EXPLORING THE BENEFITS OF A TROPICAL, LARGE-SCALE MARINE PROTECTED AREA FOR BREEDING SEABIRDS

Per Mare

Per Terram

Submitted by Peter Carr to the University of Exeter as a thesis for the degree of
Doctor of Philosophy in Biological Sciences.
In July 2021

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……………………………………………………………..

Abstract

Debate continues in scientific and popular literature into the benefits of large-scale marine protected areas (> 100,000 km^2 - LSMPAs), especially for top predators. Of top marine predators, seabirds are deemed to be the easiest to study due to their ease of observation and often colonial breeding. The Important Bird and Biodiversity Areas (IBAs) programme is a method of identifying the most important places for birds. IBAs are identified using a globally agreed standardised set of data-driven criteria and thresholds. In this thesis I explore the benefits of a LSMPA for top predators. I use IBAs on land and at sea with seabirds as the qualifying species as the means of exploration and the tropical British Indian Ocean Territory (Chagos) MPA (hereafter BIOT MPA) as the study system. Red-footed Booby *Sula sula rubripes* is the focal species of the thesis.

My research demonstrates that the BIOT MPA is extremely important regionally and globally for biodiversity and provides a breeding sanctuary for ≈ 282,000 pairs of seabirds of 18 species annually, four of which breed in internationally important numbers that trigger IBA status. However, invasive Ship Rats *Rattus rattus* and abandoned coconut *Cocos nucifera* plantations are severely restricting the islands that seabirds can breed on. I calculate by eradicating rats and managing invasive coconut plantations on a single 123 ha island, the number of seabirds breeding in the BIOT MPA could more than double. At sea, I identified sites that meet IBA status and due to their overlapping boundaries form a single ‘super’ IBA that covers ≈ 10% of the MPA.

The terrestrial and marine sites I have identified within the MPA warrant enhanced protection. Red-footed Booby is deemed an umbrella species and therefore protecting the feeding and breeding habitat of this species will afford protection on a suite of other species, including sub-surface predators. I suggest this thesis is a foundation stone from which further research into marine biodiversity hotspots in the central Indian Ocean can be launched. This thesis supports the growing evidence that tropical LSMPAs are beneficial to top predators and unequivocally demonstrates that the BIOT MPA encompasses the early stages of breeding of a highly mobile, top predator.

All photographs throughout this thesis are the property of the author.

Table of Contents

List of Figures

List of Tables

List of Boxes

Acknowledgements

First, I would like to thank those that inspired and encouraged me to become involved in science and conservation in the Chagos Archipelago over a decade ago; Professors Charles Sheppard, Jessica Meeuwig and Nick Graham. Particular thanks go to Dr. Colin Clubbe of RBG Kew for showing me on a science expedition in the Chagos Archipelago in 2010 that there is more to conservation than birds. Colin has remained a stalwart of inspiration and friend since then.

I would like to thank all of my supervisors past and present for their contribution to the production of this thesis, especially Drs. Stephen Votier and Richard Sherley from Exeter University. Dr. Malcolm Nicoll from the Zoological Society of London was there at the genesis, the conclusion and was a constant throughout. Malc, it is a fact I would not have completed this thesis without your calm and balanced approach – thank you. Dr. Alice Trevail of the Chagos Seabird Ecology research group provided support beyond the call of duty for which I am grateful.

My supervisor Professor Heather Koldewey was also a great source of inspiration and encouragement to enter the world of science and conservation after my 33 years’ service as a Royal Marine Commando. Heather has stuck by me through thick and thin and without her not only this PhD thesis but most current science and conservation in the Chagos Archipelago would not have happened. Heather, I am forever grateful for what you have done for me and the Chagos Archipelago.

Above all, my wife Zoe has borne the brunt of the consequences of my passion for the Chagos Archipelago - from being left alone for weeks at a time whilst conducting fieldwork, to being left alone for months at a time when I was writing up this thesis. For her unstinting support, I am eternally thankful.

This PhD was funded by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science.

List of other papers with Peter Carr as author / co-author published in the timeframe of the PhD but not part of PhD

Benkwitt CE, Gunn RL, Le Corre M, Carr P and Graham NA. 2021. Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. Current Biology 31: 2704-2711.

Carr P. 2020. Odonata of the Chagos Archipelago, central Indian Ocean: an update. Notulae Odonatologicae 9(6): 229-275.

Graham NA, Wilson SK, Carr P, Hoey AS, Jennings S and MacNeil MA. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559(7713): 250-253.

Harper GA, Carr P and Pitman H. 2019. Eradicating black rats from the Chagos – working towards the whole archipelago. Island invasives: Scaling up to meet the challenge, Occasional Paper SSC 62: 26-30.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Pilly SS, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MAC, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard CRC, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier SC, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H and Curnick DJ. 2020. A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. Marine Biology 167(11): 1-22.

Perez-Correa J, Carr P, Meeuwig JJ, Koldewey HJ and Letessier TB. 2020. Climate oscillation and the invasion of alien species influence the oceanic distribution of seabirds. Ecology and Evolution 10(17): 9339-9357.

CHAPTER 1

GENERAL INTRODUCTION

Tropical, Large-Scale Marine Protected Areas (LSMPAs) – Background and Context

Few now refute the dire warnings issued towards the end of the 20th Century that the planet's ocean was in perilous decline due to detrimental anthropogenic impact (Croxall 1991, Agardy 1994, Watling and Norse 1998, Pauly et al. 1998). Overexploitation of commercially profitable commodities has been identified as a primary driver of ecosystem change in the ocean (IUCN-WCPA 2005), particularly overfishing (Jackson et al. 2001, Gjerde et al. 2013). Overfishing has wider impacts on ecosystems and species, for example, non-commercial bycatch has had a catastrophic impact on marine megafauna (Lewison et al. 2004). Marine megafauna refers to seabirds, cetaceans, elasmobranchs, pinnipeds, large teleosts e.g., tunas and billfish, sirenians and marine reptiles - following Hays et al. (2016). Other "unanticipated, unprecedented and complex changes" impacting upon the chemistry, physical structure and ecological functioning of the ocean (Lubchenco et al. 2003) include but are not limited to; climate change (Hoegh-Guldberg and Bruno 2010, Bates et al. 2019), marine pollution including microplastics (Rochman et al. 2016, Beaumont et al. 2019), eutrophication (Smith et al. 1999, Malone and Newton 2020), acidification (Feely et al. 2004, Doney et al. 2020), shipping malpractices (Gertler et al. 2010), invasive species introductions (Bax et al. 2003, Giakoumi et al. 2019) and noise pollution (Duarte et al. 2021). The above threats to the ocean can and do act synergistically (Sorte et al. 2010).

As a result of the devastation of the oceanic environment much marine megafauna is perilously declining, in some cases to the point of extinction e.g., seabirds (Croxall et al. 2012); predatory fish (Myers and Worm 2003); chondrichthyans (Davidson and Dulvy 2017); pinnipeds (Kovacs et al. 2012); marine turtles (Wallace et al. 2011); general marine defaunation (McCauley et al. 2015).

This century has seen calls for protection of the marine environment increase and gain in credence (Lubchenco et al. 2003, IUCN-WCPA 2005, Game et al. 2009) and a suite of management tools have been and are being implemented to preserve biodiversity, protect marine ecosystems and resuscitate depleted populations of marine megafauna. These tools include but are not limited to changing fishing operations (Broadhurst 2000, Lewison et al. 2004), the regulating of commercial extractive operations (Allison and Ellis 2001) and the establishment of marine protected areas (MPAs) (Fernandes et al. 2005, IUCN-WCPA 2008). The foundation stone of MPAs is the 2010 United Nations (UN) Convention on Biological Diversity (CBD) agreed Aichi Biodiversity Target 11 that states that 10% of coastal and marine areas are to be conserved by 2020 (CBD 2017), later endorsed under Sustainable Development Goal 14. The UK government is leading a 30-by-30 initiative, pushing for at least 30% of the global ocean to be protected by 2030 with the hope that this goal will be ratified at the rescheduled 2021 CBD Conference of the Parties (https://www.gov.uk/government/topical-events/global-ocean-alliance-30by30-initiative/ accessed 31 January 2021).

The vast majority of MPAs are coastal, shallow water and small scale with a median size (in 2013) of 4.6 km^2 and are mostly contained within the boundaries of national Exclusive Economic Zones (Toonen et al. 2013). Latterly marine conservationists have been calling for MPAs that include Areas Beyond National Jurisdiction (ABNJ) (Visalli et al. 2020) that incorporate open ocean (High Seas) ecosystems (Hyrenbach et al. 2000, Norse 2005, Game et al. 2009) that constitute ∽ 50% of the ocean. The 21st Century has witnessed the designation of some 18 MPAs >100,000 km^2 (MCI 2021). Of these large-scale MPAs (LSMPAs – Toonen et al. 2013) 14 are deemed to be tropical having >50% of their area between the Tropic of Cancer and Capricorn (Table 1.1).

Despite there being strong support for LSMPAs in the scientific community (Koldewey et al. 2010, Sheppard et al. 2012, Toonen et al. 2013, Wilhelm et al. 2014, O'Leary et al. 2018, Gallagher et al. 2020, Hays et al. 2020), there remains criticism and debate surrounding them (reviewed in O'Leary et al. 2018). Three themes of criticism (placement, governance, and management; political expediency; socio-ecological value and cost) were addressed by O'Leary et al. (2018). Ongoing debates about the efficacy of LSMPAs in protecting biodiversity are centered upon; a). The level of protection biodiversity is afforded in MPAs with opinions covering the spectrum from "no-take" marine reserves (Costello and Ballantine 2015, Sala and Giakoumi 2017) to expanding fisheries management rather than establishing more no-take MPAs (Hilborn 2018); b). How large an MPA needs to be to protect top predators and highly mobile species, with advocates for LSMPAs of a size that could potentially cover the entire life cycle of mobile species (Hyrenbach et al. 2000, Game et al. 2009) or smaller MPAs covering critical parts of an organism's life cycle (Kerwath et al. 2009).

Recent research has demonstrated that there are linkages between the benefits that MPAs offer - in addition to biodiversity protection, they can provide essential food provision and carbon storage (Sala et al. 2021). In MPAs where seabird islands (Mulder et al. 2011) thrive in the absence of invasive rats, Graham et al. (2018) and Benkwitt et al. (2021) have demonstrated the cross-ecosystem benefits derived from nutrient transfer. This occurs via seabirds feeding in the ocean and depositing nutrients (primarily through guano) on islands that 'runs off' and enriches nearshore ecosystems.

Specific to seabird populations, the top three threats are invasive alien species, bycatch in fisheries and climate change/severe weather; overfishing, hunting/trapping and disturbance have also been identified as major threats (Dias et al. 2019).

Table 1. 1. Tropical, large-scale Marine Protected Areas (LSMPAs) as at 2021, the area they encompass, the amount that is fully protected, year of designation and sponsoring country. LSMPAs are listed in size order starting with the largest to date. Data from https://mpatlas.org/zones/ accessed July 2021.

	Marine Protected Area	Area (km^2)	Protected (No Take) Area (%)	Designation Year (Extended Year)	Sponsor
1	Papahānaumokuākea Marine National Monument	1,508,730	100	2006 (2016)	United States of America
2	Pacific Remote Islands Marine National Monument	1,265,923	100	2009 (2014)	United States of America
3	Pitcairn Islands Marine Reserve	832,694	100	2015	United Kingdom
4	British Indian Ocean Territory (Chagos) Marine Protected Area	638,097	100	2010	United Kingdom
5	Palau National Marine Sanctuary	477,148	80	2015	Palau
6	Ascension Exclusive Economic Zone	446,005	99	2019	United Kingdom
7	Phoenix Islands Protected Area	395,133	99.9	2006	Kiribati
8	Nazca-Desventuradas Marine Park	299,947	100	2015	Chile
9	Coral Sea Marine Park	238,391	24	2018	Australia
10	Aldabra Group (Marine) National Park	195,272	100	2020	Seychelles
11	Motu Motiro Hiva Marine Park	150,079	100	2010	Chile
12	Revillagigedo National Park	148,641	100	2017	Mexico
13	Niue Moana Mahu Marine Protected Area	126,650	100	2020	Cook Islands and Niue
14	Great Barrier Reef Marine Park	115,025	33	1975	Australia

Tropical Seabirds

Seabirds can give unique insights into pelagic ecosystems and offer many advantages over other marine megafauna for research because they tend to be conspicuous at sea and, as central-placed foragers when breeding, they are ideally placed for long-term population monitoring, productivity, and tracking studies (Piatt et al. 2007, Parsons et al. 2008). Compared with other groups with an equivalent role in the marine environment, seabirds are exceptionally well-studied (Schreiber and Burger 2001), providing more comprehensive and reliable information on their conservation status than for other comparable marine organisms (Vie et al. 2008). Seabirds are also indicators of the health of marine ecosystems (Cairns 1988, Piatt et al. 2007, Einoder 2009).

Compared to temperate and polar populations of seabirds, tropical seabirds are less studied (Croxall et al. 2012). Challenges exist when researching tropical seabirds e.g., immense size of the ocean, remoteness and inaccessibility of many breeding populations, secretive and/or nocturnal breeding, unknown breeding areas, a vast number of potential breeding islands and in some cases minuscule breeding populations (VanderWerf and Young 2018). There are also unique challenges to monitoring tropical seabirds (VanderWerf and Young 2017) including aseasonal and asynchronous breeding (Lack 1954, Carr et al. 2021).

Important Bird and Biodiversity Areas (IBAs)

The Important Bird and Biodiversity Areas (IBAs) programme is a method of identifying the most important places on earth for birds (BirdLife International 2009). Since the late 1970s, the BirdLife Partnership has been working to identify, document and protect all places on earth of greatest significance for the conservation of the world’s birds. As a result, over 13,000 IBAs have been identified, becoming the largest global network of significant biodiverse sites in the world (http://www.birdlife.org/worldwide/programmes/sites-habitats-ibas/ accessed 16 December 2020). Of these, some 10,000 are terrestrial IBAs (tIBAs) and the remainder are marine (mIBAs). The identification of tIBAs globally is nearing completion, the more recent concept of mIBAs is a work in progress (Lascelles et al. 2016). IBAs are identified using a globally agreed standardised set of data-driven criteria and thresholds, ensuring that the approach can be used consistently worldwide (Box 1.1).

Box 1. 1. Important Bird and Biodiversity Area selection criteria applicable outside of Europe and the Middle East (précised from Guidelines for the application of the IBA criteria. Final version July 2020. http://datazone.birdlifeorg accessed 29 April 2021).

A1: Globally Threatened Species Criterion: The site is known or thought regularly to hold significant numbers of a Globally Threatened species. The site qualifies if it is known, estimated or thought to hold a population of a species categorized on the IUCN Red List as globally threatened (Critically Endangered, Endangered and Vulnerable). Specific thresholds apply to species in the three threat categories.

A2: Restricted Range Species Criterion: The site is known or thought to hold a significant population of at least two range-restricted species. Restricted-range bird species are those having a global range size less than or equal to 50,000 km^2. This criterion can be applied to species both within their breeding and nonbreeding ranges.

A3: Bioregion-Restricted Assemblages Criterion: The site is known or thought to hold a significant component of a group of species whose distributions are largely or wholly confined to one biome-realm.

A4: Congregations Criterion: The site is known or thought to hold congregations of ≥1% of the global population of one or more species on a regular or predictable basis.

B1a: Globally Near Threatened Species: The site regularly holds significant numbers of a Near Threatened species (NT). Non-passerines – 10 pairs/30 individuals; Passerines – 30 pairs/90 individuals.

B3a: Regionally Important Congregations – biogeographical populations: The site is known or thought to hold, on a regular basis ≥ 1% of a biogeographic or other distinct population of a congregatory waterbird, breeding seabird or other species.

B3b: Regionally Important Congregations – multi-species aggregations: The site is known or thought to hold, on a regular basis ≥ 20,000 waterbirds or (formerly global A4iii) ≥ 6,700 pairs of seabirds of one or more species.

B3c: Regionally important congregations – bottleneck sites: The site is known or thought to exceed thresholds set for migratory species at bottleneck sites.

Due to their standardised qualifying criteria and global application, IBAs are a common currency that permit meaningful comparison between sites within and between regions of the world (BirdLife International 2004). IBAs can be used for spatial planning, especially for designating and delineating protected areas

(Lascelles et al. 2016). Monitoring IBA-based indicators e.g., population dynamics, gives a strong indication of the health of the surrounding and associated ecosystems and of the success of conservation measures such as protected areas (Handley et al. 2020, 2021). The number of IBAs an area holds or their species composition and richness can give an indication of the ecological richness of that space (Pavón-Jordán et al. 2020).

A prerequisite for effective conservation management of IBAs is accurate, current data on the threats to biodiversity (pressure), the status of bird populations (state), and the type and effectiveness of conservation actions (response) (BirdLife International 2004). Therefore, IBAs can be used to monitor the efficacy and assess the benefits of protected areas, for example MPAs, but the data behind the IBAs must be current for this to be meaningful.

To facilitate a discussion on the use of IBAs to assess the benefits of tropical LSMPAs for breeding seabirds, data on the IBAs within the LSMPAs had to be compiled (Table S1.1 and S1.2). Direct comparisons of the benefits between LSMPAs using IBAs as the ‘common currency’ are not possible because LSMPAs have used different scales for delineating IBAs. For example, the largest tropical LSMPA, Papahānaumokuākea Marine National Monument (1,508,870 km^2) has but one tIBA, the North-western Hawaiian Islands, whilst the smallest, the Great Barrier Reef Marine Park (115,025 km^2) holds 12. However, collectively, the IBA qualifying species’ data provides useful insights into the benefits to seabirds of LSMPAs.

Thesis Aims and Outline

The central aim of this thesis is to explore the benefits of a single tropical LSMPA to breeding seabirds to inform the wider debate on the benefits of LSMPAs to biodiversity. It uses the global currency of IBAs with tropical seabirds as the qualifying criteria as the indicator of benefits and the tropical BIOT LSMPA as the study system. The analytical chapters are written to stand alone yet, tie to together *per mare, per terram*, to explore the benefits of tropical LSMPAs to breeding seabirds. The specific aims of the chapters are:

Chapter Two – This chapter introduces the study system, the British Indian Ocean Territory / Chagos Archipelago (hereafter CA) and the associated BIOT MPA. It covers the location, basic geology and geography, climate, a brief history leading to the creation of the BIOT MPA and concludes with an introduction to the seabirds of the CA with emphasis on the thesis' focal species, the Red-footed Booby *Sula sula rubripes* L. 1766 (hereafter RfB).

Chapter Three – This chapter updates and reviews the status, distribution and phenology of breeding seabirds of the BIOT MPA and concludes with a review of its tIBAs. It combines all published records of breeding seabirds in the MPA with the author's unique personal records collected 2008-2018. It recommends the current 10 designated and two proposed (single island) tIBAs are amalgamated into three "island cluster" and a single island IBA. Chapter three has been published as:

Carr P, Votier SC, Koldewey HJ, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Chapter Four – Chapter four explores the health of the terrestrial environment of the BIOT MPA using breeding seabirds as the indicator. It researches the habitats and factors that provide optimum breeding conditions for seabirds and then measures the current extent of these requirements throughout the archipelago. It concludes that eradicating invasive rats and rehabilitating abandoned coconut plantations, especially where these conditions exist within island cluster IBAs, would greatly enhance the benefits to breeding seabirds of the BIOT MPA. Chapter four has been published as:

Carr P, Trevail A, Bárrios S, Clubbe C, Freeman R, Koldewey HJ, Votier SC, Wilkinson T and Nicoll MAC. 2021. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. Restoration Ecology .e13386.

Chapter Five – This chapter is field and laboratory-based and explored the question of how to sex the focal species, RfB, in the field. Using genomic DNA of uniquely identified birds, it assesses the potential for sexing RfBs in the field and, using the results, generalised on where the central Indian Ocean population sits morphometrically within the species and subspecies groups.

Chapter Six – The final analytical chapter reviewed the seaward extension to breeding colony mIBAs proposed by BirdLife International and explores for pelagic mIBAs within the central Indian Ocean. With the findings from Chapter Three it revisits seaward extension to colonies based on the newly designated tIBAs. It then uses tracking data of the focal species, RfB, from the three largest breeding colonies in the CA, with standardised formulae developed by BirdLife International to search for pelagic mIBAs. It updates and redefines the seaward extensions to breeding colony mIBAs and creates three pelagic mIBAs. As the boundaries of both types of mIBA overlap, one ‘super’ mIBA (62,379 km^2 ~10% of the MPA) has been proposed that if designated will be the fourth largest in the Indian Ocean and 11th largest in the world - the proposed Chagos Archipelago marine Important Bird and Biodiversity Area (CA mIBA), that lies entirely within the boundary of the BIOT MPA.

Chapter Seven –Using this research from the CA, the final chapter assesses the benefits to breeding seabirds of a tropical LSMPA. Using the t/mIBAs as the indicators, it first looks inwards at the benefits and, how these benefits could be enhanced. It then combines the BIOT MPA seabird research with IBA data from other tropical LSMPAs (Tables S1.1 and S1.2) and discusses the benefits to breeding seabirds and biodiversity of LSMPAs globally. The thesis continues by discussing its key findings and limitations and identifying future research opportunities using this thesis as the foundation. It concludes by making management recommendations to BirdLife International and the British Indian Ocean Territory Administration (BIOTA) on how to further conserve and enhance the benefits of the BIOT MPA to biodiversity.

REFERENCES

Agardy MT. 1994. Advances in marine conservation: the role of marine protected areas. Trends in Ecology & Evolution 9(7): 267-270.

Allison EH and Ellis F. 2001. The livelihoods approach and management of small-scale fisheries. Marine Policy 25(5): 377-388.

Bates AE, Cooke RS, Duncan MI, Edgar GJ, Bruno JF, Benedetti-Cecchi L, Côté IM, Lefcheck JS, Costello MJ, Barrett N and Bird TJ. 2019. Climate resilience in marine protected areas and the 'Protection Paradox'. Biological Conservation 236: 305-314.

Bax N, Williamson A, Aguero M, Gonzalez E and Geeves W. 2003. Marine invasive alien species: a threat to global biodiversity. Marine Policy 27(4): 313-323.

Beaumont NJ, Aanesen M, Austen MC, Börger T, Clark JR, Cole M, Hooper T, Lindeque PK, Pascoe C, Wyles KJ. 2019. Global ecological, social and economic impacts of marine plastic. Marine Pollution Bulletin 142: 189–195.

Benkwitt CE, Gunn RL, Le Corre M, Carr P and Graham NA. 2021. Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. Current Biology.

Billerman M, Keeney BK, Rodewald PG and Schulenberg TS. (Eds.). 2021. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA https://birdsoftheworld.org/bow/home

BirdLife International. 2004. Important Birds Areas in Asia: key sites for conservation. Cambridge, UK: BirdLife International. BirdLife Conservation Series No. 13.

BirdLife International. 2009. Designing networks of marine protected areas: exploring the linkages between Important Bird Areas and ecologically or biologically significant marine areas. Cambridge, UK: BirdLife International.

Broadhurst MK. 2000. Modifications to reduce bycatch in prawn trawls: a review and framework for development. Reviews in Fish Biology and Fisheries 10(1): 27-60.

Carr P, Votier S, Koldewey H, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and

Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Cairns DK. 1988. Seabirds as indicators of marine food supplies. Biological Oceanography 5(4): 261-271.

Convention on Biological Diversity. 2017. The Aichi Targets. https://www.cbd.int/sp/targets accessed on 09 February 2017.

Costello M and Ballantine B. 2015. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. Trends in Ecology & Evolution 30(9): 507-509.

Croxall JP. 1991. Editor's Introduction. Page 1 in: Croxall JP. (Ed.). Seabird Status and Conservation: A Supplement. International Council for Bird Preservation Technical Publication No. 11.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A and Taylor P. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22(10): 1-34.

Davidson LNK and Dulvy NK. 2017. Global marine protected areas to prevent extinctions. Nature, Ecology and Evolution 1: 1-6.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Doney SC, Busch DS, Cooley SR and Kroeker KJ. 2020. The impacts of ocean acidification on marine ecosystems and reliant human communities. Annual Review of Environment and Resources 45: 83-112.

Duarte CM, Chapuis L, Collin SP, Costa DP, Devassy RP, Eguiluz VM, Erbe C, Gordon TA, Halpern BS, Harding HR and Havlik MN. 2021. The soundscape of the Anthropocene ocean. Science 371(6529).

Einoder LD. 2009. A review of the use of seabirds as indicators in fisheries and ecosystem management. Fisheries Research 95(1): 6-13.

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ and Millero FJ. 2004. Impact of Anthropogenic CO^2 on the $CaCO^3$ System in the Oceans. Science 305(5682): 362-366.

Fernandes L, Day JON, Lewis A, Slegers S, Kerrigan B, Breen DAN, Cameron D, Jago B, Hall J, Lowe D and Innes J. 2005. Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conservation Biology 19(6): 1733-1744.

Gallagher AJ, Amon D, Bervoets T, Shipley ON, Hammerschlag N and Sims DW. 2020. The Caribbean needs big marine protected areas. Science 367(6479): 749.

Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP and Richardson AJ. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecological Evolution 24: 360-369.

Gertler C, Yakimov MM, Malpass MC and Golyshin PN. 2010. Shipping-related accidental and deliberate release into the environment. Pages 243-256 in: Timmis K.N. (Ed.) Handbook of hydrocarbon and lipid microbiology. Springer Berlin Heidelberg.

Giakoumi S, Katsanevakis S, Alban, PG, Azzurro E, Cardoso AC, Cebrian E, Deidun A, Edelist D, Francou, P, Jimenez C and Mačić V. 2019. Management priorities for marine invasive species. Science of the Total Environment 688: 976-982.

Gjerde KM, Currie D, Wowk K and Sack K. 2013. Ocean in peril: Reforming the management of global ocean living resources in areas beyond national jurisdiction. Marine Pollution Bulletin 74(2): 540-551.

Graham NA, Wilson SK, Carr P, Hoey AS, Jennings S and MacNeil MA. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559(7713): 250.

Handley JM, Pearmain EJ, Oppel S, Carneiro AP, Hazin C, Phillips RA, Ratcliffe N, Staniland IJ, Clay TA, Hall J and Scheffe A. 2020. Evaluating the effectiveness of a large multi-use MPA in protecting Key Biodiversity Areas for marine predators. Diversity and Distributions 26(6): 715-729.

Handley J, Rouyer MM, Pearmain EJ, Warwick-Evans V, Teschke K, Hinke JT, Lynch H, Emmerson L, Southwell C, Griffith G and Cárdenas CA. 2021. Marine Important Bird and Biodiversity Areas for Penguins in Antarctica, Targets for Conservation Action. Frontiers in Marine Science 7: 1-17.

Hays GC, Ferreira LC, Sequeira AM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP and Eguíluz VM. 2016. Key questions in marine megafauna movement ecology. Trends in Ecology and Evolution 31(6): 463-475.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Pilly SS, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MAC, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard CRC, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier SC, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H and Curnick DJ. 2020. A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. Marine Biology 167(11): 1-22.

Hilborn R. 2018. Are MPAs effective? ICES Journal of Marine Science 75(3): 1160-1162.

Hoegh-Guldberg O and Bruno JF. 2010. The impact of climate change on the world's marine ecosystems. Science 328(5985): 1523-1528.

Hyrenbach KD, Forney KA and Dayton PK. 2000. Marine protected areas and ocean basin management. Aquatic Conservation: Marine and Freshwater Ecosystems 10(6): 437-458.

IUCN World Commission on Protected Areas (IUCN-WCPA). 2005. Parks. High Seas Marine Protected Areas, Vol 15(3). Switzerland, IUCN.

IUCN World Commission on Protected Areas (IUCN-WCPA). 2008. Establishing Marine Protected Area Networks—Making It Happen. Washington, D.C.: IUCN-WCPA, National Oceanic and Atmospheric Administration and The Nature Conservancy.

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA and Hughes TP. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530): 629-637.

Kerwath SE, Thorstad EB, Naesje TF, Cowley PD, Økland F, Wilke C and Attwood CG. 2009. Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon Marine Protected Area as a harvest refuge for a migratory fish species in South Africa. Conservation Biology 23(3): 653-661.

Koldewey HJ, Curnick D, Harding S, Harrison LR and Gollock M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. Marine Pollution Bulletin 60(11): 1906-1915.

Kovacs KM, Aguilar A, Aurioles D, Burkanov V, Campagna C, Gales N, Gelatt T, Goodman SD, Hofmeyr GJ and Härkönen T. 2012. Global threats to pinnipeds. Marine Mammal Science 28(2): 414-436.

Lack D. 1954. The natural regulation of animal numbers. The Clarendon Press, Oxford.

Lascelles BG, Taylor PR, Miller MGR, Dias MP, Oppel S, Torres L, Hedd A, Le Corre M, Phillips RA, Shaffer SA and Weimerskirch H. 2016. Applying global criteria to tracking data to define important areas for marine conservation. Diversity and Distributions 22(4): 422-431.

Lewison RL, Crowder LB, Read AJ and Freeman SA. 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology and Evolution 19(11): 598-604.

Lubchenco J, Palumbi SR, Gaines SD and Andelman S. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13(1): S3-S7.

Malone TC and Newton A. 2020. The globalization of cultural eutrophication in the coastal ocean: causes and consequences. Frontiers in Marine Science 7: 670.

Marine Conservation Institute (MCI). 2021. MPAtlas [On-line]. Seattle, WA. http://www.mpatlas.org accessed on 15 July 2021.

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH and Warner RR. 2015. Marine defaunation: Animal loss in the global ocean. Science 347(6219).

McGowan A, Broderick AC and Godley BJ. 2008. Seabird populations of the Chagos Archipelago, Indian Ocean: an evaluation of IBA sites. Oryx 42(03): 424-429.

Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). 2011. Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Myers RA and Worm B. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423: 280-283.

Norse E. 2005. Pelagic protected areas: the greatest parks challenge of the 21st century. In: IUCN World Commission on Protected Areas (IUCN-WCPA), 2005. Parks. High Seas Marine Protected Areas, Vol 15(3): 32-39. Switzerland, IUCN.

O’Leary BC, Ban NC, Fernandez M, Friedlander AM, García-Borboroglu P, Golbuu Y, Guidetti P, Harris JM, Hawkins JP, Langlois T and McCauley DJ. 2018. Addressing criticisms of large-scale marine protected areas. Bioscience 68(5): 359-370.

Parsons M, Mitchell I, Butler A, Ratcliffe N, Frederiksen M, Foster S and Reid JB. 2008. Seabirds as indicators of the marine environment. ICES Journal of Marine Science: Journal du Conseil 65(8): 1520-1526.

Pauly D, Christensen V, Dalsgaard J, Froese R and Torres Jr. F. 1998. Fishing down marine food webs. Science 279: 860-863.

Pavón-Jordán D, Azafzaf H, Balaž M, Bino T, Borg JJ, Božič L, Butchart SH, Clausen P, Sniauksta L, Dakki M and Devos K. 2020. Positive impacts of important bird and biodiversity areas on wintering waterbirds under changing temperatures throughout Europe and North Africa. Biological Conservation 246: 108549.

Piatt JF, Sydeman WJ and Wiese F. 2007. Introduction: Seabirds as indicators of marine ecosystems. Marine Ecology Progress Series 352: 199-204.

Rochman CM, Browne MA, Underwood AJ, van Franeker JA, Thompson RC and Amaral-Zettler LA. 2016. The ecological impacts of marine debris: unravelling the demonstrated evidence from what is perceived. Ecology 97: 302–312.

Sala E and Giakoumi S. 2017. No-take marine reserves are the most effective protected areas in the ocean. ICES Journal of Marine Science 75(3): 1166-1168.

Sala E, Mayorga J, Bradley D, Cabral RB, Atwood TB, Auber A, Cheung W, Costello C, Ferretti F, Friedlander AM and Gaines SD. 2021. Protecting the global ocean for biodiversity, food and climate. Nature 592(7854): 397-402.

Sanders SM. (Ed.). 2006. Important Bird Areas in the United Kingdom Overseas Territories. Sandy, UK: RSPB.

Schreiber EA and Burger J. 2001. Seabirds in the marine environment. Pages 19-34 in: Schreiber EA and Burger J. (Eds.) Biology of Marine Birds. CRC Press, Florida, USA.

Sheppard CRC, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, Fitzsimmons N, Gaither MR, Gan CH, Gollock M, Guzman N, Graham NAC, Harris A, Jones R, Keshavmurthy S, Koldewey H, Lundin CG, Mortimer JA, Obura D, Pfeiffer M, Price AR, Purkis S, Raines P, Readman JW, Riegl B, Rogers A, Schleyer M, Seaward MR, Sheppard AL, Tamelander J, Turner JR, Visram S, Vogler C, Vogt S, Wolschke H, Yang JM, Yang SY and Yesson C. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. Aquatic Conservation 22(2): 232-261.

Smith VH, Tilman GD and Nekola JC. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution 100(1): 179-196.

Sorte CJ, Williams SL and Zerebecki RA. 2010. Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91(8): 2198-2204.

Toonen RJ, Wilhelm TA, Maxwell SM, Wagner D, Bowen BW, Sheppard CR, Taei SM, Teroroko T, Moffitt R, Gaymer CF and Morgan L. 2013. One size does not fit all: the emerging frontier in large-scale marine conservation. Marine Pollution Bulletin 77(1): 7-10.

VanderWerf EA and Young LC. 2017. A Summary and Gap Analysis of Seabird Monitoring in the US Tropical Pacific. Report prepared for the US Fish and Wildlife Service, Region, 1. Portland, OR. Pacific Rim Conservation, Honolulu, HI.

VanderWerf EA and Young LC. 2018. U.S. Tropical Pacific seabird surveying guide. Report prepared for the U.S. Fish and Wildlife Service, Region 1, Portland, OR. Pacific Rim Conservation, Honolulu, HI.

Vie JC, Hilton-Taylor C and Stuart SN. (Eds.). 2008. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species. Gland, Switzerland: IUCN.

Visalli ME, Best BD, Cabral RB, Cheung WW, Clark NA, Garilao C, Kaschner K, Kesner-Reyes K, Lam VW, Maxwell SM and Mayorga J. 2020.

Data-driven approach for highlighting priority areas for protection in marine areas beyond national jurisdiction. Marine Policy 122: 1-14.

Wallace BP, DiMatteo AD, Bolten AB, Chaloupka MY, Hutchinson BJ, Abreu-Grobois FA, Mortimer JA, Seminoff JA, Amorocho D, Bjorndal KA and Bourjea J. 2011. Global conservation priorities for marine turtles. PloS ONE 6(9): e24510.

Watling L and Norse EA. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology 12: 1180-1197.

Wilhelm TA, Sheppard CR, Sheppard AL, Gaymer CF, Parks J, Wagner D and Lewis NA. 2014. Large marine protected areas – advantages and challenges of going big. Aquatic Conservation: Marine and Freshwater Ecosystems 24(S2): 24-30.

SUPPLEMENTARY MATERIAL TO CHAPTER 1

Table S1. 1. Important Bird and Biodiversity Area triggering populations of seabirds in the 14 tropical Large-Scale Marine Protected Areas (LSMPAs), their IUCN Red List category, global population, the LSMPA population's size and percentage of the global population breeding in LSMPAs (as at 2021). Taxonomy follows Billerman et al. (2021). IUCN Red List category is from https://www.iucnredlist.org/ accessed July 2021. Global and LSMPA populations are breeding pairs unless stated. Global populations are from https://www.iucnredlist.org/ and Billerman et al. (2021). LSMPA populations are from http://datazone.birdlife.org/. Percentage of global population breeding in LSMPAs is the maximum figure.

SPECIES	IUCN RED LIST CATEGORY	GLOBAL POPULATION	LSMPA POPULATION	% BREEDING POPULATION IN LSMPAs
Laysan Albatross *Phoebastria immutabalis*	NT	1,600,000 individuals	617,000	>95
Black-footed Albatross *Phoebastria nigripes*	NT	69,900	55,900	80
Kermadec Petrel *Pterodroma neglecta*	LC	150,000 – 200,00 individuals	43,500	≅ 87
Herald Petrel *Pterodroma heraldica*	LC	150,000 individuals	111,100 individuals	74
Murphy's Petrel *Pterodroma ultima*	LC	800,000 – 1,000,000 individuals	265,000	53
Henderson Petrel *Pterodroma atrata*	EN	19,987	19,987	100
Bonin Petrel *Pterodroma hypoleuca*	LC	1,000,000 individuals	315,000	63

Masatierra Petrel *Pterodroma defilippiana*	VU	2,227	2,227	100
Phoenix Petrel *Pterodroma alba*	EN	10,000	10,000	100
Bulwer’s Petrel *Bulweria bulwerii*	LC	250,000 - 500,000	90,000	18
Wedge-tailed Shearwater *Ardenna pacifica*	LC	5,200,000 individuals	566,200 – 756,200	29
Christmas Shearwater *Puffinus nativitatis*	LC	75,000	18,105 – 18,610	25
Townsend’s Shearwater *Puffinus auricularis*	CR	250 - 999	999	100
Tropical Shearwater *Puffinus bailloni*	LC	Unknown (115,0000)	2,920	2.5
Polynesian Storm-petrel *Nesofregetta fuliginosa*	EN	500	500	100
Band-rumped Storm-petrel *Hydrobates castro*	LC	150,000	20,829	13.9
Tristram’s Storm-petrel *Hydrobates tristrami*	LC	10,000	5,500	55
Red-billed Tropicbird *Phaethon aethereus*	LC	8,000 – 15,000	3,126	20.8
Red-tailed Tropicbird *Phaethon rubricauda*	LC	45,000	19,951 – 22,363	49.7
White-tailed Tropicbird *Phaethon lepturus*	LC	400,000 individuals	3,500	1.75
Lesser Frigatebird *Fregata ariel*	LC	250,000	29,597 – 31,707	12.7

Great Frigatebird *Fregata minor*	LC	700,000	10,000	1.4
Ascension Frigatebird *Fregata aquila*	VU	21,000 individuals	12,600	100
Masked Booby *Sula dactylatra*	LC	700,000	11,564 – 13,469	1.9
Nazca Booby *Sula granti*	LC	20,000	1,070	5.35
Brown Booby *Sula leucogaster*	LC	100,000	9,641 – 36,741	36.7
Red-footed Booby *Sula sula*	LC	1,000,000	43,344 – 46,120	4.6
Red-legged Cormorant *Phalacrocorax gaimardi*	NT	20,000	15	0.08
Brown Noddy *Anous stolidus*	LC	500,000	89,000	17.8
Black Noddy *Anous minutus*	LC	500,000	121,000 – 134,000	26.8
Lesser Noddy *Anous tenuirostris*	LC	120,0000	33,000	2.75
Blue Noddy *Procelsterna cerulea*	LC	100,000	10,585 – 12,085	12.1
Common White Tern *Gygis alba*	LC	100,000	29,000 – 31,000	31
Sooty Tern *Onychoprion fuscatus*	LC	2,000,0000	4,751,571	23.8
Grey-backed Tern *Onychoprion lunatus*	LC	100,000 – 1,000,000	46,600	46.6

Bridled Tern *Onychoprion anaethetus*	LC	1,000,000	12,000 – 26,000	2.6
Roseate Tern *Sterna dougallii*	LC	200,000 – 220,000	23,750	11.8
Black-naped Tern *Sterna sumatrana*	LC	Unknown	260	Unknown
Great Crested Tern *Thalasseus bergii*	LC	2,000,000	2,000 – 6,080	00.3
Lesser Crested Tern *Thalasseus bengalensis*	LC	225,000	5,228 – 24,913	11.1

Table S1. 2. Overview of Important Bird and Biodiversity Areas designated for seabirds within the 14 tropical Large-Scale Marine Protected Areas designated as of 2021. All data from http://datazone.birdlife.org/home except where referenced.

