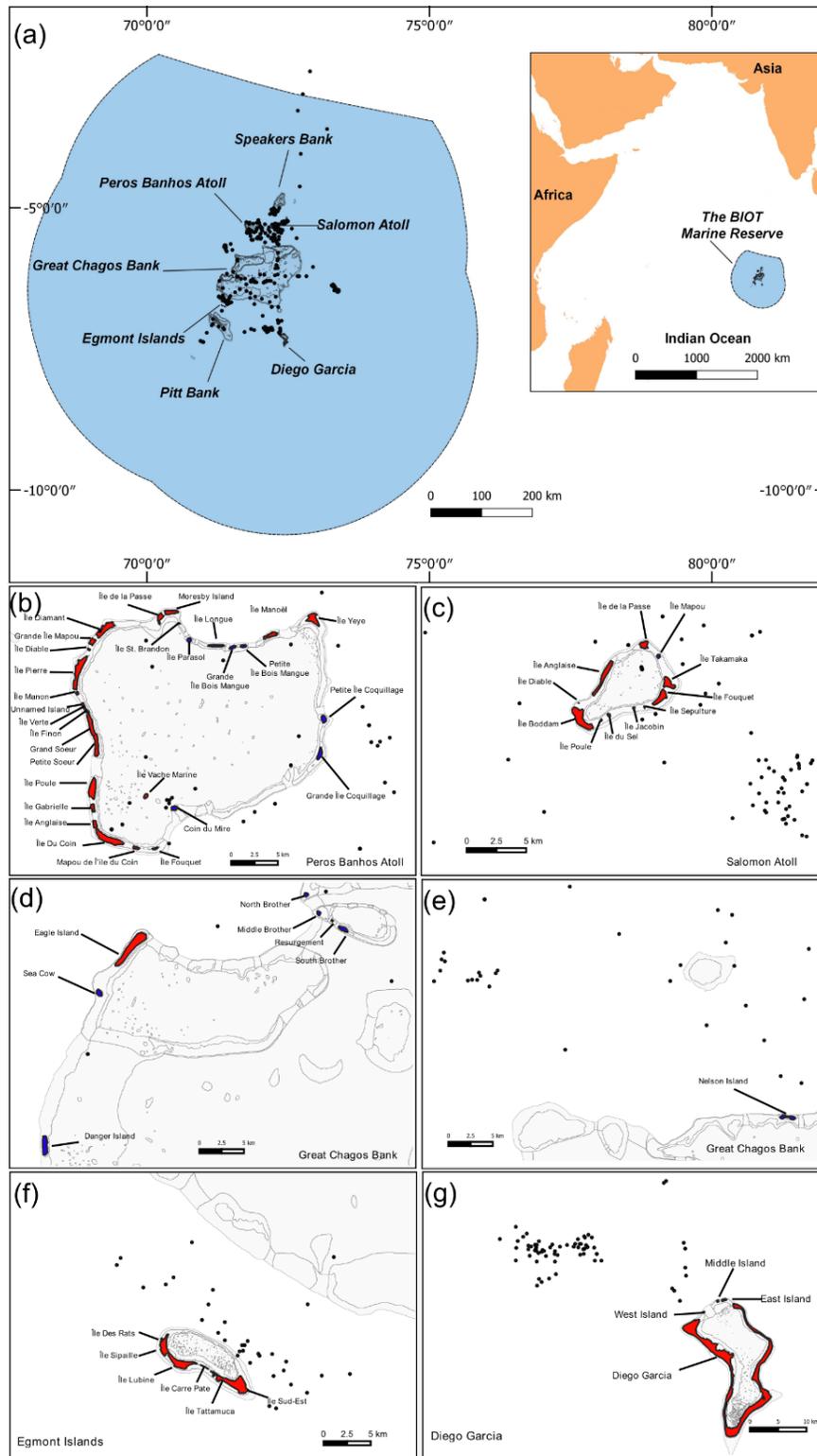


FIGURE 1. Seabird sampling effort within the Chagos Archipelago and the British Indian Ocean Territory.

Boundaries of the marine protected area (a, black lines), and location within the Indian Ocean (inset). (b-g) indicates close-ups of individual atolls and islands. Black dots represent the location of individual bird count samples. Rat-infested islands are coloured in red and rat-free islands in blue. Six islands have been reported with uncertain rat status and are for representation purposes considered as rat-infested here.