Large-Scale Marine Protected Area	Important Bird and Biodiversity Area	IBA Qualifying Species (IUCN Red-List Status)
Papahānaumokuākea Marine National Monument	HI01: North-western Hawaiian Islands	Red-tailed Tropicbird *Phaethon rubricauda* (LC) Tristram's Storm-petrel *Hydrobates tristrami* (LC) Black-footed Albatross *Phoebastria nigripes* (NT) Laysan Albatross *Phoebastria immutabalis* (NT) Bonin Petrel *Pterodroma hypoleuca* (LC) Wedge-tailed Shearwater *Ardenna pacifica* (LC) Christmas Shearwater *Puffinus nativitatis* (LC) Bulwer's Petrel *Bulweria bulwerii* (LC) Great Frigatebird *Fregata minor* (LC) Red-footed Booby *Sula sula* (LC) Masked Booby *Sula dactylatra* (LC) Brown Noddy *Anous stolidus* (LC) Black Noddy *Anous minutus* (LC) Blue Noddy *Procelsterna cerulea* (LC) Common White Tern *Gygis alba* (LC) Sooty Tern *Onychoprion fuscatus* (LC) Grey-backed Tern *Onychoprion lunatus* (LC)
Totals	1 tIBA	17
Pacific Remote Islands Marine National Monument	00000: Baker Island 00000: Howland Island	Polynesian Storm-petrel *Nesofregetta fuliginosa* (EN) Red-tailed Tropicbird *Phaethon rubricauda* (LC)

	00000: Jarvis Island 00000: Johnston Atoll 00000: Palmyra Atoll 00000: Wake Island 00000: Howland and Baker Marine 00000: Jarvis Island Marine 00000: Palmyra Atoll Marine 00000: Johnstone Atoll Marine 00000: Wake Island Marine	Red-footed Booby *Sula sula* (LC) Brown Booby *Sula leucogaster* (LC) Masked Booby *Sula dactylatra* (LC) Lesser Frigatebird *Fregata ariel* (LC) Sooty Tern *Onychoprion fuscatus* (LC) Brown Noddy *Anous stolidus* (LC) Blue Noddy *Procelsterna cerulea* (LC)
	6 tIBA + 5mIBA	7
Pitcairn Islands Marine Reserve	00000: Ducie Island 00000: Henderson Island 00000: Oeno Island	Murphy's Petrel *Pterodroma ultima* (LC) Kermadec Petrel *Pterodroma neglecta* (LC) Herald Petrel Pterodroma heraldica (VU) Henderson Petrel *Pterodroma atrata* (EN) Phoenix Petrel *Pterodroma alba* (EN) Christmas Shearwater *Puffinus nativitatis* (LC) Red-tailed Tropicbird *Phaethon rubricauda* (LC) Common White Tern *Gygis alba* (LC)
	3 tIBA	8
British Indian Ocean Territory Marine Protected Area	Eastern Diego Garcia island group Eastern Peros Banhos island group Nelson's Island Western Great Chagos Bank island group Chagos Archipelago Marine	Tropical Shearwater *Puffinus bailloni* (LC) Red-footed Booby *Sula sula* (LC) Sooty Tern *Onychoprion fuscatus* (LC) Lesser Noddy *Anous tenuirostris* (LC)
	4 tIBA + 1 proposed mIBA	4
Palau National Marine Sanctuary	PW007: Fana Island PW008: Helen Island, Hatohobei	Red-footed Booby *Sula sula* (LC) Black Noddy *Anous minutus* (LC)

	PW009: Fana Island Marine PW010: Helen Island Marine	Common White Tern *Gygis alba* (LC)
	2 tIBA + 2 mIBA	3
Ascension Exclusive Economic Zone	SH002: Boatswainbird Island SH009: Wideawake Fairs SH010: Letterbox Hill	Band-rumped Storm-petrel *Hydrobates castro* (LC) Red-billed Tropicbird *Phaethon aethereus* (LC) White-tailed Tropicbird *Phaethon lepturus* (LC) Masked Booby *Sula dactylatra* (LC) Ascension Frigatebird *Fregata aquila* (VU) Sooty Tern *Onychoprion fuscatus* (LC) Common White Tern *Gygis alba* (LC)
	3 tIBA	7
Phoenix Islands Protected Area	KI001: McKean Island KI002: Nikumaroro (Gardner Island) KI003: Abariranga (Canton Island) KI004: Orona Atoll (Hull Island) KI005: Enderbury Island KI006: Rawaki (Phoenix Island) 00000: McKean Island Marine 00000: Orona Atoll Marine 00000: Phoenix Island Marine	Polynesian Storm-petrel *Nesofregetta fuliginosa* (EN) Phoenix Petrel *Pterodroma alba* (EN) Christmas Shearwater *Puffinus nativitatis* (LC) Tropical Shearwater *Puffinus bailloni* Red-tailed Tropicbird *Phaethon rubricauda* (LC) Masked Booby *Sula dactylatra* (LC) Lesser Frigatebird *Fregata ariel* (LC) Sooty Tern *Onychoprion fuscatus* (LC) Grey-backed Tern *Onychoprion lunatus* (LC) Brown Noddy *Anous stolidus* (LC) Blue Noddy *Procelsterna cerulea* (LC)
	6 tIBA + 3mIBA	11
Nazca-Desventuradas Marine Park	CL019: Islas Desventuradas	Masatierra Petrel *Pterodroma defilippiana* (VU)
	1 tIBA	1
Coral Sea Marine Park	0000: Coringa-Herald Reefs	Wedge-tailed Shearwater *Ardenna pacifica* (LC) Red-tailed Tropicbird *Phaethon rubricauda* (LC) Red-footed Booby *Sula sula* (LC)

		Lesser Frigatebird *Fregata ariel* (LC) Black Noddy *Anous minutus* (LC)
	1 tIBA	5
Aldabra group (marine) National Park	SC012: African Banks SC014: Etoile Island SC016: Marie-Louise Island SC017: Desnoeufs Island SC019: Cosmoledo SC020: Aldabra Special Reserve	Red-tailed Tropicbird *Phaethon rubricauda* (LC) White-tailed Tropicbird *Phaethon lepturus* (LC) Red-footed Booby *Sula sula* (LC) Great Frigatebird *Fregata minor* (LC) Lesser Frigatebird *Fregata ariel* (LC) Greater Crested Tern *Thalasseus bergii* (LC) Roseate Tern *Sterna dougallii* (LC) Black-naped Tern *Sterna sumatrana* (LC) Sooty Tern *Onychoprion fuscatus* (LC) Brown Noddy *Anous stolidus* (LC) Lesser Noddy *Anous tenuirostris* (LC) Common White Tern *Gygis alba* (LC)
	6 m/tIBAs	12
Motu Motiro Hivu	00000: Isla Sala y Gómez	Polynesian Storm-petrel *Nesofregetta fuliginosa* (EN) Christmas Shearwater *Puffinus nativitatis* (LC) Red-legged Cormorant *Phalacrocorax gaimardi* (NT) Blue Noddy Procelsterna cerulea (LC)
	1 tIBA	4
Revillagigedo National Park	MX031: Islas Revillagigedo	Townsend’s Shearwater *Puffinus auricularis* (CR) Red-billed Tropicbird *Phaethon aethereus* (LC) Red-footed Booby *Sula sula* (LC) Nazca Booby *Sula granti* (LC)
	1 m/tIBA	4
Niue Moana Mahu	00000: Suwarrow Atoll National Park	Red-tailed Tropicbird *Phaethon rubricauda* (LC)

	00000: Takutea Wildlife Sanctuary 00000: Suwarrow Atoll Marine 00000: Takutea Marine	Lesser Frigatebird *Fregata ariel* (LC) Sooty Tern *Onychoprion fuscatus* (LC)
	2 tIBA + 2 mIBA	3
Great Barrier Reef Marine Park Data from: http://datazone.birdlife.org/country/australia http://www.birdlife.org.au/documents/OTHPUB-IBA-supp.pdf	00000: Brook Islands 00000: Cape York to Cape Grenville Islands 00000: Capricornia Cays 00000: Islands North of Port Stewart 00000: Michaelmas Cay 00000: Piper Islands 00000: Raine Island, Moulter and Maclennan Cays 00000: South Barnard Islands 00000: Stapleton Island 00000: Sudbury Reef 00000: Swain Reef 00000: Wilson Reef (Great Barrier Reef)	Wedge-tailed Shearwater *Ardenna pacifica* (LC) Lesser Frigatebird *Fregata ariel* (LC) Brown Booby *Sula leucogaster* (LC) Masked (Tasman) Booby *Sula dactylatra* (LC) Brown Noddy *Anous stolidus* (LC) Black Noddy *Anous minutus* (LC) Bridled Tern *Onychoprion anaethetus* (LC) Roseate Tern *Sterna dougallii* (LC) Greater Crested Tern *Thalasseus bergii* (LC) Lesser Crested Tern *Thalasseus bengalensis* (LC)
	12 tIBA	10

CHAPTER 2

STUDY SYSTEM

The British Indian Ocean Territory (Chagos Archipelago)

The CA lies at the southern end of the Lakshadweep-Maldives-Chagos ridge that was formed as the Indian subcontinent moved northwards from Early Cretaceous time (*c.*130 Ma BP) passing over a volcanic hot-spot, the oldest rocks thought to be formed in this movement being the Deccan traps in western India. The CA is in the geographical centre of the tropical Indian Ocean stretching approximately 240 km north to south and 140 km east to west within a latitude and longitudinal box bounded by 05°15’ - 07°27’S and 71°15’ - 72°30’E (Fig. 2.1) (Eisenhauer et al. 1999).

There are five islanded atolls in the CA comprising of Diego Garcia in the south, the Solomons and Peros Banhos in the north, the Egmonts (historically called the Six Islands) in the southwest, whilst the centre holds the largest submerged atoll in the world, the Great Chagos Bank. The atoll rims have 55 islands and islets on them.

The terrestrial component of the CA comprises of an area slightly < 1% of the *c.* 640,000 km^2 of the total area. The island of Diego Garcia at 2,719.5 ha. is an order of magnitude larger than its nearest contender, Eagle Island on the western rim of the Great Chagos Bank at 243.5 ha. (Sheppard et al.1999, Symens 1999). The islands are those of typical atolls, located on the rims with a low elevation of generally < 2 m (Sheppard et al. 1999). The CA is one of the most intense sources of oceanic seismicity apart from the conventionally defined plate boundaries. This has resulted in at least one submerged island in Peros Banhos; the small (6 ha.) raised island of North Brother (3-4 masl) and two tiny (≈ 0.5 ha.) atypical, raised limestone rocks, Coin du Mire in southern Peros Banhos and Resurgent in the Three Bothers group (Symens 1999, Eisenhauer et al. 1999 and references therein).

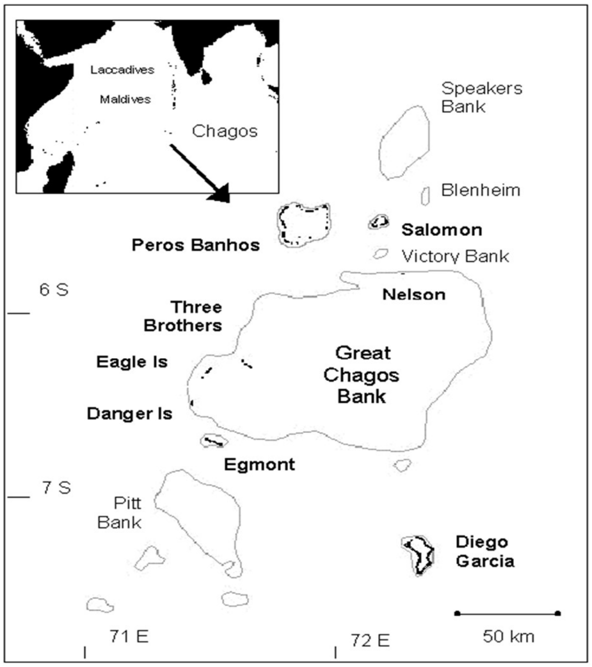


Figure 2. 1. The British Indian Ocean Territory (Chagos Archipelago).

Underwater, there are the prominent (> 20 km^2) completely submerged reefs and banks of Speaker's and Victory in the north and Pitt, Ganges and Centurion in the southwest. Blenheim Reef northwest of the Solomons is emerged at low tide and it is reported that in the 1700s it had three vegetated islands (Sheppard et al. 2012). There are also numerous pinnacles, seamounts and knolls, especially to the west of the Great Chagos Bank with an abyssal plain to the east (Sheppard et al. 2012). To the east of the Great Chagos Bank running north-south is the dominant feature of the Chagos Trench that drops to at least 5,904 m that has had a novel bacterium discovered in its depths (Bhadra et al. 2008).

The first claim of sighting of any island of the CA comes from Portuguese mariners in the sixteenth century. It was over 200 years later that it became continuously inhabited by man in the 1780s. Over the ensuing centuries, the economy of the entire archipelago has been dominated by the growing and harvesting of coconuts *Cocos nucifera*, principally to produce copra oil. This industry declined throughout the 20th century. Other short-lived and less successful economic ventures have included whaling, a coaling station, guano mining and exporting native hardwood timber (Scott 1961, Edis 1994, Wenban-Smith and Carter 2018).

The military have had a long association with the CA. The first British settlers in 1786 were accompanied by military personnel. Royal Navy hydrographers have been amongst those who have charted the archipelago's seas and mapped the islands and the 20th century saw a British military presence based on the largest island, Diego Garcia, particularly during World War II, which included the Royal Air Force and Royal Marines (Edis 1994, Wenban-Smith and Carter 2018). Since the Exchange of Notes (EoN) in 1966 between the United Kingdom and the United States of America, all the islands and seas of the CA have been given over to the defence needs of both Governments. This EoN resulted in the final closure of the coconut plantations, the clearing of all the islands of their inhabitants, the creation of a military support facility on Diego Garcia and the renaming of the CA as the British Indian Ocean Territory (BIOT). The 1966 EoN was renewed in 2016 and the Territory will remain dedicated to defence purposes for a further 25 years (http://www.fco.gov.uk accessed 19 March 2021).

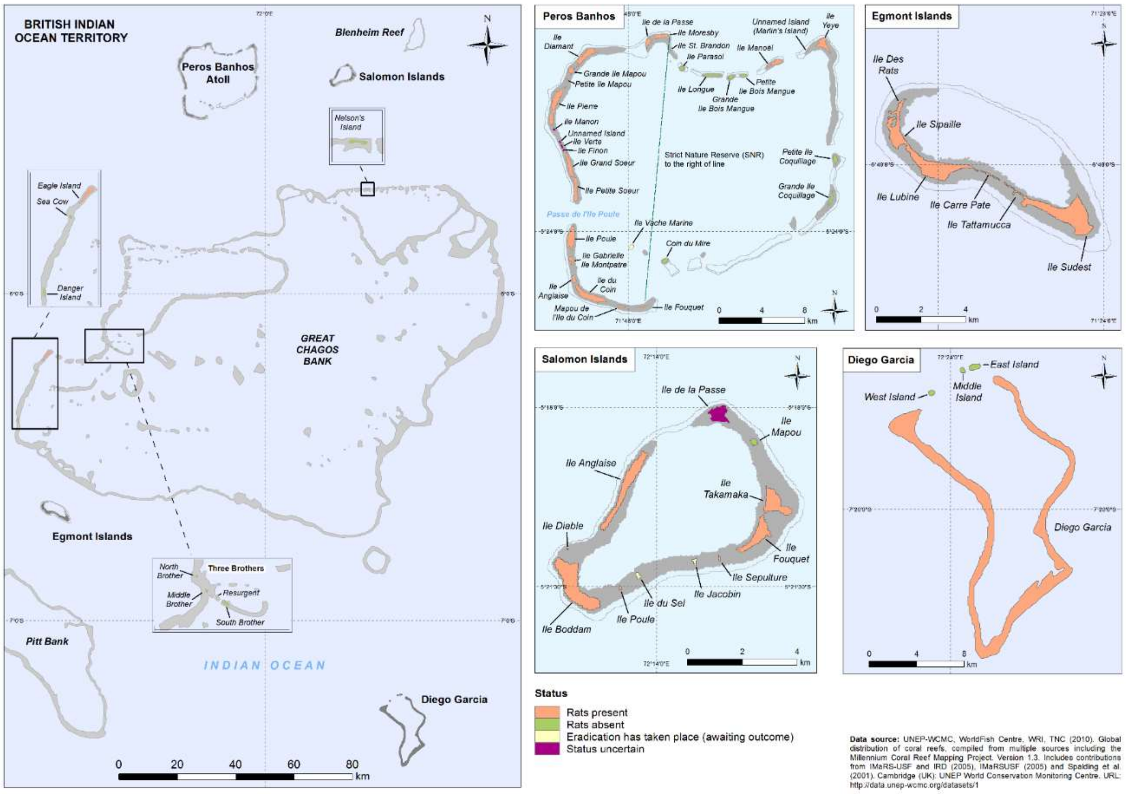
Presently, the CA remains a British Overseas Territory and as such has its own government, the BIOT Administration (BIOTA), a department of the United Kingdom Foreign and Commonwealth and Development Office in London. It has a British Representative to the Commissioner, a Royal Navy officer based on Diego Garcia who administrates on behalf of BIOTA. There is a small UK military contingent based on Diego Garcia who perform military and civic duties (principally Police and Customs) along with US military personnel and supporting contractors, the number of which varies depending upon active US military operations being supported from the island.

The Impact of Man on the Chagos Archipelago Environment

The devastating impact of man's presence on the terrestrial environment of the CA is principally due to the replacement of native forest with coconut groves (Stoddart and Taylor 1971; Bourne 1971; Clubbe 2010; Carr 2011a); the introduction of invasive plants (Topp and Sheppard 1999; Clubbe 2010) and the introduction of invasive mammalian predators. In the case of the CA, the main invasive mammalian predators have been humans *Homo sapiens*, cats *Felis catus*, dogs *Canis lupus familiaris*, pigs *Sus scrofa domesticus* and Black/Ship Rats *Rattus rattus* (hereafter rats) (Scott 1961, Bourne 1971, Edis 1993, Symens 1999, Hilton and Cuthbert 2010, Harper et al. 2019). The two historic anthropogenic factors that are still negatively impacting the environment is the introduction of invasive rats and the clearing of native forest for coconut groves that are now abandoned and unmanaged due to the cessation of the plantation regimes (Carr et al. 2013).

Although direct anthropogenic pressure on seabirds, e.g., collecting of adults, chicks and eggs for food; guano extraction and habitat destruction, (Bourne GC 1886, Bourne WRP 1971, Edis 1993) has all but ceased, the catastrophic legacy of rat introduction lives on. Symens (1999) assessed that 11 islands of the 45 he visited were rat free and that the nest density on most rat-infested islands was significantly lower than on rat-infested islands. Hilton and Cuthbert (2010), using Symens' data, calculated that 4.7% of the CA was invasive mammalian predator free. Latterly, the RSPB (2014) prioritised Ile de la Passe 25th in an assessment of eradication benefit to islands within the UK Overseas Territories (see Carr et al. 2013 for counter arguments). Harper et al. (2019) reassessed the distribution of rats in the CA based on over ten years of observations and trapping (by Carr) and following the successful eradication of rats from three islands. They concluded that of the 55 islands, rats are present on 26, absent from at least 20 and their status uncertain on the remaining nine (Fig. 2.2). Subsequent research has demonstrated that as of 2021 there are rats present on 30 islands, absent from 24 and their status remains uncertain on one, equating to ≈ 94% of the terrestrial landmass being rat-infested (Carr et al. 2021b).

Of the other invasive mammalian predators introduced by man it is believed that only feral cats remain on one island, Diego Garcia. Intense control measures since 2002 have reduced this population from > 6,000 individuals to < 50 (Vogt et al. 2015).



Data source: UNEP-WCMC, WorldFish Centre, WRI, TNC (2010). Global distribution of coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 1.3. Includes contributions from IMaRS-USF and IRD (2005), IMaRSUSF (2005) and Spalding et al. (2001). Cambridge (UK): UNEP World Conservation Monitoring Centre. URL: http://data.unep-wcmc.org/datasets/1

Figure 2. 2. Black Rat *Rattus rattus* distribution in the Chagos Archipelago. (Reproduced from Harper et al. 2019, with the permission of the authors).

Climate

The climate of the CA is governed primarily by the seasonal migration north and south across the area of a zone of equatorial westerlies separating the north-west and Southeast Trade winds. The zones of convergence between the equatorial westerlies and the trades form shear zones with unsettled and often squally weather (Stoddart 1971a). Four wind seasons have been identified: First, during December - March winds are variable but mainly westerly, these are most pronounced in February when easterly winds are near absent. This is followed in April – May by transitional conditions with the westerlies weakening and the south-easterlies becoming more important. Next, during June – September the South-east Trades blow, with the dominant direction being 120 - 150°, come September the trades begin to weaken and spread from east round to south. Finally, October – November represents a second transitional period with variable winds though still concentrated at 90 - 120°. By December, season one is again established, with approximate co-dominance of easterlies and westerlies (Stoddart 1971a). Because of the low latitude, tropical cyclones are rare, though maverick cyclones do occur and can cause substantial damage such as the one that passed through Diego Garcia the night of 15/16 September 1944 (Edis 2004).

The temperature regime follows the seasonal wind pattern. During the period of equatorial westerlies and calms, temperatures are higher than during the Trades. Mean monthly temperature varies from a maximum of 30.75°C in March to a minimum of 28.03°C in August, an annual range of 2.7°C (Stoddart 1971a).

The CA has the highest annual rainfall totals of all Indian Ocean atolls. Rainfall distribution is approximately bimodal, (generally) with peaks in January-February and October. Variability is high, especially on Solomon and Peros Banhos atolls (Stoddart 1971b). Figure 2.3 shows the annual rainfall distribution from the southern atoll of Diego Garcia in 2009, demonstrating the variability in precipitation referred to by Stoddart (1971b). The atolls of the CA are the only Indian Ocean atolls where completely dry months do not occur. Very high monthly totals are frequently recorded, with a maximum rainfall of 1,037 mm in June 1952 - the second highest monthly total recorded on an Indian Ocean coral island - the highest being 2,208 mm in January 1965 at Cocos-Keeling Atoll (Stoddart 1971b).

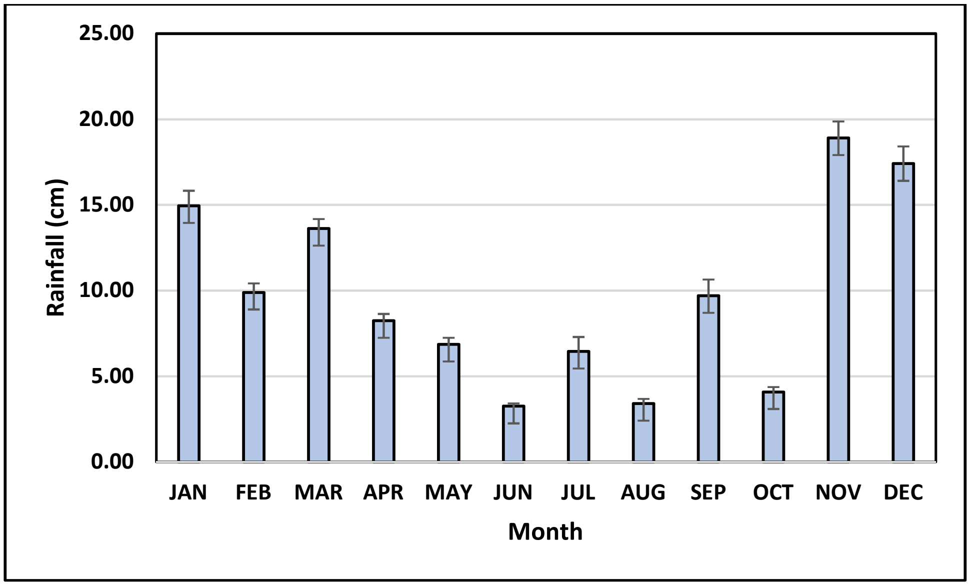


Figure 2. 3. Mean monthly rainfall (cm) on Diego Garcia in 2014 (data supplied by NSF Diego Garcia METOC). Error bars are standard deviation.

The British Indian Ocean Territory (Chagos) Marine Protected Area

On the 1st April 2010, the United Kingdom Foreign Secretary announced that the British Indian Ocean Territory was to be a no-take marine protected area where commercial fishing will be banned. This was executed in the name of the Queen in Proclamation Number 1 of 2010. Diego Garcia atoll to its three nautical mile boundary is excluded. At the time of declaration, the BIOT MPA at ≈ 640,000 km^2 was the largest no-take marine reserve on the planet.

The enforcement of the no-take policy is undertaken by the BIOT Patrol Vessel with the physical policing being undertaken by a Senior Fisheries Patrol Officer (SFPO - presently supplied by the Marine Resources Assessment Group). On a regular basis the SFPO is augmented by armed UK military personnel, police and customs. The military perform sovereignty duties while the police and customs check on the small number of yachts that are permitted to visit designated areas of Peros Banhos and the Solomon Islands.

Seabirds of the Chagos Archipelago

There has been no funded, structured long-term monitoring programme implemented of the internationally important seabird populations, though temporally and spatially limited censuses of the breeding seabirds occurred in 1974/75 (Baldwin 1975), February/March 1996 (Symens 1999) and March 2006 (McGowan et al. 2008).

Eighteen species of seabird are now known to breed in the CA (Carr 2011b). All 18 species are of Least Concern on the IUCN Red List of Threatended Species and occur throughout the western Indian Ocean (https://www.iucnredlist.org/en accessed 25 October 2021). Historically, there is evidence that seabird populations were much wider distributed across the archipelago and of greater abundance. For example, Bourne (1886) recorded "tens of thousands" of Sooty Tern *Onychoprion fuscatus* breeding on Diego Garcia in the late 19th Century, this species is now extinct as a breeding species on this atoll and is restricted to breeding only on the rat-free islands of the CA (Carr et al. 2021a) Edis (2004) states that "….from the mid-1950s guano for fertiliser was dug at the north-west end of the island (of Diego Garcia), carted to shore by tractors….", indicating extensive seabird colonies across the island. There appears no reason why such colonies did not exist across all islands of the archipelago.

Bourne (1971) states the decline in CA breeding seabird populations occurred following the colonisation by man in the late 18th Century. This resulted in the direct persecution of adult birds, nestlings and eggs for food; destruction of breeding habitat, mainly through the clearance of native habitats for coconut plantations and; the introduction of alien, invasive species. Direct persecution of seabirds has all but ceased following the removal of humans from all islands except Diego Garcia in the early 1970s (Edis 2004). However, the catastrophic legacy of invasive species remains extant and severely impacts the islands that seabirds breed on throughout the CA (Carr et al. 2021b).

Post the human depopulation of the northern atolls of the CA, the numbers of breeding seabirds remains dynamic. Three species (White-tailed Tropicbird *Phaethon lepturus,* Roseate Tern *Sterna dougallii* and Little Tern *Sternula albifrons*) have tiny (≥ 5 pairs/annum) breeding populations or do not breed annually and therefore their population dynamics cannot be assessed (Carr et al. 2021a). There appears to have been an inexplicable decline in Brown Noddy *Anous stolidus* since the 1970s (Baldwin 1975, McGowan et al. 2008, Carr et al. 2021a), yet, an increase in distribution and abundance of Brown Booby *Sula leaucogaster* and RfB (Carr et al. 2021a). Other breeding populations appear stable (Carr et al. 2021).

The most abundant large, easily recognised seabird that breeds in all months on all atolls on both rat-free and rat-infested islands throughout the archipelago is RfB. Therefore, RfB was selected as the focal breeding seabird of this thesis. It is a pantropical breeding species with a global breeding population estimated at well over 1,000,000 pairs (Carboneras et al. 2018). The global population is thought to be declining owing to habitat loss, predation by invasive species and unsustainable levels of exploitation (BirdLife International 2018). In the tropical Indian Ocean, the population decline is primarily through loss of breeding colonies (Feare 1982) though where they are left unmolested such as in the BIOT MPA, breeding populations are increasing in distribution and abundance (Carr 2011b).

The RfB is a highly polymorphic species with three recognised subspecies; *S. s. rubripes* is the form occurring in the central Indian Ocean. Sub-specific classification is complicated due to its selectively un-penalised polymorphism; *S.s. rubripes* is the lightest and longest winged of all the Sulids (Nelson 1978) and in the CA, > 99% of the population are the all-white morph (Carr 2011b). It is sexually reverse size dimorphic, females being larger than males though not to the extent of other Sulid species (Nelson 1978).

Throughout its range, RfB nests on small or very small oceanic islands or peninsulas of larger islands and never on large land masses (Nelson 1978). It invariably nests in trees or on shrubs with exceptions on treeless islands where it will nest on cliffs, walls, and buildings or by exception the ground (Nelson 1978 and references therein). It is a gregarious breeder that can form large colonies e.g., 140,000 breeding pairs on Genovesa, Galapagos (Carboneras et al. 2018). Breeding can occur anytime throughout the year and even in individual colonies there is often a wide spread of laying dates (Carr et al. 2021). It lays a single egg in a loosely woven stick nest. Incubation varies by location but is generally *c*. 45 days. Fledgling period is 100–139 days with a post-fledging period where the offspring is still fed daily by the parents lasting *c*. 190 days (Carboneras et al. 2018).

The diet consists of mainly flying-fish (Exocoetidae) and squid (Ommastrephidae) caught by plunge-diving; flying-fish are also taken in flight (Carboneras et al. 2018). In the central Indian Ocean, it is a near-obligate associate of tuna species (Thunnini) that drive prey to the surface and it typically feeds in flocks, often in association with other pelagic species such as shearwaters and Brown Noddy *Anous stolidus* (P. Carr, pers. obs.).

Study Site Summary

Its' remoteness and lack of human disturbance provide a sanctuary on land for breeding seabirds on rat-free islands (Carr et al. 2021a, 2021b). The no-take status of the MPA substantially reduces the at-sea threats (Dias et al. 2019) applicable to tropical seabirds (Hays et al. 2020, Carr et al. 2021c). RfB is an iconic species in the CA. It is (re)colonising depopulated islands and atolls, is an easily recognisable centralised breeder that breeds throughout the year. It is a robust species that does not appear to desert its' breeding colonies due to scientific research activities. RfB is an excellent focal species to assess the use of a large-scale MPA by seabirds (Chapter 5, Carr et al. 2021c) and the the CA and associated BIOT MPA provide an ideal stude site (Hays et al. 2020).

REFERENCES

Baldwin EA. (Ed.). 1975. Report on the Joint Services Expedition to Danger Island 1975. MOD internal Publication, London.

Bhadra B, Raghukumar C, Pindi PK and Shivaji S. 2008. *Brevibacterium oceani* sp. *nov*., isolated from deep-sea sediment of the Chagos Trench, Indian Ocean. International Journal of Systematic and Evolutionary Microbiology 58(1): 57-60.

BirdLife International. 2018. Species factsheet: *Sula sula*. http://www.birdlife.org/ accessed 16 March 2018.

Bourne GC. 1886. General Observations on the fauna of Diego Garcia. Proceedings of the Zoological Society of London 1886: 331-334.

Bourne WRP. 1971. The Birds of the Chagos Group, Indian Ocean. Atoll Research Bulletin 149: 175-207.

Carboneras C, Christie DA, Jutglar F, Garcia EFJ and Kirwan GM. 2018. Red-footed Booby (*Sula sula*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E. (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/52624/ accessed 16 March 2018.

Carr P. 2011a. Important Bird Areas: The British Indian Ocean Territory. British Birds 104: 642-659.

Carr P. 2011b. Birds of the British Indian Ocean Territory. Published by Pisces Publications for the RSPB. Sandy, Bedfordshire, England.

Carr P, Hillman JC, Seaward MRD, Vogt S and Sheppard CRC. 2013. Coral Islands of the British Indian Ocean Territory (Chagos Archipelago). Pages 271–282 in: Sheppard CRC (Ed.). Coral Reefs of the United Kingdom Overseas Territories, Coral Reefs of the World 4, © Springer Science+Business Media Dordrecht.

Carr P, Votier S, Koldewey H, Godley B, Wood H, Nicoll MAC. 2021a. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Carr P, Trevail A, Bárrios S, Clubbe C, Freeman R, Koldewey HJ, Votier SC, Wilkinson T & Nicoll MAC. 2021b. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. Restoration Ecology .e13386.

Carr P, Trevail A, Koldewey HJ, Sherley R, Votier SC, Wilkinson T and Nicoll MAC. 2021c. Marine Important Bird and Biodiversity Areas in the Chagos Archipelago. Bird Conservation International. Submitted 07 July 2021.

Clubbe CP. 2010. Trouble in Paradise. Conservation (Kew Winter) 31-35.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Edis R. 2004. Peak of Limuria. The story of Diego Garcia and the Chagos Archipelago. Second edition. Chagos Conservation Trust, London.

Eisenhauer A, Heiss GA, Sheppard CRC and Dullo WC, 1999. Reef and island formation and Late Holocene sea-level changes in the Chagos islands. Pages 21–31 in: Sheppard CRC and Seaward MRD. (Eds.). Ecology of the Chagos Archipelago. The Linnean Society Occasional Publications, Westbury Academic and Scientific Publishing, Otley.

Feare CJ. 1982. Seabird status and conservation in the tropical Indian Ocean. In: Croxall JP, Evans PGH and Schreiber RW. (Eds.). Status and conservation of the world’s seabirds. ICBP Technical Publications No. 2.

Harper GA, Carr P and Pitman H. 2019. Eradicating black rats from the Chagos – working towards the whole archipelago. Pages 26–36 in: Veitch CR, Clout MN, Martin AR, Russell JC and West CJ. (Eds.). Island Invasives: Scaling up to meet the challenge. Occasional Paper SSC no 62. Gland, Switzerland: IUCN.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Pilly SS, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MAC, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard CRC, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier SC, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H and Curnick DJ. 2020. A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key challenges. Marine Biology 167(11): 1-22.

Hilton GM and Cuthbert RJ. 2010. The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. Ibis 152: 443-458.

McGowan A, Broderick AC and Godley BJ. 2008. Seabird populations of the Chagos Archipelago: an evaluation of Important Bird Area sites. Oryx 42(3): 424-429.

Nelson JB. 1978. The Sulidae: Gannets and Boobies. Oxford University Press.

RSPB. 2014. Eradication of Invasive Alien Vertebrates in the UK Overseas Territories. RSPB, Sandy, UK.

Scott R. 1961. Limuria. The Lesser Dependencies of Mauritius. Oxford University Press, London.

Sheppard CRC, Seaward MRD, Klaus R and Topp JMW. 1999. The Chagos Archipelago: an introduction. Pages 1–20 in: Sheppard CRC and Seaward MRD. (Eds.). Ecology of the Chagos Archipelago. The Linnean Society Occasional Publications, Westbury Academic and Scientific Publishing, Otley.

Sheppard CRC, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Elbe J, Fitzsimmons N, Gaither MR, Gan H-C, Gollock M, Guzman N, Graham NAJ, Harris A, Jones R, Keshauvmurthy S, Koldewey H, Lundin CG, Mortimer JA, Obura D, Pfeiffer M, Price ARG, Purkis S, Raines P, Readman JW, Riegl B, Rogers A, Schleyer M, Seaward MRD, Sheppard ALS, Tamelander J Turner JR, Visram S, Vogle, C, Vogt S, Wolschke H, Yang JM-C, Yang S-Y and Yesson C. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. National Institute of Health, Public Access pp1-53.

Stoddart DR. 1971a. Diego Garcia climate and marine environment. In: Stoddart DR and Taylor JD. (Eds.). Geography and Ecology of Diego Garcia Atoll, Chagos Archipelago. Atoll Research Bulletin 149: 27-30.

Stoddart DR. 1971b. Rainfall on Indian Ocean coral islands. Atoll Research Bulletin 147: 1-21.

Stoddart DR and Taylor J. (Eds.).1971. Geology and ecology of Diego Garcia atoll, Chagos Archipelago. Atoll Research Bulletin 149: 1-237.

Symens P. 1999. Breeding seabirds of the Chagos Archipelago. Pages 257–272 in: Sheppard CRC and Seaward MRD. (Eds.). Ecology of the Chagos Archipelago. The Linnean Society Occasional Publications, Westbury Academic and Scientific Publishing, Otley.

Topp JMW and Sheppard CRC. 1999. Higher Plants of the Chagos Archipelago. Pages 225-240 in: Sheppard CRC and Seaward MRD. (Eds.). Ecology of the Chagos Archipelago. Linnean Society Occasional Publications 2, Westbury Publishing.

Vogt S, Guzman AN and Necessario E. 2015. Feral cat control on Diego Garcia: current population estimate, evaluation and recommendations. Appendix J. Diego Garcia Integrated Natural Resources Management Plan (DGINRMP), Naval Facilities Engineering Command, Pacific (NAVFACPAC), for the United States (U.S.) Navy Support Facility (NSF) Diego Garcia.

Wenban-Smith N and Carter M. 2017. Chagos: A History. Chagos Conservation Trust, London.

CHAPTER 3

STATUS AND PHENOLOGY OF BREEDING SEABIRDS AND A REVIEW OF IMPORTANT BIRD AND BIODIVERSITY AREAS IN THE BRITISH INDIAN OCEAN TERRITORY

Chapter published as:

Carr P, Votier SC, Koldewey HJ, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

ABSTRACT

Seabirds are one of the most threatened avian taxa and are hence a high conservation priority. Managing seabirds is challenging, requiring conservation actions at sea (e.g., Marine Protected Areas - MPAs) and on land (e.g., protection of breeding sites). Important Bird and Biodiversity Areas (IBAs) have been successfully used to identify sites of global importance for the conservation of bird populations, including breeding seabirds. The challenge of identifying suitable IBAs for tropical seabirds is exacerbated by high levels of dispersal, aseasonal and asynchronous breeding. The western Indian Ocean supports ~19 million breeding seabirds of 30 species, making it one of the most significant tropical seabird assemblages in the world. Within this is the British Indian Ocean Territory (BIOT), encompassing 55 islands of the CA, which supports 18 species of breeding seabird and one of the world's largest no-take MPAs. Between January and March in 1975 and 1996, eight and 45 islands respectively were surveyed for seabirds and the data used to designate 10 islands as IBAs. A further two were proposed following an expedition to 26 islands in February/March 2006. Due to the historic and restricted temporal and spatial nature of these surveys, the current IBA recommendations may not accurately represent the archipelago's present seabird status and distribution. To update estimates of the BIOT breeding seabird assemblage and reassess the current IBA recommendations, I used seabird census data collected in every month except September from every island, gathered during 2008-2018. The maximum number of breeding seabirds for a nominal year was 281,596 pairs of 18 species, with three species making up 96% - Sooty Tern *Onychoprion fuscatus* (70%), Lesser Noddy *Anous tenuirostris* (18%) and RfB (8%). Phenology was a complex species-specific mix of synchronous and asynchronous breeding, as well as seasonal and aseasonal breeding. Nine of the 10 designated IBAs and the two proposed IBAs qualified for IBA status based on breeding seabirds. However, not every IBA qualified each year because Sooty Terns periodically abandoned breeding islands and Tropical Shearwater *Puffinus bailloni* breeding numbers dropped below IBA qualifying criteria in some years. Further, one survey per year does not always capture the periodic breeding of

some tropical seabirds. I propose therefore, that IBAs in BIOT are better designated at the island cluster level rather than by specific island and require two surveys six months apart per year. This work highlights the merits of long-term, systematic, versus incidental surveys for breeding tropical seabirds and the subsequent associated designation of IBAs.

INTRODUCTION

The global health of the ocean is under severe pressure from anthropogenic intervention (Jackson 2008, Game et al. 2009), with profoundly negative consequences for marine biodiversity. Marine megafauna has been particularly negatively impacted (McCauley et al. 2015) and of these seabirds (Phaethontiformes, Sphenisciformes, Procellariiformes, Suliformes, Laridae, Stercorariidae and Alcidae) are more threatened than other comparable groups of birds (Croxall et al. 2012). At sea, the greatest threat is from bycatch (Dias et al. 2019), as well as competition with fisheries (Sherley et al. 2018) and pollution (Votier et al. 2005). On land, the principal threat is from alien invasive predators (Hilton and Cuthbert 2010, Dawson et al. 2015, Dias et al. 2019), as well as habitat degradation (Croxall et al. 2012), hunting and trapping (Dias et al. 2019) and disturbance (Burger and Gochfeld 1994, Carney and Sydeman 1999, Dias et al. 2019).

Internationally significant breeding sites for seabirds have been identified globally through terrestrial Important Bird and Biodiversity Areas (Donald et al. 2019). At sea, Marine Protected Area (MPAs) are part of a suite of tools available to combat the rapid depletion of seabirds and other marine megafauna (McCauley et al. 2015), especially if they are "no-take" reserves (Koldewey et al. 2010). In the Tropics, 14 large-scale MPAs > 100,000 km^2 have been designated (http://www.mpatlas.org accessed 16 July 2021) and these surround 49 terrestrial IBAs (tIBAs) that have at least one breeding seabird as their qualifying species (data from http://www.datazone.birdlife.org accessed 16 July 2021). Although none of the 14 large-scale MPAs were designated specifically for seabirds, where MPAs are no-take and the seabird breeding sites in them are in protected IBAs, it provides a very powerful conservation tool.

Despite tropical MPAs being an important seabird conservation tool, there has been little published on seabird status and distribution within them. This is likely due to a combination of their recent creation (of the 14 large-scale tropical MPAs designated to date only one, the Great Barrier Reef Marine Park was designated in the 20th Century) and therefore a lack of data from long-term studies (Maxwell et al. 2014), remoteness (VanderWerf and Young 2018), immense size (Maxwell and Morgan 2012) and the logistical challenges of monitoring them (Wilhelm et al. 2014). In addition, tropical seabirds can present unique challenges to census work (VanderWerf and Young 2017) due to aseasonal and asynchronous breeding (Lack 1954, Nelson 1978), secretive and/or nocturnal breeding (Newman et al. 2009), inaccessible breeding areas (VanderWerf and Young 2018), extensive potential breeding sites and in some cases small, mobile breeding populations. This has resulted in at least some of the large-scale tropical MPAs having the tIBAs situated within them designated based upon *ad hoc* data (e.g., Brooke 2006, Carr 2006) rather than comprehensive multi-year data sets. However, designation of tIBAs based upon spatially and temporally limited data may be necessary as a pragmatic, but limited solution to initiate the identification of hitherto unrecognised priority sites (BirdLife International 2004).

In 2010 the CA was designated, at that time, as the world's largest no-take MPA (Fig. 3.1 - https://biot.gov.io/environment/marine-protected-area/ accessed 6 March 2019). The MPA includes the 55 islands of the CA, 10 of which are designated as tIBAs (BirdLife International 2004, Carr 2006) and a further two have been proposed (McGowan et al. 2008) (Table 3.1, Fig. 3.1 - Nelson's Island, Figs. 3.2 and 3.3 - all other IBAs). The initial designation of 10 IBAs was based on two spatially and temporally limited breeding seabird censuses from eight islands in January/March 1975 (Baldwin 1975) and 45 islands in February/March 1996 (Symens 1999), with revisions to these designations proposed following a census of 26 islands in March 2006 (McGowan et al. 2008). Due to the time elapsed and the limited spatial and temporal nature of the censuses, they may not have captured the true, present day status and distribution of breeding seabirds in BIOT.

Table 3. 1. Designated and proposed terrestrial Important Bird and Biodiversity Areas of the Chagos Archipelago as at 2018.

IBA	Criteria of designated status (from BirdLife International 2004, Carr 2006)	Criteria of proposed status (from McGowan et al. 2008)
IO001 Barton Point Nature Reserve, Diego Garcia	A4ii Red-footed Booby (16,067); A4iii > 10,000 pairs of seabirds	A4ii Red-footed Booby (4061) retain A4iii
IO002 Danger Island	A4i Brown Noddy (11,100); A4ii Red-footed Booby (3,470); A4iii > 20,000 waterbirds	Not surveyed in 2006, retain until next survey
IO003 Sea Cow	A4i Brown Noddy (11,500); A4iii > 20,000 waterbirds	Failed to requalify; retain until annual monitoring implemented
IO004 North Brother	A4ii Tropical (Audubon's) Shearwater (420); A4iii > 10,000 pairs of seabirds	A4ii Tropical (Audubon's) Shearwater (183); retain A4iii
IO005 Middle Brother	A4i Sooty Tern (12,500); A4iii > 20,000 waterbirds	Failed to requalify; retain until annual monitoring implemented
IO006 South Brother	A4i Lesser Noddy (7,300); A4i Brown Noddy (6,100); A4iii > 20,000 waterbirds	Failed to requalify; retain until annual monitoring implemented
IO007 Nelson's Island	A4i Lesser Noddy (13,700); A4i Brown Noddy (8,300); A4iii > 20,000 waterbirds	Not surveyed in 2006, retain until next survey
IO008 Petite Bois Mangue	A4i Lesser Noddy (12,000); A4iii > 20,000 waterbirds	A4i Sooty Tern (9,186); A4iii > 20,000 waterbirds
IO009 Parasol	A4i Sooty Tern (14,000); A4iii > 20,000 waterbirds	A4i Sooty Tern (9,186); A4iii > 20,000 waterbirds
IO010 Longue	A4i Sooty Tern (32,000); A4iii > 20,000 waterbirds	Failed to requalify; retain until annual monitoring implemented
Proposed, Petite Coquillage		A4i Sooty Tern (34,669); A4iii > 20,000 waterbirds
Proposed, Grande Coquillage		A4i Sooty Tern (15,429); A4iii > 20,000 waterbirds

Since 2008, breeding seabirds in CA have been monitored annually, including intra-annual repeat surveys and during this period every island has been surveyed at least once. Eighteen species of seabird breed in the CA (Carr 2011), all of which are of Least Concern on the IUCN Red List (https://www.iucnredlist.org/ accessed 16 July 2021). The long-term nature of these surveys has enabled me to overcome previous sampling limitations. Here I update the status and distribution of breeding seabirds in CA, describe their breeding phenology and then assess whether the present designation and delimitation of tIBAs effectively captures the conservation requirement.

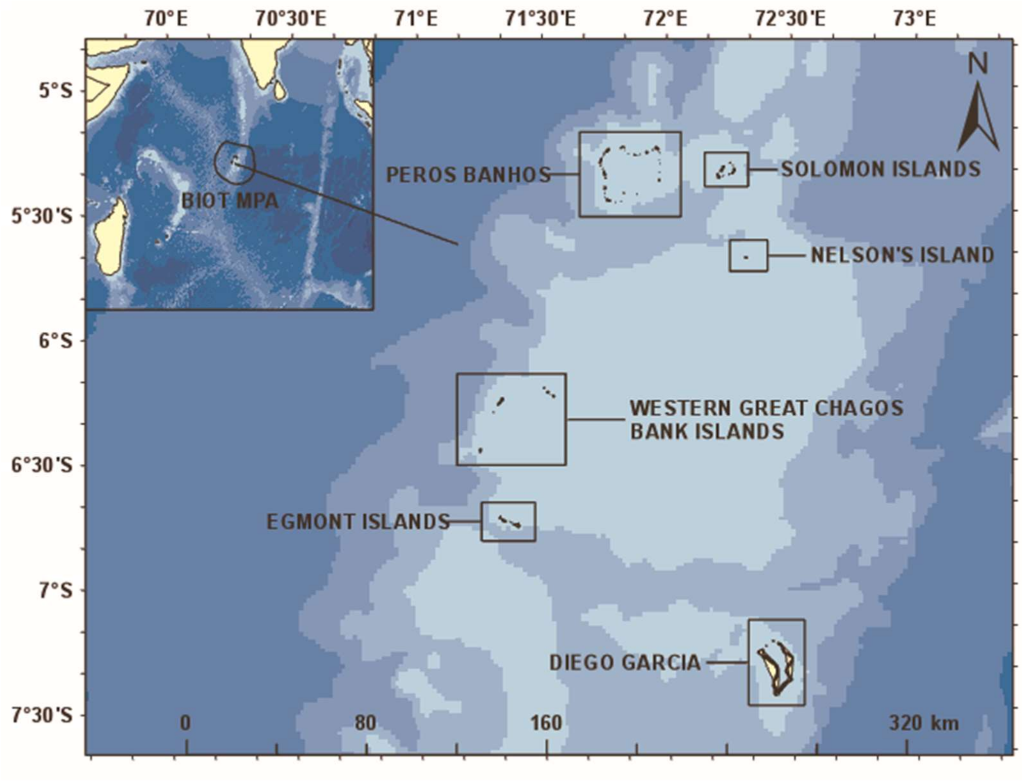


Figure 3. 1. The British Indian Ocean Territory (BIOT) Marine Protected Area in an Indian Ocean context showing major atolls and islands.

METHOD

Study Site

The CA is a United Kingdom Overseas Territory situated in the central Indian Ocean. It totals ≈ 644,000 km^2 of which ≈ 60 km^2 is permanently above the high-water mark (Sheppard et al. 1999). Declared in 2010, the BIOT MPA encompasses the entire Territory and is an IUCN category 1a. strict no-take marine reserve. Except for a UK/US Naval Support Facility on Diego Garcia, CA has been uninhabited since 1974 (Edis 1994, Wenban-Smith and Carter 2017). Historically, native forests were cleared (Bourne 1971) and invasive alien predators introduced (Symens 1999, Wenban-Smith and Carter 2017). Of those remaining, the Black Rat (*Rattus rattus*) is the most pervasive being present on 30 islands totalling 94% of the BIOT landmass (Carr and Harper 2015, Harper et al. 2019). The archipelago is made up of five atolls, Diego Garcia, Egmont Islands, Great Chagos Bank, Peros Banhos and the Salomon Islands (Fig. 3.1). The rat-free islands of the Great Chagos Bank and north-eastern Peros Banhos (Figs.3.2 and 3.3) are of the greatest importance to breeding seabirds. The rat-infested, deforested atolls of the Egmonts and Solomons (except the island of Mapou) and the islands of western Peros Banhos are ecologically devastated and will not support large colonies of breeding seabirds in their present environmental condition. The rat-infested island of Diego Garcia is an anomaly, as it supports an extensive colony of RfB in its remaining oceanic island rainforest (this study).

Breeding Seabird Status and Distribution

Between November 2008 – November 2010, every island of BIOT was censused at least once for breeding seabirds. This period was used to validate the 10 designated and two proposed IBAs, identify hitherto unknown islands that were important for breeding seabirds and identify islands that were unlikely to ever support numbers of breeding seabirds in their present ecological condition. Thereafter (2011-2018), efforts were concentrated on monitoring the 12 IBA islands and, when possible, as many other islands as feasible within the constraints of the visit. Counts were made between 08h00 - 17h00 and lasted from one to four hours. Breeding seabird populations were estimated for all islands using Apparently Occupied Nests (AONs) following Bibby et al. (2012). The same survey methods as previously used in CA by Symens (1999) and McGowan et al. (2008) were employed, refined as outlined below:

Shearwaters (Procellariidae): Wedge-tailed *Ardenna pacifica* and Tropical Shearwater breed in BIOT. In the two largest colonies on North and South Brother (Fig. 3.3) the species breed sympatrically. On all breeding islands burrows are generally dug into sandy substrates and are extremely susceptible to collapsing. Burrows are often hidden under dense vegetation. These factors make accurate counts of the two species problematic. On islands where few nests have been detected (Diego Garcia, Danger, Sea Cow, Resurgent, Nelson, Coin du Mire, Petite Coquillage – Figs. 3.2 and 3.3) all burrows were inspected for occupancy. Burrows were deemed occupied (= 1 AON / one breeding pair / two adult individuals) when adults or chicks were present, feathers, fresh faeces or scratch marks were noted or the smell of preen oil was strong in the burrow. On islands with many nests, notably South and North Brother, breeding numbers were estimated by obtaining the mean number of AONs from a minimum of ten, 100 m^2 plots (sum of AONs for each plot divided by the number of plots), dividing this number by 100 to produce a mean number of AONs per m^2 and then multiplying this figure by the colony surface area in m^2 (Walsh et al. 1995). Plots were not randomly selected due to the potential of burrow damage but were distributed throughout both colonies. Colony surface area was calculated by mapping the colony circumference using the Area Calculation function on a handheld Global Positioning System on South Brother and was the whole island area on North Brother.

Tropicbirds (Phaethontidae): White-tailed *Phaethon lepturus* and Red-tailed Tropicbird *P. rubricauda* breed in CA. The former breeds on all atolls and has been recorded nesting in holes in trees (Bourne 1971) and epiphytic *Asplenum nidus* boles (this study). The latter breed on the ground near human habitation on rat-infested Diego Garcia (Carr 2011). Counts of Red-tailed Tropicbird were made by locating calling birds above the colonies and then searching the area underneath where AONs were directly counted. White-tailed Tropicbird was the hardest species to accurately count of all the seabirds due to its very low density and preference for nesting in dense forest; to date only two nests have ever actually been located (Bourne 1971, P. Carr, pers. obs.). AONs were estimated from the number of individual birds recorded in the interior of forests nest prospecting or counting pairs conducting aerial courtship displays above islands.

Boobies (Sulidae): Red-footed, Brown *Sula leucogaster* and Masked Booby *S. dactylatra* breed in loose colonies throughout the year in BIOT. The latter two are terrestrial nesters and restricted to rat-free islands, the former is an arboreal breeder and widely distributed including on rat-infested islands (Carr 2011). Masked Booby breeds on Coin du Mire and Resurgent (Figs. 3.2 and 3.3) and AONs either counted directly or from the sea when landing was not possible. Brown Booby breed on seven islands and AONs were counted directly on each. RfB breed on 38 islands. AONs were counted directly while walking the circumference of an island. Islands with obvious open areas in the interior sometimes held breeding birds and required checking (all IBAs plus Moresby and Grand Bois Mangue – Fig.3.2). Two islands, Danger and Nelson's had birds breeding throughout the interior as well as on the coast. During visits when high numbers were breeding on these islands, direct counts of AONs was not possible. On these occasions random 100 m^2 plot counts throughout the colonies were made and the same calculations used for shearwaters were followed. The colony on Diego Garcia extends ~40 km around the coast and AONs were counted directly with some birds (<0.1%) breeding in the interior that were located by calling nestlings and visually from a maintained dirt road.

Frigatebirds (Fregatidae): Greater *Fregata minor* and Lesser Frigatebird *F. ariel* breed in loose colonies throughout the year in CA. Both nest on the rat-free islands of Nelson's, North Brother and Grand Coquillage and Greater only occasionally on

Middle Brother (Fig.3.3). Nests are sited on low vegetation on all islands except North Brother where they are positioned above 10 m in *Pisonia grandis* trees. AONs were counted directly, care was taken with species identification on high or distant, partially concealed nests. When time was short or identification not possible both species were lumped together and recorded as frigatebird sp.

Terns (Sterninae): Nine species of terns breed in BIOT. Colonies of all terrestrial nesting terns (Table 3.3) was made by direct counts except Sooty Tern. This species' breeding numbers were estimated when possible during incubation and birds were less easily flushed. A minimum of ten, 100 m^2 plots were censused from throughout the colonies and the same calculations as for shearwaters were followed. To prevent unnecessary disturbance plots were counted from the perimeter of the colony.

Three species of tern nested in trees or shrubs, Common White Tern *Gygis alba*, Brown *Anous stolidus* and Lesser Noddy. Where Lesser Noddy was breeding in colonies too large for direct counts of AONs (South Brother, Nelson's and Petite Bois Mangue – Fig. 3.2) the AONs in a minimum of ten 100 m^2 random plots were counted within the colony area and the same calculations as for shearwaters were followed. AONs of lone pairs of Common White Tern and Brown Noddy were made by direct counts or from breeding behaviour displays of courtship, copulation, nest defence, food carrying or calling nestlings.

When counting mass breeding events of Sooty Tern and Lesser Noddy and time prohibited the methods above, the breeding population was estimated by comparing the size of the colony and density of nests with known-size colonies.

For each island in the archipelago the maximum number of breeding pairs of any species recorded between 2008-2018 was taken as the estimate of the breeding population. (An average number of breeding pairs over the survey period could not be accurately calculated due to the complicated breeding phenology of tropical seabirds not facilitating a non-skewed distribution of data, i.e., an over-abundance of zero counts).

Breeding Phenology

Breeding phenology data were collected for all species focussing upon seasonality and, synchronicity of breeding in relation to conspecifics. If the total population bred at the same time annually it was termed seasonal. If the total population bred at the same time but not annually it was termed periodic. If the species bred throughout the year with defined spikes in laying it was termed episodic. If there was no set breeding period, it was termed aseasonal. When breeding, if the total population laid eggs within a 14-day period it was termed synchronised. If there was some coordination between laying dates, for example, within a RfB colony "sub-colonies" lay in a synchronised manner it was termed partially synchronised. If there was no coordination in egg laying it was termed asynchronised. Assessments of seasonality and synchronicity were made at the archipelago, atoll and island level.

Terrestrial Important Bird and Biodiversity Area Criteria

IBA qualifying criteria followed BirdLife International (2004), Sanders (2006) (Table 3.2) and BirdLife International (2020). Biogeographically BIOT is classified as part of South Asia (BirdLife International 2004), hence regional and global population figures used for IBA qualification are from BirdLife International (2004). IBA criteria were assessed at island, atoll and the archipelago scale.

Table 3. 2. Important Bird and Biodiversity Area qualification criteria.

Category		Criterion
A1	Species of global conservation concern	The site regularly holds significant numbers of a Globally Threatened species or other species of global conservation concern.
A2	Assemblage or restricted range species	The site is known or thought to hold a significant component of the restricted-range species whose breeding distributions define an Endemic Bird Area (EBA) or Secondary Area (SA).
A3	Assemblage of biome-restricted species	The site is known or thought to hold a significant component of the group of species whose distributions are largely or wholly confined to one biome.
A4i	Congregations	The site is known or thought to hold, on a regular basis >1% of a biogeographic population of a congregatory waterbird species.
A4ii		The site is known or thought to hold, on a regular basis >1% of the global population of a congregatory seabird or terrestrial species.
A4iii		The site is known or thought to hold, on a regular basis, >20,000 waterbirds or >10,000 pairs of seabirds of one or more species.
A4iv		The site is known or thought to exceed thresholds set for migratory species at bottleneck sites.

RESULTS

Breeding Seabird Status and Distribution

Excluding zero counts, the surveys produced 1,547 records of 18 species breeding on 55 islands over 10 years (one record = the total number of one species breeding on a given island during a single census visit). Using maximum counts from all islands of all species from the survey period (Table S3.1) CA holds 281,596 pairs of breeding seabirds of which ≈ 96% is made up of three species, Sooty Tern (70%), Lesser Noddy (18%) and RfB (8%).

Every island in CA had at least one seabird recorded breeding and North Brother, with 12 breeding species, was the most diverse. Longue (Fig. 3.2) held the greatest number of breeding seabirds with 48,000 pairs of Sooty Tern recorded in 2012, the embryonic island of Saint Brandon (Fig. 3.2) held the least over the decade with a single pair of Black-naped Tern *Sterna sumatrana* in 2016. Eight species nested exclusively on rat-free islands, of these, six are ground-nesting. The 11 rat-free islands that are currently designated/proposed IBAs (Table 3.1, Figs. 3.1, 3.2 and 3.3) accounted for ≈ 94% of the total number of breeding birds - over half a million individual adult birds (Table S3.1).

CA holds breeding seabird populations of significance at the regional and global scale for six species: Tropical Shearwater - 5.44% of global population; RfB - 7.62% of global population; Greater Crested Tern *Thallaseus bergii* - 2.82% of regional population; Black-naped Tern - 2.77% of regional population; Sooty Tern - 19.75% of regional population and Lesser Noddy - 10.16% of regional population.

Breeding Phenology

Of the 18-breeding species, eight were synchronised, three were partially synchronised and five were asynchronous. Brown Noddy adopts two strategies: lone pairs nesting arboreally throughout the year, including on rat-infested islands (aseasonal and asynchronised); and synchronised in dense terrestrial colonies exclusively on rat-free islands at unknown periods (periodic). Two species were seasonal, seven were periodic, three were episodic and five were aseasonal. Three species, White-tailed Tropicbird, Little *Sternula albifrons* and Roseate Tern *Sterna dougallii* had too few data to accurately determine their synchronicity and seasonality (Table 3.3).

Table 3. 3. Seabird breeding phenology in BIOT 2008-2018.

SPECIES	SYNCHRONISED	PARTIALLY SYNCHRONISED	ASYNCHRONISED	SEASONAL	PERIODIC	EPISODIC	ASEASONAL	UNKNOWN	COMMENTS
Wedge-tailed Shearwater *Ardenna pacifica*	■			■					Terrestrial breeding species. Breeds October – April. Exceptional breeding of > 5 pairs was recorded on Diego Garcia in July and August 2009 and June 2018
Tropical Shearwater *Puffinus bailloni*	■			■					Terrestrial breeding species. Breeds October – April
Red-tailed Tropicbird *Phaethon rubricauda*		■			■				Terrestrial breeding species. Has been recorded breeding semi-colonially from February through to July. When breeding the spread of laying dates is > 21 days
White-tailed Tropicbird *Phaethon lepturus*								■	Arboreal breeding species
Masked Booby *Sula dactylatra*			■				■		Terrestrial breeding species. Limited data, continuous breeder possibly with laying spikes like Red-footed Booby
Red-footed Booby *Sula sula*		■				■			Arboreal breeding species. Egg laying spikes occur in December/January and June/July
Brown Booby *Sula leucogaster*		■				■			Terrestrial breeding species. Limited data, continuous breeder possibly with laying

		■				■			spikes. Laying spikes differ by island
Greater Frigatebird *Fregata minor*			■				■		Arboreal breeding species. Breeds continuously throughout year with no noticeable spikes
Lesser Frigatebird *Fregata ariel*			■				■		Arboreal breeding species. Breeds continuously throughout year with no noticeable spikes
Greater Crested Tern *Thalasseus bergii*	■				■				Terrestrial breeding species. Nomadic breeder, colonies are synchronised though periodic. Colonies on the same island may not be synchronised with each other
Roseate Tern *Sterna dougallii*								■	Terrestrial breeding species
Black-naped Tern *Sterna sumatrana*	■				■				Terrestrial breeding species. Nomadic breeder, colonies are synchronised though periodic. Has nested on man-made structures such as floating platforms and roofs on Diego Garcia
Little Tern *Sternula albifrons*								■	Terrestrial breeding species
Bridled Tern *Onychoprion anaethetus*	■				■				Terrestrial breeding species. Synchronised breeding occurs on individual islands throughout the year. Possible egg laying spikes like Red-footed Booby
Sooty Tern *Onychoprion fuscatus*	■				■				Terrestrial breeding species. Synchronised breeding occurs at unknown intervals. Has been recorded breeding sub-annually in BIOT MPA

Brown Noddy *Anous stolidus*	■		■		■		■		Terrestrial and arboreal breeding species. When terrestrial it is colonial, synchronised and periodic at an unknown interval. Lone pairs breed arboreally, aseasonally and asynchronised
Lesser Noddy *Anous tenuirostris*	■					■			Arboreal breeding species. Individual colonies are synchronised. Breeds at unknown intervals and colonies on different islands can have very different breeding dates
Common White Tern *Gygis alba*			■				■		Arboreal breeding species. Lone pairs breed aseasonally

Terrestrial Important Bird and Biodiversity Area Qualification

Surveys of the designated and proposed IBAs were conducted an average of 13.7 times (range 11-19, n = 12) during 2008-18 (Table S3.2). None of the 18 species of breeding seabird in CA are globally threatened, endemic, restricted-range species or largely confined to one biome (del Hoyo et al. 2018), therefore no site qualifies for IBA status under A1, A2 or A3 criteria (BirdLife International 2004). All islands that qualified were under the A4 (congregations) criteria. Using decadal data (Table 3.4), of the 10 currently designated IBAs, 9 qualified under either A4i, ii or iii or combinations thereof. One IBA never qualified at all. Both proposed IBAs qualified under A4i and iii criteria. However, when assessed on an annual timescale (Table 3.4), only a single IBA, Petite Bois Mangue (Fig. 3.2), qualified every time it was surveyed. Every other island failed to qualify at least twice (range 2–6) during the ten years.

Table 3. 4. Counts of species that originally qualified the ten designated and two proposed Important Bird Areas (IBAs) in the British Indian Ocean Territory, censused between 2008–2018. Records of newly qualifying species are in *italics*. **Bold text** denotes a species' count met IBA qualifying criteria A4i, A4ii or A4iii. NC = IBA was not censused in that year.

IBA	ORIGINAL QUALIFYING SPECIES (QUALIFYING COUNT OF BREEDING PAIRS) *NEW QUALIFYING SPECIES*	YEAR COUNT OF IBA QUALIFYING SPECIES (IBA QUALIFYING CRITERIA – IF APPLICABLE)										
		2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
DIEGO GARCIA	RED-FOOTED BOOBY (16,067)	NC	2,880	**4,625 (A4ii)**	**3,530 (A4ii)**	2,932	NC	**3,663 (A4ii)**	NC	NC	NC	**9,969 (A4ii)**
DANGER ISLAND	RED-FOOTED BOOBY (3,470)	NC	700	**3,500 (A4ii)**	NC	63	1,145	400	45	45	NC	NC
	BROWN NODDY (11,100)		35	40		40	24	45	12	12		
SEA COW	BROWN NODDY (11,100)	NC	130	140	NC	30	42	52	22	NC	NC	NC
SOUTH BROTHER	BROWN NODDY (6,100)	NC	60	50	0	30	40	41	7	6	NC	NC
	LESSER NODDY (7,300)		**10,000 (A4i/A4iii)**	0	0	0	57	**9,800 (A4i/A4iii)**	**11,500 (A4i/A4iii)**	30		
	SOOTY TERN		**10,000**	0	800	800	0	0	0	5,000		

	(10,000)		**(A4i/A4iii)**									
	TROPICAL SHEARWATER (400)		0	0	0	0	2	**400 (A4ii)**	**345 (A4ii)**	0		
MIDDLE BROTHER	SOOTY TERN (12,500)	NC	**10,000 (A4i/A4iii)**	**10,500 (A4i/A4iii)**	400	**32,000 (A4i/A4iii)**	10	2,200	5,000	NC	NC	NC
NORTH BROTHER	TROPICAL SHEARWATER (420)	200	120	166	NC	0	0	120	**1,200 (A4ii)**	NC	NC	NC
	SOOTY TERN (10,000)	0	**10,000 (A4i/A4iii)**	0		0	0	0	0			
NELSON'S ISLAND	BROWN NODDY (8,300)	14	70	80	20	650	64	41	14	12	NC	350
	LESSER NODDY (13,700)	50	**10,000 (A4i/A4iii)**	1,400	0	**11,000 (A4i/A4iii)**	820	**12,000 (A4i/A4iii)**	50	**10,000 (A4i/A4iii)**		**6,500 (A4i/A4iii)**
	RED-FOOTED BOOBY (3,300)	490	600	500	300	**3,300 (A4ii)**	996	957	310	12		683
PARASOL	SOOTY TERN (20,000)	NC	**15,000 (A4i/A4iii)**	**31,250 (A4i/A4iii)**	NC	**37,500 (A4i/A4iii)**	0	**10,000 (A4i/A4iii)**	0	5,000	0	NC
LONGUE	SOOTY TERN (32,000)	NC	**20,000 (A4i/A4iii)**	0	NC	**48,000 (A4i/A4iii)**	0	0	0	**11,000 (A4i/A4iii)**	0	NC
PETITE BOIS MANGUE	SOOTY TERN (20,424)	NC	0	0	NC	0	0	0	0	0	NC	NC
	LESSER NODDY (12,000)		**10,000 (A4i/A4iii)**	**10,000 (A4i/A4iii)**		**10,000 (A4i/A4iii)**	**11,500 (A4i/A4iii)**	**14,000 (A4i/A4iii)**	**11,000 (A4i/A4iii)**	**12,500 (A4i/A4iii)**		
PETITE COQUILLAGE	SOOTY TERN (34,669)	300	**20,000 (A4i/A4iii)**	**10,000 (A4i/A4iii)**	NC	0	NC	0	0	8,000	NC	NC
GRAND COQUILLAGE	SOOTY TERN (15,429)	**10,000 (A4i/A4iii)**	NC	0	NC	**38,000 (A4i/A4iii)**	0	1,000	0	0	0	2,304

Between 2008–2018 (Table 3.4), of the five original qualifying species, Brown Noddy never met IBA qualifying numbers. On the two islands designated due to RfB, this species made IBA criteria five times during 13 censuses. It met IBA criteria for the first time in 2012 on Nelson's Island when 3,300 breeding pairs were present. On the three islands that qualified through breeding numbers of Lesser Noddy, IBA criteria were met 14 times out of 25 visits. One island originally qualified for IBA status via Tropical Shearwater. On this island (North Brother) it met IBA status once in the decade, in 2015, though qualified for the first time on South Brother in 2014 and again in 2015. Six islands qualified for IBA status through the presence of Sooty Tern colonies 14 times during 46 visits over 10 years.

At the atoll level (Table S3.1), five species qualify three atolls as IBAs; Diego Garcia - RfB (A4ii); Great Chagos Bank – Tropical Shearwater (A4ii), RfB (A4ii); Greater Crested Tern (A4i), Sooty Tern (A4i) and Lesser Noddy (A4i); Peros Banhos - Sooty Tern (A4i) and Lesser Noddy (A4i). These three atolls would all qualify for A4iii. The qualifying criteria for Black-naped Tern is 150 individual birds, and while the Egmont Islands atoll only held 70 breeding pairs (140 individuals), if chicks and non-breeding birds are counted this atoll would qualify with this species under A4i.

At the archipelago level (Table S3.1), six species have IBA qualifying populations – Tropical Shearwater (A4ii); RfB (A4ii); Greater Crested Tern (A4i); Black-naped Tern (A4i); Sooty Tern (A4i) and Lesser Noddy (A4i). The archipelago would further qualify under A4iii criteria for holding > 20,000 waterbirds or > 10,000 pairs of seabirds.

DISCUSSION

Prior to 2008 there had only been three spatially and temporally limited breeding seabird censuses in CA (Baldwin 1975, Symens 1999, McGowan et al. 2008). The surveys reported here during 2008–2018 instead provide a more detailed annual picture of breeding seabirds on the archipelago and reveal in a nominal year, 281,596 pairs of breeding seabirds of 18 species. The counts also demonstrate that the present system of delimiting IBAs in CA at an island scale does not capture the present status and distribution of its qualifying breeding seabird species. It has further exposed the limitations of using temporally and spatially limited censuses due to the complex nature of tropical seabird breeding phenology.

Terrestrial Important Bird and Biodiversity Area Species' Monitoring in the BIOT MPA

Appropriate census methods for tropical seabirds requires an understanding of their breeding phenology (VanderWerf and Young 2017, 2018). The long-term survey data have revealed much of the breeding phenology of CA seabirds, though the periodicity of breeding Lesser Noddy and Sooty Tern is not yet understood (Table 3.3).

When assessed at an island level, CA now has four seabird species breeding in IBA qualifying numbers: Tropical Shearwater, RfB, Sooty Tern and Lesser Noddy (Tables 3.4, S3.1). I discuss the status and monitoring of these species in turn.

Globally, Tropical Shearwater is synchronised and both a seasonal and aseasonal breeding species, with the season dependent upon location and the length of cycle variable with locality. Generally, it breeds in the austral winter, e.g., Reunion, July – October, but year-round close to the equator, e.g., on Seychelles (del Hoyo et al. 2019). In CA, it is seasonal (October - March) and synchronised with a breeding population of 1,000–2,000 pairs. The largest colonies are found on the rat-free islands of North and South Brother (Tables 3.3, S3.1) where it nests in amongst the more abundant Wedge-tailed Shearwater. The colony on South Brother was discovered in 2014 and another, unsurveyed, large colony may exist on Nelson's Island (Carr et al. 2018).

Nocturnal burrow-nesting seabirds are difficult and/or labour intensive to accurately census (e.g., Dyer and Hill 1991, Bonnet-Lebrun et al. 2016), therefore inter-annual variation in counts may relate to a lack of sampling precision. Tropical Shearwater is the only IBA qualifying species where a single annual survey of the archipelago conducted between November and March would capture the entire breeding population.

Globally, RfB is aseasonal, episodic, asynchronised (Carboneras et al 2019) and a partially synchronised breeder (Nelson 1978). In CA, it is a partially synchronised, episodic breeder with a total annual breeding population that could reach ≈ 21,000 pairs in years when peak breeding across the archipelago was synchronised (Tables 3.3, S3.1). There are two breeding spikes: one in January when the prevailing winds are north-west and a second larger event in June/July when the stronger Southeast Trades blow. This species is not difficult to accurately census when breeding but due to the two spikes in egg laying some six months apart, it requires two surveys *per annum* to capture the entire breeding population (as in 2018 on Diego Garcia – Tables 3.4, S3.1). (The original IBA qualifying count of 16,067 breeding pairs [BirdLife International 2004] is erroneous as it was assumed at that time that birds bred throughout the forested interior of the eastern arm of Diego Garcia – see Carr 2005 for further information).

Globally, Sooty Tern breeds year-round in some places and is seasonal in others (Gochfeld et al. 2019d). It can breed sub-annually and the breeding cycle takes 9·5 months, both at population and individual levels (Hughes 2014). It breeds in the western Indian Ocean at many locations from 04° S (Seychelles) to 26° S (S Madagascar) and the breeding season is related to latitudinal variations in food availability (Gochfeld et al. 2019d). In CA, it is the most numerous bird species with a maximum breeding population of ≈ 200,000 pairs (Tables 3.4, S3.1) and is highly synchronised within colonies and, all colonies throughout the archipelago nest at the same time. However, it breeds at unknown intervals and like on Ascension Island (Reynolds et al. 2014) it has bred subannually. In CA, it is not island philopatric, having inter-annual variation in breeding island selection (this study). Feare (1976) and Feare and Feare (1984) found periodic desertion of breeding colonies in the western Indian Ocean due to tick infestation, and this is the likely cause in CA (Carr et al. 2013, Carr 2014). Periodic desertions of breeding islands make IBA designation at the island level in CA challenging.

In the western Indian Ocean, Lesser Noddy of the race *tenuirostris* on Seychelles laid eggs between late May and late June in most years during 1995–2002 (Gochfeld et al. 2019b). Elsewhere race *melanops* on Houtman Abrolhos Island (off Western Australia) laid August–early December. Some colonies are stable but others shift location from year to year (Gochfeld et al. 2019b). In CA, I estimated ≈ 50,000 breeding pairs (Tables 3.4, S3.1) where it is a highly synchronised breeder and strongly philopatric. However, it is asynchronous between colonies and breeds at unknown intervals. There are three epicentres of breeding in CA holding ≈ 10,000 pairs in peak years – on rat-free Petite Bois Mangue, Nelson's Island and South Brother. In 2009, when repeat surveys of islands were undertaken, the former held peak breeding numbers in February, the latter two islands peaked in July. A single, temporally limited count of the archipelago may not necessarily account for the year's entire breeding population. Previous predictions of a population decline seem unfounded (McGowan et al. 2008).

Brown Noddy formerly qualified four islands for IBA status but no longer breeds in sufficient numbers with a current estimate of ≈ 3,000 breeding pairs (Tables 3.4, S3.1). This species is of Least Concern (BirdLife International 2018), with a globally stable population and no known large-scale threats or declines (Gochfeld et al. 2018). Some small populations are believed to be vulnerable to introduced predators (Gochfeld et al. 2018) though this cannot be the cause of decline in CA because the large breeding colonies (< 7,500 individual birds) recorded by Baldwin (1975) and Symens (1999) were on predator free islands – that have remained predator free (Harper et al. 2019). McGowan et al (2008) first noted the decline of this species; why it declined so rapidly from 1996 to its present-day stable population remains a mystery.

Greater Crested Tern and Black-naped Tern had confirmed or potential IBA qualifying breeding populations at the atoll level (Table S3.1). The former nests in large dense colonies in Australia and elsewhere in very small colonies and the breeding season varies with location – with April - June recorded in the Indian Ocean. In Aldabra and Southwest Australia is has two annual breeding peaks but individual birds only nest once a year (Gochfeld et al. 2019c). The latter breeds September - November elsewhere in the Indian Ocean. It usually breeds in small colonies of 5-20 pairs but sometimes up to 200 (Gochfeld et al. 2019a). In CA, both species breed in colonies of up to 50 pairs at unknown intervals throughout the year. Occasionally two colonies of the same species are sited on the same beach on an island but will be at different breeding stages. Both species are not philopatric and locating colonies requires extensive searching of all islands including those that are rat-infested.

To conclude, an accurate estimate of CA breeding seabirds requires biannual censuses during January/February and July/August. These censuses should occur at least every four years to meet IBA monitoring guidelines and IUCN Red List review periodicity (BirdLife International 2006).

Terrestrial Important Bird and Biodiversity Area Designation in the BIOT MPA

As part of the ongoing IBA monitoring process, IBAs should meet the criteria they were listed for and boundaries identified and mapped (BirdLife International 2006). This review demonstrates that the present site boundaries of the CA IBAs does not reflect the current status and distribution of breeding seabirds, thus requiring a revision.

IBA site boundaries are usually determined based on environmental, administrative, and practical factors (Fishpool & Evans 2001 in Harris et al. 2011) and the larger the area included, the more likely the population thresholds for IBA site designation will be reached (Harris et al. 2011). Options for larger spatial scale IBAs in CA are to designate at the archipelago, atoll or parts of atoll (island cluster) level, all of which have been incorporated in other UK Overseas Territories (UKOTs - Sanders 2006).

In CA, the lack of granularity when recording species at the archipelago level is thought to preclude this option. Consisting of five atolls up to 200 km apart (Diego Garcia – Peros Banhos Fig. 3.1) that have differing climatic conditions north to south (Stoddart 1971), monitoring at the archipelago scale may not capture finer scale shifts in population dynamics. Hence, this scale of IBA may not detect population dynamics of seabirds and therefore cannot be used to assess the efficacy of the MPA. Further, conservation management requires a finer scale than archipelago to identify specific islands in need of environmental rehabilitation, i.e., rat eradication and/or reforestation.

Atoll scale IBA designation and monitoring would be a better option. At this level, fine-scale changes can be identified, and atolls are unique, readily defined units. However, the access to visiting yachts, military presence, protection status and ecological quality of islands in Peros Banhos and Diego Garcia may preclude this option. Peros Banhos is an atoll of two distinct halves (Carr 2011). One half, all islands west of Vache Marine and Passe (Fig. 3.2), are ecologically impoverished with invasive rats and the clearance of native forest for coconut, the eastern half holds five IBAs and is a Strict Nature Reserve (Fig. 3.2 - Carr 2011, Carr et al. 2013, Harper et al. 2019). Similarly, on Diego Garcia, the eastern arm is a RAMSAR site, Strict Nature Reserve and IBA, the western arm a sophisticated military facility with very little native habitat left (Carr et al. 2013). Therefore, designating these entire atolls as IBAs would not reflect the true status and distribution of seabirds.

The final option is to designate parts of atolls, e.g., clusters of islands as IBAs. Clusters of islands have been made IBAs elsewhere in the UKOTs, e.g., Beaver

Island Group, Falklands (Sanders 2006) and elsewhere in the western Indian Ocean, e.g., Farquhar - South Island and islets IBA in the Seychelles (BirdLife International 2019). Globally, no “cluster of islands” IBAs have been created to cater for shifting populations of breeding seabirds. In CA, this grouping would capture the periodic desertion of breeding islands by Sooty Tern. It is also a defined unit that can be readily censused, does not misrepresent or over-inflate the importance of the breeding seabirds due to spatial scale and is manageable in terms of size, protection and conservation measures if needed.

Removing invasive predators aids the recovery of seabird populations (Hilton and Cuthbert 2010, Bedolla-Guzmán et al. 2019, Holmes et al. 2019), with rat eradication a priority not only for seabirds, but also for surrounding reef ecosystems (Graham et al. 2018; Savage 2019). For conservation practitioners, including ecologically impoverished islands into a discrete cluster of IBA islands would give a focus to environmental rehabilitation projects. Adopting the island cluster strategy would align well with proposed management recommendations relating to the control of invasives. For example, having the islands of eastern Peros Banhos (Fig. 3.2) designated would focus rat eradication efforts on the three islands where they are still present (Passe, Moresby and Yéyé – Fig. 3.2). Similarly, the western islands of the Great Chagos Bank should include Eagle Island (Fig. 3.3).

Using Important Bird and Biodiversity Areas to Monitor the Efficacy of Marine Protected Areas (MPAs)

Seabirds are used to identify and delineate MPAs (Thaxter et al. 2012, Ronconi et al. 2012). Monitoring the efficacy of the BIOT MPA could be achieved through seabird tracking to establish their use of the no-take zone for foraging and non-breeding. Further, demographic monitoring of tIBAs within MPAs could quantify the level of protection afforded, both at sea and on land. Monitoring breeding seabirds within the BIOT MPA is also a method for globally testing the validity and effectiveness of a large-scale tropical, strict no-take MPA for the conservation and protection of top predators, a subject of which the requirement and efficacy is still debated (Game et al. 2009, De Santo et al. 2011, De Santo 2013, McCauley et al. 2015, Hilborn 2018, O'Leary et al. 2018).

RECOMMENDATIONS

To address the shortcomings in seabird data collection, CA requires a standardised, systematic breeding seabird monitoring programme. To accurately reflect the present status and distribution of breeding seabirds in CA, it is recommended that the boundaries of the tIBAs are redrawn. The data collected between 2008–2018 presented in this study will facilitate an effective monitoring programme and redrawing of tIBA boundaries. It also provides the opportunity, with baseline figures provided, to initiate credible assessments of the role of the BIOT MPA in seabird conservation using a suite of seabirds from different foraging guilds. Taking into consideration the complicated breeding phenology of tropical seabirds, the shifting nature of breeding Sooty Tern and the challenges of monitoring a vast area/MPA, I make four recommendations:

1. Terrestrial IBAs are delimited and refined as follows (Table 3.5, Figs. 3.2, 3.3):

Table 3. 5. Recommendations for the revision of terrestrial Important Bird and Biodiversity Areas in the British Indian Ocean Territory.

IBA name	Qualifying criteria (breeding pairs)	Comments
Eastern Diego Garcia island group	A4ii Red-footed Booby (9,969)	Site includes West, Middle and East Islands. On Diego Garcia island, IBA includes all land from the Plantation Gate (-7.411°S 72.453°E) to Barton Point (-7.234°S 72.434°E)
Western Great Chagos Bank island group	A4i Sooty Tern (52,000), Lesser Noddy (15,735) A4ii Red-footed Booby (5,469), Tropical Shearwater (1,615) A4iii site holds at least 20,000 waterbirds	IBA includes Danger Island, Sea Cow, Eagle Island, the Three Brothers and Resurgent
Nelson's Island	A4i Lesser Noddy (12,000) A4ii Red-footed Booby (3,300) A4iii site holds at least 20,000 waterbirds	
Eastern Peros Banhos island group	A4i Sooty Tern (145,000), Lesser Noddy (20,850) A4iii site holds at least 20,000 waterbirds	IBA includes all islands from Ile du Passe to Vache Marine inclusive

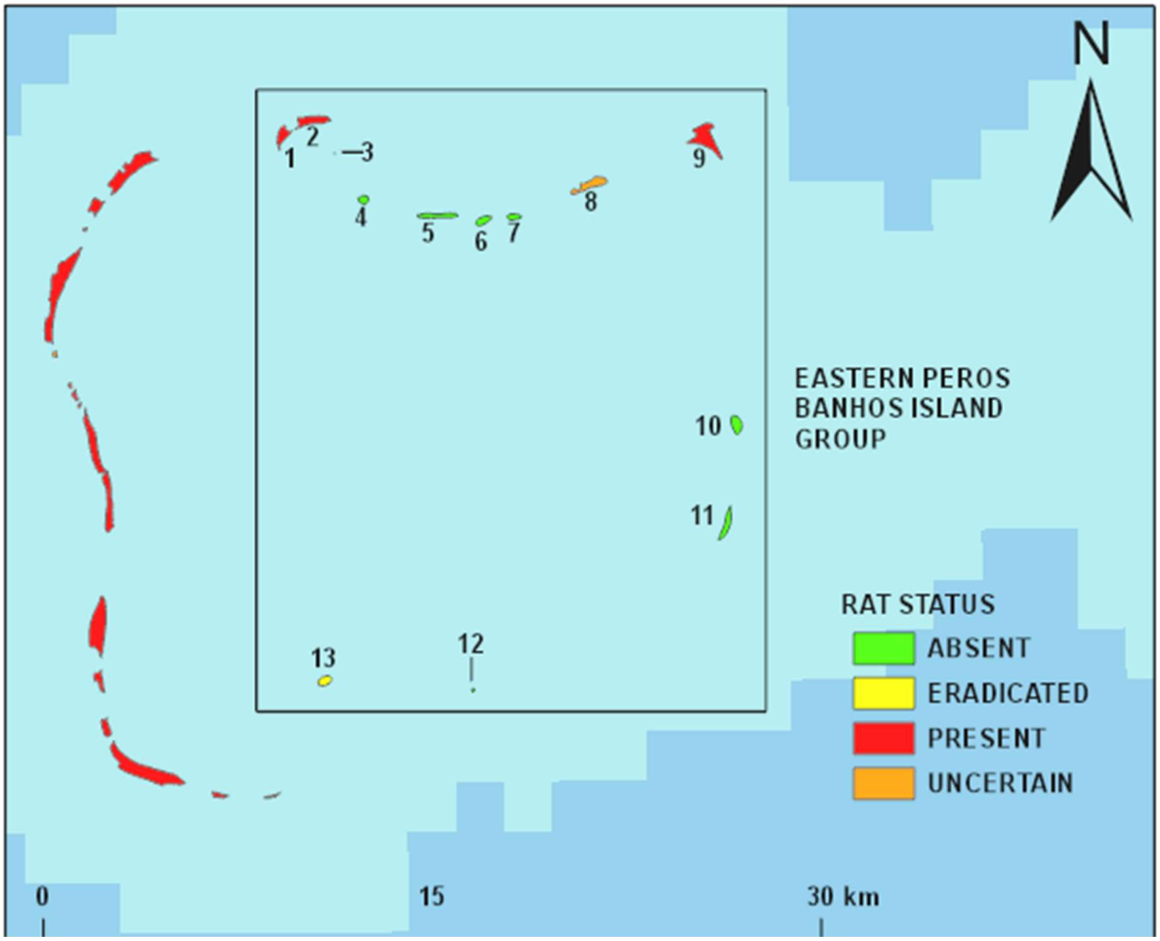


Figure 3. 2. Proposed Eastern Peros Banhos island group terrestrial Important Bird and Biodiversity Area. 1 = Passe, 2 = Moresby, 3 = Saint Brandon, 4 = Parasol, 5 = Longue, 6 = Grand Bois Mangue, 7 = Petite Bois Mangue, 8 = Manoel, 9 = Yeye, 10 = Petite Coquillage, 11 = Grand Coquillage, 12 = Coin du Mire and 13 = Vache Marine.