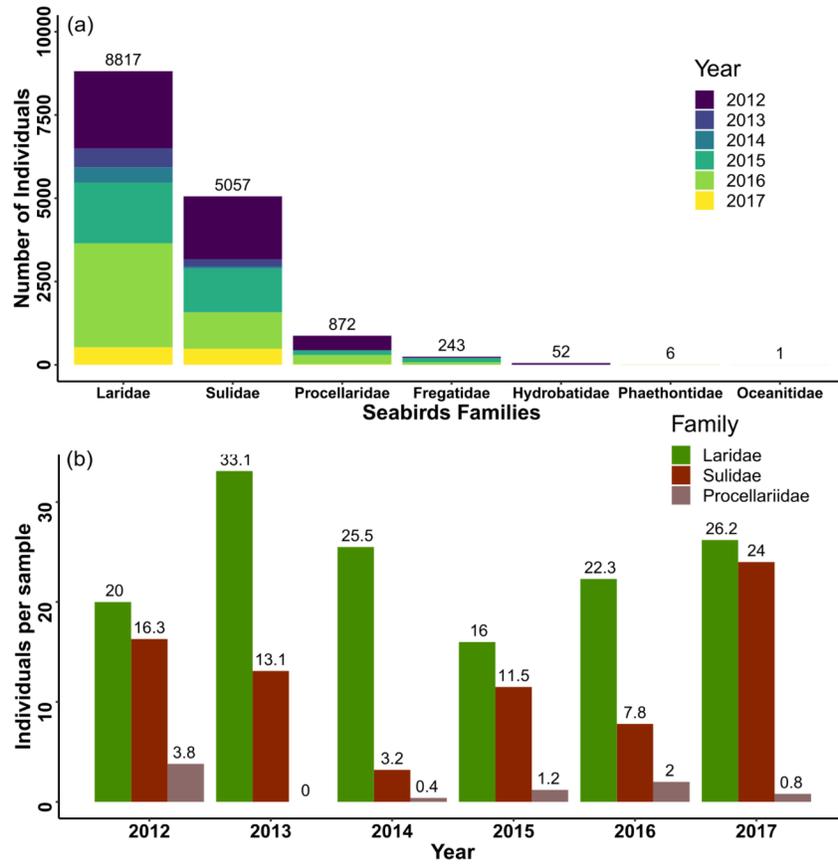


FIGURE 2. Number of individual seabirds by family summed across all samples (a) and for the three most abundant families Laridae, Sulidae and Procellariidae, standardised by the number of samples for each year (b).

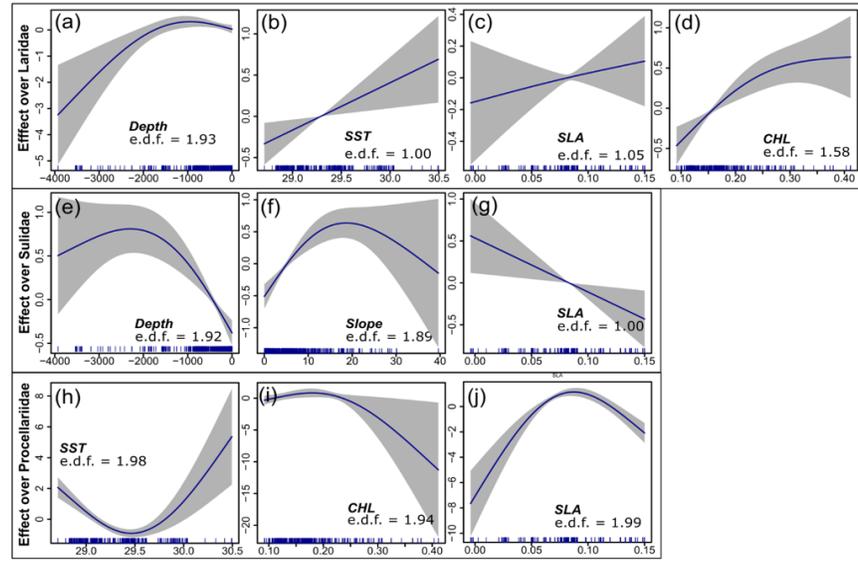


FIGURE 3. Smooth functions for selected variables for each seabird family (ind. per sample). The blue-solid line in each graph represents the smooth function estimate. Shaded regions represent the 95% confidence intervals in each smoother. SST = sea surface temperature, SLA = sea levels anomalies, CHL = chlorophyll-a.