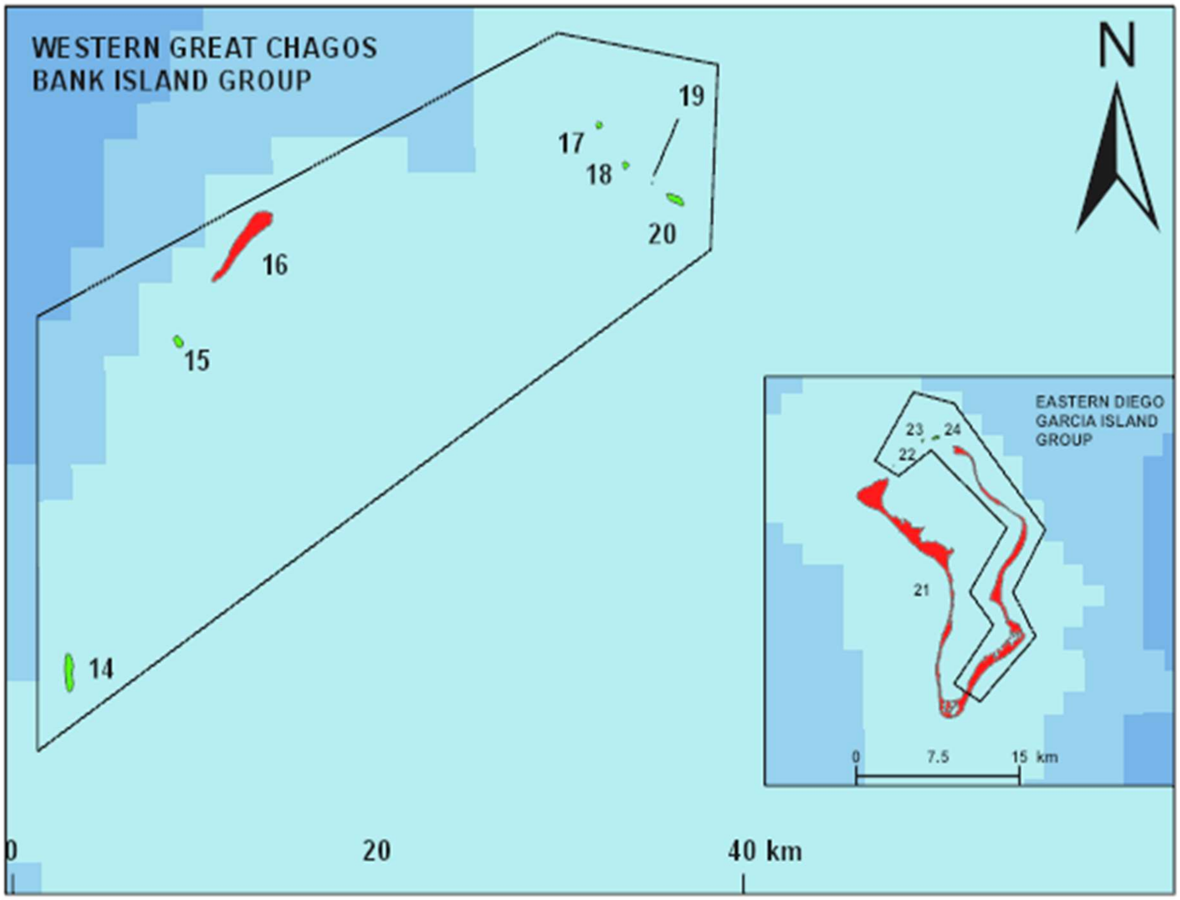


Figure 3. 3. Proposed Western Great Chagos Bank island group terrestrial Important Bird and Biodiversity Area. 14 = Danger, 15 = Sea Cow, 16 = Eagle, 17 = North Brother, 18 = Middle Brother, 19 = Resurgent, 20 = South Brother. Inset: Eastern Diego Garcia island group revised terrestrial Important Bird and Biodiversity Area. 21 = Diego Garcia, 22 = West Island, 23 = Middle Island and 24 = East Island.

2. Every four years, two breeding seabird censuses of all islands should be undertaken six months apart, one in January/February and the other in July/August.
3. The revised designation of IBAs is used to inform and prioritise the rehabilitation of ecologically impoverished islands in CA, with a focus upon islands of currently low ornithological importance within the revised IBAs.
4. The results of IBA monitoring are used as a tool to assess the efficacy of the BIOT MPA for the conservation of seabirds.

REFERENCES

Arcos JM, Bécares J, Villero D, Brotons L, Rodríguez B and Ruiz A. 2012. Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine Important Bird Areas (IBAs) in Spain. Biological Conservation 156: 30-42.

Baldwin EA. (Ed.). 1975. Report on the Joint Services Expedition to Danger Island 1975. MOD internal Publication, London.

Bedolla-Guzmán Y, Méndez-Sánchez F, Aguirre-Muñoz A, Félix-Lizárraga M, Fabila-Blanco A, Bravo-Hernández E, Hernández-Ríos A, Corrales-Sauceda M, Aguilar-Vargas A, Aztorga-Ornelas A, Solís-Carlos F, Torres-García F, Luna-Mendoza L, Ortiz-Alcaraz A, Hernández-Montoya J, Latofski-Robles M, Rojas-Mayoral E and Cárdenas-Tapia A. 2019. Recovery and current status of seabirds on the Baja California Pacific Islands, Mexico, following restoration actions. Pages 531-538 in: Veitch CR, Clout MN, Martin AR, Russell JC and West (Eds.). Proceedings of the Island Invasives 2017 Conference. Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

Bibby CJ, Burgess ND and Hill DA. 2012. Bird Census Techniques. Academic Press, Cambridge, UK.

BirdLife International. 2004. Important Birds Areas in Asia: key sites for conservation. Cambridge, UK: BirdLife International. (BirdLife Conservation Series No. 13).

BirdLife International. 2006. Monitoring Important Bird Areas: a global framework. Cambridge, UK. BirdLife International version 1.2.

BirdLife International. 2018. *Anous stolidus*. The IUCN Red List of Threatened Species 2018: e.T22694794A132573846. http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694794A132573846.en accessed on 14 February 2019.

BirdLife International. 2019. Important Bird Areas factsheet: Farquhar - South Island and islets. http://www.birdlife.org accessed on 09 April 2019.

BirdLife International. 2020. Guidelines for the application of the IBA criteria. Final version July 2020. http://datazone.birdlife.org/userfiles/images/Guidelines accessed 7 July 2021.

Bonnet-Lebrun AS, Calabrese L, Rocamora G and López-Sepulcre A. 2016. Estimating the abundance of burrow-nesting species through the statistical analysis of combined playback and visual surveys. Journal of Avian Biology 47(5): 642-649.

Bourne WRP. 1971. The Birds of the Chagos Group, Indian Ocean. Atoll Research Bulletin 149: 175-207.

Brooke M de L. 2006. Pitcairn Islands. Pages 185–190 in: Sanders SM (Ed.). Important Bird Areas in the United Kingdom Overseas Territories. Sandy, UK, RSPB.

Burger J and Gochfeld M. 1994. Predation and effects of humans on islands-nesting seabirds. Pages 39-67 in: Nettleship DN, Burger J and Gochfeld M (Eds.). Seabirds on islands, threats, case studies and action plans. BirdLife Conservation Series No.1. Cambridge, UK: BirdLife International.

Carboneras C, Christie DA, Jutglar F, Garcia EFJ and Kirwan GM. 2019. Red-footed Booby (*Sula sula*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona https://www.hbw.com/node/52624 accessed on 5 April 2019

Carney KM and Sydeman WJ. 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22(1): 68-79.

Carr P. 2005. Diego Survey II (2005) - Expedition Report. Sea Swallow 54: 6-40.

Carr P. 2006. British Indian Ocean Territory. Pages 37-55 in: Sanders SM (Ed.). Important Bird Areas in the United Kingdom Overseas Territories. Sandy, UK, RSPB.

Carr P. 2011. Birds of the British Indian Ocean Territory. Published by Pisces Publications for the RSPB. Sandy, Bedfordshire, England.

Carr P. 2014. New and interesting bird records from the British Indian Ocean Territory (BIOT). Sea Swallow 63: 78-86.

Carr P, Wood H and Nicoll M. 2018. Seabird ecology on Nelson's Island. Private post.

Carr P, Hillman JC, Seaward MRD, Vogt S and Sheppard CRC. 2013. Coral Islands of the British Indian Ocean Territory (Chagos Archipelago). Pages 271-282 in: Sheppard CRC (Ed.). Coral Reefs of the United Kingdom Overseas Territories, Coral Reefs of the World 4, © Springer Science+Business Media Dordrecht.

Carr P and Harper GA. 2015. The Distribution of Ship Rat *Rattus rattus* in the Chagos Archipelago. Chagos News. The Periodical Newsletter of the Chagos Conservation Trust and Chagos Conservation Trust US 47: 20-31.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A and Taylor P. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22(1): 1-34.

Dawson J, Oppel S, Cuthbert RJ, Holmes N, Bird JP, Butchart SH, Spatz DR and Tershy B. 2015. Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. Conservation Biology 29(1): 143-153.

De Santo EM. 2013. Missing marine protected area (MPA) targets: How the push for quantity over quality undermines sustainability and social justice. Journal of Environmental Management 124: 137–146.

De Santo EM, Jones PJS, Miller AMM. 2011. Fortress conservation at sea: A commentary on the Chagos marine protected area. Marine Policy 35: 258–260.

del Hoyo J, Collar N and Kirwan GM. 2019. Tropical Shearwater (Puffinus bailloni). In del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/467279 Accessed on 5 April 2019.

del Hoyo J, Elliott A, Sargata J, Christie DA and de Juana E (Eds.). 2018. Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com accessed 31 October 2018.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips R, Yates O, Lascelles B, Borboroglu PG. and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Donald PF, Fishpool LD, Ajagbe A, Bennun LA, Bunting G, Burfield IJ, Butchart SH, Capellan S Crosby, MJ, Dias MP and Diaz D. 2019. Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. Bird Conservation International 29(2): 177-198.

Dyer PK and Hill GJE. 1991. A solution to the problem of determining the occupancy status of Wedge-tailed Shearwater *Puffinus pacificus* burrows. Emu 91(1): 20-25.

Edis R. 2004. Peak of Limuria. The story of Diego Garcia and the Chagos Archipelago. Second edition. Chagos Conservation Trust, London.

Feare CJ. 1976. Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infected ticks. Ibis 118(1): 12-115.

Feare CJ and Feare FC. 1984. Seabird ecology and tick distribution in the western Indian Ocean. National Geographic Society: 341-358

Game ET, Grantham HS, Hobday AJ, Pressey RL Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP and Richardson AJ. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecological Evolution 24: 360-369.

Gochfeld M, Burger J, Kirwan GM and Garcia EFJ. 2018. Brown Noddy (*Anous stolidus*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E. (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/54049 accessed on 4 December 2018.

Gochfeld M, Burger J and Garcia EFJ. 2019a. Black-naped Tern (Sterna sumatrana). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/54043 accessed on 7 April 2019.

Gochfeld M, Burger J and Garcia EFJ. 2019b. Lesser Noddy (Anous tenuirostris). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/54043 accessed on 7 April 2019.

Gochfeld M, Burger J, Kirwan GM, Christie DA and Garcia EFJ. 2019c. Greater Crested Tern (Thalasseus bergii). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/54043 accessed on 7 April 2019.

Gochfeld M, Burger J, Kirwan GM, Christie DA, de Juana E and Garcia EFJ. 2019d. Sooty Tern (Onychoprion fuscatus). In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E (Eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. https://www.hbw.com/node/54043 accessed on 7 April 2019.

Graham NA, Wilson SK, Carr P, Hoey AS, Jennings S and MacNeil MA. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559(7713): 250.

Harper G, Carr P and Pitman H. 2019. Eradicating black rats from the Chagos – working towards the whole archipelago. Pages 26–30 in: Veitch CR, Clout MN, Martin AR, Russell JC and West CJ (Eds.). Proceedings of the Island Invasives 2017 Conference. Island invasives: scaling up to meet the challenge, Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

Harris CM, Carr R, Lorenz K and Jones S. 2011. Important Bird Areas in Antarctica: Antarctic Peninsula, South Shetland Islands, South Orkney Islands – Final Report. Prepared for BirdLife International and the Polar Regions Unit of the UK Foreign & Commonwealth Office. Environmental Research & Assessment Ltd., Cambridge.

Hilborn R. 2018. Are MPAs effective? ICES Journal of Marine Science 75(3): 1160-1162.

Hilton GM and Cuthbert RJ. 2010. Review article: The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. Ibis 152(3): 443-458.

Holmes N, Spatz DR, Oppel S, Tershy B, Croll DA, Keitt B, Genovesi P, Burfield IJ, Will DJ, Bond AL, Wegmann A, Aguirre-Muñoz A, Raine AF, Knapp CR, Hung C-H, Wingate D, Hagen E, Méndez-Sánchez F, Rocamora G, Yuan H-W, Fric J, Millett J, Russell J, Liske-Clark J, Vidal E, Jourdan H, Campbell K, Springer K, Swinnerton K, Gibbons-Decherong L, Langrand O, Brooke, MdL, McMinn M, Bunbury N, Oliveira N, Sposimo P, Geraldes P, McClelland P, Hodum P, Ryan PG, Borroto-Páez R, Pierce R, Griffiths R, Fisher RN, Wanless R, Pasachnik SA, Cranwell S, Micol T and Butchart SHM. 2019. Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. PLoS ONE 14: e0212128.

Hughes BJ. 2014. Breeding and population ecology of Sooty Terns on Ascension Island. (Doctoral dissertation, University of Birmingham).

Jackson JBC. 2008. Ecological extinction and evolution in the brave new ocean. PNAS 105(Supp. 1): 11458-11465.

Koldewey HJ, Curnick D, Harding S, Harrison LR and Gollock M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. Marine Pollution Bulletin 60(11): 1906-1915.

Lack D. 1954. The natural regulation of animal numbers. The Clarendon Press, Oxford.

Maxwell SM and Morgan LE. 2012. Examination of pelagic marine protected area management with recommendations for the Pacific Remote Islands Marine National Monument. Marine Conservation Institute, Seattle, WA.

Maxwell SM, Ban NC and Morgan LE. 2014. Pragmatic approaches for effective management of pelagic marine protected areas. Endangered Species Research 26(1): 59-74.

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH and Warner RR. 2015. Marine defaunation: Animal loss in the global ocean. Science 347(6219): 1255641-7.

McGowan A, Broderick AC and Godley BJ. 2008. Seabird Populations in the Chagos Archipelago: an Evaluation of Important Bird Area Sites. Oryx 42: 24-429.

Nelson JB. 1978. The Sulidae: Gannets and Boobies. Oxford: Published for the University of Aberdeen by Oxford University Press. ISBN 978-0-19-714104-5.

Newman J, Fletcher D, Moller H, Bragg C, Scott, D and McKechnie S. 2009. Estimates of productivity and detection probabilities of breeding attempts in the sooty shearwater (Puffinus griseus), a burrow-nesting petrel. Wildlife Research 36(2): 159-168.

O’leary BC, Ban NC, Fernandez M, Friedlander AM, García-Borboroglu P, Golbuu Y, Guidetti P, Harris JM, Hawkins JP, Langlois T and McCauley DJ. 2018. Addressing criticisms of large-scale marine protected areas. Bioscience 68(5): 359-370.

Reynolds SJ, Martin GR, Dawson A, Wearn CP and Hughes BJ. 2014. The sub-annual breeding cycle of a tropical seabird. PLoS One 9(4) p.e93582.

Ronconi RA, Lascelles BG, Langham GM, Reid JB and Oro D. 2012. The role of seabirds in Marine Protected Area identification, delineation, and monitoring: introduction and synthesis. Biological Conservation 156: 1-4.

Sanders SM (Ed.). 2006. Important Bird Areas in the United Kingdom Overseas Territories. Sandy, UK: RSPB.

Savage C. 2019. Seabird nutrients are assimilated by corals and enhance coral growth rates. Scientific Reports 9(1): 4284.

Sheppard CR, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, Fitzsimmons N, Gaither MR, Gan CH, Gollock M, Guzman N, Graham NA, Harris A, Jones R, Keshavmurthy S, Koldewey H, Lundin CG, Mortimer JA, Obura D, Pfeiffer M, Price AR, Purkis S, Raines P, Readman JW, Riegl B, Rogers A, Schleyer M, Seaward MR, Sheppard AL, Tamelander J, Turner JR, Visram S, Vogler C, Vogt S, Wolschke H, Yang JM, Yang SY and Yesson C. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. Aquatic Conservation 22(2): 232-261.

Sheppard CRC (Ed.). 2013. Coral Reefs of the United Kingdom Overseas Territories, Coral Reefs of the World 4, © Springer Science+Business Media Dordrecht.

Sheppard CRC and Seaward MR (Eds.). 1999. Ecology of the Chagos. Linnean Society Occasional Publications 2, Westbury Publishing, UK.

Sheppard CRC, Seaward MR, Klaus R and Topp JMW. 1999. The Chagos Archipelago: an introduction. Pages 1-20 in: Sheppard CRC and Seaward MR (Eds.). Ecology of the Chagos. Linnean Society Occasional Publications 2, Westbury Publishing, UK.

Sherley RB, Barham BJ, Barham PJ, Campbell KJ, Crawford RJ, Grigg J, Horswill C, McInnes A, Morris TL, Pichegru L and Steinfurth A. 2018. Bayesian inference reveals positive but subtle effects of experimental fishery closures on marine predator demographics. Biological Sciences 285(1871): 2017-2443.

Stoddart DR. 1971. Rainfall on Indian Ocean coral islands. Atoll Research Bulletin 147: 1-21.

Symens P. 1999. Breeding seabirds of the Chagos Archipelago. Pages 257-272 in: Sheppard CRC and Seaward MR (Eds.). Ecology of the Chagos. Linnean Society Occasional Publications 2, Westbury Publishing, UK.

Thaxter CB, Lascelles B, Sugar K, Cook AS, Roos S, Bolton M, Langston RH and Burton NH. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biological Conservation 156: 53-61.

VanderWerf EA and Young LC. 2017. A Summary and Gap Analysis of Seabird Monitoring in the US Tropical Pacific. Report prepared for the US Fish and Wildlife Service, Region, 1. Portland, OR. Pacific Rim Conservation, Honolulu, HI.

VanderWerf EA and Young LC. 2018. U.S. Tropical Pacific seabird surveying guide. Report prepared for the U.S. Fish and Wildlife Service, Region 1, Portland, OR. Pacific Rim Conservation, Honolulu, HI.

Votier SC, Hatchwell BJ, Beckerman A, McCleery RH, Hunter FM, Pellat J, Trinder M and Birkhead TR. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. Ecological Letters 8: 1157-1164.

Walsh PM, Halley DJ, Harris MP, Del Nevo A, Sim IMW and Tasker ML. 1995. Seabird monitoring handbook for Britain and Ireland: a compilation of methods for survey and monitoring of breeding seabirds. JNCC/RSPB/ITE/Seabird Group.

Wenban-Smith N and Carter M. 2017. Chagos: A History. Chagos Conservation Trust, London.

Wilhelm TA, Sheppard CRC, Sheppard AL, Gaymer CF, Parks J, Wagner D and Lewis NA. 2014. Large marine protected areas–advantages and challenges of going big. Aquatic Conservation: Marine and Freshwater Ecosystems 24(S2): 24-30.

SUPPLEMENTARY MATERIAL TO CHAPTER 3

Table S3. 1. Maximum number of breeding pairs of seabirds recorded between 2008-2018 from all islands in the Chagos Archipelago. Zero counts = the species was not recorded breeding on an island. Top figure = breeding pairs, brackets = year the record was made. **Bold** text = number of breeding pairs recorded qualifies for IBA status. Black Rat *Rattus rattus* presence (P), absence (A), eradicated (E) or uncertain status (U) is recorded (data from Carr and Harper 2015; Harper et al. 2019). IBA qualifying population from BirdLife International 2004 pp. 296-297.

Island	Atoll	Rattus rattus	*Ardenna pacifica*	***Puffinus bailloni***	*Phaethon lepturus*	*Phaethon rubricauda*	*Sula dactylatra*	***Sula sula***	*Sula leucogaster*	*Fregeta minor*	*Fregeta ariel*	***Thalasseus bergii***	*Sterna dougallii*	***Sterna sumatrana***	*Sternula albifrons*	*Onychoprion anaethetus*	***Onychoprion fuscatus***	*Anous stolidus*	***Anous tenuirostris***	*Gygis alba*
Diego Garcia	Diego Garcia	P	18 (2010)	2 (2009)	6 (2015)	5 (2009)	0	**8,068** **(2018)**	0	0	0	14 (2018)	0	5 (2009)	5 (2009)	0	0	400 (2015)	25 (2014)	200 (2009)
West Island	Diego Garcia	A	0	0	0	0	0	268 (2018)	0	0	0	0	0	0	0	8 (2018)	0	240 (2018)	0	0
Middle Island	Diego Garcia	A	0	0	0	0	0	520 (2018)	0	0	0	0	0	1 (2018)	0	0	0	22 (2014)	10 (2015)	10 (2009)
East Island	Diego Garcia	A	0	0	0	0	0	1,113 (2018)	3 (2018)	0	0	0	0	0	0	0	0	34 (2012)	40 (2014)	15 (2014)
Diego Garcia atoll		NA	18	2	6	5	0	**9,969**	3	0	0	14	0	6	5	8	0	696	75	225
Sudest complex	Egmont Islands	P	0	0	2 (2016)	0	0	123 (2013)	0	0	0	70 (2009)	0	40 (2009)	0	0	0	24 (2014)	0	17 (2009)
Lubine complex	Egmont Islands	P	0	0	0	0	0	1 (2015)	0	0	0	0	0	30 (2013)	0	0	0	40 (2009)	0	30 (2009)
Egmont Islands atoll		NA	0	0	2	0	0	124	0	0	0	70	0	70	0	0	0	64	0	47
Danger	Great Chagos Bank	A	40 (2015)	10 (2015)	0	0	0	**3,500** **(2010)**	141 (2009)	0	0	0	0	0	0	0	0	45 (2014)	2,400 (2014)	35 (2010)
Sea Cow	Great Chagos Bank	A	150 (2009)	5 (2015)	0	0	0	1,400 (2009)	0	0	0	5 (2009)	0	14 (2009)	0	11 (2009)	0	140 (2010)	1,200 (2010)	25 (2010)
Eagle Island	Great Chagos Bank	P	0	0	1 (2013)	0	0	10 (2010)	0	0	0	0	0	0	0	0	0	40 (2013)	10 (2013)	20 (2015)

North Brother	Great Chagos Bank	A	3,200 (2012)	**1,200 (2015)**	0	0	0	377 (2009)	740 (2014)	300 (2009)	15 (2015)	10 (2009)	0	0	0	6 (2012)	**10,000 (2009)**	124 (2014)	600 (2009)	55 (2009)
Middle Brother	Great Chagos Bank	A	0	0	0	0	0	77 (2014)	0	10 (2010)	0	40 (2009)	0	8 (2013)	0	0	**32,000 (2012)**	80 (2013)	25 (2009)	35 (2009)
Resurgent	Great Chagos Bank	A	1 (2009)	0	0	0	140 (2010)	0	7 (2009)	0	0	6 (2009)	0	0	0	4 (2009)	0	0	0	0
South Brother	Great Chagos Bank	A	300 (2010)	**400 (2014)**	0	0	0	105 (2009)	0	0	0	40 (2009)	0	0	0	2 (2009)	**10,000 (2009)**	55 (2009)	**11,500 (2015)**	30 (2009)
Nelson's Island	Great Chagos Bank	A	32 (2013)	5 (2015)	0	0	0	**3,300 (2012)**	25 (2015)	250 (2012)	50 (2010)	0	0	0	0	9 (2018)	0	650 (2012)	**12,000 (2014)**	25 (2014)
Great Chagos Bank atoll		NA	3,723	**1,620**	1	0	140	**8,769**	913	560	65	**101**	0	22	0	32	**52,000**	1,134	**27,735**	225
Coin	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21 (2014)	10 (2013)	20 (2009)
Anglaise	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20 (2009)	0	20 (2009)
Monpatre complex	Peros Banhos	P	0	0	0	0	0	0	0	0	0	10 (2015)	0	1 (2015)	0	0	0	2 (2015)	0	2 (2014)
Poule	Peros Banhos	P	0	0	1 (2015)	0	0	0	0	0	0	0	3 (2012)	2 (2015)	0	0	0	8 (2015)	0	2 (2015)
Petit Souer	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5 (2012)	0	4 (2009)
Grand Souer	Peros Banhos	P	0	0	0	0	0	4 (2016)	0	0	0	0	0	0	0	0	0	7 (2014)	0	4 (2009)
Finon	Peros Banhos	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1 (2016)	0	1 (2016)
Verte	Peros Banhos	U	0	0	0	0	0	3 (2015)	0	0	0	0	0	0	0	0	0	1 (2016)	0	1 (2016)
Unnamed (Burtle)	Peros Banhos	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1 (2016)
Manon	Peros Banhos	U	0	0	0	0	0	3 (2015)	0	0	0	0	0	0	0	0	0	15 (2009)	10 (2016)	5 (2009)
Pierre	Peros Banhos	P	0	0	0	0	0	3 (2015)	0	0	0	0	0	0	0	0	0	7 (2012)	0	3 (2012)
Petite Mapou	Peros Banhos	P	0	0	0	0	0	22 (2012)	0	0	0	0	0	0	0	0	0	5 (2014)	0	2 (2014)
Grande Mapou	Peros Banhos	P	0	0	0	0	0	10 (2015)	0	0	0	0	0	0	0	0	0	10 (2009)	15 (2014)	10 (2009)
Diamant	Peros Banhos	P	0	0	0	0	0	12 (2013)	0	0	0	0	0	0	0	0	0	20 (2009)	15 (2013)	10 (2010)
Passe	Peros Banhos	P	0	0	0	0	0	54 (2013)	0	0	0	0	0	0	0	0	0	15 (2010)	40 (2016)	15 (2010)
Moresby	Peros Banhos	P	0	0	1 (2016)	0	0	540 (2013)	0	0	0	14 (2017)	0	0	0	0	0	45 (2012)	105 (2013)	25 (2010)
Saint Brandon	Peros Banhos	A	0	0	0	0	0	0	0	0	0	0	0	1 (2016)	0	0	0	0	0	0

Parasol	Peros Banhos	A	0	0	0	0	0	96 (2013)	1 (2016)	0	0	0	0	0	0	3 (2009)	**37,500 (2012)**	30 (2010)	140 (2013)	10 (2009)
Longue	Peros Banhos	A	0	0	0	0	0	490 (2009)	3 (2016)	0	0	0	0	0	0	0	**48,000 (2012)**	140 (2013)	1,100 (2014)	25 (2009)
Grand Bois Mangue	Peros Banhos	A	0	0	0	0	0	127 (2012)	0	0	0	0	0	0	0	0	0	50 (2009)	2,000 (2009)	10 (2016)
Petite Bois Mangue	Peros Banhos	A	0	0	0	0	0	120 (2013)	0	0	0	0	0	0	0	0	2,000 (2009)	82 (2013)	**14,000 (2014)**	13 (2009)
Manoel	Peros Banhos	U	0	0	0	0	0	3 (2015)	0	0	0	0	0	0	0	0	0	15 (2009)	10 (2016)	15 (2009)
Unnamed (Marlin)	Peros Banhos	A	0	0	0	0	0	0	0	0	0	0	0	3 (2009)	0	0	0	0	0	0
Yeye	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	15 (2009)	0	0	0	32 (2014)	55 (2014)	45 (2009)
Petite Coquillage	Peros Banhos	A	0	0	0	0	0	125 (2009)	0	0	0	0	0	0	0	0	**20,000 (2009)**	140 (2008)	1,850 (2014)	20 (2009)
Grand Coquillage	Peros Banhos	A	0	10 (2009)	0	0	0	750 (2014)	0	80 (2016)	5 (2016)	23 (2012)	0	0	0	2 (2012)	**38,000 (2012)**	125 (2013)	1,500 (2009)	30 (2009)
Coin de Mire	Peros Banhos	A	2 (2012)	0	0	0	24 (2015)	0	0	0	0	0	4 (2010)	1 (2012)	0	21 (2015)	0	0	0	0
Vache Marine	Peros Banhos	E	0	0	0	0	0	0	0	0	0	25 (2016)	0	0	0	0	0	5 (2009)	0	7 (2018)
Fouquet	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5 (2012)	0	3 (2009)
Mapou de Coin	Peros Banhos	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5 (2010)	0	5 (2012)
Peros Banhos atoll		NA	2	10	2	0	24	2,362	4	80	5	72	7	33	0	26	**145,000**	791	**20,850**	308
Boddam	Salomon Islands	P	0	0	1 (2013)	0	0	0	0	0	0	0	0	0	0	0	0	25 (2013)	10 (2014)	30 (2009)
Diable	Salomon Islands	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1 (2015)	0	0
Anglaise	Salomon Islands	P	0	0	0	0	0	0	0	0	0	0	0	1 (2015)	0	0	0	20 (2012)	10 (2010)	15 (2010)
Passe	Salomon Islands	A	0	0	2 (2015)	0	0	27 (2013)	4 (2015)	0	0	0	0	0	0	0	0	40 (2015)	400 (2016)	25 (2009)
Mapou	Salomon Islands	A	0	0	1 (2014)	0	0	100 (2014)	0	0	0	0	0	0	0	0	0	60 (2012)	1,600 (2014)	13 (2009)
Takamaka	Salomon Islands	P	0	0	5 (2015)	0	0	302 (2016)	0	0	0	0	0	25 (2009)	0	0	0	65 (2014)	100 (2016)	25 (2010)
Fouquet	Salomon Islands	P	0	0	1 (2012)	0	0	17 (2012)	0	0	0	0	3 (2013)	53 (2013)	0	0	0	25 (2012)	0	10 (2009)
Sepulture	Salomon Islands	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6 (2013)	0	1 (2014)
Jacobin	Salomon Islands	E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5 (2013)	0	2 (2010)

Sel	Salomon Islands	E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3 (2012)	0	1 (2015)
Poule	Salomon Islands	P	0	0	0	0	0	0	0	0	0	25 (2010)	0	0	0	0	0	1 (2014)	0	1 (2012)
Salomon Islands atoll		NA	0	0	10	0	0	446	4	0	0	25	3	77	0	0	0	251	2,120	123
Chagos Archipelago		NA	3,743	**1,632**	21	5	164	**21,670**	924	640	70	**282**	10	**200**	5	66	**197,500**	2,956	**50,780**	928
IBA qualifying population		NA	15,000 pairs	300 pairs	250 pairs	160 pairs	1,000 pairs	3,000 pairs	1,000 pairs	1,700 pairs	1,000 pairs	200 individuals	50 individuals	150 individuals	250 individuals	5,000 individuals	20,000 individuals	7,500 individuals	10,000 individuals	5,000 individuals

Table S3. 2. The date surveys of the proposed and designated terrestrial Important Bird and Biodiversity Areas in the Chagos Archipelago were undertaken (2008-2018).

ISLAND	MONTH (- MONTH) YEAR																										
	11 08	1 09	2 09	4 09	5 09	6 09	7 09	8 09	10 09	2 10	5 10	8 10	3 11	2-3 12	7 12	12 12	2-3 13	1 14	3-4 14	8 14	3-4 15	8 15	2 16	3 16	4 17	1-2 18	6-7 18
DIEGO GARCIA			■				■	■		■			■	■	■		■		■		■					■	■
DANGER ISLAND			■				■	■	■	■	■			■			■		■		■		■	■			
SEA COW			■	■			■	■	■	■	■			■			■		■		■						
NORTH BROTHER	■	■	■		■		■		■	■	■			■			■		■		■						
MIDDLE BROTHER			■		■		■	■	■	■		■	■	■		■	■		■		■	■					
SOUTH BROTHER			■		■	■	■	■	■	■	■		■	■		■	■		■		■		■	■			
NELSON	■	■	■		■		■		■	■			■	■	■	■	■		■	■	■		■	■		■	■
PETITE BOIS MANGUE		■	■		■	■	■		■	■	■			■	■		■		■		■		■	■			
PARASOL			■		■		■		■	■	■			■			■	■	■		■		■	■	■		
LONGUE		■	■				■		■	■				■			■		■		■		■	■	■		
PETITE COQUILLAGE	■		■		■		■		■	■	■			■			■		■		■		■				
GRAND COQUILLAGE	■		■		■		■		■	■	■			■			■		■	■	■		■		■	■	

CHAPTER 4

POTENTIAL BENEFITS TO BREEDING SEABIRDS OF CONVERTING ABANDONED COCONUT PLANTATIONS TO NATIVE HABITATS AFTER INVASIVE PREDATOR ERADICATION.

Chapter published as:

Carr P, Trevail A, Bárrios S, Clubbe C, Freeman R, Koldewey HJ, Votier SC, Wilkinson T & Nicoll MAC. 2021. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. Restoration Ecology .e13386.

ABSTRACT

On many Pacific and Indian Ocean islands, colonisation by humans brought invasive species, native vegetation destruction and coconut plantations, leading to the decimation of seabird populations. The coconut industry on oceanic islands has since crashed, leaving the legacy of altered, impoverished ecosystems. Many island restoration projects eradicate invasive species, particularly rats, with the goal of restoring seabird-driven ecosystems. However, in the absence of converting abandoned plantations to habitat conducive to breeding seabirds, seabird-driven ecosystems may not fully recover after rat eradication. Here I quantify and, by resource selection function, confirm seabird habitat selection within the CA, before estimating the potential difference in breeding abundance following rat eradication with and without active management of abandoned plantations. Using Ile du Coin as my primary example, I estimate that following rat eradication, but without plantation conversion, this island could potentially support 4,306 (+/- 93) pairs of breeding seabird; if restored to habitat representative of associated rat-free islands, 138,878 (+/- 1,299) pairs. If 1 km^2 of plantation is converted to produce 0.5 km^2 each of native forest and savanna, it could theoretically support 319,762 (+/- 2,279) breeding pairs – more than the entire archipelago at present. My research indicates that when setting restoration goals in the CA, at least 55% of the restored habitat should be comprised of native forest and savanna in order to support a viable seabird community. My research enhances the prospects of successfully restoring seabird islands across the tropical landscape with wider benefits to native biodiversity.

INTRODUCTION

Islands contribute disproportionally to global biodiversity relative to their comparatively small land mass (Whittaker 1998). With their high rates of endemism and relative isolation they have incurred 61% of all documented extinctions and currently support 37% of all critically endangered species (Tershy et al. 2015). The conservation (and restoration) of islands and their associated biodiversity is therefore a global priority (CBD 2020).

Seabirds are key components of island ecosystems (Smith et al. 2011), transporting nutrients from the open ocean to islands, enhancing the productivity of island flora and fauna and surrounding marine ecosystems (Graham et al. 2018). Yet, seabird islands have been severely degraded by human activities worldwide (Mulder et al. 2011a) due in part to deforestation (Anderson & Mulder 2011), and the introduction of invasive species (Jones et al. 2016). Indeed, invasive species, particularly rats and cats, are the greatest threat to global seabird populations (Dias et al. 2019) as well as to island biodiversity generally (Millennium Ecosystem Assessment 2015).

Repairing damage to degraded seabird islands by eradicating invasive mammals has proven extremely effective (Jones et al. 2016). However, predator eradication may not necessarily lead to (re)colonisation and ecosystem recovery because of ecological factors such as distances to source populations, metapopulation dynamics, philopatry strength, reproductive rates, and competition with other colonisers (Kappes & Jones 2014). Moreover, the recovery of a seabird island post eradication is strongly influenced by the availability of suitable breeding habitat (Smith et al. 2011, Mulder et al. 2011a).

In the tropical Indian and Pacific Oceans, many seabird islands became degraded following human colonisation, the introduction of invasive mammals and clearance of native vegetation for coconut *Cocos nucifera* plantations (Maunder et al. 1998, Samways et al. 2010, von Brandis 2012, Wenban-Smith and Carter 2017). With the demise of coconut farming on oceanic islands (Wenban-Smith and Carter 2017) many former plantations were abandoned and > 50% of the 1.3 million trees on Pacific islands are classified as senile and unproductive (McGregor and Sheehy 2017). These abandoned plantations are considered invasive (Young et al. 2017), break natural ecological interactions (McCauley et al. 2012), reduce floristic diversity and change soil characteristics (Young et al. 2010a, Mulder et al. 2011b), resulting in impoverished ecosystems that support few breeding seabirds (Young et al. 2010b, Carr et al. 2013). Therefore, even if invasive mammals are eradicated, seabird-driven ecosystems are unlikely to recover fully in the absence of vegetation management. Conversion of abandoned plantations to seabird breeding habitat is thus essential for ecological rehabilitation (Norton and Miller 2000), although more evidence is required to quantify such effects.

The CA, central Indian Ocean (Fig. 4.1) formerly held seabird colonies at least an order of magnitude greater than today (Bourne 1886, Gardiner and Cooper 1907, Bourne 1971). The decline was due to invasive mammalian predators, harvesting, and clearance of native habitat for monospecific coconut plantations (Bourne 1971, Wenban-Smith and Carter 2017). Copra (coconut kernel for oil production) was so successful that by 1880 the archipelago was known as the Oil Islands (Scott 1961). Coconut farming ceased in the 1970s and except for a transient military population on one island (Diego Garcia), all islands are now uninhabited. Abandoned plantations are the dominant vegetation throughout the archipelago (Carr et al. 2013) and on all 30 islands where plantations were established, invasive *Rattus rattus* (ship/black rats – hereafter rat) are present (Harper et al. 2019).

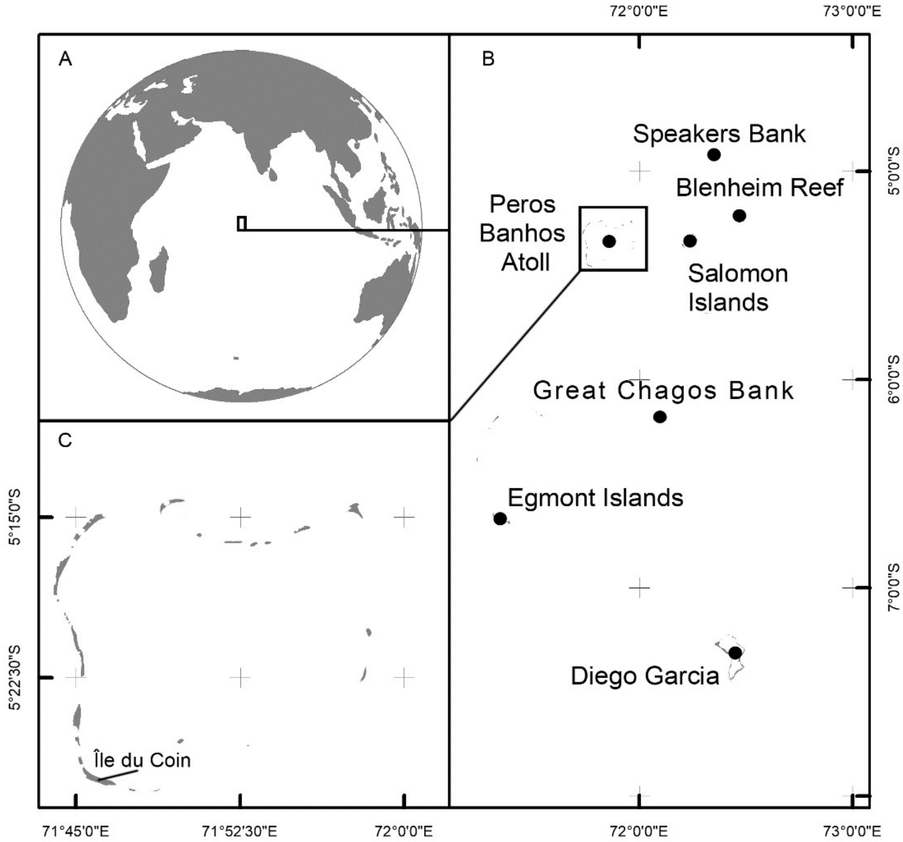


Figure 4. 1. The Chagos Archipelago, A). Location within the Indian Ocean, B). Major reef, banks and atolls, C). Ile du Coin within Peros Banhos atoll.

However, islands not farmed for coconut (n = 24) are in a near-natural vegetative state and rat-free (Scott 1961, Edis 2004, Wenban-Smith and Carter 2017, Harper et al. 2019) with seabird-driven ecosystems (Graham et al. 2018, Benkwitt et al. 2019). Collectively, these 24 islands form a contemporaneous reference site (CTR) (Mulder et al. 2011a). CTRs are sites (here islands) that are used to set targets for island restoration projects, especially where historical data are lacking (Mulder et al. 2011a), such as in the CA, as they represent present day climatic and environmental regimes and have properties that can be explicitly measured to evaluate restoration progress against (Jones et al. 2011). The measured properties in this studies' CTR are the six types of breeding habitat and the number of species and abundance of breeding seabirds in them. The numbers of breeding seabirds in the CTR are what the restored islands will be evaluated against.

Here, in the CA, I quantify the hypothetical potential increase in breeding seabird numbers with and without conversion of abandoned coconut plantations to breeding seabird habitats, post rat eradication.

METHOD

Overview

To estimate breeding seabird numbers, post hypothetical rat eradication and vegetation management, I first defined seabird breeding habitats (n = 6) and measured their availability on every island. I recorded the number of different species of seabirds and their abundance breeding in each habitat and used resource selection modelling to identify species-specific preferred nesting habitats. Using the (rat-free) CTR breeding seabird data, I calculated population density (breeding pairs/km^2) for each species in each breeding habitat. I used these habitat-specific breeding seabird densities to estimate breeding seabird abundance on a former coconut plantation island (Ile du Coin, 1.26 km^2, hereafter Coin), following rat eradication, under three plantation conversion scenarios.

There are assumptions in the calculations that require consideration. It is assumed that throughout the data gathering period (2008-2018) the habitat remained constant and the breeding bird's selection of habitat remained consistent. It is also assumed that all breeding habitats were identified, and birds had access to these all the time. It is accepted that recolonisation post ecological intervention by tropical seabirds can be unpredictable with extenuating circumstances impacting (Jones et al. 2011), can take decades (Dunlop et al. 2015), and that the marine resources capable of supporting increased seabird populations must be extant (e.g., Danckwerts et al. 2014).

Study Site

The CA, central Indian Ocean (05°15' - 07°27'S, 71°15' - 72°30'E) holds 55 low lying (1-3 m AMSL) porous, coralline islands sited on five atolls (Fig. 4.1). The southernmost island of Diego Garcia constitutes ~50% (~27 km^2) of the terrestrial landmass of the archipelago and the remaining islands' median size is 0.14 km^2 (range 0.025 – 2.65 km^2).

Coin is the former plantation headquarters of Peros Banhos atoll and has been uninhabited since 1973 (Wenban-Smith and Carter 2017). At 1.26 km^2 it is the fourth largest island in the archipelago. Abandoned coconut plantations form ~92% of vegetation cover (Wilkinson 2017) that, when combined with invasive rat presence mean it supports an impoverished biome including only 51 breeding pairs of three seabird species (Carr et al. 2021). The extant vegetation communities on Coin are representative of all rat-infested former plantation islands > 0.5 km^2 in the CA (n = 13 - Figs. 4.3a; S4.1).

Breeding Seabird Habitat Mapping

I defined and mapped six seabird breeding habitat types (see Figs. 4.2a-f) for ~90% of the CA based on Wilkinson (2017) and Bárrios and Wilkinson (2018). The unmapped 10% were categorized using expert local knowledge, satellite imagery and aerial photographs (see Table S4.1).

4.2a. Beach: IUCN habitat class 13.1/13.3. Sea cliffs and rocky offshore islands/coastal sand dunes. Beach is comprised of any substrate that forms the shoreline above the highwater mark up to the point that vegetation starts. Photo Credit: P. Carr.

4.2b. Mixed Shrub: IUCN habitat class 3.6. Tropical moist shrubland. Mixed shrub is found mainly on the beach crest but occurs inland on islands not yet extensively colonised by native forest. Photo Credit: L. Kedding.

4.2c. Native Forest: IUCN habitat class 1.6. Tropical moist lowland forest. Native forest is made up of 11 species of tree and occurs on shorelines and inland. Photo Credit: P. Carr.

4.2d. Non-native Forest: IUCN habitat class 14. 3 Plantations. Over 92% of non-native forest is made up of abandoned *Cocos nucifera* (coconut) plantations. Photo Credit: P. Carr.

4.2e. Savanna: IUCN habitat class 2.2. Moist savanna. Bare ground and, sand with sparse cover are included as savanna where they are not part of the beach habitat, i.e. where they are found inland behind the beach crest. Photo Credit: A. Williams.

4.2f. Wetlands: IUCN habitat classes 5.14/5.16. Permanent saline, brackish or alkaline lakes/ponds. 1.7. Subtropical/Tropical mangrove forest vegetation above high tide level. Wetland habitats are areas of permanent fresh or brackish water not connected to the open sea. Photo Credit: C. Clubbe.

Figure 4. 2. Tropical seabird breeding habitat classification in the Chagos Archipelago adapted from Wilkinson (2017) and Bárrios & Wilkinson (2018).

Breeding Seabird Habitat Selection

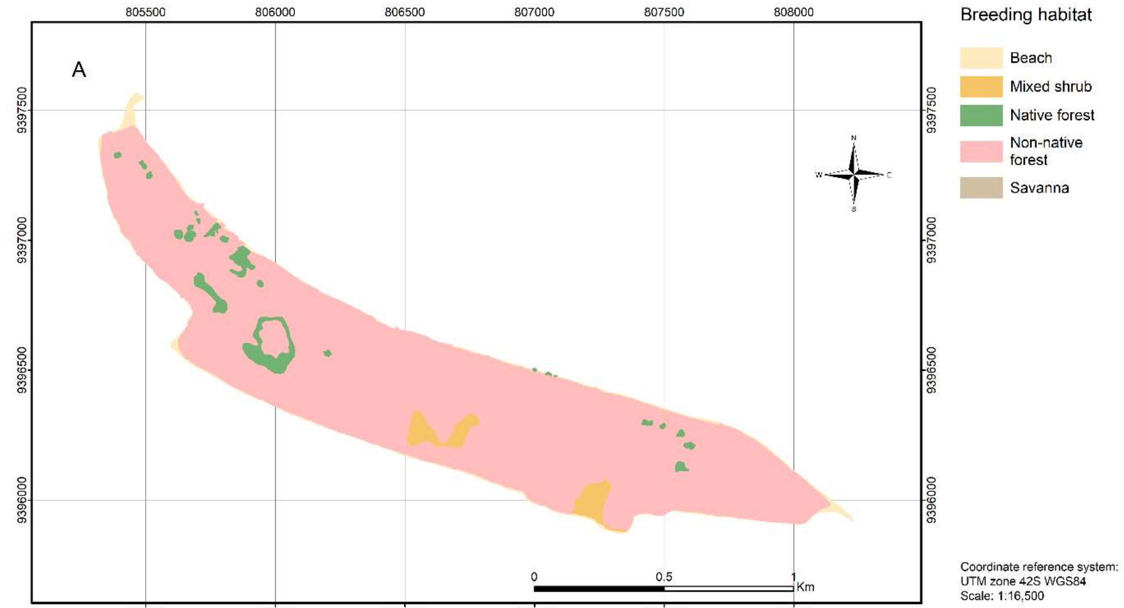
Breeding seabird populations were surveyed between 2008-2018 (for details see Carr et al. 2021 and chapter 3). Across the archipelago the maximum annual population was estimated at 281,149 breeding pairs of 18 species (Carr et al. 2021) and all nests were assigned to a breeding habitat (Figs. 4.2a-f). To test whether seabirds were preferentially selecting breeding habitats over others, I used resource selection functions (Manly et al. 1993). As a measure of available habitat, I modelled 10 pseudo-absences for each nest for 14 species across the 24 islands of the rat-free CTR. Four species, White-tailed Tropicbird *Phaethon lepturus*, Red-tailed Tropicbird *P. rubricauda*, Roseate Tern *Sterna dougallii* and Little Tern *Sternula albifrons* were omitted from the analysis because of small numbers (< 5 pairs) and irregular (not annual) breeding and two, Red-tailed Tropicbird and Little Tern only breed on rat-infested Diego Garcia (Carr et al. 2021). I randomly assigned each nest a vegetation type based on the percentage vegetation cover on the island that the corresponding 'used' nest was located in. Habitat use (binary response variable; 1 = used, 0 = available) was modelled in response to a two-way interaction between vegetation type and species, to explore species specific nest-site habitat selection. Island and size were included as fixed effects to account for potential effects on breeding numbers. I was unable to fit island as a random effect because of issues with convergence and rank deficiency.

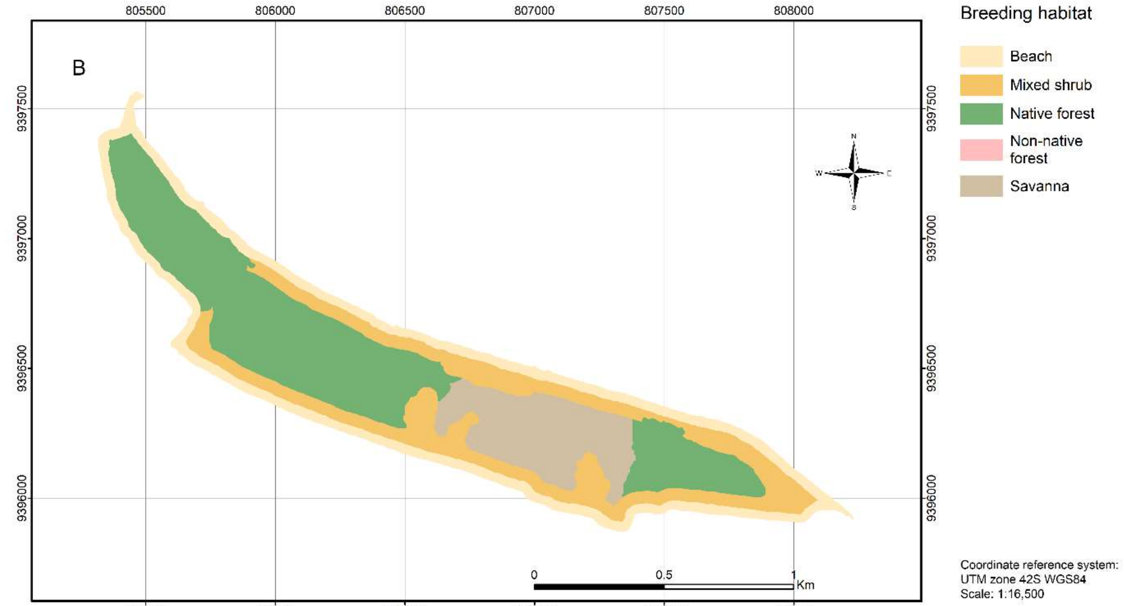
Models were run using the glm function in lme4 (Bates et al. 2015), with a binomial error structure and logit link. Used and available points were given weightings of 10 and 1 respectively, thereby weights were proportionally equal between all used and available locations (Barbet-Massin et al. 2012). I selected the most suitable fixed effects structure based on corrected Akaike information criterion (AICc) values in backward stepwise selection (Table S4.2). I ensured model fit by calculating the area under the receiving operator characteristic curve (AUC – Zweig and Campbell 1993), predictive power and sensitivity and specificity (Warwick-Evans et al. 2016) (Table S4.3). All analysis were conducted in the statistical software package R, version 4.0.3 (R Core Team 2017).

Estimating Breeding Seabird Populations Post Management

I employed a two-step process to estimate the number of breeding seabirds that could potentially be supported by Coin, following rat eradication, under three plantation conversion scenarios.

First, I calculated for each of the six habitats the breeding density (pairs per km^2) of all seabird species across the CTR (Tables 4.1; S4.4). Second, I applied these habitat-specific population densities to Coin, following rat eradication, where; (A) the vegetation composition remained the same as the current situation (Fig. 4.3a); (B) the plantation was converted to the habitat composition in the CTR (Fig. 4.3b), and (C) 1 km^2 of plantation was converted to 0.5 km^2 of native forest and 0.5 km^2 of savanna habitat, which were identified as the two habitats supporting the greatest abundance and number of species of breeding seabirds in the CTR (Fig. 4.3c; Table 4.1). Coin holds 1.154 km^2 of non-native forest (SI Worked Example), 1 km^2 was selected for conversion as this is the figure that would likely be used in a real-time conversion operation. A working example of calculating seabird breeding density following rat eradication on Coin is provided for scenario (A) in the SI Worked Example.


A
805500
806000
806500
807000
807500
808000
9397500
9397000
9396500
9396000
Breeding habitat
Beach
Mixed shrub
Native forest
Non-native forest
Savanna
N
W
E
S
0
0.5
1
Km
Coordinate reference system:
UTM zone 42S WGS84
Scale: 1:16,500


B
805500
806000
806500
807000
807500
808000
9397500
9397000
9396500
9396000
Breeding habitat
Beach
Mixed shrub
Native forest
Non-native forest
Savanna
N
W
E
S
0
0.5
1
Km
Coordinate reference system:
UTM zone 42S WGS84
Scale: 1:16,500

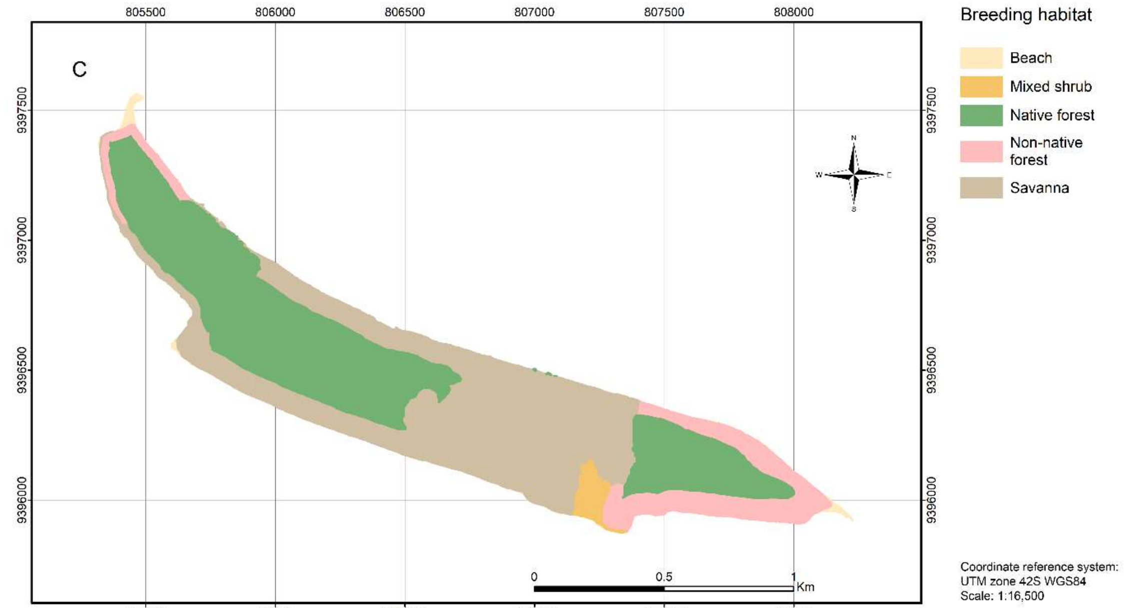


Figure 4. 3. Ile du Coin, Peros Banhos atoll, Chagos Archipelago. (A) Extant vegetation cover; (B) vegetation cover after hypothetical conversion of coconut *Cocos nucifera* plantations to proportionately represent the extant vegetation cover on the contemporaneous reference site and; (C) after converting 1 km^2 of plantation to produce 0.5 km^2 each of native forest and savanna (adapted from Wilkinson 2017).

RESULTS

Breeding Seabird Habitat Mapping

Archipelago-wide, there was ~ 12x more rat-infested than rat-free habitat (Table 4.1). Non-native forest on rat-infested islands covers the greatest area (15.87 km^2/~55%) of which 92% constitutes abandoned coconut plantations (Wilkinson 2017, Bárrios and Wilkinson 2018). Wetland on rat-free islands is the scarcest habitat (0.004 km^2/0.33%). Savanna on rat-free islands supported the greatest abundance of breeding pairs with a total of 197,409 (580,615/km^2), while no seabirds bred in savanna on rat-infested islands. Native forest supported the second highest abundance with 61,280 (51,471/km^2) breeding pairs and the highest number of species (n = 10) on rat-free islands. Wetland only had a single species breeding in it regardless of rat status.

Table 4. 1. The physical area and mean percentage area with standard deviation (SD) covered by six breeding habitats across the Chagos Archipelago; the actual number of breeding pairs and breeding pairs/km^2 per habitat and number of species breeding in a habitat, on rat-free (RF) and rat-infested (RI) islands. BEAC = beach, MISH = mixed shrub, NATF = native forest, NONF = non-native forest, SAVA = savanna, WETL = wetlands.

Habitat	Area (km^2)		% Area/SD				Breeding pairs		Breeding pairs/km^2		No. of breeding species in habitat	
	RF	RI	RF		RI		RF	RI	RF	RI	RF	RI
BEAC	0.280	7.860	20.790	5.040	7.350	1.950	434	316	1,550	40	4	3
MISH	1.110	2.800	23.770	3.810	20.260	4.020	9,900	3,047	8,919	1,088	7	4
NATF	1.210	10.900	36.990	5.850	13.200	3.500	61,280	7,001	51,471	697	10	5
NONF	0.240	15.870	5.200	3.180	54.860	5.270	136	1,121	588	71	3	2
SAVA	0.340	1.200	12.930	2.990	3.360	1.290	197,409	0	580,615	0	6	0
WETL	0.004	0.300	0.330	0.310	0.980	0.440	55	450	13,750	1,500	1	1
TOTALS	3.184	38.930	—	—	—	—	269,214	11,935	—	—	—	—

Breeding Seabird Habitat Selection

Resource selection modelling (RSM) demonstrates scientifically the habitat selection made by breeding seabirds (use versus availability, not use because of availability). The model (Fig. 4.4) shows that beach is the only habitat selected by Black-naped Tern *Sterna sumatrana* and Great Crested Tern *Thalasseus bergii*. Wetland is only selected for by RfB. Savanna is the only habitat selected by two terrestrial nesting boobies, Brown Booby *S. leucogaster* and Masked Booby *S. dactylatra* and is the preferred habitat of the super-abundant breeding Sooty Tern *Onychoprion fuscatus*. Native forest is positively selected for by the highest diversity of species (n = 7), one of which is the second most abundant breeding species, Lesser Noddy *Anous tenuirostris*, which only breeds in this habitat. Non-native forest is selected by Common White Tern *Gygis alba*, Brown Noddy *Anous stolidus* and Great Frigatebird *Fregata minor*, these three species breed in trees in other habitats - the latter species appears to select for non-native forest above all others.

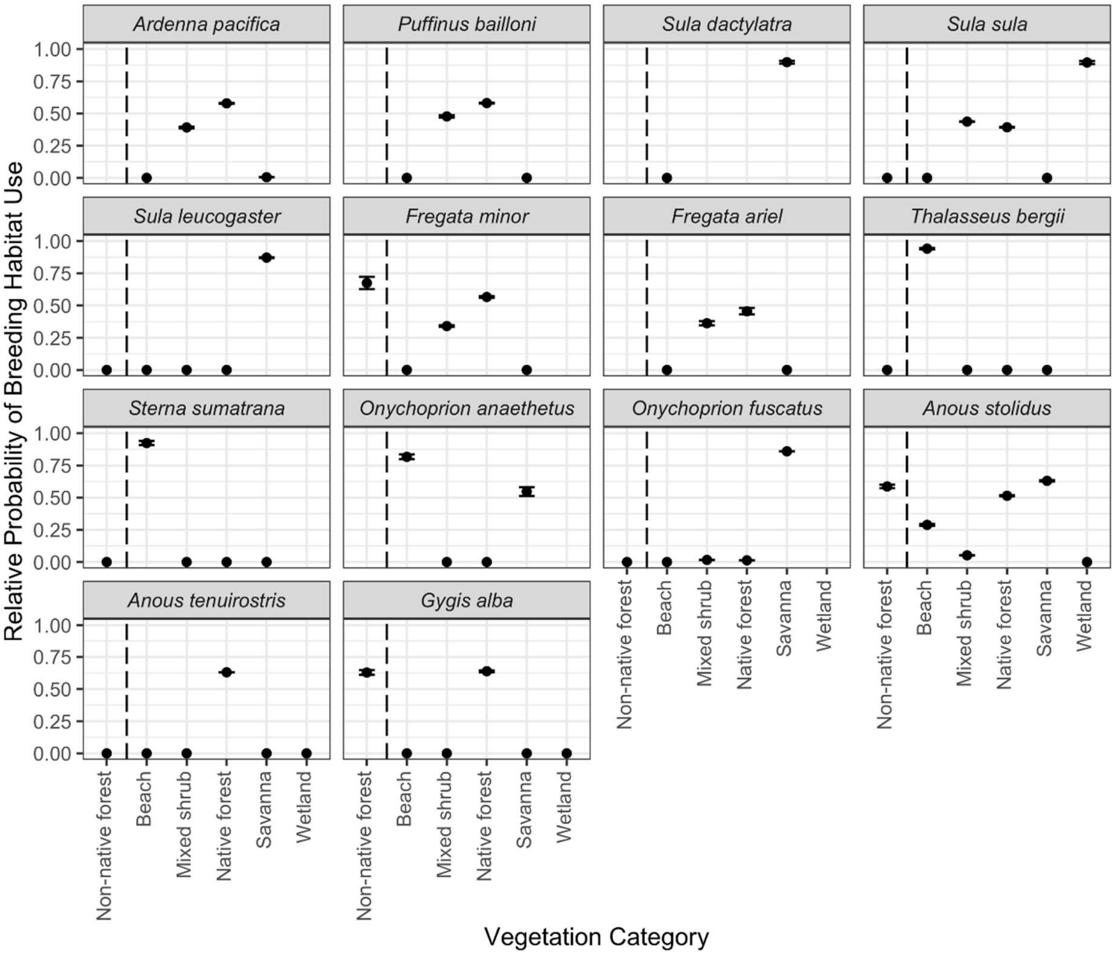


Figure 4. 4. Breeding habitat selection for 14 species of tropical seabird from the (rat-free) contemporaneous reference site in the Chagos Archipelago. Error bars show standard error.

Predicting Breeding Seabird Populations Post Management

At present, Coin supports an impoverished biome that includes 51 breeding pairs of three species of seabird - Brown and Lesser Noddy and, Common White Tern. Following rat eradication without plantation conversion (scenario A), I estimate 4,306 (+/- 93) breeding pairs of 14 species. If the abandoned plantations are converted to breeding habitat proportionately representative of the CTR (scenario B), this increases to 138,878 (+/- 1,299) pairs. In scenario C, where 1 km^2 of abandoned plantation is converted to 0.5 km^2 each of native forest and savanna, 319,762 (+/- 2,279) breeding pairs of 16 species are estimated. Savanna, that is not currently present on Coin, supports the greatest number of breeding pairs when created through habitat conversion in scenarios B and C (Table 4.2).

Table 4. 2. Ile du Coin, Chagos Archipelago, breeding seabird population (breeding pairs +/-SD) from the present day and, after Scenario A: following rat eradication with no vegetation management; Scenario B: after theoretically converting abandoned coconut plantations on the island to a habitat ratio equivalent of the contemporaneous reference site and Scenario C: after 1 km^2 of abandoned coconut plantation is theoretically converted equally between savanna and native forest. BEAC = beach, MISH = mixed shrub, NATF = native forest, NONF = non-native forest, SAVA = savanna, WETL = wetlands.

Habitat Type	**Breeding Pairs Per Habitat**			
	Present day	Scenario A	Scenario B	Scenario C
Beach	0	17 +/- 0	391 +/- 3	17 +/- 0
Mixed shrub	0	214 +/- 6	2,809 +/- 72	214 +/- 5
Native forest	13	3,397 +/- 91	25,941 +/- 633	29,133 +/- 709
Non-native forest	38	678 +/- 15	0	90 +/- 1
Savanna	0	0	109,736 +/- 591	290,307 +/-1,564
Wetland	0	0	0	0
TOTAL	51 (3 ssp.)	4,306 +/- 93 (14 ssp.)	138,878 +/- 1,299 (16 ssp.)	319,762 +/- 2,279 (16 ssp.)

DISCUSSION

I believe my research is the first to combine quantitative analysis and resource selection modelling to demonstrate the potential benefits to breeding tropical seabirds of ecologically restoring abandoned coconut plantations on oceanic islands. The results also reveal the limits of ecological restoration programmes involving rat removal without including restoration of degraded habitat.

The habitat modelling showed that seabirds selected natural habitats, with very weak selection for or, more commonly, selection against breeding in non-native forest (i.e., coconut plantations). These results highlight the importance of restoring abundant natural habitats for breeding seabirds in restoration programmes.

In the worked example of Coin, this island could potentially support an ~84-fold increase in breeding pairs to 4,306 pairs of 14 species following rat eradication but without converting plantations. Intuitively, with 92% of the island remaining covered by the suboptimum, invasive habitat of abandoned plantations, this option does not constitute “restoration” of a seabird island and, because of the lack of seabird breeding habitat, is highly unlikely to lead to the full recovery of a seabird-driven ecosystem.

On the CTR, it is assumed that the mean breeding habitat ratio represents the habitat proportions necessary for supporting seabird-driven ecosystems. This assumption is supported by the cross-ecosystem benefits bestowed by nutrient transfer through abundant seabirds demonstrated by Graham et al. (2018) and Benkwitt et al. (2019) from some of these islands. Therefore, theoretically, if seabirds are breeding in these habitats on ecologically restored islands at similar breeding abundance and number of species, the island should be functional as a seabird island ecosystem. In the worked example of Coin, eradicating rats followed by converting abandoned plantations to habitat in proportion with what is present on the CTR produces a total of 138,878 breeding pairs of 16 species. Although reproducing habitat proportionately representative of a CTR appears the obvious target for ecological restoration, there are practical reasons why it cannot be applied.

Creating beach habitat in a remote environment where its extent and distribution naturally changes seasonally (Sheppard & Sheppard 2019) would be an expensive logistical challenge. The two Sternidae that only select this habitat are IUCN Red-Listed Least Concern (BirdLife International 2018) and, at least in the CA, are nomadic breeders displaying little natal philopatry (Carr et al. 2021). The expense of creating beach would not justify the possible improved outcome. Creating wetland habitat on porous coralline islands, that only has a single species selecting it as breeding habitat is also not justified.

Mixed shrub is a pioneering habitat that rapidly colonizes open areas and is an essential component of island formation (Hyland et al. 2010). In any restoration project, mixed shrub would occur naturally as successional growth (Mueller-Dombois and Fosberg 1998).

Non-native forest, which in the CA is 92% abandoned coconut plantations (Wilkinson 2017, Bárrios and Wilkinson 2018), is invasive (Young et al. 2010a, 2010b) and a species poor biome (Carr et al. 2013). In this study it supports the least breeding pairs/km^2 and only two generalist breeding species of Least Concern, Brown Noddy and Common White Tern, (BirdLife International 2018) regularly breed in it. The five pairs of Great Frigatebird that bred in non-native forest are an anomaly and were only ever recorded once, in 2010 (Carr et al. 2021).

Therefore, in any ecological restoration project in the CA, non-native forest in the form of abandoned coconut plantations, would be the habitat to convert. Due to the impracticalities of creating beach and wetland, and the way that mixed shrub (particularly *Scaevola taccarda*) colonises open areas naturally, native forest and savanna would become the replacement habitats. These two habitats also hold the greatest abundance of breeding pairs and number of species of all breeding habitats and RSM demonstrates they are the preferentially selected breeding habitats of nine of the 14 species modelled. This conclusion holds true for other island rehabilitation projects in the Western Indian Ocean. Abandoned coconut plantations on Denis Island, Republic of Seychelles, were successfully converted to savanna-type habitat for Sooty Tern recovery (Feare et al. 2015); on Cousine (Samways 2010) and D’Arros Island (von Brandis 2012) native forest has been the goal. Further afield on Palmyra atoll, Northern Line Islands, Pacific Ocean, invasive abandoned coconut plantations are being converted to native *Pisonia* (*Coedes*) forest (Hathaway et al. 2011).

The breeding seabird habitat ratio of the CTR (that has functional seabird-driven ecosystems), combined with estimations of breeding abundance and number of species in these habitats, informs habitat cover requirements to restore seabird-driven ecosystems post rat eradication. Based on this research, a minimum of 55% of an island must be composed of native forest (36.99% on CTR) and savanna (12.93% on CTR) and, savanna must constitute at least 15% of the total land coverage for a seabird-driven ecosystem to fully recover. In the CA, ecological restoration to this habitat ratio is essential to restore seabird-driven ecosystems. This is because all rat-infested islands are dominated by abandoned coconut plantations and seabird breeding abundance and numbers of species in native forest and savanna, coupled with the habitat selection results of RSM demonstrate these are the two habitats required for seabirds to recolonise in sufficient numbers to drive ecosystem recovery.

The CA provides a good example of the potential benefits of converting abandoned coconut plantations to native habitats post invasive predator eradication. However, this quantitative approach to predicting results of ecological restoration is relevant and widely applicable elsewhere. Tropical seabirds are declining and with them the quality of environmental services they provide to associated ecosystems that are stressed from global threats such as climate warming. This research has shown that the ‘panacea’ of rat eradication alone is unlikely to restore seabird-driven ecosystems on islands previously used as coconut plantations. Restoration practitioners must consider the recovery of these islands as a two-phase operation: firstly, removing the invasive predators; secondly managing and converting non-native habitat.

REFERENCES

Anderson WB and Mulder CPH. 2011. An introduction to seabird islands. Pages 3-16 in: Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Barbet-Massin M, Jiguet F, Albert CH and Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3: 327-338.

Bárrios S and Wilkinson T. 2018. Mapping the vegetation of Diego Garcia island, British Indian Ocean Territory, November 2018. Fieldwork report. Overseas Fieldwork Committee registration number 893. Royal Botanic Garden, Kew, Richmond, Surrey, UK.

Bates D, Mächler M, Bolker B and Walker S. 2015. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software 67: 1-48.

Benkwitt CE, Wilson SK and Graham NA. 2019. Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Global Change Biology 25(8): 2619-2632.

BirdLife International. 2018. IUCN Red List of Threatened Species https://www.iucnredlist.org/ accessed 24 July 2020.

Bourne GC. 1886. General Observations on the fauna of Diego Garcia. Proceedings of the Zoological Society London 1886: 331-334.

Bourne WRP. 1971. The Birds of the Chagos Group, Indian Ocean. Atoll Research Bulletin 149: 175-207.

Carr P, Hillman JC, Seaward MRD, Vogt S, Sheppard CRC. 2013. Coral Islands of the British Indian Ocean Territory (Chagos Archipelago). Pages 271-282 in: Sheppard CRC (Ed.). Coral Reefs of the United Kingdom Overseas Territories, Coral Reefs of the World 4., © Springer Science+Business Media Dordrecht.

Carr P, Votier S, Koldewey H, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Convention on Biological Diversity. 2020. CBD overview https://www.cbd.int/island/ accessed 17 September 2020.

Danckwerts DK, McQuaid CD, Jaeger A, McGregor GK, Dwight R, Le Corre M and Jaquemet S. 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. ICES Journal of Marine Science 71(9): 2589-2598.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Dunlop JN, Rippey E, Bradshaw LE and Burbidge AA. 2015. Recovery of seabird colonies on Rat Island (Houtman Abrolhos) following the eradication of introduced predators. Journal of the Royal Society of Western Australia 98: 29-36.

Edis R. 2004. Peak of Limuria. The story of Diego Garcia and the Chagos Archipelago. Second edition. Chagos Conservation Trust, London, UK.

Feare CJ, French GC, Nevill JE, Pattison-Willits VS, Wheeler V, Yates TL, Hoareau C and Prescott C. 2015. Attempted re-establishment of a sooty tern *Onychoprion fuscatus* breeding colony on Denis Island, Seychelles. Conservation Evidence 12: 19-24.

Gardiner JS and Cooper C. 1907. The Percy Sladen Trust Expedition to the Indian Ocean. Description of the expedition. Transactions of the Linnean Society London (Zoology) 12: 111-175.

Graham NA, Wilson SK, Carr P, Hoey AS, Jennings S and MacNeil MA. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559(7713): 250-253.

Harper GA, Carr P and Pitman H. 2019. Eradicating black rats from the Chagos – working towards the whole archipelago. Pages 26–30 In: Veitch CR, Clout MN, Martin AR, Russell JC and West CJ (Eds). Proceedings of the Island Invasives 2017 Conference. Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. IUCN, Gland, Switzerland.

Hathaway SA, McEachern K and Fisher RN. 2011. Terrestrial forest management plan for Palmyra Atoll: U.S. Geological Survey Open-File Report 2011–1007.

Hyland BPM, Whiffin T, Zich FA, Duffy S, Gray B, Elick R, Venter F and Christophel D. 2010. Factsheet – *Scaevola taccada.* Australian Tropical Rainforest Plants (6.1 online version) Australian Tropical Herbarium, James Cook University, Cairns, Australia.

Jones HP, Towns DR, Bodey T, Miskelly CM, Ellis JC, Rauzon MJ, Kress SW and McKown M. 2011. Recovery and restoration on seabird islands. Pages 460-531 in: Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Jones HP, Holmes ND, Butchart SH, Tershy BR, Kappes PJ, Corkery I, Aguirre-Muñoz A, Armstrong DP, Bonnaud E, Burbidge AA and Campbell K. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113(15): 4033-4038.

Kappes PJ and Jones HP. 2014. Integrating seabird restoration and mammal eradication programs on islands to maximize conservation gains. Biodiversity and Conservation 23(2): 503-509.

Manly BFJ, McDonald LL and Thomas DL. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.

Maunder M, Culham A and Hankamer C. 1998. Picking up the pieces: Botanical conservation on degraded oceanic islands. Pages 317-344 In: Fiedler PL and Kareiva PM (Eds.). Conservation Biology. Springer, Boston, MA.

McCauley DJ, DeSalles PA, Young HS, Dunbar RB, Dirzo R, Mills MM and Micheli F. 2012. From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. Scientific Reports 2(1): 1-5.

McGregor A and Sheehy M. 2017. An overview of the market for Pacific Island coconut products and the ability of industries to respond. Pacific Island Farmers Organisation Network, Fiji. ISBN: 978-982-00-1084-0.

Millennium Ecosystem Assessment. 2015. MEA overview https://www.millenniumassessment.org/ accessed 07 September 2020.

Mueller-Dombois D and Fosberg FR. 1998. Vegetation of the Tropical Pacific Islands. Springer, New York.

Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). 2011a. Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Mulder CPH, Jones HP, Kameda K, Palmborg C, Schmidt S, Ellis JC, Orrock JL, Wait DA, Wardle DA, Yang L, Young H, Croll DA and Vidal E. 2011b. Impacts of seabirds on plant and soil properties. Pages 135-176 n: Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Norton DA and Miller CJ. 2000. Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecological Management and Restoration 1: 26–34.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Samways MJ, Hitchins PM, Bourquin O and Henwood J. 2010. Restoration of a tropical island: Cousine Island, Seychelles. Biodiversity and Conservation 19(2): 425-434.

Scott R. 1961. Limuria. The Lesser Dependencies of Mauritius. Oxford University Press, London, UK.

Sheppard CRC and Sheppard A. 2019. British Indian Ocean Territory (Chagos Archipelago). Pages 237-252 In: Sheppard CRC. (Ed.). World Seas: an Environmental Evaluation. Academic Press.

Smith JL, Mulder CPH and Ellis JC. 2011. Seabirds as Ecosystem Engineers: Nutrient Inputs and Physical Disturbance. Pages 27-55 in: Mulder CPH, Anderson WB, Towns DR and Bellingham PJ (Eds.). Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Tershy BR, Shen KW, Newton KM, Holmes ND and Croll DA. 2015. The importance of islands for the protection of biological and linguistic diversity. Bioscience 65(6): 592-597.

von Brandis RG. 2012. Rehabilitation of abandoned coconut plantations at D'Arros Island, Republic of Seychelles. Ocean & Coastal Management 69: 340-346.

Warwick-Evans VC, Atkinson PW, Robinson LA, Green JA and Jackson A. 2016. Modelling to identify near-shore, fine-scale seabird distributions during the breeding season. PLOS ONE 11: e0150592.

Wenban-Smith N and Carter M. 2017. Chagos: A History. Chagos Conservation Trust, London, UK.

Whittaker RJ. 1998. Island biogeography: Ecology, evolution and conservation. Oxford University Press, Oxford, UK.

Wilkinson T. 2017. Vegetation maps in support of Chagos Atoll Restoration Expedition (CAREX). https://www.chagosinformationportal.org/ accessed 29 December 2019.

Young HS, Raab TK, McCauley DJ, Briggs AA and Dirzo R. 2010a. The coconut palm, *Cocos nucifera*, impacts forest composition and soil characteristics at Palmyra Atoll, Central Pacific. Journal of Vegetation Science 21(6): 1058-1068.

Young HS, McCauley DJ, Dunbar RB and Dirzo R. 2010b. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. Proceedings of the National Academy of Science USA 107: 2072–2077.

Young HS, Miller-ter Kuile A, McCauley DJ and Dirzo R. 2017. Cascading community and ecosystem consequences of introduced coconut palms (Cocos nucifera) in tropical islands. Canadian Journal of Zoology 95: 139-148.

Zweig MH and Campbell G. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. Clinical Chemistry 39: 561-577.

SUPPLEMENTARY MATERIAL TO CHAPTER 4

Figure S4. 1. Ile du Coin extant vegetation cover in relation to all other rat-infested, ecologically degraded islands > 0.5 km^2 in the Chagos Archipelago. Dieg = Diego Garcia, Eagl = Eagle, Lunc = Lubine complex, Sudc = Sudest complex, Pier = Pierre, Coin = Coin, Bodd = Boddam, Poup = Poule (Peros Banhos), Diam = Diamant, Angs = Anglaise (Solomon Islands), Gras = Grand Souer, Yeye = Yeye and Taka = Takamaka.

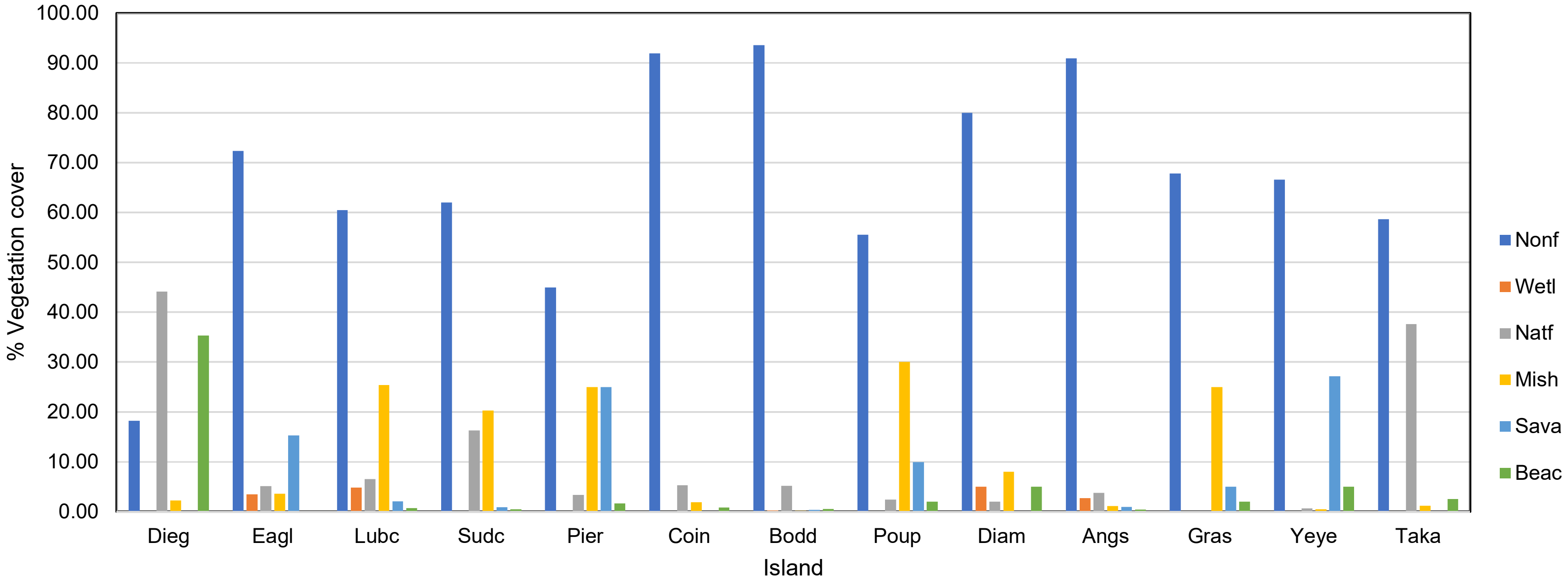


Table S4. 1. Breeding habitat classification in the Chagos Archipelago. Twenty-four original categories as defined and mapped by Wilkinson (2017) and Bárrios and Wilkinson (2018) condensed in to six tropical seabird breeding habitats.

Original categories	Breeding seabird habitat	Definition
Manmade structures Ornamental vegetation Manmade wetlands	Omitted	All manmade structures were omitted from the analysis. These were only present on the inhabited western arm of Diego Garcia and constitute ~20% of the total landmass of the archipelago and held very few breeding seabirds (<50 breeding pairs combined of *Anous stolidus* (Brown Noddy) and *Gygis alba* (Common White Tern). Included in these omissions are an airport and a port; ornamental vegetation included a golf course, flowered-garden areas and lawns. Manmade wetlands are sewage settling ponds and an artificial lake.
Brackish water	Wetlands (WETL) IUCN habitat class 5.14/5.16 Permanent saline, brackish or alkaline lakes/ponds	Wetland habitat are areas of permanent fresh or brackish water not connected to the open sea. On Eagle and Moresby Island the wetlands are mangrove forest of the species *Lumnitzera racemosa* Willd. *Pemphis acidula* J.R Forst & G. Forst.is the other dominant wetland plant.
Broadleaf woodland Mixed broadleaf and coconut Asplenum sp. Unknown sp. Cordia Pisonia (Ceodes) Coconut with broadleaf Dead Cordia	Native forest (NATF) IUCN habitat class 1.6. Tropical moist lowland forest	Native forest is made up of 11 species of tree: *Barringtonia asiatica* (L.) Kurz, *Calophyllum inophyllum* L., *Ceodes (Pisonia) grandis* (R.Br.) D.Q.Lu, *Cocos nucifera* L., *Cordia subcordata* Lam, *Guettarda speciosa* L, *Hernandia nymphaeifolia* (C. Presl) Kubitzki, *Intsia bijuga* (Colebr.) Kuntze, *Morinda citrifolia* L, *Ochrosia (Neisosperma) oppositifolia* (Lam.) K.Schum. and *Heliotropium (Tournefortia) arboretum* (Blanco) Mabb. where it occurs as a tree. *Lumnitzera racemosa* Willd. is the remaining native tree and is dealt with under the separate habitat of wetland. Asplenum is included as this fern is invariably associated with native forest, especially under Hernandia. Unknown species are included in native forest as there are no extensive tracts of non-native trees on any island that are not known and were not identified when being mapped.