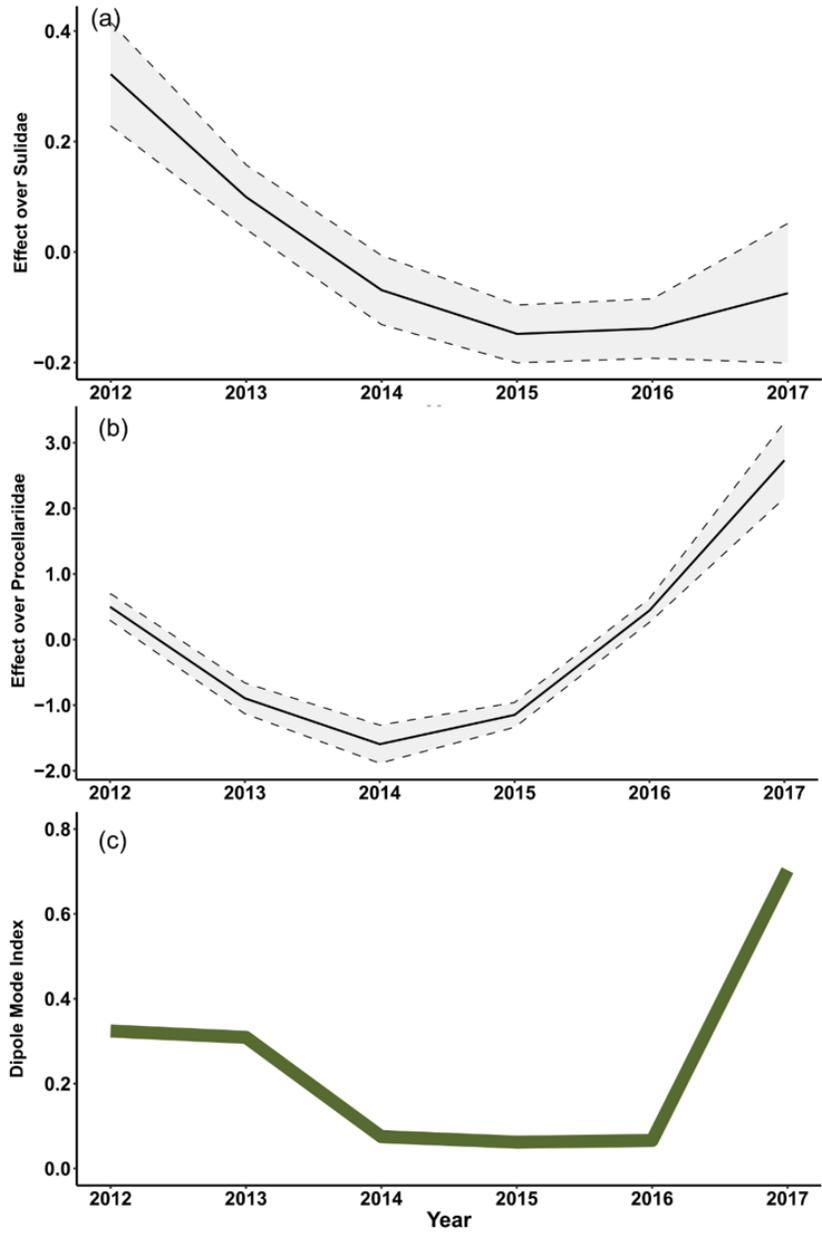


FIGURE 4. Yearly variability in abundance (ind. per sample), as represented by GAM smooth functions for Sulidae (a) and Procellariidae (b). Climate oscillation event, due to the Indian Dipole mode, as represented by the Dipole Mode Index (DMI) value, during the month of sampling (c). DMI values represent the SST anomalies gradient between the western and eastern tropical Indian Ocean (Saji & Yamagata, 2003).