Bare ground Grass Sand with sparse cover Herbaceous savanna	Savanna (SAVA) IUCN habitat class 2.2. Moist savanna	Bare ground and sand with sparse cover are included as savanna where they are not part of the beach habitat, i.e. where they are found inland behind the beach crest. The principle native floral components of savanna are the grasses *Lepturus repens* (G. Forst.) R. Br. and *Stenotaphrum micranthum* (Desv.) C.E. Hubb., the sedge *Fimbristylis cymosa* R. Br. and the vascular plants *Portulaca mauritiensis* Poelln., *P. oleracea* L., *Ipomoea macrantha* Roem. & Schultes, *Achyranthes aspera* var. *velutina* (Hook & Arn.), *Boerhavia repens* L., *Sida pusilla* Cav. and *Triumfetta procumbens* G. Forst. Included in savanna is the non-native *Stachytarpheta jamaicensis* (L.) Vahl.
Scaevola Thicket	Mixed shrub (MISH) IUCN habitat class 3.6. tropical moist shrubland	Mixed shrub is comprised of *Scaevola taccada* (Gaertn.) Roxb. and *Heliotropium* (*Tournefortia*) *arboretum* (Blanco) Mabb. where it occurs in bush form, normally in the interior of islands. Other shrub species are present but are not nested in by seabirds.
Beach Beach littoral	Beach (BEAC) IUCN habitat class 13.1/13.3 Sea cliffs and rocky offshore islands/coastal sand dunes	Beach is comprised of any substrate that forms the shoreline up to the point that vegetation starts. The usual substrate is sand or limestone. Beach is not vegetated.
Casuarina Papaya Coconut	Non-natural or non-native forest (NONF) IUCN habitat class 14.3 Plantations	Non-native forest is comprised of *Casuarina equisetifolia* L., *Carica papaya* L. and *Cocos nucifera* L. In the Chagos Archipelago, *C. nucifera* occurs as a natural colonist and is found on shorelines and the interior where storm surges have pushed nuts inland. It also occurs unnaturally inland as an abandoned commercial crop planted where native vegetation has been cleared. Only *C. nucifera* planted as a commercial crop is included as non-natural forest.

Table S4. 2. AICc values for model selection for models of rat-free islands.

Model	Fixed effect structure	AICc	Difference in AIC relative to most parsimonious model
Rat-free islands			
Without size	Vegetation type * Species + Island	3703368	0
Without island	Vegetation type * Species + Size	3792935	89566
Without two-way interaction or size	Vegetation type + Species + Island	4690585	987217
Full model	Vegetation type * Species + Island + Size	83505181	79801813

Table S4. 3. Model scores from receiving operator characteristic curves of most parsimonious models by model selection.

Model	Correct classification (%)	Positive Predictive Power (%)	Negative Predictive Power (%)	Sensitivity	Specificity	Area under curve
Rat-free islands	74.4	25.8	99.5	0.97	0.72	0.84

Table S4. 4. Mean breeding population estimates for all 18 species of tropical seabird in the Chagos Archipelago for the six breeding habitats. Population estimates come from the contemporaneous reference site of the 24 rat-free islands. Red-tailed Tropicbird and Little Tern have only ever been found breeding on rat-infested Diego Garcia.

HABITAT	*Ardenna pacifica* (Wedge-tailed Shearwater	*Puffinus bailloni* Tropical Shearwater	, *Phaethon lepturus* White-tailed Tropicbird	*Phaethon. Rubricauda* Red-tailed Tropicbird	Sula dactylatra Masked Booby	Sula sula Red-footed Booby	Sula leucogaster Brown Booby	Fregata minor Great Frigatebird	Fregata ariel Lesser Frigatebird	*Thalasseus bergii* Great Crested Tern	*Sterna dougallii* Roseate Tern	Sterna sumatrana Black-naped Tern	*Sternula albifrons* Little Tern	Onychoprion aenathetus Bridled Tern	Onychoprion fuscatus Sooty Tern	Anous stolidus Brown Noddy	Anous tenuirostris Lesser Noddy	*Gygis alba* Common White Tern
Beach	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	532 +/- 2.6	14 +/- 0.2	100 +/- 0.7	0.0	189 +/- 1	0.0	714 +/- 8.3	0.0	0.0
Mixed shrub	240 +/- 9	135 +/- 5	0.0	0.0	0.0	7276 +/- 155	0.0	238 +/- 10.4	45 +/- 2.1	0.0	0.0	0.0	0.0	0.0	900 +/- 42	82 +/- 1.5	0.0	0.0
Native forest	2,855 +/- 125	1,223 +/- 50	2.5 +/- 0.1	0.0	0.0	3,605 +/- 174	0.0	305 +/- 12.7	16 +/- 0.7	0.0	0.0	0.0	0.0	0.0	826 +/- 42	734 +/- 8.5	41,624 +/- 838.1	276 +/- 2.9
Non-native forest	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20 +/- 0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	354 +/- 2.3	0.0	212 +/- 1.2
Savanna	8.8 +/- 0.1	0.0	0.0	0.0	482 +/- 6	0.0	2,717 +/- 31	0.0	0.0	0.0	0.0	0.0	0.0	38 +/- 0.4	575,000 +/- 3,065	2,367 +/- 25.2	0.0	0.0
Wetland	0.0	0.0	0.0	0.0	0.0	13,750 +/- 2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Supplementary Material Working Example. Hypothetical future breeding seabird populations on a rat-cleared Ile du Coin, Chagos Archipelago, without conversion of abandoned plantations to native habitats.

Legend: BEAC = beach, MISH = mixed shrub, NATF = native forest, NONF = non-native forest, SAVA = savanna, WETL = wetland. WETS = *Ardenna pacifica* (Wedge-tailed Shearwater), TROS = *Puffinus bailloni* (Tropical Shearwater), WHTT = *Phaethon lepturus* (White-tailed Tropicbird), REFB = *Sula sula* (Red-footed Booby), GREF = *Fregata minor* (Great Frigatebird), LESF = *Fregata ariel* (Lesser Frigatebird), GRCT = *Thalasseus bergii* (Great Crested Tern), ROST = *Sterna dougallii* (Roseate Tern), BLNT = *Sterna sumatrana* (Black-naped Tern), BRIT = *Onychoprion aenathetus* (Bridled Tern), SOOT = *Onychoprion fuscatus* (Sooty Tern), BRON = *Anous stolidus* (Brown Noddy), LESN = *Anous tenuirostris* (Lesser Noddy), COWT = *Gygis alba* (Common White Tern).

Estimating breeding abundance of seabirds in the CA for islands where rats have been eradicated. Worked example: Ile du Coin, Peros Banhos (1.26 km^2).

To estimate breeding abundance (e.ba) post rat eradication on Ille du Coin, we sum (Σ) the abundance of every species (sp_{1-18}) breeding in every habitat (hab_{1-6}) using the present-day mean breeding abundance of species (μ) from the contemporaneous reference sites of 24 rat-free islands in Chagos (Equation 2).

$e.ba = \Sigma(hab_{1-6} \times \mu sp_{1-18})$

Where, Hab $_{1-6}$ is the area (km^2) covered by the six breeding habitats on Ile du Coin (BEAC = 0.011, MISH = 0.024, NATF = 0.066, NONF = 1.154, SAVA = 0, WETL 0) and, μsp_{1-18} = is the mean breeding abundance of species breeding in $habitat_{1-6}$, extracted from Table S4.

BEAC: GRCT (0.011 x 532.1 +/- 2.6) + ROST (0.011 x 14.3 +/- 0.2) + BLNT (0.011 x 100 +/- 0.7) + BRIT (0.011 x 189.3 +/- 1) + BRON (0.011 x 714.3 +/- 8.3)

MISH: WETS (0.024 x 240.5 +/- 9) + TROS (0.024 x 135.1 +/- 5) + REFB (0.024 x 7,276.6 +/- 155) + GREF (0.024 x 238.7 +/- 10.4) + LESF (0.024 x 45.1 +/- 2.1) + SOOT (0.024 x 900.9 +/- 42) + BRON (0.024 x 82 +/- 1.5)
NATF: WETS (0.066 x 2,855.4 +/- 125) + TROS (0.066 x 1,223.1 +/- 50) + WHTT (0.066 x 2.5 +/- 0.1) + REFB (0.066 x 3,605.8 +/- 174) + GREF (0.066 x 305.8 +/- 12.7) + LESF (0.066 x 16.5 +/- 0.7) + SOOT (0.066 x 826.5 +/- 42) + BRON (0.066 x 734.7 +/- 8.5) + LESN (0.066 x 41,624 +/- 838.1) + COWT (0.066 x 276.9 +/- 2.9)
NONF: GREF (1.154 x 20.8 +/- 0.2) + BRON (1.154 X 354.2 +/- 2.3) + COWT (1.154 x 212.5 +/- 1.2)

This condenses down to:

BEAC: GRCT (5.85 +/- 0.03) + ROST (0.16) + BLNT (1.1 +/- 0.01) + BRIT (2.08 +/- 0.01) + BRON (7.86 +/- 0.09) = 17.05 (+/- 0.14)
MISH: WETS (5.77 +/- 0.22) + TROS (3.24 +/- 0.12) + REFB (174.64 +/- 3.72) + GREF (5.73 +/- 0.25) + LESF (1.08 +/- 0.05) + SOOT (21.62 +/- 1.01) + BRON (1.97 +/- 0.03) = 214.05 (+/- 5.4)
NATF: WETS (188.46 +/- 8.25) + TROS (80.72 +/- 3.3) + WHTT (0.17) + REFB (237.98 +/- 11.49) + GREF (20.18 +/- 0.84) + LESF (1.09+/- 0.05) + SOOT (54.55 +/- 2.77) + BRON (48.49 +/- 0.56) + LESN (2747.18 +/- 55.32) + COWT (18.28 +/- 0.19) = 3397.1 (+/- 82.76)
NONF: GREF (24 +/-0.23) + BRON (408.75 +/- 2.65) + COWT (245.23 +/- 1.38) = 677.98 (+/- 4.26)

This condenses down to:

17.05 (+/- 0.14) + 214.05 (+/- 5.4) + 3397.1 (+/- 82.76) + 677.98 (+/- 4.26)

Without conversion of abandoned coconut plantations to native habitats conducive to breeding seabirds post rat eradication, the six breeding habitats on Ile du Coin, of which only four are present, could support 4,306 +/- 93 breeding pairs of 14 species.

CHAPTER 5

USING MOLECULAR ANALYSIS TO DEFINE SEX SPECIFIC MORPHOMETRICS OF RED-FOOTED BOOBY *SULA SULA RUBRIPES* L. IN THE CHAGOS ARCHIPELAGO, CENTRAL INDIAN OCEAN

ABSTRACT

Molecular analysis has opened research avenues in ornithology that have advanced the science on numerous fronts. The ability to accurately determine sex of species with little or no morphometric differences has greatly expanded the boundaries of research. Genetic identification of sex in seabirds has assisted in confirming or designing alternative methods of determining sex that are less expensive and readily available to field workers. In the CA, central Indian Ocean, research is being undertaken into the ecology of tropical seabirds breeding in the archipelago, the focal species being RfB. Researchers found that study birds could not be reliably sexed by methods used elsewhere for this species (body measurements and vocalisation) and time constraints precluded such methods as witnessing copulatory position or sex specific behaviour. Therefore, using molecular analysis to definitively determine sex, a field-ready method using simple to measure biometrics was designed. Using a generalised linear model, the approach developed for CA RfB sexed 93% of captured birds with 80% accuracy. The accuracy of this method might be enhanced if additional body measurements were included, particularly bill length and depth that were found to differ statistically at one colony, though further research at different colonies in the archipelago is required to confirm whether bill measurements are consistently different at all locations. Having the first morphometrics of RfB from the central Indian Ocean allowed a general comparison of this subspecies from a distinct location with the species group and within the subspecies. A generalisation is that the Indian Ocean *S.s. rubripes* appears longer winged and has a greater mass than the Atlantic/Caribbean centred nominate subspecies. Within the *S.s. rubripes* group, it appears Indian Ocean birds tend to be larger than Pacific Ocean populations and that the central Indian Ocean population lay within the morphometric parameters of other Indian Ocean populations. This research has contributed towards unravelling the complex taxonomy and morphology of a pan-tropical top predator.

INTRODUCTION

Molecular approaches have revolutionised marine ornithology. It has advanced knowledge in phylogenetics, population genetics, species limits and introgression, as well as providing a powerful tool to determine species' historical and contemporary abundance, distributions and movements (Friesen et al. 2007, Taylor and Friesen 2012). Moreover, sex-linked markers now enable us to accurately sex birds that could not previously be assigned (Kocijan et al. 2011, Dawson et al. 2016). This is especially significant for seabirds since many species have no or only subtle sex differences in terms of phenotype (Votier and Sherley 2017).

Seabirds can be sexed in a variety of different ways including plumage, integument colour, voice, copulatory position, agonistic behaviours, play-back response, cloacal inspection and morphometrics, across a range of seabird families e.g., Magellanic Penguin *Spheniscus magellanicus* (Bertellotti et al. 2002), European Storm-petrel *Hydrobates pelagicus* (Castro et al. 2013), White-winged (Gould's) Petrel *Pterodroma leucoptera* (O'Dwyera et al. 2006), Wedge-tailed Shearwater *Ardenna pacifica* (Totterman 2015), Streaked Shearwater *Calonectris leucomelas* (Arima et al. 2014), Yelkouan Shearwater *Puffinus yelkouan* (Bourgeois et al. 2007), Sooty Tern *Onychoprion fuscatus* (Reynolds et al. 2008), Long-tailed Skua *Stercorarius longicaudus* (Seyer et al. 2019). Sexing techniques can be confirmed by or designed using molecular analysis, however, even this scientifically advanced technique is not infallible (Shizuka and Lyon 2008) and only internal examination of the sexual organs is 100% accurate.

Sulidae (gannets and boobies) are globally distributed seabirds comprising 10 species, found in temperate to tropical waters. They show rather limited or subtle sexual dimorphism and differences are associated with reverse size sexual dimorphism (RSD), whereby the females tend to be larger than males (Nelson 1978). Molecular approaches have been influential for studying sex differences among the Sulidae, including foraging (Young et al. 2010a/b, Weimerskirch et al. 2006, 2009a, Clark et al. 2021), migration and demography (Deakin et al. 2019), sex specific behaviour (Daniel et al. 2008), genetic distinctiveness (Kingsley et al. 2020) and the evolutionary role of RSD (Weimerskirch et al. 2006, 2009b).

Within the Sulidae, RfB is the smallest of the Sulids (Nelson 1978). This pelagic species is generally split into three subspecies, *S.s. sula* (Caribbean, south Atlantic islands), *S.s. websteri* (tropical east Pacific including Galapagos) and, *S.s. rubripes* that breeds across the Hawaiian Islands, Indian Ocean, central, west and south Pacific, south China Sea, Banda Sea and Australia (Schreiber et al. 2021). They are polymorphic throughout their range but have no reliable intra-sex plumage differences (Schreiber et al. 2021). They exhibit RSD, although there is overlap and RfB is the least dimorphic of all the sulids (Nelson 1978).

RfB morphometrics vary across their global range both between subspecies (Fig 5.2) and within a subspecies group (Fig. 5.3) (Nelson 1978, Weimerskirch et al. 2006, Young et al. 2010b). Other studies have sexed RfB through detailed observation of pairs (Nelson 1978), morphometrics (Nelson 1978, Weimerskirch et al. 2006, Young et al. 2010b), vocalisations (Nelson 1978, Weimerskirch et al. 2006, Young et al. 2010b), and integument colouration (Young et al. 2010b). Studies since 2000 confirmed their sex determination with molecular analysis. Recent research has used Discriminant Function Analysis to calculate the Fisher’s classification coefficients for wing length, bill length and body mass that together determine RfB sex with 93% accuracy in a Caribbean population of the nominate subspecies (Austin et al. 2021).

However, due to the variation in morphometrics from across its pan-tropical range and the subjectivity inherent when assessing bare part colours or vocalisations in the field, there is not a single, simple, infallible method for sexing RfB and sex determination using morphometrics needs to be range or even colony specific.

In the Indian Ocean the breeding range of RfB encompasses the CA (Fig. 5.1). Recent population estimates indicate that there are 21,670 breeding pairs (Carr et al. 2021) and all are white morph (Carr 2011). To the best of our knowledge no data exist on morphometrics of the RfB in the CA, though Nelson (1978) gives biometrics by sex of birds from within this subspecies range. Hence, no precedent is available to sex RfBs using in-field morphometrics in the CA.

When breeding, Sulidae are known to sexually segregate the feeding and foraging areas and hence their at sea disttribution (Cape Gannet *Morus capensis* – Botha et al. 2017, Northern Gannet *Morus bassanus* – Cleasby et al. 2015, Brown Booby *Sula leucogaster* – Miller et al. 2017), including the focal specie RfB (Weimerskirch et al. 2006, 2009a, 2009b). To research the benefits of large-scale MPAs to breeding seabirds based upon RfB I had to be able to determine the sex of the individuals being tracked.

Therefore, the aim of this study is to explore the potential for sexing RfBs in the field in CA via morphometrics, using a set of known-sex individuals confirmed by molecular methods. This is required to understand the at-sea distribution of breeding RfB in relation to the BIOT MPA – though analysis by sex was not used in chapter six. I then add the CA population morphometrics to other studied populations of subspecies *S.s.rubripes* and view this subspecies within the species group and the CA population within the *S.s. rubripes* complex.

METHODS

Study Area

The CA lies entirely in the Tropics at the southern end of the Lakshadweep-Maldives-Chagos ridge in the geographical centre of the Indian Ocean (Fig. 5.1). It has 55 islands in five atolls that form < 1% of the ~ 640,000 km^2 total area of the UK Overseas Territory. The entire Exclusive Economic Zone was designated a category 1 strict no-take marine protected area in 2010, the largest in the world at that time (Koldewey et al. 2010).

Data Collection

Data were collected from three atolls, in the south (Diego Garcia), along the Great Chagos Bank (Danger Island and Nelson's Island) and in the north (Peros Banhos) of the archipelago (Fig. 5.1). Adult birds ≥ 4 calendar years old that were incubating eggs or guarding small chicks (≤ 21 days old) were captured by hand and both sexes were fitted with a British Trust for Ornithology (BTO) G size Incoloy® metal ring (internal diameter 11.00 mm) for unique identification. Maximum wing length of birds not moulting the longest primary (rounded to whole mm using a 500 mm butted wing rule) and mass (rounded to whole g using a 2 kg Pesola Spring Scale) were taken at all locations. Bill tip to feathering, bill depth and tarsus width (rounded to 0.1 mm using BTO dial callipers) were taken only from the Diego Garcia colony (Table 5.1). As the latter three biometrics were only sampled from one location, they were omitted from further analysis. A subset of birds from all colonies had a sample of breast feathers removed and stored in paper envelopes for molecular analysis (Table S5.1).

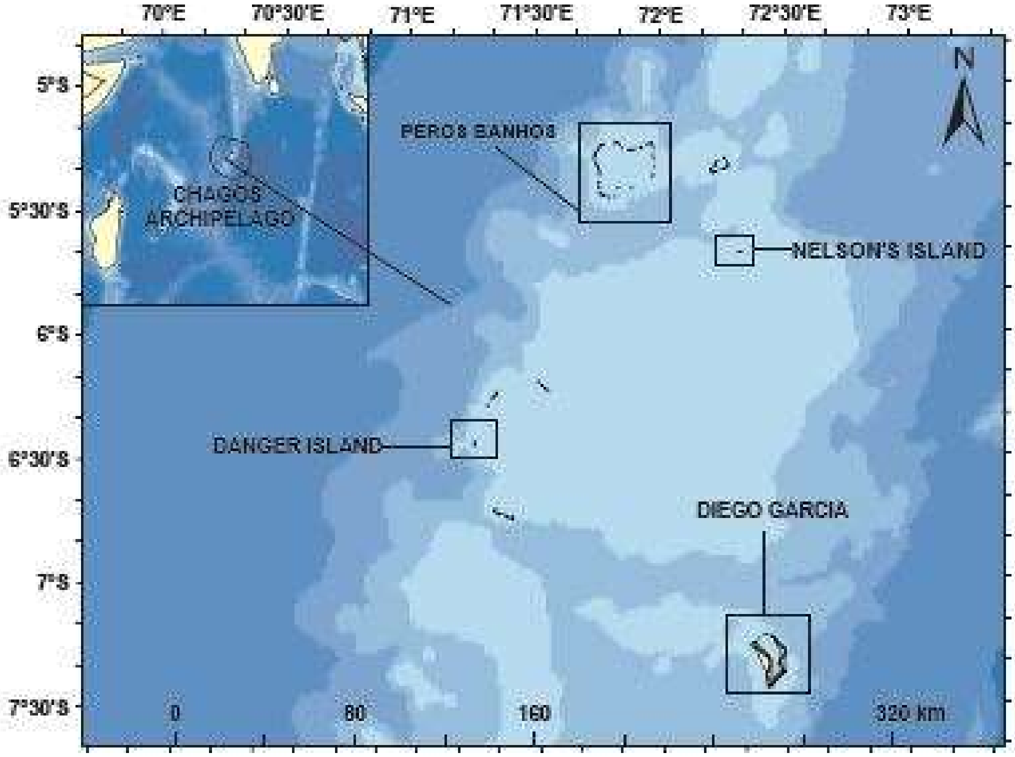


Figure 5. 1. The Chagos Archipelago, central Indian Ocean, showing the locations where Red-footed Booby morphometric data and feather samples for DNA analysis were collected. Danger and Nelson’s Island lie on the Great Chagos Bank atoll.

Molecular Analysis

We extracted genomic DNA from breast feathers of RfB using DNeasy Tissue kit (QIAGEN). Individual feather follicles were cut into small pieces and digested in 180µl of ATP buffer and 20µl of Proteinase K, overnight at 56°C. After ethanol precipitation and washing with buffers AW1 and AW2, DNA was diluted in 200µl elution buffer. We amplified the genetic marker Z43B (Forward primer CTTGAGACTAATTCCACTCC/ Reverse primer TTTACATGGCAGCyTGA) (Dawson et al 2016) in a 6µl PCR reaction containing 3.5µl Multiplex PCR Master Mix (QIAGEN), 1.5µl (0.2M) Primer Mix (with the forward primer fluorescently labelled with 6-FAM), and 1µl DNA (approx. 10ng). To confirm reliability each DNA sample was separately amplified 3 times. PCR amplification conditions were an initial enzyme activation cycle at 95°C for 15', followed by 45 cycles of denaturing at 94°C for 30", annealing at 50°C for 30" and extension at 72°C for 30", and a final extension at 72°C for 10'. To visualize the fragments, 1 µl of diluted (1:50) PCR product was mixed with 9ml HiDi Formamide containing Liz500 size standard before separation on a 16-capillary array ABI 3130 Genetic Analyser (Life Technologies). The data were analysed on GeneMappper v.5 (Life Technologies) that showed 2 alleles sizes 262 basepairs (located in the W-chromosome) and 268 bp (located in the Z-chromosome) for females and one allele 268 bp for males. Laboratory analysis was conducted at the Institute of Zoology, Zoological Society of London, UK.

Data Analysis

Hartley's F_{max} test was used to test for homogeneity of variance and normality of all morphometric data. Single Factor ANOVA was used to test if there were significant differences in the means of morphometrics between colonies by sex or whether the birds were all derived from the same population. All birds of both sexes at all colonies were found to be from the same population (Table S5.2). As there were no statistically significant differences between birds from the three atolls, data were pooled from across the archipelago to test for statistically significant differences between sexes. Statistically significant differences existed between the sexes in wing length and body mass (Figs, S5.1 and S5.2). Knowing there were no statistically significant differences between populations across the CA and that there were statistically significant differences between the sexes supported analysis to determine morphometric parameters of the sexes of the CA population of subspecies *S.s. rubripes*.

To determine the morphometric parameters of the sexes I used a generalised linear model (GLM) with binomial errors and a logit link function incorporating a subset of data (body mass and wing length) from birds of known sex through molecular analysis from three atolls in the CA (Fig. 5.1, Table S5.1). The data were split randomly into a training (70%) and a test (30%) dataset. The GLM was built using the training data set, then the model was used to predict the sex of the birds in the test dataset (cross-validation) and the predictions were checked against the known, molecular sexed individuals. All statistical analysis and modelling were conducted in the package R version 2.6.0 (R Core Team 2020).

RESULTS

A total of 333 RfB had biometrics recorded from ten islands on three atolls, of these, a subset of 125 (65 female, 60 male) were sexed using genomic DNA (Table S5.1). Hartley's F_{max} test indicated no deviation from homogeneity of variance in the morphometric data (male wing length $F_{3,2} = 2.06$, $p < 0.05$; male mass $F_{3,2} = 2.08$, $p < 0.05$; female wing length $F_{3,2} = 2.34$, $p < 0.05$; female mass $F_{3,2} = 2.00$, $p < 0.05$). Single factor ANOVA demonstrated there was no significant difference in wing length or mass in either sex between atolls (Table S5.2). Between sex morphometrics were significantly different (t-Tests assuming equal variance, $p < 0.05$) except tarsus width (Table 5.1).

Table 5. 1. Morphometrics of molecular sexed Red-footed Booby ssp. *S.s. rubripes* breeding in the Chagos Archipelago. (Mean ± standard error, range, lower and upper confidence limits, (n)), * indicates a significant difference between sexes (t-Tests assuming equal variance, $p \leq 0.05$).

Wing length * (mm)	Mass * (g)	Bill length * (mm)	Bill depth * (mm)	Tarsus width (mm)
FEMALE				
394 ± 1.76 375 - 417 390 - 397 (65)	998 ± 21.2 820 - 1420 956 - 1040 (65)	110 ± 0.832 100.8 - 119 109 - 112 (37)	32.5 ± 0.34 29.5 - 36.5 31.8 - 33.2 (37)	9.35 ± 0.2 8 - 10.5 8.93 - 9.78 (18)
MALE				
383 ± 1.78 362 - 404 379 - 386 (60)	833 ± 21.4 700 - 1060 791 - 876 (60)	105 ± 1.08 101 - 111.3 103 - 107 (21)	30.6 ± 0.44 27 - 34.4 29.7 - 31.4 (21)	9.35 ± 0.29 8 - 10.5 8.73 - 9.96 (7)

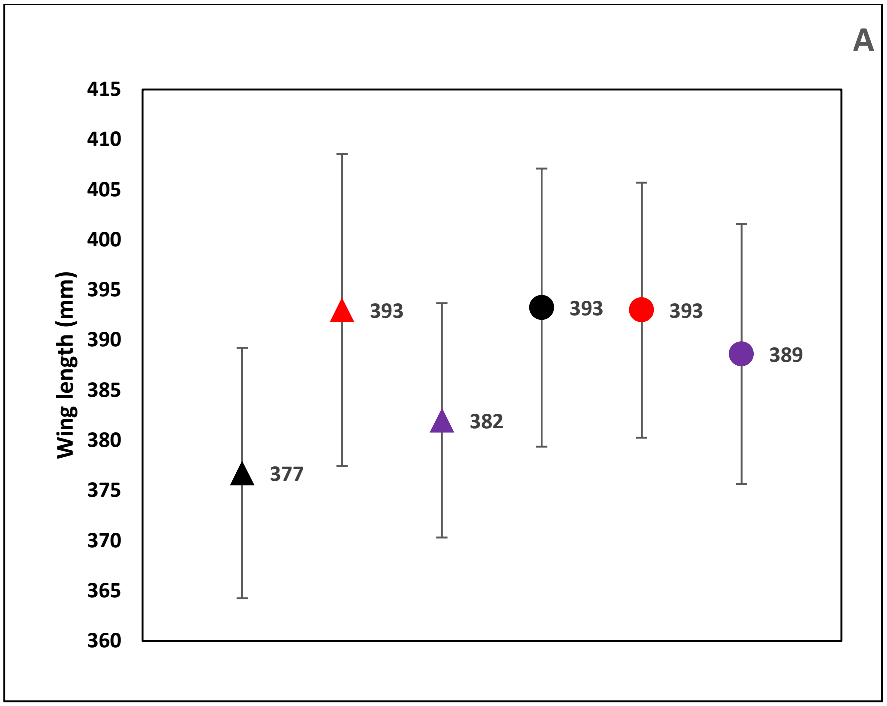
Predicting Sex Using General Linear Modelling (GLM)

The GLM predicted sex with an accuracy ~82% against the 30% known sex test data using the fixed effects of wing length and body mass. Plotting a specificity versus sensitivity curve (false negative versus false positive) showing the trade off in predicting male when female vs predicting female when male gave a prediction threshold of 0.5 for a bird being female (Fig. S5.3). Using this threshold, the GLM prediction of being female based on all known sex birds (n = 125) led to an overall accuracy of 76.8% (45/65 females correctly assigned and 51/60 males). When 0.25 / 0.75 buffers were incorporated to the GLM threshold (that ruled out a percentage of birds in the biometric overlap zone) the prediction percentage accuracy was 80.0% and left 6.9% of birds unsexed. Using the coefficients of the 0.5 threshold, the following equation to predict sex is produced:

$$\text{Female} = 51.21536543 + (0.01641796 * \text{mass}) + (0.09269796 * \text{wing length}) = > 0.5$$
$$\text{Male} = 51.21536543 + (0.01641796 * \text{mass}) + (0.09269796 * \text{wing length}) = < 0.5 \quad \text{(Eqn. 5.1)}$$

Red-footed Booby Subspecies' Morphometrics in a Global Context

Globally, with the inclusion of the CA RfB wing length and body mass biometrics to other studied populations, the subspecies *S.s. rubripes* remains within the morphometric parameters of the species. It appears that subspecies *S.s. websteri* displays less RSD than other subspecies (Fig. 5.2 A/B). Within the *S.s. rubripes* subspecies' group, both sexes of the Line Islands (Kiribati - Pacific Ocean) population appear shorter-winged and lighter than all three Indian Ocean populations (Fig. 5.3A/B), though there is overlap and the differences cannot be statistically tested from the data available. In the three Indian Ocean populations, there seems to be RSD in both wing length and mass, though there is much biometric overlap and a lack of statistical analysis. Along with the Europa population, females of the CA population appear long-winged compared with other Indian Ocean colonies and, both male and females look to be the lightest of Indian Ocean populations, again with no statistical analysis to lend credence to the data.



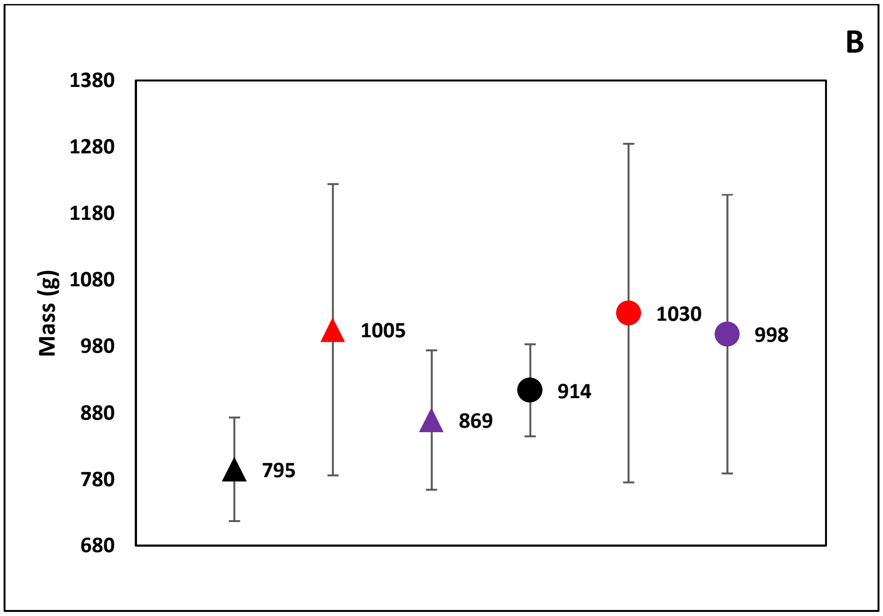
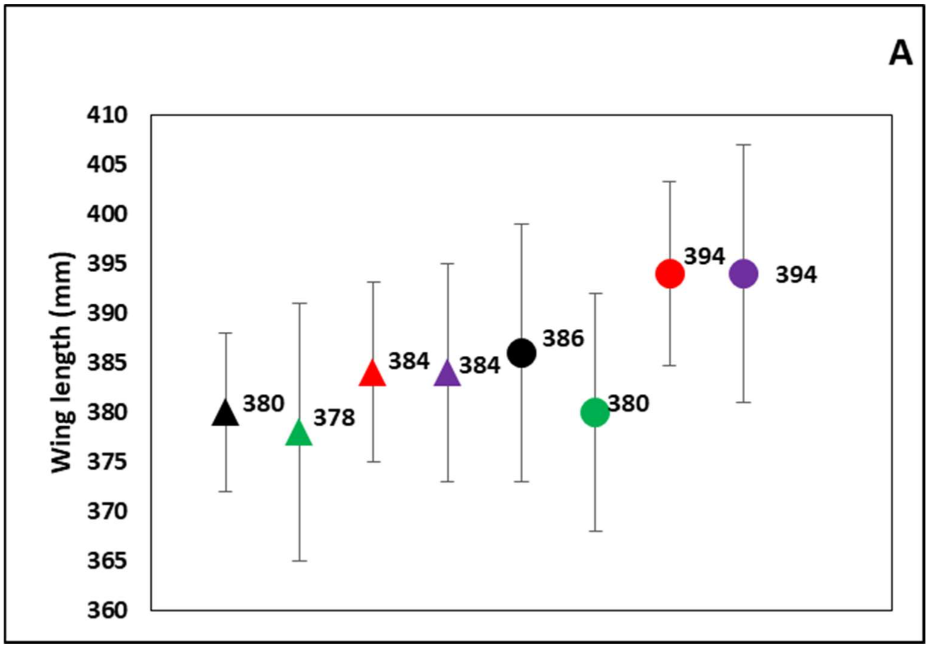


Figure 5. 2 A/B. Mean wing length (**A**) and mass (**B**) of male (▲) and female (●) Red-footed Booby. Black symbols are *Sula sula sula*, red is *S.s. websteri*, purple is *S.s. rubripes*. Data from the Caribbean (*S.s. sula* Nelson 1978, Austin et al. 2021), Galapagos/Revillagigedos (*S.s.websteri* – Nelson 1978), Tromelin (*S.s.rubripes* – Kappes et al. 2011), Line Islands (*S.s.rubripes* – Nelson 1978), Chagos Archipelago (*S.s.rubripes*) and Europa Island (*S.s.rubripes* – Weimerskirch et al. 2006). Error bars are 1 standard deviation.



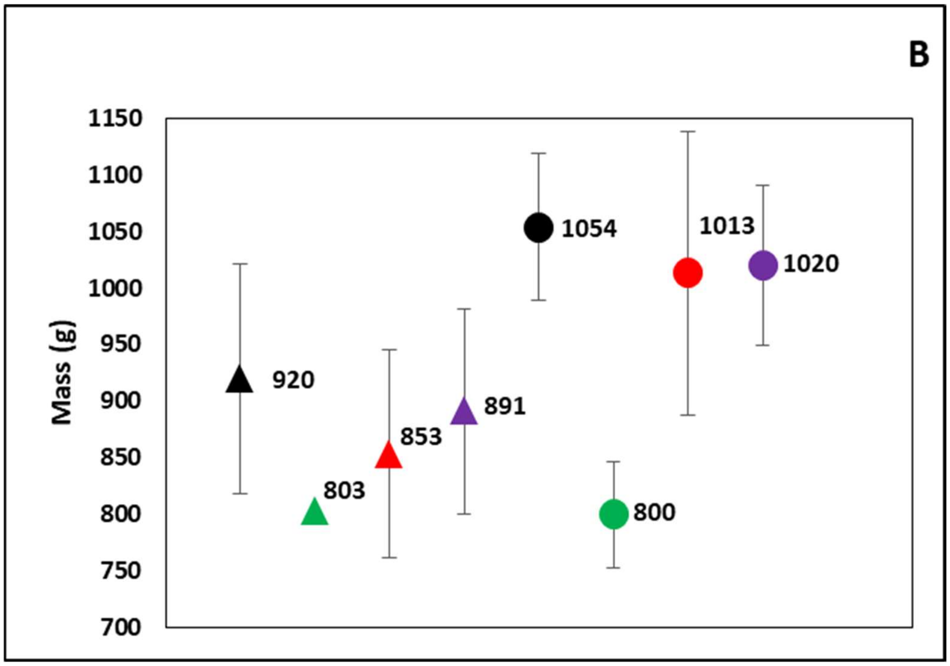


Figure 5. 3 A/B. Mean wing length (**A**) and mass (**B**) of male (▲) and female (●) Red-footed Booby of subspecies *S.s. rubripes*. Black symbols are Tromelin (Kappes et al. 2011), green symbols Line Islands (Nelson 1978), red symbols Chagos Archipelago, purple symbols Europa Island (Weimerskirch et al. 2006). Error bars are 1 standard deviation – Line Islands males has no standard deviation.

DISCUSSION

Whilst statistically significant differences between the sexes were found for four of the five morphometrics of the CA population of RfB, there was considerable overlap in the ranges of measurements. This deviation, theoretically, could result in a CA breeding pair having a longer-winged male with greater mass than the female. Sex determination through vocalisation (Nelson 1978, Weimerskirch et al. 2006, Young et al. 2010b) in the CA proved inconsistent between observers through subjectivity and other methods, e.g., detailed observation of pairs, copulatory position (Nelson 1978), too time-consuming to be considered for use within the expeditionary nature of research in the CA. For research purposes, it was desirable to devise an accurate, simple to apply field method that does not incur the expense and time-delay penalty of genetic analysis.

Equation 5.1 provides a morphometric method that will assign sex to ~ 93% of research birds with 80% accuracy and can be used under field conditions. However, only offering the capability of correctly assigning sex to 4:5 (or 40:50) does incur an additional time penalty, whereby that more birds would be required to be included in any study where known sex is required.

For a Caribbean population of the nominate subspecies, using three biometrics (wing length, mass and bill length) Austin et al. (2021) attained 93% accuracy in determining the correct sex. With bill length and bill depth of the CA population being statistically different between the sexes, with further data on these morphometrics being gathered from other colonies than Diego Garcia, it could be that by incorporating a third or fourth factor into the determining equation, greater accuracy could be attained. It appears for the CA population that at present, the most accurate, non-intrusive method for determining sex remains molecular analysis.

Having the first morphometric data from known-sex individuals in the CA allows meaningful comparison to be made with the species elsewhere across its range. Globally, Schreiber et al. (2021) generalised that subspecies *S.s. websteri* is slightly smaller and *S.s. rubripes* slightly larger than the nominate. With the limited information available and with the CA *S.s. rubripes* morphometric data added, Schreiber's (2021) statement appears to not hold true. Based on viewing the population means, both sexes of the nominate subspecies have the least mass, males have the shortest wing length, whilst females have the equal largest wing length. Further biometric data allowing statistical analysis from across its' pan-tropical range would greatly enhance the understanding of how this species has morphologically adapted to life dependent upon tropical oceans.

The global distribution of the *S.s. rubripes* complex ranges across two vast oceans, the Pacific and Indian (Schreiber et al. 2021). The limited data available suggest that both sexes of the Line Islands (Kiribati), Pacific Ocean population are the shortest-winged, lightest and least RSD of the subspecies, indeed, female mean mass is actually less than males, though the sample size is very small. Within the three Indian Ocean populations studied, the central ocean population appears to fall comfortably within the morphometric parameters of other studied populations.

The ecology of seabirds breeding in the central Indian Ocean is relatively poorly understood due to lack of research, despite four species being present in internationally significant numbers (Carr et al. 2021). This study has advanced the knowledge of one of these species and this has added to the growing compendium of data informing the complex global morphology of RfB. Equation 5.1. has not proved to be the panacea for determining sex of RfB in the field, though it does provide a foundation stone to build upon. Future research in the CA should endeavour to acquire further morphometric data from colonies outside of Diego Garcia, focussing on bill length and depth, to rerun this analysis to potentially improve the accuracy of determining the sex of RfB subspecies *S.s. rubripes* in the central Indian Ocean. In the interim, molecular analysis remains the most reliable method for determining sex in this remote population.

REFERENCES

Arima H, Oka N, Baba, Y, Sugawa H and Ota T. 2014. Gender identification by calls and body size of the Streaked Shearwater examined by CHD genes. Ornithological Science 13(1): 9-17.

Austin RE, De Pascalis, F, Votier SC, Haakonsson J, Arnould JPY, Ebanks-Petrie G, Newton J, Harvey J and Green JA. 2021. Interspecific and intraspecific foraging differentiation of neighbouring tropical seabirds. Movement Ecology 9(1): 1-16.

Ballance LT, Pitman RL and Reilly SB. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78(5): 1502-1518.

Bertellotti M, Tella JL, Godoy JA, Blanco G, Forero MG, Donázar JA and Ceballos O. 2002. Determining sex of Magellanic Penguins using molecular procedures and discriminant functions. Waterbirds 25(4): 479-484.

Botha JA, Rishworth GM, Thiebaul A, Green DB and Pistorius PA. 2017. Sex-specific foraging over space and time in Cape Gannets during chick rearing. Marine Ecology Progress Series 579: 157-167.