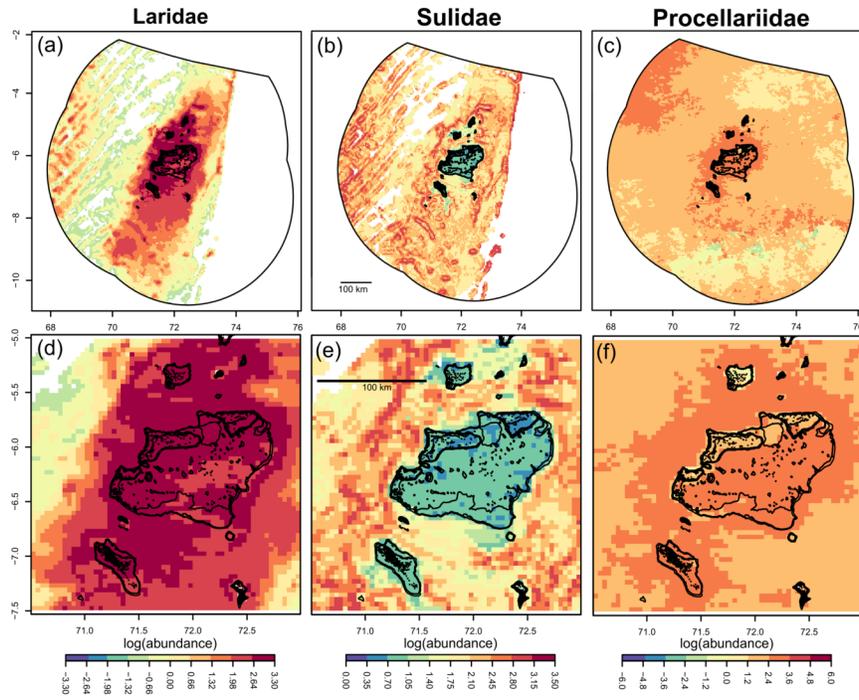


FIGURE 5. Predicted distribution of Laridae, Sulidae and Procellariidae on the logarithmic scale, at the scale of the Chagos Archipelago (a, c, e) and of the BIOT Marine Protected Area (b, d, and f). Blank spaces denotes areas outside the range of the variables used for modelling.