Bourgeois K, Curé C, Legrand J, Gomez-Diaz E, Vidal E, Aubin T and Mathevon N. 2007. Morphological versus acoustic analysis: what is the most efficient method for sexing yelkouan shearwaters *Puffinus yelkouan*? Journal of Ornithology 148(3): 261-269.

Carr P. 2011. Birds of the British Indian Ocean Territory. Pisces Publications for the RSPB. Sandy, Bedfordshire, England.

Carr P, Votier S, Koldewey H, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Castro GD, Delgado JD, González J and Wink M. 2013. Sexual size dimorphism in the extreme SW breeding population of the European Storm Petrel *Hydrobates pelagicus* (Aves: Procellariformes). Vertebrate Zoology 63: 313-320.

Clark BL, Cox SL, Atkins KM, Bearhop S, Bicknell AW, Bodey TW, Cleasby IR, Grecian WJ, Hamer KC, Loveday BR and Miller PI. 2021. Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. Marine Ecology Progress Series 661: 1-16.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J, Votier SC, Bearhop S and Hamer KC. 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. Marine Ecology Progress Series 518: 1-12.

Daniel C, Millar CD, Ismar SM, Stephenson BM and Haube, ME. 2008. Evaluating molecular and behavioural sexing methods for the Australasian gannet (Morus serrator). Australian Journal of Zoology 55(6): 377-382.

Dawson DA, Dos Remedios N and Horsburgh GJ. 2016. A new marker based on the avian spindlin gene that is able to sex most birds, including species problematic to sex with CHD markers. Zoo Biology 35(6): 533-545.

Deakin Z, Hamer KC, Sherley RB, Bearhop S, Bodey TW, Clark BL, Grecian WJ, Gummery M, Lane J, Morgan G and Morgan L. 2019. Sex differences in migration and demography of a wide-ranging seabird, the northern gannet. Marine Ecology Progress Series 622: 191-201.

Friesen VL, Burg TM & McCoy KD. 2007. Mechanisms of population differentiation in seabirds. Molecular Ecology 16(9): 1765-1785.

Kappes MA, Weimerskirch H, Pinaud D and Le Corre M. 2011. Variability of resource partitioning in sympatric tropical boobies. Marine Ecology Progress Series 441: 281-294.

Kingsley MR, Lavers JL, Steeves TE and Burridge CP. 2020. Genetic distinctiveness of masked booby (Sula dactylatra) on Bedout Island, Western Australia. Emu-Austral Ornithology 120(2): 150-155.

Kocijan I, Dolenec P, Sinko T, Nenadic DD, Pavokovic G and Dolenec Z. 2011. Sex-typing bird species with little or no sexual dimorphism: an evaluation of molecular and morphological sexing. Journal of Biological Research 15: 145.

Koldewey HJ, Curnick D, Harding S, Harrison LR and Gollock M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. Marine Pollution Bulletin 60(11): 1906-1915.

Longhurst AR and Pauly D. 1987. Ecology of tropical oceans. Academic Press. San Diego, USA.

Miller MG, Silva FR, Machovsky-Capuska G. and Congdon BC. 2018. Sexual segregation in tropical seabirds: drivers of sex-specific foraging in the Brown Booby *Sula leucogaster*. Journal of Ornithology 159(2): 425-437.

Nelson B. 1978. The Sulidae: gannets and boobies (No. 154). Oxford University Press.

O'Dwyera TW, Priddel D, Carlile N, Bartle JA and Buttemer WA. 2006. An evaluation of three field techniques for sexing Gould's Petrels (Pterodroma leucoptera) (Procellariidae). Emu-Austral Ornithology 106(3): 245-252.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reynolds SJ, Martin GR, Wallace LL, Wearn CP and Hughes BJ. 2008. Sexing sooty terns on Ascension Island from morphometric measurements. Journal of Zoology 274(1): 2-8.

Schreiber EA, Schreiber RW and Schenk GA. 2021. Red-footed Booby (Sula sula), version 1.0. In: Billerman SM. (Ed.). Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.refboo.01.

Seyer Y, Gauthier G, Bernatchez L and Therrien JF. 2019. Sexing a monomorphic plumage seabird using morphometrics and assortative mating. Waterbirds 42(4): 380-392.

Shizuka D and Lyon BE. 2008. Improving the reliability of molecular sexing of birds using a W-specific marker. Molecular Ecology Resources 8(6): 1249-1253.

Taylor SA and Friesen VL. 2012. Use of molecular genetics for understanding seabird evolution, ecology and conservation. Marine Ecology Progress Series 451: 285-304.

Totterman SL. 2015. A comparative evaluation of four field methods for sexing Wedge-tailed Shearwaters *Puffinus pacificus*. Marine Ornithology 43: 83-93.

Votier SC and Sherley RB. 2017. Seabirds. Current Biology 27(11): R448-R450.

Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A and Marsac F. 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. Oecologia 146(4): 681-691.

Weimerskirch H, Le Corre M, Gadenne H, Pinaud D, Kato A, Ropert-Coudert Y and Bost CA. 2009a. Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. Oecologia 161(3): 637-649.

Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K and Aurioles D. 2009b. Species-and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Marine Ecology Progress Series 391: 267-278.

Young HS, McCauley DJ, Dirzo R, Dunbar RB and Shaffer SA. 2010a. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. Marine Ecology Progress Series 416: 285-294.

Young HS, Shaffer SA, McCauley DJ, Foley DG, Dirzo R and Block BA. 2010b. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. Marine Ecology Progress Series 403: 291-301.

SUPPLEMENTARY MATERIAL TO CHAPTER 5

Table S5. 1. The locations and number of Red-footed Booby processed (ringed, body mass and wing length recorded) and identified by sex using genomic DNA analysis.

Atoll	Island	Processed	DNA sex	
			♂	♀
Diego Garcia	Diego Garcia	165	26	42
	East Island	2	0	0
	West Island	2	0	0
Totals		169	26	42
Great Chagos Bank	Danger Island	31	0	0
	Nelson’s Island	96	18	8
Totals		127	18	8
Peros Banhos	Grand Coquillage	15	9	5
	Longue	5	3	2
	Moresby	5	0	4
	Parasol	11	3	4
	Verte	1	1	0
Totals		37	16	15
Grand Total	10	333	60	65

Table S5. 2. Single factor ANOVA results comparing wing length and mass between atolls in the Chagos Archipelago of known sex Red-footed Booby, sexed through genomic DNA analysis (d.f. = Degrees of Freedom, SS = Sum of Squares, MS = Mean Sum of Squares, NS = not statistically significant).

Morphometric		**d.f.**	**SS**	**MS**	**F-value**	**P-value**
Female wing length	Between atolls	2	54.37	27.18	0.31	0.74 (NS)
	Within atoll	62	5529.41	89.18		
	Total	64	5583.78			
Male wing length	Between atolls	2	191.83	95.91	1.174	0.316 (NS)
	Within atoll	58	4737.85	81.69		
	Total	60	4929.67			
Female mass	Between atolls	2	13188.46	6594.23	0.41	0.66 (NS)
	Within atoll	62	993140	16018.39		
	Total	64	1006328			
Male mass	Between atolls	2	38648.96	19324.48	2.420797	0.097778 (NS)
	Within atoll	58	462996.1	7982.692		
	Total	60	501645.1			

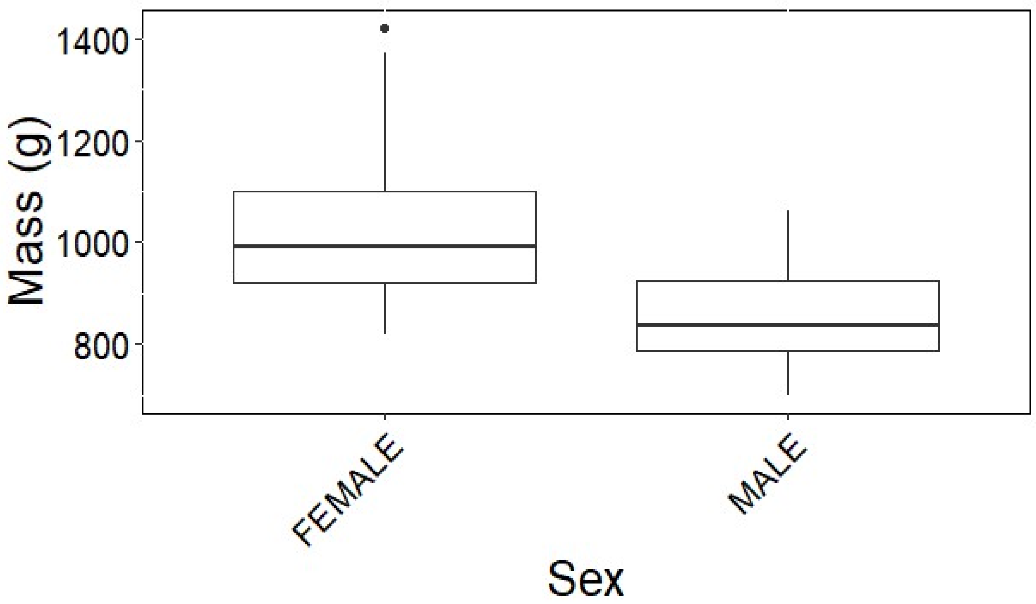


Figure S5. 1. Mass (g) of Red-footed Booby of molecular determined, known sex birds (n = ♀ 65, ♂ 60) from three atolls combined data in the Chagos Archipelago. There is a significant difference in mass between the sexes, taking into consideration location (F = 64.9, P < 0.001).

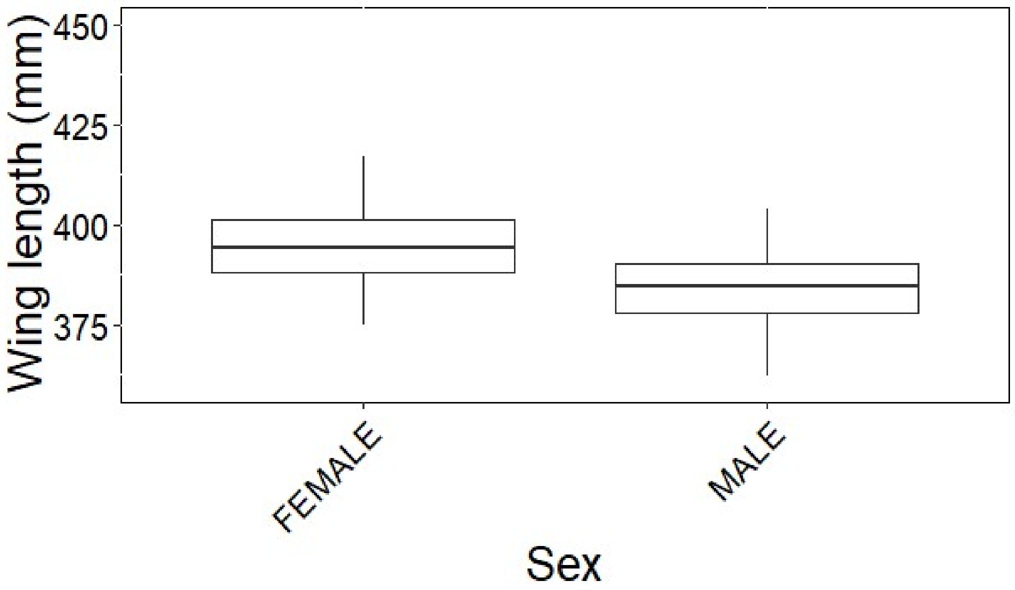


Figure S5. 2. Wing length (mm) of Red-footed Booby of molecular determined, known sex birds (n = ♀ 65, ♂ 60) from three atolls combined data in the Chagos Archipelago. There is a significant difference in wing length between the sexes, taking into consideration location (F = 40.4, P < 0.001).

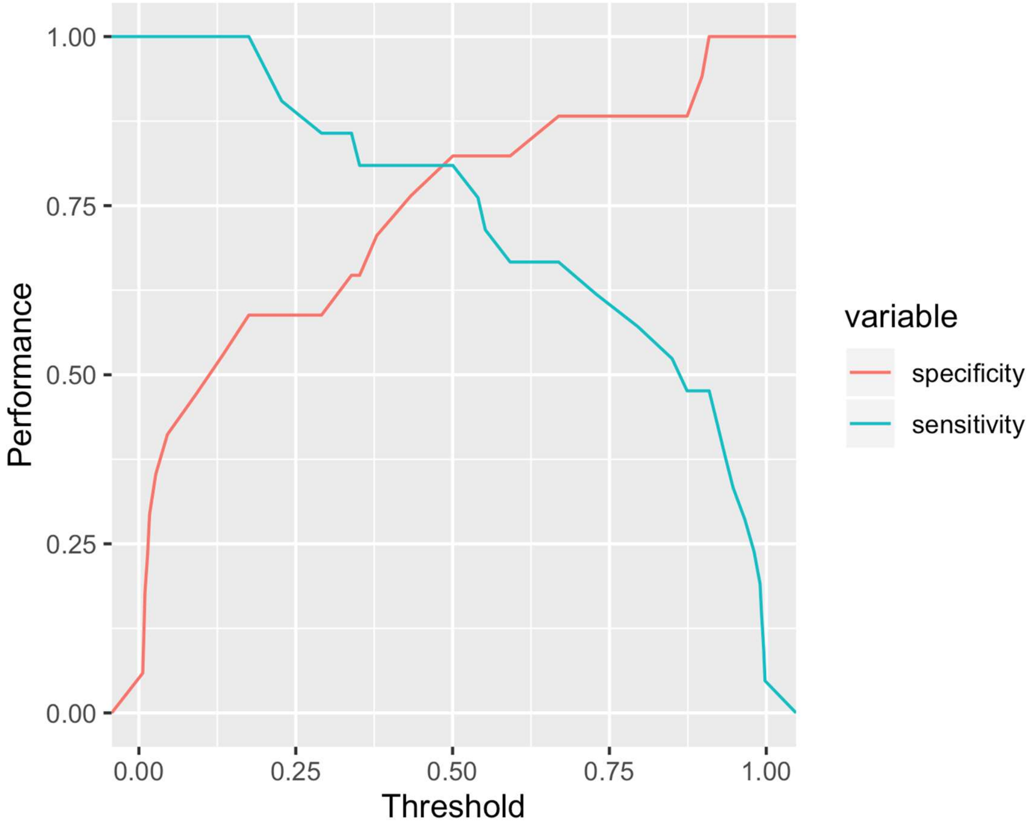


Figure S5. 3. Specificity versus sensitivity plot (false negative versus false positive) demonstrating the trade off in predicting male when female vs predicting female when male. The threshold is ~ 0.5 for a bird being female.

CHAPTER 6

MARINE IMPORTANT BIRD AND BIODIVERSITY AREAS IN THE CHAGOS ARCHIPELAGO

Chapter published as:

Carr P, Trevail A, Koldewey HJ, Sherley R, Votier SC, Wilkinson T and Nicoll MAC. 2021. Marine Important Bird and Biodiversity Areas in the Chagos Archipelago. Bird Conservation International. Submitted 07 July 2021.

ABSTRACT

Seabirds are declining globally and are one of the most threatened groups of birds. To halt or reverse this decline they need protection both on land and at sea, requiring site-based conservation initiatives based on seabird abundance and diversity. The Important Bird and Biodiversity Area (IBA) programme is a method of identifying the most important places for birds based on globally agreed standardised criteria and thresholds. However, while great strides have been made identifying terrestrial sites, at-sea designation is lacking. The CA, central Indian Ocean, supports four terrestrial IBAs (tIBAs) and two proposed marine IBAs (mIBAs). The mIBAs are seaward extensions to breeding colonies based on outdated information and, other types of mIBA have not been explored. Here, I review the proposed seaward extension mIBAs using up-to-date seabird status and distribution information and, use GPS tracking from RfB – one of the most widely distributed breeding seabirds on the archipelago – to identify any pelagic mIBAs. I demonstrate that due to overlapping boundaries of seaward extension to breeding colony and pelagic areas of importance there is a single mIBA in the central Indian Ocean that lays entirely within the Chagos Marine Protected Area (MPA). Covering 62,379 km^2 it constitutes ~10% of the MPA and if designated would become the 11th largest mIBA in the world and 4th largest in the Indian Ocean. My research strengthens the evidence of the benefits of large-scale MPAs for the protection of top predators and provides a scientific foundation stone for marine biodiversity hotspot research in the central Indian Ocean.

Author’s Note

Chapter 3 covering terrestrial IBAs in CA and this chapter covering marine IBAs were written four years apart. When writing chapter 3, the BirdLife region of reference for the “1% of biogeographic populations” IBA qualifying thresholds was South Asia (BirdLife International 2004), as used in previous CA IBA designations by Birdlife International (2004) and Carr (2006). Following discussions with BirdLife (pers. comm.), the region of reference for CA has been amended to the western Indian Ocean, as used by IUCN (e.g., Bullock et al. 2021) and in this chapter.

INTRODUCTION

Globally, at least 40% of bird species are in decline and as of 2017, 1,469 (13% of the total number of species, or one in eight) are threatened with extinction (BirdLife International 2018a). Seabirds are one of the most threatened groups of birds (Croxall et al. 2012) with almost half of all species (47%) having declining population trends (BirdLife International 2018b). To reverse the decline in seabird populations, conservation measures are required on land, especially at breeding colonies, and at sea where species feed (Dias et al. 2019). The conservation measures required are wide ranging. For example, on land these range from the ecological restoration of whole (seabird) island ecosystems (Mulder et al. 2011), to providing artificial breeding chambers for a single species (Bolton et al. 2004). At sea, intervention is required to counter overfishing and bycatch – the threats causing the most negative impacts on average to all seabird species (Dias et al. 2019). Key to the implementation of site-based conservation initiatives, both on land and at sea, is to identify sites of biodiversity significance (Donald et al. 2018).

The Important Bird and Biodiversity Areas (IBAs) programme is a method of identifying the most important places for birds (BirdLife International 2009). Since the late 1970s, the BirdLife Partnership has been working to identify, document and protect all places of greatest significance for the conservation of the world's birds. As a result, over 13,000 IBAs have been identified, becoming the largest global network of significant biodiverse sites in the world (http://www.birdlife.org/worldwide/programmes/sites-habitats-ibas/ accessed 16 December 2020). IBAs are identified using a globally agreed standardised set of data-driven criteria and thresholds, ensuring that the approach can be used consistently worldwide (Box 6.1). IBAs do not afford protection to a site in themselves, they identify sites that warrant protection.

Box 6. 1. Important Bird and Biodiversity Area selection criteria applicable outside of Europe and the Middle East (précised from Guidelines for the application of the IBA criteria. Final version July 2020. http://datazone.birdlifeorg accessed 29 April 2021).

A1: Globally Threatened Species Criterion: The site is known or thought regularly to hold significant numbers of a Globally Threatened species. The site qualifies if it is known, estimated or thought to hold a population of a species categorized on the IUCN Red List as globally threatened (Critically Endangered, Endangered and Vulnerable). Specific thresholds apply to species in the three threat categories.

A2: Restricted Range Species Criterion: The site is known or thought to hold a significant population of at least two range-restricted species. Restricted-range bird species are those having a global range size less than or equal to 50,000 km^2. This criterion can be applied to species both within their breeding and nonbreeding ranges.

A3: Bioregion-Restricted Assemblages Criterion: The site is known or thought to hold a significant component of a group of species whose distributions are largely or wholly confined to one biome-realm.

A4: Congregations Criterion: The site is known or thought to hold congregations of ≥1% of the global population of one or more species on a regular or predictable basis.

B1a: Globally Near Threatened Species: The site regularly holds significant numbers of a Near Threatened species (NT). Non-passerines – 10 pairs/30 individuals; Passerines – 30 pairs/90 individuals.

B3a: Regionally Important Congregations – biogeographical populations: The site is known or thought to hold, on a regular basis ≥ 1% of a biogeographic or other distinct population of a congregatory waterbird, breeding seabird or other species.

B3b: Regionally Important Congregations – multispecies aggregations: The site is known or thought to hold, on a regular basis ≥ 20,000 waterbirds or (formerly global A4iii) ≥ 6,700 pairs of seabirds of one or more species.

B3c: Regionally important congregations – bottleneck sites: The site is known or thought to exceed thresholds set for migratory species at bottleneck sites.

Whilst the identification of tIBAs has neared completion globally (Birdlife International 2009), the identification of mIBAs is more challenging and ongoing (Lascelles et al. 2016). Osieck (2004) recognised four types of mIBA (Box 6.2), designed to encompass the spatial distribution of seabirds (and other coastal waterbirds) throughout their annual lifecycle.

Box 6. 2. Types of marine Important Bird and Biodiversity Areas (from Osieck 2004).

Seaward extensions to breeding colonies: These extensions, which are used for feeding, maintenance behaviour and social interactions, are limited by the foraging range and depth of the species concerned. The breeding colonies themselves will have, in most cases, already been identified as IBAs, which will therefore require their boundaries to be extended into the marine environment. The seaward boundary would, as far as possible, be colony and/or species-specific, based on known or estimated foraging and maintenance information.

Non-breeding (coastal) concentrations: These include sites, usually in coastal areas, which hold feeding and moulting concentrations of waterbirds, such as divers, grebes and benthos feeding ducks. They could also refer to coastal feeding areas for auks, shearwaters etc.

Migratory bottlenecks: These are sites whose geographic position means that seabirds fly over or round in the course of regular migration. These sites are normally determined by topographic features, such as headlands and straits.

Areas for pelagic species: These sites comprise marine areas remote from land at which pelagic seabirds regularly gather in large numbers, whether to feed or for other purposes. These areas usually coincide with specific oceanographic features, such as shelf-breaks, eddies and upwellings, and their biological productivity is invariably high.

Within the main island groups of the tropical Indian Ocean - CA, Christmas Island, Cocos Keeling, Lakshadweep, Maldives, the Mascarenes (Mauritius, Reunion and Rodrigues) and Seychelles - there have been 52 tIBAs and 29 mIBAs proposed or designated to date. Of the mIBAs, the vast majority are seaward extension to breeding colonies. Throughout the Indian Ocean high seas (areas beyond national jurisdiction) there have been a further 25 mIBAs proposed which are all areas for pelagic species (http://datazone.birdlife.org accessed 26 April 2021).

The CA is situated in the central Indian Ocean (Fig. 6.1). Carr et al. (2021) reviewed the tIBAs of the archipelago using updated status and distribution information for the 18 species of breeding seabird. This review condensed the 10 designated and two proposed (all single island) tIBAs into three island clusters and one single island tIBA (Fig. 6.1) based upon four IBA triggering species; Tropical Shearwater *Puffinus baillonii* (formerly Audubon's Shearwater *Puffinus lherminieri*), RfB, Sooty Tern *Onychoprion fuscatus,* and Lesser Noddy *Anous tenuirostris*. The IBA qualifying criteria and thresholds have advanced since this review and now include qualification at the global ('A' criteria) and regional ('B' criteria) level (Box 6.1, Table 6.1). The CA is part of the Western Indian Ocean region as defined by Fischer and Bianchi (1984), and used by the IUCN (e.g., Bullock et al. 2021). All four tIBAs retain their status at the global level, in some cases with revised qualifying species (Table 6.2).

Table 6. 1. Global and regional 1% threshold values for the Chagos Archipelago Important Bird and Biodiversity Area triggering species. Global populations are from IUCN (2021). For regional populations see Table S6.1.

Species	Global 1% threshold	Regional 1% threshold
Tropical Shearwater	Population unknown	3,769 mature individuals 1,256 breeding pairs
Red-footed Booby	10,000 mature individuals 3,333 breeding pairs	2,987 mature individuals 996 breeding pairs
Sooty Tern	230,000 mature individuals 76,667 breeding pairs	136,560 mature individuals 45,520 breeding pairs
Lesser Noddy	12,000 mature individuals 4,000 breeding pairs	10,404 mature individuals 3,468 breeding pairs

Table 6. 2. Chagos Archipelago - terrestrial Important Bird and Biodiversity Areas (tIBA) with their qualifying criteria (from Carr et al. 2021) and revised status as of 2021.

tIBA name	Qualifying criteria (breeding pairs)	Revised qualifying criteria as at 2021 (breeding pairs)
Eastern Diego Garcia island group	A4ii Red-footed Booby (9,969)	A4/B3b Red-footed Booby (11,170)
Western Great Chagos Bank island group	A4i Sooty Tern (52,000), Lesser Noddy (15,735) A4ii Red-footed Booby (5,469), Tropical Shearwater (1,615) A4iii site holds at least 20,000 waterbirds	A4 Red-footed Booby (5,469) A4/B3b Lesser Noddy (15,735) B3a/B3b Sooty Tern (52,000) B3a Tropical Shearwater (1,615)
Nelson's Island	A4i Lesser Noddy (12,000) A4ii Red-footed Booby (3,300) A4iii site holds at least 20,000 waterbirds	A4/B3b Lesser Noddy (12,000)
Eastern Peros Banhos island group	A4i Sooty Tern (145,000), Lesser Noddy (20,850) A4iii site holds at least 20,000 waterbirds	A4/B3b Sooty Tern (145,000) A4/B3b Lesser Noddy (20,850)

Birdlife International have proposed two mIBAs for the CA (Fig. S6.1) (http://datazone.birdlife.org accessed 26 April 2021). These mIBAs were delineated using seaward extension to breeding colony (SEBC) criteria (Osieck 2004) based upon historical data from Birdlife International (2004), Carr (2006) and foraging radii from the (now defunct) BirdLife Seabird Foraging Range Database (Lascelles 2008).

Here, the two SEBC mIBAs proposed by BirdLife International are reviewed and, for the first time in the CA, I assess the potential for pelagic mIBAs. When reviewing the SEBC IBAs the updated tIBA designations are used (http://datazone.birdlife.org/site/results accessed 14 May 2021) coupled with the latest information on seabird foraging behaviour in the CA. When exploring for pelagic mIBAs, I analyse tracking data from a single species (RfB – considered to be representative of all the archipelago's pelagic species and therefore a useful umbrella species), from across the archipelago using the standardised methodology presented in the 'Marine IBA toolkit' (BirdLife International 2010) and the associated R package 'track2KBA' (Beal et al. 2020). My goal was to identify marine areas of significance to the internationally important breeding seabirds of the CA and, to understand seabirds' use of the BIOT MPA, to gauge the efficacy of the MPA at affording protection to central-place foraging seabirds and top predators.

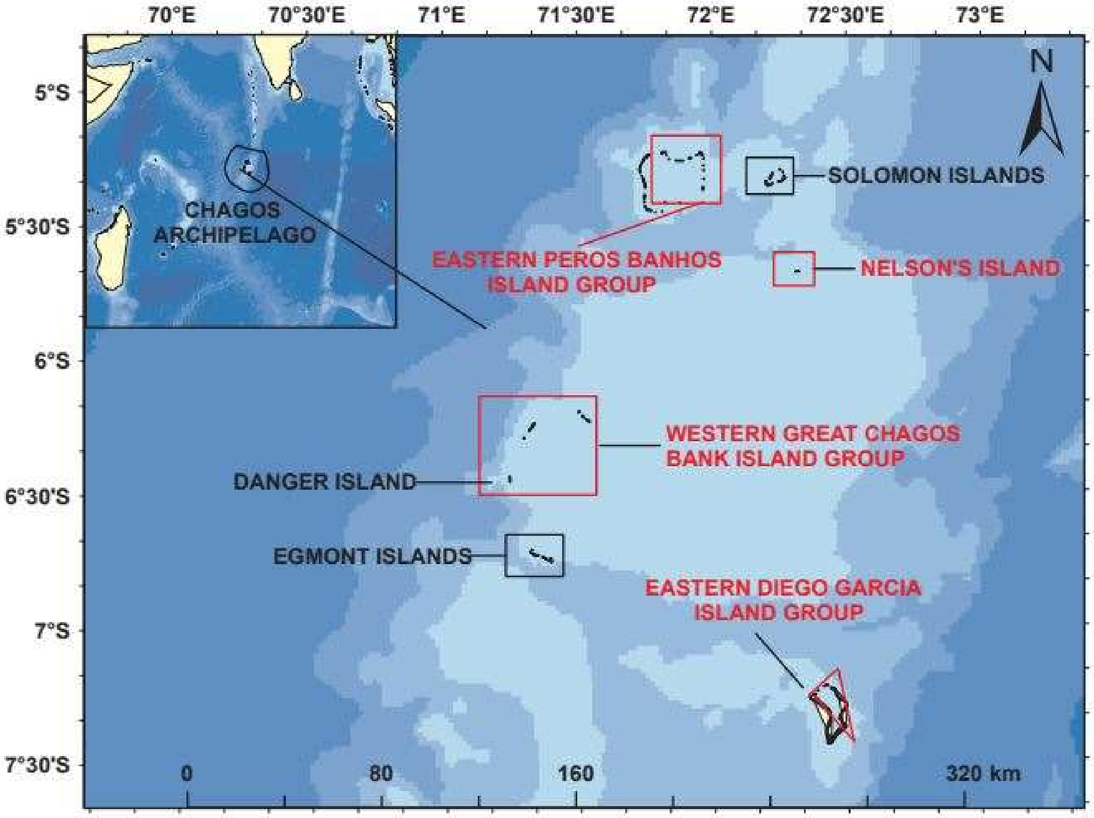


Figure 6. 1. The Chagos Archipelago in an Indian Ocean context showing the four terrestrial Important Bird and Biodiversity Areas (in red) within the five atolls of Peros Banhos, Solomon Islands, Great Chagos Bank (includes Nelson's Island), Egmont Islands and Diego Garcia.

METHOD

Study Site

The CA is the southern termini of the Lakshadweep-Maldives-Chagos ridge. It is comprised of 55 islands in five atolls between 05°15’ - 07°27’S and 71°15’ - 72°30’E (Fig. 6.1). The coralline islands are located on atoll rims with elevations generally no more than 2–3 m Above Mean Sea Level (Eisenhauer et al. 1999). About 282,000 breeding pairs of 18 species of tropical seabird nest annually in the archipelago (Carr et al. 2021). All *c.* 640,000 km^2 of the CA Exclusive Economic Zone was designated as a no-take marine protected area (BIOT MPA) in 2010, at that time the largest no-take MPA in the world (Koldewey et al. 2010). The archipelago has two monsoon seasons: from October to April, winds are light or moderate and blow generally from the north-west; for the rest of the year, the Southeast trades blow strongly (Sheppard et al. 1999).

Marine Important Bird and Biodiversity Area Qualifying Criteria

Of the 18 breeding seabird species in the CA, there are no globally threatened (A1) or restricted range species (A2), nor any biome restricted assemblages (A3) (Carr et al. 2021). Therefore, all IBAs qualify under congregations at a global threshold (A4) or regional threshold (B3) (Box 6.1). Of the four mIBA types (Osiek 2004), no non-breeding concentrations or migration bottlenecks are known to occur – all potential mIBAs qualify as seaward extensions to breeding colonies or, possibly, areas for pelagic species (Box 6.2).

Seaward Extension to Breeding Colonies (SEBC) mIBAs

Globally, these are normally based upon tIBAs designated for breeding seabirds (Box 6.2, in the CA Table 6.2 and Fig. 6.1) based upon their foraging ranges. How a seabird species uses a SEBC mIBA is strongly influenced by their foraging strategy, for example, neritic species will feed and conduct maintenance (e.g., bathing) primarily within an SEBC mIBA. Pelagic species generally feed far beyond SEBC boundaries in the open ocean and only use the SEBC for maintenance and social interaction (e.g., rafting). As a result, BirdLife

International (2010) suggest that SEBC delineation using the foraging radius approach may be more suitable/accurate based upon coastal rather than pelagic foragers. For this reason, the foraging radius of Lesser Noddy, which is a coastal species in the CA (Carr et al. 2021), has been used to delineate SEBC mIBAs – the remaining three IBA triggering species, Tropical Shearwater, RfB and Sooty Tern all being pelagic foragers (Billerman et al. 2020).

If the foraging radius of the species breeding in a specific tIBA is not known, it is accepted practice to use the foraging radius of the same species from elsewhere based upon tracking data or, expert opinion if no tracking data are available (Lascelles 2011). No foraging radius data exist for Lesser Noddy from the CA. Lascelles (2011), using the opinion of experts from across the species' range gives a foraging radius of 50 km. Surman et al. (2017) using tracking data from Houtman Abrolhos, Western Australia, offer a mean trip distance of 79.5 km (SE 9.8 km, range 4.8 – 112 km) for subspecies *A.t. melanops*. In the CA, the nominate subspecies is primarily a lagoon and nearshore forager (Carr et al. 2021), therefore, I have followed Lascelles (2011) and used the lesser foraging radius of 50 km to delineate SEBC mIBA boundaries. Where SEBC boundaries overlapped they were joined to form one continuous mIBA.

The predicting of marine areas of significance for seabirds using foraging radius can be made more robust by the inclusion of potential drivers for foraging, e.g., prey distribution, diving depth, bathymetry (BirdLife International 2010, Soanes et al. 2016). I only had access to depth data within delineation of mIBA boundaries. However, depth was excluded as a factor impacting SEBC mIBA delineation because prior at-sea survey data from the CA found that feeding aggregations of the four IBA triggering species varied from shallow atoll lagoons (< 30 m, typically Lesser Noddy) to deep-ocean abysses (> 1,000 m, Tropical Shearwater, RfB and Sooty Tern). Such habitats can all exist within 500 m of breeding colonies in the CA (Fig. S6.2A/B), and therefore all feeding depths are accommodated for all species within the 50 km foraging radius used.

Pelagic mIBAs

These are best denoted from tracking data, identify areas usually much further from the breeding colony than SEBC mIBAs, are normally for pelagic species, and are often in the high seas areas beyond national jurisdictions (Lascelles et al. 2016).

Breeding RfB were tracked during both monsoon seasons in 2016, 2018 and 2019 (dates in Table 6.3) at the three largest colonies in the CA (Fig. 6.1, Carr et al. 2021) in order to ascertain foraging areas. Adult birds ≥ 4 calendar year old that were incubating eggs or guarding small chicks (1 – 3 weeks old) were caught on the nest by hand and fitted with a British Trust for Ornithology (BTO) G size Incoloy® metal ring for unique identification and a tail-mounted GPS logger (18g, IGotU GT-120, Mobile Action Technology Inc.). Loggers were fixed to the tail using tape (Tesa® 4651, Beiersdorf AG) and deployed for between three and 10 days. Tracking birds across two breeding stages (egg incubation and small chick guarding) gives a greater representation of foraging areas as elsewhere Sulidae use different foraging strategies dependent upon breeding stage (Lerma et al. 2020).

Pelagic mIBAs were based on the BirdLife International Marine IBA toolkit (BirdLife 2010) using the ‘track2KBA’ package (Beal et al. 2020) for R (Version 3.6.0, R Core Team 2020). Tracks were split by colony and monsoon period but pooled by year (Table 6.3). Foraging trips was defined as movements > 1 km and > 1 hour to distinguish between true foraging and short maintenance forays (e.g., bathing). For each trip, the 50% isopleth utilisation distribution (UD) was calculated as a measure of the core foraging grounds and used the scale of the area-restricted search (ARS) from first passage time for the smoothing factor (*h*) (Lascelles et al. 2016) (Table 6.3, example shown in Fig. S6.3). The 50% UD of each trip were overlayed onto a 0.01 x 0.01° grid in a Lambert Equal-area Azimuthal projection, and it was assumed a grid cell was in a core area if it intersected the 50% UD. To identify core-use areas, I summarised how often each 0.01 x 0.01° cell was included in a core-use area of individual trips. The representativeness threshold (a value that estimates how well a tracked sample represents a population after running 100 iterations) for each data group (Table 6.3, example at Fig. S6.4) was set at 70% (Lascelles et al. 2016).

The number of birds using each grid cell was calculated by multiplying the breeding colony population by the proportion of the tracked population which had a core-use area in each grid cell (example at Fig. S6.5). RfB breeds throughout the year in the CA with two spikes in breeding, one in each monsoon season (Carr et al. 2021). I adopted the precautionary approach (Cooney and Dickson 2012) and used the largest breeding colony figure available from the most recent review (Carr et al. 2021 - Table 6.3). Maximum and minimum numbers of birds using the core-use area were calculated using the *potSite* function in the 'track2KBA' package (Beal et al. 2020) and the mean values (Table 6.3) were measured against the global and regional 1% species' threshold (Table 6.1) to assess whether an area meets IBA criteria. Shapefiles of global or regionally significant areas were produced using the R package 'sf' (Pebesma 2018) and mapped using ArcGIS Pro 2.7.0. Where pelagic mIBAs overlapped with other pelagic mIBAs, they were joined to form one continuous mIBA.

Diego Garcia had RfB tracking data from both monsoon seasons (Table 6.3). To assess the kernel overlap of the 95% UD of the two seasonal pelagic mIBAs, I used Bhattacharyya's affinity (BA - Bhattacharyya 1943) within the R 'adehabitatHR' package (Fieberg and Kochanny 2005). BA ranges from 0 (no overlap) to 1 (complete overlap). I further calculated the overlap of the mIBA shapefile boundaries in ArcGIS Pro 2.7.0. If the BA was ≥ 0.75 and the overlap of boundaries ≥ 75%, I combined the two mIBAs into a single entity. Variation in the trip metrics between monsoon seasons from the colony on Diego Garcia were tested using (parametric) students two-sample equal variance t-Tests (p = 0.05) for the number of trips and ARS values and, (non-parametric) Wilcoxon rank sum tests with continuity corrections (p = 0.05) for trip duration, total track and mean maximum track distance following tests for homogeneity of variance and normality of all data.

The marine Important Bird and Biodiversity Areas of the Chagos Archipelago

To produce the consolidated map of mIBAs for the CA, the SEBC and pelagic mIBAs were combined where overlap occurred into a single spatial polygon using ArcGIS Pro 2.7.0.

RESULTS

Seaward Extension to Breeding Colonies mIBAs

Seaward extensions to the four tIBAs (North-eastern Peros Banhos, Nelson's Island, Great Chagos Bank and Eastern Diego Garcia; Table 6.2) had overlapping foraging radii for the three northern atolls, producing two mIBAs (Fig. 6.3A). Both qualified based on congregations of ≥1% of the global populations (criteria A4, Box 6.1) of RfB (Diego Garcia) and RfB, Sooty Tern and Lesser Noddy (northern atolls) (Box 6.1, Tables 6.1, 6.2).

Pelagic mIBAs

The 194 tracked birds (female = 35, male = 35, unsexed = 124) produced 511 foraging trips (Fig. 6.2, Table 6.3). No statistically significant differences were found between the number of trips (t = 1.97, df = 2, p = 0.19) and the ARS values (t = 1.41, df = 2, p = 0.3) recorded in the opposing monsoon seasons. Representativeness values all exceeded the minimum 70% threshold (Table 6.3). All pelagic mIBAs met the regional 1% threshold for RfB (criteria B3a – Table 6.1) - the colony on Diego Garcia met the regional 1% threshold in both monsoon seasons (Table 6.3). At the Diego Garcia colony Wilcoxon rank sum tests demonstrated statistically significant differences between the track metrics recorded in the two monsoon seasons (Table 6.4) - trip duration ($p = 0.006$), total track distance ($p = 0.008$), mean track distance ($p = 0.001$). Four pelagic mIBAs were identified (Figs. 6.3B/C). Despite significantly different track metrics, the two Diego Garcia mIBAs had a BA of 0.81 and 95% of the NW monsoon mIBA area lay inside the SE monsoon mIBA area. Therefore, the boundaries of these two mIBAs were amalgamated and as a result, this mIBA met the global 1% threshold for RfB (criteria A4, Table 6.1, Fig. 6.3C).

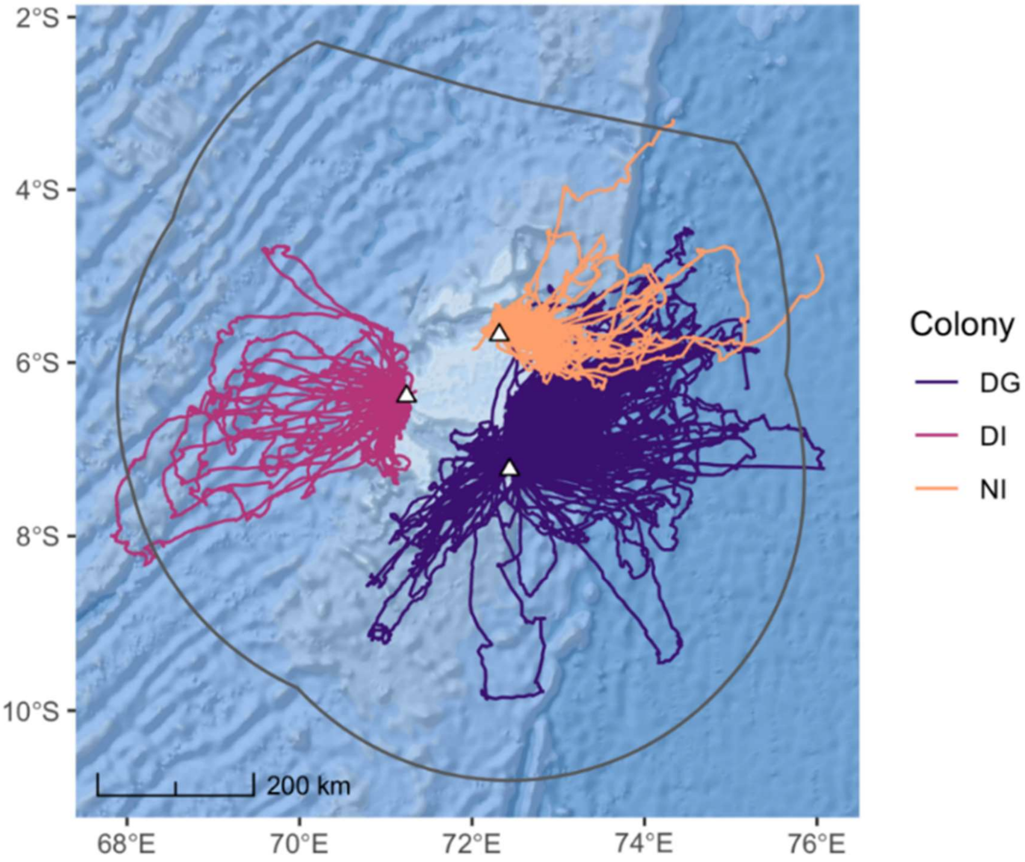


Figure 6. 2. 511 foraging trips conducted by 194 Red-footed Booby from the three largest breeding colonies in the Chagos Archipelago. Tracking took place during 2016, 2018 and 2019 in both monsoon seasons. White triangles denote breeding colonies. DG = Diego Garcia, DI = Danger Island, NI = Nelson's Island.