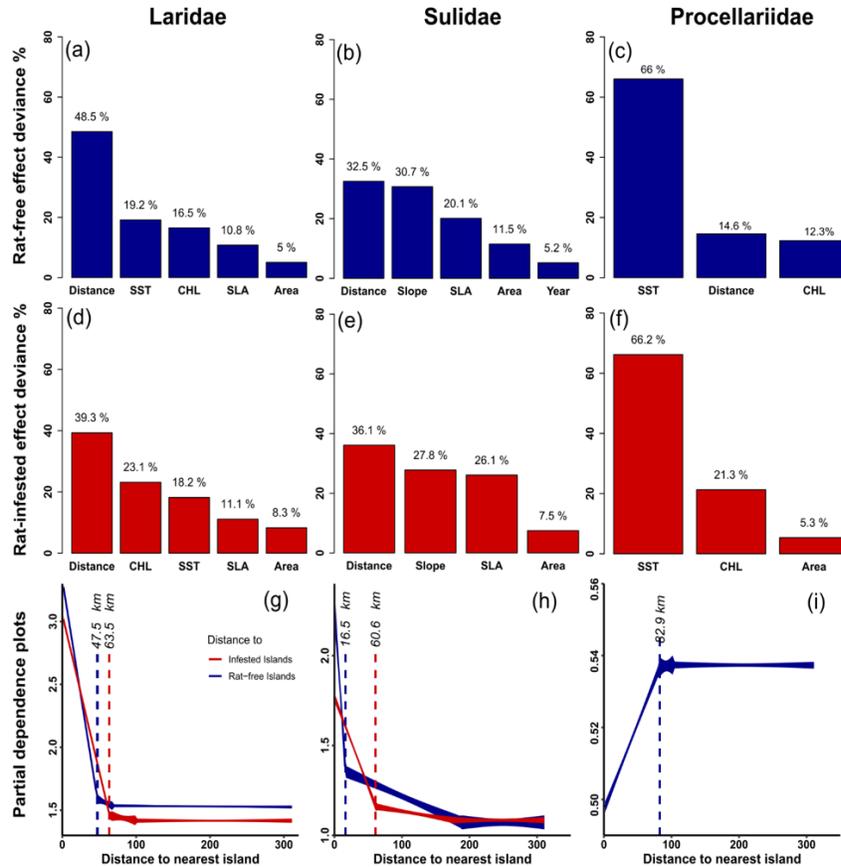


FIGURE 6. Sensitivity of seabird distribution to presence or absence of rats on nearby islands. Boosted Regression Trees (BRT) relative contribution, in the vicinity of rat-free island (a-c) or rat-infested islands (d-f). Variables with less than 5% contribution were not included in the plots. Partial dependence plot (g-i) of the effects of rat-free (blue lines) and rat-infested (red lines) islands. Contribution of Distance to infested islands on Procellariidae was not >5% therefore it was not retained. Stippled line denotes location of 1st breaking point threshold for each partial plot. Breaking points for Laridae were 63.6 km and 100.7 km from rat-infested islands, and 47.5 km and 67.4 km from rat-free islands. Breaking point for Sulidae were 60.5 and 176.4 from rat-infested islands and 16.5 and 188.1 from rat-free islands. Breaking point for Procellariidae were 73.5 and 175.3 from rat-infested islands and 82.9 and 102.6. The 2nd breaking point on each partial plot was no significant, hence no plotted (Appendix S3). SST = sea surface temperature, SLA = sea levels anomalies, CHL = chlorophyll-a, Distance = distance to the nearest rat-free or rat infested island, depending on the model, Area = area of the nearest rat-free or rat infested island.

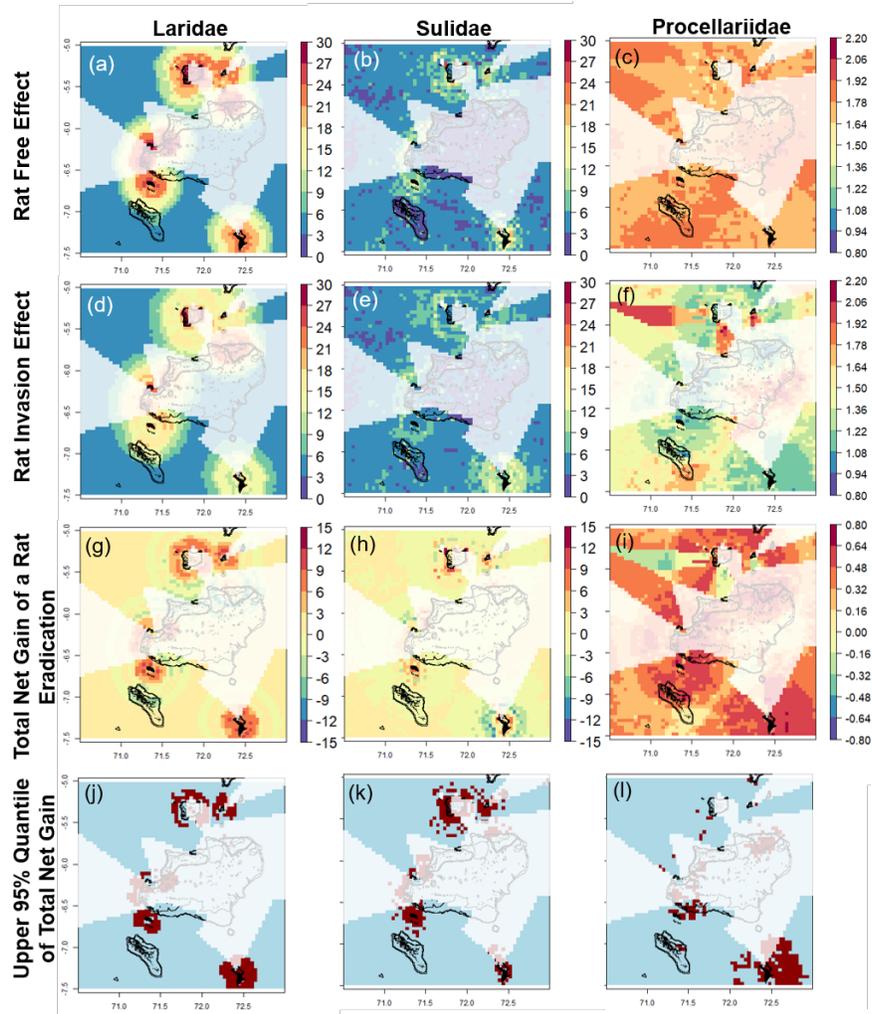


FIGURE 7. Predicted areas of increase in seabird abundance under a scenario of rat-eradication. Rat-free distribution predicted from BRT model using distance to the nearest rat-free island as a variable (a-c), rat-infested distribution, predicted from BRT model using distance to the nearest rat-infested island (d-f), the net gain in bird abundance under a scenario of rat eradication (rat-free distribution minus rat-infested distribution g-i), and upper 85% quantile of the net gain j-l). Light shaded areas indicate areas closest to rat-free islands, already at the theorised maxima.