The marine Important Bird and Biodiversity Areas of the Chagos Archipelago

Combining the SEBC and pelagic IBAs into a single spatial polygon produced one mIBA for the CA due to overlapping boundaries (Fig. 6.3D) – this is the proposed Chagos Archipelago marine Important Bird and Biodiversity Area (CA mIBA).

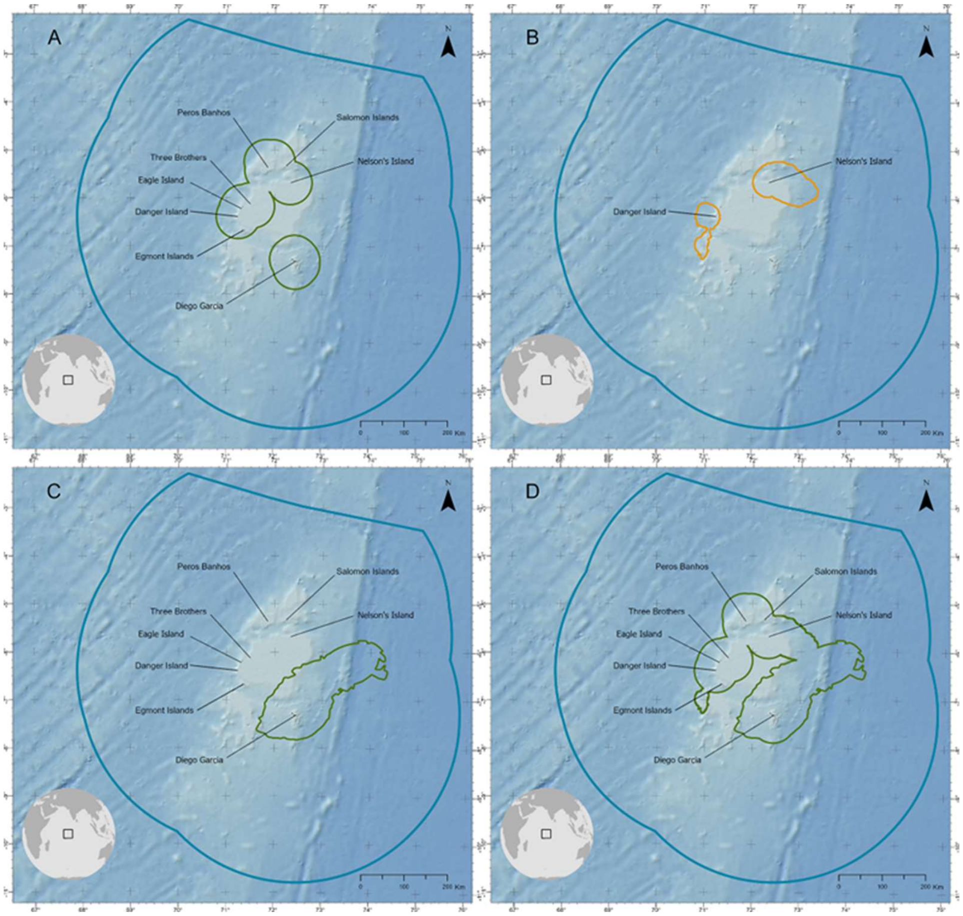


Figure 6. 3 (**A**). Seaward extension to breeding colony marine Important Bird and Biodiversity Areas (mIBAs) in the Chagos Archipelago, qualifying at the global (A4) level based upon three terrestrial IBAs (tIBAs), Western Great Chagos Bank island group, Nelson's Island and Eastern Peros Banhos island group (upper shape) and, the tIBA of the Eastern Diego Garcia island group (lower shape). Blue border is the boundary of the Chagos Marine Protected Area (MPA). Inset globe shows location of the Chagos Archipelago in the Indian Ocean. Green border denotes mIBA qualifies at the global scale. (**B**). Pelagic

mIBAs based upon tracked Red-footed Booby *Sula sula rubripes* from breeding colonies on Nelson's and Danger Island, Great Chagos Bank atoll, qualifying at the regional (B3a) level. Orange borders denote mIBA qualification at the regional level. (**C**). Pelagic mIBA based upon tracked Red-footed Booby from the breeding the colony on Diego Garcia, qualifying at the global level (A4). The tracking data from opposing monsoon seasons have been amalgamated. (**D**). Overlaying 6.3A/B/C results in the proposed mIBA - The Chagos Archipelago marine Important Bird and Biodiversity Area (62,379 km2).

Table 6. 3. Red-footed Booby tracking data from the three largest breeding colonies and population sizes (individual mature birds) used to identify pelagic marine Important Bird and Biodiversity Areas in the Chagos Archipelago. NW = Northwest Monsoon, SE = Southeast Monsoon. Representativeness value is a value that demonstrates whether a sample set of data represents the population from which the sample came from. The threshold value is 70% below which a sample was deemed non-representative (Lascelles et al. 2016). * indicates the value meets Important Bird and Biodiversity Area qualifying threshold.

Colony / Season / Individual mature birds	**Number tracked**	**Dates tracked**	**Number of trips**	**Area restricted value (km)**	**Representative value (%)**	**Mean number of individual mature birds in IBA**
Diego Garcia NW 15,252	15 21	05 – 17/12/2016 13 – 22/01/2018	71	29	99.6	7,626*
Diego Garcia SE 18,258	35 30	25/06 – 07/07/2016 09 – 18/06/2018	127	45	99.6	8,980*
Danger Island NW 10,500	30	16 – 24/01/2019	76	11.5	94	4,595*
Nelson’s Island SE 9,900	36 27	08 – 16/07/2018 04 – 10/07/2019	237	29	99.6	4,950*

Table 6. 4. Red-footed Booby track metrics from the three largest breeding colonies in the Chagos Archipelago. NW = Northwest Monsoon; SE = Southeast Monsoon; Total track distance is the distance travelled by a bird in a single trip calculated from when it left the nest to when it returned; Mean max distance is the mean of the furthest point a bird travelled from a colony calculated from using all trips of all tracked birds from a colony; Direction is the mean of the direction a bird travelled on the outward leg of a trip. Figures have been rounded to whole numbers.

Colony / Season	**Mean duration ± SD (hrs)**	**Duration range (hrs)**	**Mean total track distance ± SD (km)**	**Total track distance range (km)**	**Mean max distance ± SD (km)**	**Max distance range (km)**	**Direction ± SD (°)**
Diego Garcia NW	62 ± 8	1 – 233	520 ± 51	4 – 1767	184 ± 16	2 – 402	55 ± 19
Diego Garcia SE	43 ± 5	1 – 216	380 ± 29	4 – 1450	112 ± 7	2 – 311	32 ± 32
Danger Island NW	14 ± 2	1 – 111	253 ± 29	14 – 1254	92 ± 10	6 – 418	264 ± 12
Nelson’s Island SE	8 ± 1	1 – 63	108 ± 8	1 – 919	43 ± 4	1 – 423	40 ± 37

DISCUSSION

This research reviewed the two proposed SEBC mIBAs of the CA using contemporary information on seabird breeding populations. For the first time in the archipelago, tracking data from an IBA triggering species, RfB, was used to identify pelagic IBAs. Where the revised SEBC IBAs and identified pelagic mIBAs overlapped, they were combined into one proposed mIBA, the CA mIBA, that is situated entirely within the BIOT MPA. Covering 62,379 km^2 it constitutes ~10% of the MPA and if designated would become the 11th largest mIBA in the world and 4th largest in the Indian Ocean (http://datazone.birdlife.org/site/results accessed 10 June 2021).

Debate continues into the merits of single- versus multi-species approaches to conservation planning (Ronconi et al. 2012). To date, in the CA only RfB has been researched as an indicator of marine biodiversity hotspots; however, as an umbrella species (Roberge and Angelstam 2004) this top predator is representative of several of the breeding species. In the extremely low-resource environments of the tropical ocean (Longhurst and Pauly 1987) prey distribution and associated predators are often centred upon areas of productivity such as upwellings (Hyrenbach et al. 2000). For tropical pelagic seabirds, the deep blue oceans of their foraging grounds are more homogenous than other oceanic areas and prey distribution is patchy, rare and unpredictable (Balance et al. 1997). In these expanses, many seabird species rely on sub-surface predators such as tuna (Scombridae) and dolphin (Delphinidae) to drive epipelagic prey to the surface and have been described as ‘near-obligate associates’ (Au and Pitman 1986). In the western Indian Ocean, regular feeding associations with sub-surface predators have been recorded for at least seven species of seabird (Jaquemet et al. 2004). In the CA all four IBA triggering species have been recorded at multi-species feeding aggregations, all associated with tuna species (Carr, unpubl. data). It is likely that a mIBA in the CA that covers the pelagic foraging areas of RfB would encompass foraging grounds for several other species. This is because the ‘near-obligate associate’ foraging strategy of many tropical seabirds means that wherever underwater predators are driving prey to the surface, RfB that rely on them will be accompanied by other near obligates – RfB feeding aggregations associated with tuna witnessed in the archipelago have involved Tropical Shearwater, Wedge-tailed Shearwater *Ardenna pacifica*, Masked *Sula dactylatra* and Brown Booby *S. leucogaster*, Sooty Tern, Brown Noddy *Anous stolidus* and Common White Tern *Gygis alba* (Carr, unpubl. data.). However, further research is required to confirm the umbrella species status of RfB, especially as Sooty Tern – the most numerous bird in the central Indian Ocean – have seldom been encountered at multi-species feeding aggregations in the archipelago (Fig. S6.2A/B).

Despite the declaration of the BIOT no take MPA in 2010 (Koldewey et al. 2010), illegal, unregulated and unreported (IUU) fishing still occurs (Ferretti et al. 2018, Hays et al. 2020). Authorities of the BIOT MPA now have scientifically credible evidence of a marine biodiversity hotspot within the MPA, the 62,379 km^2 CA mIBA. This area should be a focus for enforcement against IUU, safeguarding seabirds against bycatch and by proxy, through the umbrella species theory, also protect a suite of associated biodiversity.

Seabird foraging behaviours may vary between colonies and years (e.g., Osborne et al. 2020). Despite there being statistically significant differences in the track metrics at the Diego Garcia colony where tracking was undertaken in both monsoon seasons, the colony appears to feed and forage in broadly the same area in the two seasons - this may not be the case throughout the archipelago. Therefore, further tracking is desirable at all three locations to smooth out possible anomalies by having multi-year/season data and to confirm whether or not all colonies forage in a similar fashion to Diego Garcia where there is apparently little variation in the pelagic foraging area between seasons - despite how they forage being significantly different in the opposing monsoon seasons.

Marine IBAs can be triggered by both breeding and non-breeding concentrations (A4 criteria. Box 6.1) of seabirds (BirdLife International 2010, Lascelles et al. 2016, Osiek 2004). Research into the non-breeding behaviour and distribution of the IBA triggering species may also highlight more areas of IBA status. Le Corre et al. (2012) identified a major foraging area for western Indian Ocean non-breeding Wedge-tailed Shearwater and White-tailed Tropicbird *Phaethon lepturus*, centred upon the Afanasy Nikitin seamount (03°

S - 85° E) to the east of the BIOT MPA. Tracking of non-breeding seabirds from the central Indian Ocean may reveal overlap in areas of importance with western Indian Ocean populations and may further inform the ongoing debate on the merits of large-scale MPAs for both breeding and non-breeding seabirds.

The BIOT MPA at *c*. 640,000 km^2 is a ‘large-scale’ MPA (LSMPA) (Toonen et al. 2013). Despite there being strong support for LSMPAs in the scientific community (Koldewey et al. 2010, Sheppard et al. 2012, Gallagher et al. 2020, Hays et al. 2020), there remains criticism and debate surrounding them. One theme of criticism is how large an MPA needs to be to protect top predators and highly mobile species, with advocates for both LSMPAs of a size that could potentially cover the entire life cycle of mobile species (Game et al. 2009, Hyrenbach et al. 2000) and networks of smaller MPAs covering critical parts of an organism’s life cycle (Kerwath et al. 2009). This research has informed this debate by demonstrating that the BIOT MPA is large enough to entirely support a vagile, highly pelagic top predator (and umbrella species) through the most vulnerable phase of the critically important breeding cycle. Further research throughout other phases of the annual and entire RfB life cycle is required to assess whether LSMPAs can encompass the entire life stages of highly mobile top predators.

RECOMMENDATION

It is recommended that BirdLife International designate a marine Important Bird and Biodiversity Area in the CA, the CA mIBA (62,379 km^2). Shapefiles of this proposed mIBA are available from the author.

REFERENCES

Au DW and Pitman RL. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. The Condor 88(3): 304-317.

Ballance LT, Pitman RL and Reilly SB. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78(5): 1502-1518.

Bhattacharyya A. 1943. On a measure of divergence between two statistical populations defined by their probability distributions. Bulletin of the Calcutta Mathematical Society 35: 99-109.

Beal M, Oppel S, Handley J, Pearmain L, Morera-Pujol V, Miller M, Taylor P, Lascelles B and Dias M. 2020. BirdLife International/track2kba: First Release (Version 0.5.0). Zenodo.

Billerman SM, Keeney BK, Rodewald PG and Schulenberg TS. (Eds.) 2020. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home

BirdLife International. 2004. Important Birds Areas in Asia: key sites for conservation. Cambridge, UK: BirdLife International. (BirdLife Conservation Series No. 13).

BirdLife International. 2009. Designing networks of marine protected areas: exploring the linkages between Important Bird Areas and ecologically or biologically significant marine areas. Cambridge, UK: BirdLife International.

BirdLife International. 2010. Marine Important Bird Areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. BirdLife International, Cambridge UK. Version 1.2: February 2011.

BirdLife International. 2018a. State of the world's birds: taking the pulse of the planet. Cambridge, UK: BirdLife International.

BirdLife International. 2018b. IUCN Red List for birds. http://www.birdlife.org.

Bolton M, Medeiros R, Hothersall B and Campos A. 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran storm petrel (Oceanodroma castro). Biological Conservation 116(1): 73-80.

Bullock R, Ralph G, Stump E, Al Abdali F, Al Asfoor J, Al Buwaiqi B, Al Kindi A, Ambuali A, Birge T, Borsa P, Di Dario F, Everett B, Fennessy S, Fonseca C, Gorman C, Govende, A, Ho H, Holleman W, Jiddawi N, Khan M, Larson H, Linardich C, Matiku P, Matsuura K, Maunde C, Motomura H, Munroe T, Nair R, Obota C, Polidoro B, Russell B, Shaheen S, Sithole Y, Smith-Vaniz W, Uiblein F, Weerts S, Williams A, Yahya S and Carpenter K. 2021. The conservation status of marine biodiversity of the Western Indian Ocean. Gland, Switzerland: IUCN. vii + 32 pp.

Carr P. 2006. British Indian Ocean Territory. Pages 37 – 55 in: Sanders S.M (Ed.). Important Bird Areas in the United Kingdom Overseas Territories. Sandy, UK, RSPB.

Carr P, Votier SC, Koldewey HJ, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Cooney R and Dickson B. (Eds.). 2012. Biodiversity and the precautionary principle: risk, uncertainty and practice in conservation and sustainable use. Earthscan from Routledge, Oxon. UK.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A and Taylor P. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22: 1–34.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Donald PF, Fishpool LD, Ajagbe A, Bennun LA, Bunting G, Burfield IJ, Butchart SH, Capellan S, Crosby MJ, Dias MP and Diaz D. 2019. Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. Bird Conservation International 29(2): 177-198.

Eisenhauer A, Heiss GA, Sheppard CRC and Dullo WC. 1999. Reef and island formation and Late Holocene sea-level changes in the Chagos islands. Pages 21-31 in: Sheppard CRC and Seaward MRD (Eds.). Ecology of the Chagos Archipelago. The Linnean Society Occasional Publications, Westbury Academic and Scientific Publishing, Otley, UK.

Ferretti F, Curnick D, Liu K, Romanov EV and Block BA. 2018. Shark baselines and the conservation role of remote coral reef ecosystems. Science Advances 4(3): eaaq0333.

Fieberg J and Kochanny CO. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69: 1346--1359.

Fischer W and Bianchi G. (Eds.). 1984. FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). Prepared and printed with the support of the Danish International Development Agency (DANIDA). Rome, Italy: FAO. Vol. 1–6.

Gallagher AJ, Amon D, Bervoets T, Shipley ON, Hammerschlag N and Sims DW. 2020. The Caribbean needs big marine protected areas. Science 367(6479): 749.

Game ET, Grantham HS, Hobday AJ, Pressey RL, Lombard AT, Beckley LE, Gjerde K, Bustamante R, Possingham HP and Richardson AJ. 2009. Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecological Evolution 24: 360-369.

Gochfeld M, Burger J and Garcia EFJ. 2020. Lesser Noddy (Anous tenuirostris), version 1.0. In: del Hoyo J, Elliott A, Sargatal J, Christie DA and de Juana E (Eds.). Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Pilly SS, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MAC, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard CRC, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier SC, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H and Curnick DJ. 2020. A review of a decade of lessons from one of the world’s largest MPAs: conservation gains and key challenges. Marine Biology 167(11): 1-22.

Hyrenbach KD, Forney KA and Dayton PK. 2000. Marine protected areas and ocean basin management. Aquatic Conservation: Marine and Freshwater Ecosystems 10(6): 437-458.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org accessed on 04 May 2021.

Jaquemet S, Le Corre M and Weimerskirch H. 2004. Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). Marine Ecology Progress Series 268: 281-292.

Kerwath SE, Thorstad EB, Naesje TF, Cowley PD, Økland F, Wilke C and Attwood CG. 2009. Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon Marine Protected Area as a harvest refuge for a migratory fish species in South Africa. Conservation Biology 23(3): 653-661.

Koldewey HJ, Curnick D, Harding S, Harrison LR and Gollock M. 2010. Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. Marine Pollution Bulletin 60(11): 1906-1915.

Lascelles B. 2008. The BirdLife Seabird Foraging Database: guidelines and examples of its use. BirdLife International. Internal report.

Lascelles B. 2011. BirdLife special session on marine Important Bird Areas. WIOMSA 2011. 7th WIOMSA Scientific Symposium. Mombasa, Kenya. 24-29 October 2011. http://datazone.birdlife.org/userfiles/file/Marine/WesternIndianOceanMarineIBAWorkshopReport.pdf accessed 15 December 2020.

Lascelles BG, Taylor PR, Miller MGR, Dias MP, Oppel S, Torres L, Hedd A, Le Corre M, Phillips RA, Shaffer SA and Weimerskirch H. 2016. Applying global criteria to tracking data to define important areas for marine conservation. Diversity and Distributions 22(4): 422-431.

Le Corre M, Jaeger A, Pinet P, Kappes MA, Weimerskirch H, Catry T, Ramos JA, Russell JC, Shah N and Jaquemet S. 2012. Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. Biological Conservation 156: 83-93.

Lerma M, Dehnhard N, Luna-Jorquera G, Voigt CC and Garthe S. 2020. Breeding stage, not sex, affects foraging characteristics in masked boobies at Rapa Nui. Behavioral Ecology and Sociobiology 74(12): 1-16.

Longhurst AR and Pauly D. 1987. Ecology of tropical oceans. Academic Press. San Diego, USA.

Mulder CP, Anderson WB, Towns DR and Bellingham PJ. (Eds.). 2011. Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

Osborne OE, Hara PD, Whelan S, Zandbergen P, Hatch SA and Elliott KH. 2020. Breeding seabirds increase foraging range in response to an extreme marine heatwave. Marine Ecology Progress Series 646: 161-173.

Osieck ER. 2004. Towards the identification of marine IBAs in the EU: an exploration by the Birds and Habitat Directives Task Force. Cambridge, UK: BirdLife International (unpublished report).

Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10(1): 439-446.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Roberge JM and Angelstam PER. 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18(1): 76-85.

Ronconi RA, Lascelles BG, Langham GM, Reid JB and Oro D. 2012. The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. Biological Conservation 156: 1-4.

Sheppard CRC, Seaward MRD, Klaus R and Topp JMW. 1999. The Chagos Archipelago: an introduction. Pages 1 - 20 in: Sheppard CRC and Seaward MRD (Eds.). Ecology of the Chagos Archipelago. Linnean Society Occasional Publications 2, Westbury Publishing, Otley, UK.

Sheppard CR, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, Fitzsimmons N, Gaither MR, Gan CH, Gollock M, Guzman N, Graham NA, Harris A, Jones R, Keshavmurthy S, Koldewey H, Lundin CG, Mortimer JA, Obura D, Pfeiffer M, Price AR, Purkis S, Raines P, Readman JW, Riegl B, Rogers A, Schleyer M, Seaward MR, Sheppard AL, Tamelander J, Turner JR, Visram S, Vogler C, Vogt S, Wolschke H, Yang JM, Yang SY and Yesson C. 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. Aquatic Conservation 22(2): 232-261.

Soanes LM, Bright JA, Angel LP, Arnould JPY, Bolton M, Berlincourt M, Lascelles B, Owen E, Simon-Bouhet B and Green JA. 2016. Defining marine important bird areas: Testing the foraging radius approach. Biological Conservation 196: 69-79.

Surman CA, Nicholson LW and Ayling S. 2017. Foraging behaviour of the Lesser Noddy *Anous tenuirostris melanops* from the eastern Indian Ocean: insights from micro-geologging. Marine Ornithology 45: 123–128.

Toonen RJ, Wilhelm TA, Maxwell SM, Wagner D, Bowen BW, Sheppard CR, Taei SM, Teroroko T, Moffitt R, Gaymer CF and Morgan L. 2013. One size does not fit all: the emerging frontier in large-scale marine conservation. Marine Pollution Bulletin 77(1): 7-10.

SUPPLEMENTARY MATERIAL TO CHAPTER SIX

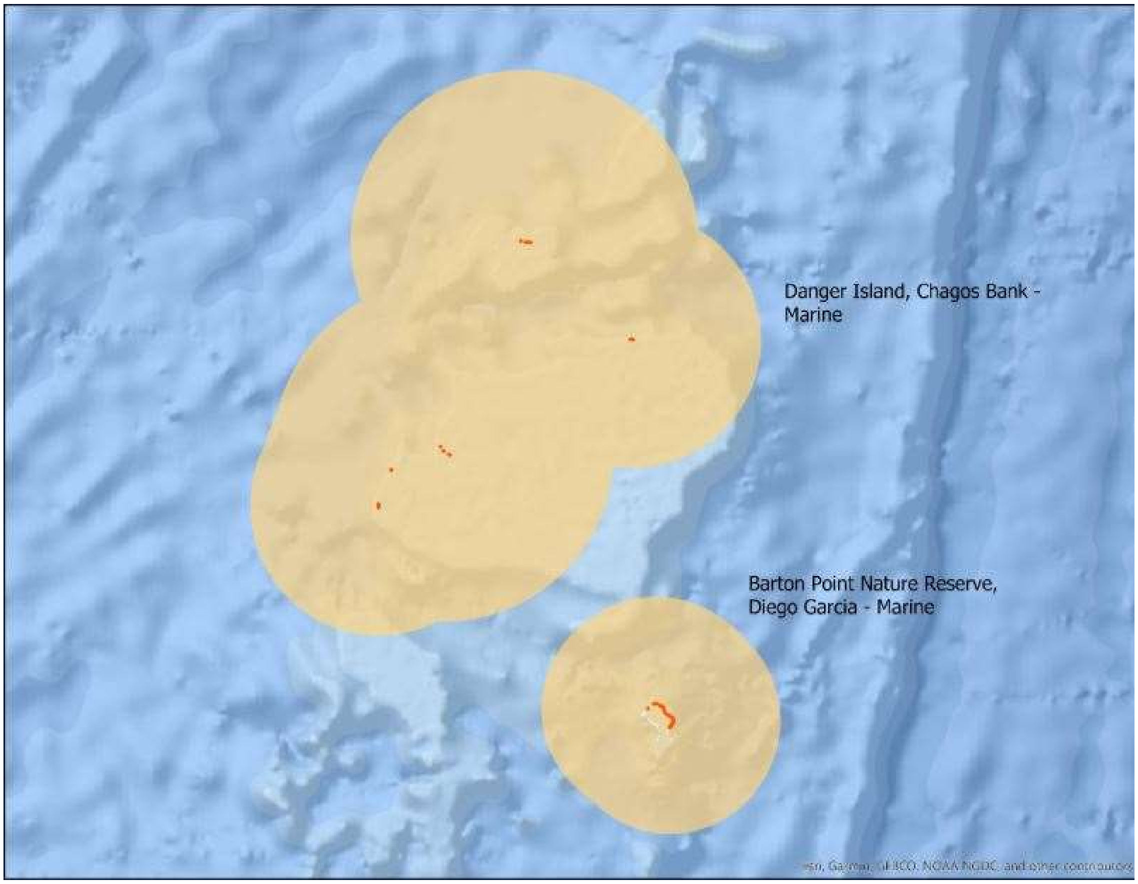


Figure S6. 1. Two BirdLife International proposed marine Important Bird and Biodiversity Areas (mIBAs) in the Chagos Archipelago. Downloaded from http://www.birdlife.org on 02 June 2021.

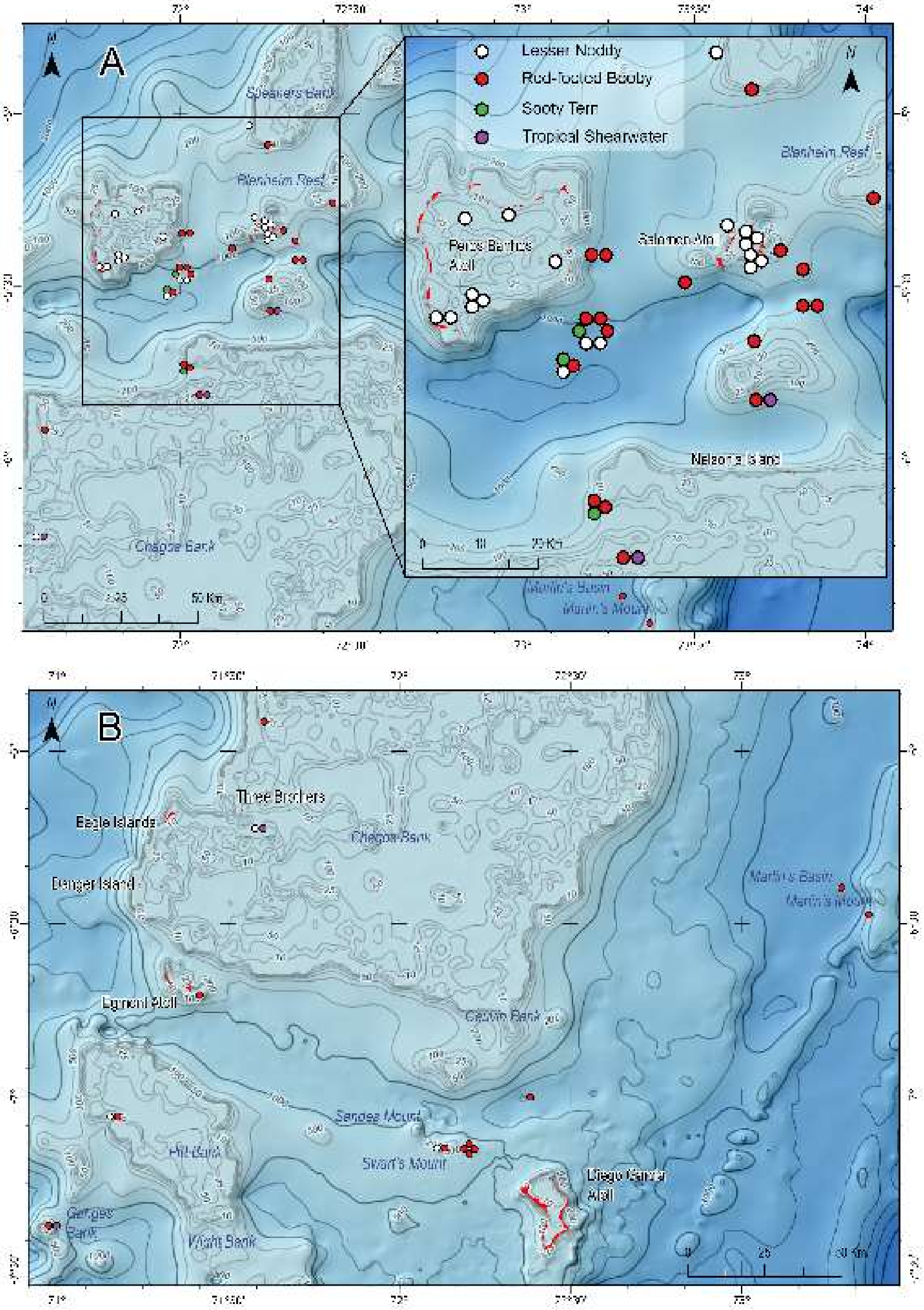


Figure S6. 2. A/B. Feeding aggregation locations in the northern (a) and southern (b) halves of the Chagos Archipelago of the four Important Bird and Biodiversity Area triggering species, recorded through 2012 – 2015.

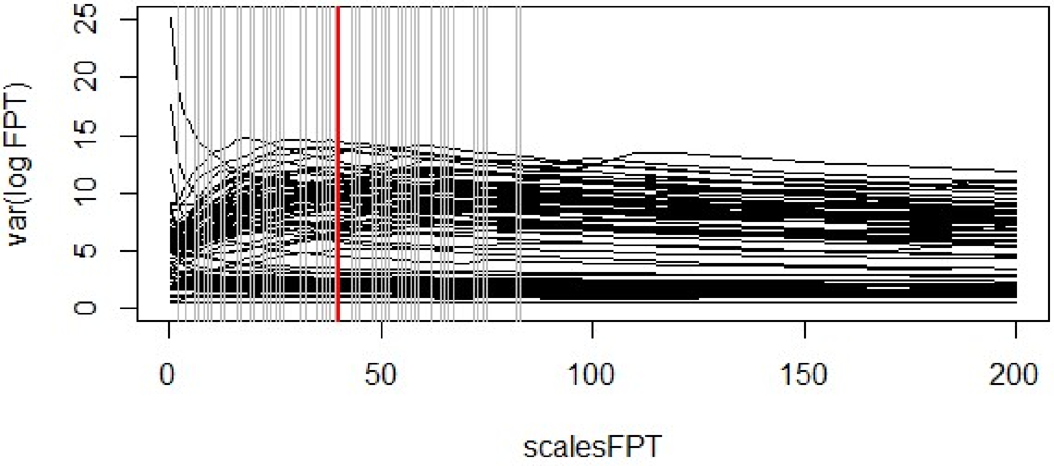


Figure S6. 3. An example of the calculation of the smoothing factor (*h*) for the Red-footed Booby colony on Diego Garcia (monsoon seasons combined), Chagos Archipelago, used to define Kernel Density Estimates (KDEs) following Lascelles et al. (2016), and derived from Area-Restricted Search (ARS) using First Passage Time (FPT). The calculation is from *hVals* function in the R package 'track2KBA' (Beal et al. 2020). The red line denotes where the ARS value lies.

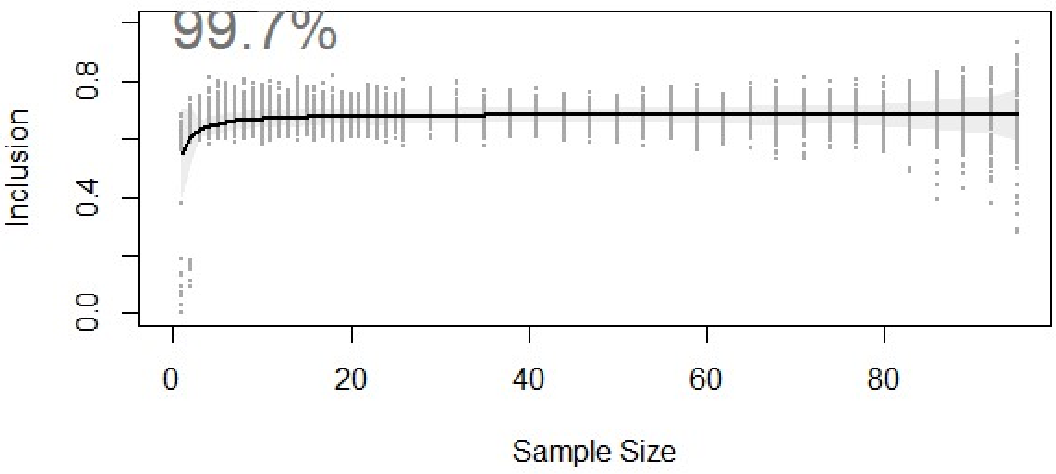


Figure S6. 4. An example of the calculation of the representativeness (99.7%) of the tracked sample of Red-footed Booby to the entire breeding population from the breeding colony on Diego Garcia (monsoon seasons combined), Chagos Archipelago after 100 iterations. The calculation is from the *repAssess* function in the R package 'track2KBA' (Beal et al. 2020).

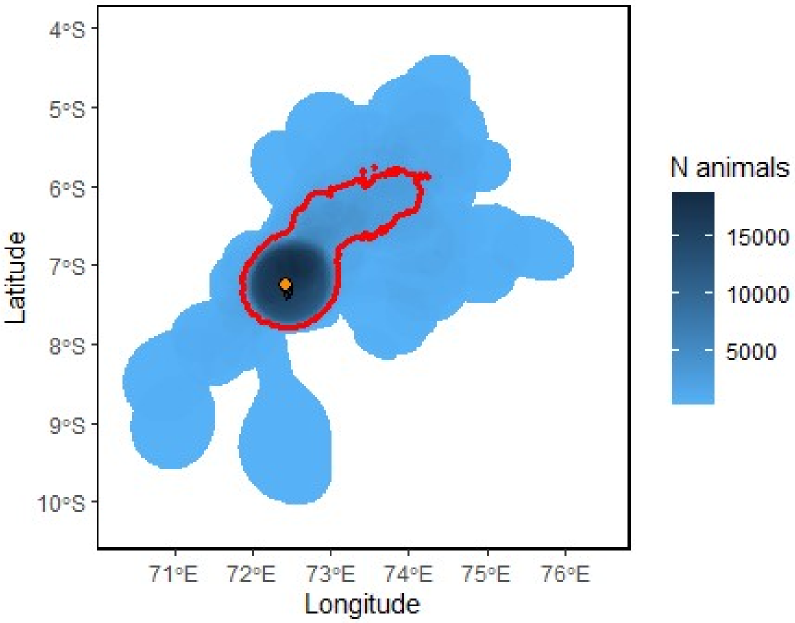


Figure S6. 5. The ‘core-use area’ of Red-footed Booby from the Diego Garcia colony (monsoon seasons combined) demonstrating the number of individuals estimated to be using the area. The area within the red boundary qualifies as an IBA at the global (A4) scale. Orange diamond denotes the colony location.

Table S6. 1. Western Indian Ocean regional breeding populations and 1% IBA qualifying populations and associated calculations. Mascarenes, Seychelles, South Mozambique, Somalia and Red Sea and North Mozambique regions follow Danckwerts et al. (2014).

Breeding colony area	Tropical Shearwater	Red-footed Booby	Sooty Tern	Lesser Noddy
Mascarenes	4,000[1]	0[5]	734,271[6]	106,250[6]
Seychelles	120,000[1]	70,437[6]	6,381,354[6]	883,333[6]
South Mozambique	Unknown[1]	6,250[6]	1,583,542[6]	0[7]
Somalia and Red Sea	Unknown[1]	0[5]	Unknown	0[7]
North Mozambique	Unknown[1]	0[5]	4,758,333[6]	0[7]
Chagos Archipelago	1,632[2]	22,871[2]	197,500[2]	50,780[2]
Maldives	Unknown[3]	0[5]	Unknown[3]	0[3]
Lakshadweep	0[4]	0[5]	4,750[4]	0[4]
Total breeding pairs	125,632	99,558	4,553,250	346,788
Total individuals	376,896	298,674	13,659,750	1,040,363
1% Regional breeding pairs	1,256	996	45,533	3,468
1% Regional individuals	3,769	2,987	136,598	10,403

Notes:

[1] Kirwan GM, del Hoyo J. and Collar N. 2020. Tropical Shearwater (*Puffinus bailloni*), version 1.0. In: Billerman SM, Keeney BK, Rodewald PG and Schulenberg TS. (Eds.). Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

[2] Carr P, Votier SC, Koldewey HJ, Godley B, Wood H and Nicoll MAC. 2021. Status and phenology of breeding seabirds and a review of Important Bird and

Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

3. Anderson RC and Shimal M. 2020. A checklist of birds of the Maldives. *Indian*BIRDS Monographs 3: 1–52.

4. Mondreti R, Priya D and Gremillet D. 2018. Illegal egg harvesting and population decline in a key pelagic seabird colony of the Eastern Indian Ocean. Marine Ornithology.

5. Nelson B. 1978. The Sulidae: gannets and boobies (No. 154). Oxford University Press, USA.

6. Danckwerts DK, McQuaid CD, Jaeger A, McGregor GK, Dwight R, Le Corre M and Jaquemet S. 2014. Biomass consumption by breeding seabirds in the western Indian Ocean: indirect interactions with fisheries and implications for management. ICES Journal of Marine Science 71(9): 2589-2598.

7. BirdLife International. 2021. Species factsheet: *Anous tenuirostris*. http://www.birdlife.org/ accessed on 12/05/2021.

Appendix S1

Danckwerts et al. (2014) regional totals included a single chick produced by every adult (breeding) pair corrected with a 50% breeding success correction factor. To be able to use the Danckwerts' figures, they needed to be converted back to breeding pairs (*B*), then to individuals (*I*). This was achieved using the equation:

$$B = D - \frac{D/3}{2},$$

$$I = B \times 3$$

Where *D* = the Danckwerts et al. (2014) total figure for the population of a colony/country. A factor of 3 was used to convert breeding pairs to individuals following advice from BirdLife International (Pearmain, pers. com.).

CHAPTER 7

GENERAL DISCUSSION

Recap

The aim of this thesis was to explore the benefits of a tropical, large-scale MPA (LSMPA, > 100,000 km^2) (Toonen et al. 2013) to breeding seabirds in order to determine the value of LSMPAs in protecting highly mobile species of seabirds (Chapter 1). The study site has been the CA that contains a 'no-take' LSMPA that offers a relatively undisturbed sanctuary for biodiversity (Chapter 2). By recording the breeding seabirds on all 55 islands of the archipelago over a decade, I produced a dataset from which it was possible to explore both the terrestrial and marine importance of the BIOT MPA for breeding seabirds.

Important Bird and Biodiversity Areas (IBAs) have a globally standardised method for assessing the importance of an area for birds. They are present in all LSMPAs across the planet. Using contemporary breeding seabird data, I reviewed the tIBAs of the CA (Chapter 3) and assessed the potential impact to breeding seabirds of ecologically restoring degraded islands in the MPA (Chapter 4). I researched whether morphometrics of a single species, RfB can be used to determine the sex of breeding pairs in the central Indian Ocean in the field, tested against molecular analysis (Chapter 5). The analytical chapters conclude by using a subset of the breeding seabird dataset (Tropical Shearwater *Puffinus bailloni*, RfB, Sooty Tern *Onychoprion fuscatus* and Lesser Noddy *Anous tenuirorostris*) to review two BirdLife International proposed seaward extension to breeding colony mIBAs and, for the first time in the CA, used tracking data to identify pelagic mIBAs. Having accurate, current knowledge of the status of t/mIBAs in the BIOT MPA, facilitates an assessment of the importance to breeding seabirds of the MPA. Adding this thesis' results to IBA data from the other (13) tropical LSMPAs offers a general examination of the benefits to breeding seabirds and, by proxy, biodiversity in LSMPAs throughout the tropical ocean.

Below, I draw together the key findings of this thesis, discuss the benefits of the BIOT MPA to breeding seabirds and follow with a broad assessment of how tropical LSMPAs benefit biodiversity. I discuss the potential applied implications of the thesis results, the thesis' limitations and, potential future research based upon the findings. I conclude by making recommendations to BirdLife International and the BIOTA arising from this thesis.

Key Findings

In Chapter 3, I presented the status and distribution of the breeding seabirds of the CA (Carr et al. 2021a). Using this dataset, I reviewed the tIBAs of the CA and concluded that 'clusters' of islands rather than single-island IBAs is a better representation of how the breeding seabirds use the area. This decision was driven by data from Sooty Tern that periodically desert individual breeding islands but, appear to remain faithful to clusters of islands. Desertion of breeding colonies by this species (due to tick infestations) has been recorded before in the western Indian Ocean (Converse et al. 1975, Feare 1976). However, this appears to be the first time that any tIBA designation has been made that takes into consideration the mobility of breeding colonies of a seabird. How mobile a Sooty Tern colony can be in the CA is dictated by the extent of ecological degradation of the surrounding islands – it normally requires open areas for breeding (Schreiber et al. 2021) and in the CA, rat-free islands.

In Chapter 4, I explored the potential benefits to breeding seabirds of vegetation management post rat-eradication on degraded islands. This identified the critical importance of conducting vegetation management post rat-eradication on islands dominated by abandoned coconut *Cocos nucifera* plantations. My research demonstrated that ecologically restoring 1 km^2 of native habitat by eradicating rats and converting abandoned plantations to savannah and native forest could potentially support ~ 320,000 breeding pairs of 16 species of tropical seabird - more than double the number of breeding seabirds in the entire CA. Without vegetation management, the same island would support ~

4,000 breeding pairs post rat-eradication. With seabird populations in decline globally (Croxall et al. 2012) and threats to seabirds remaining dire (Dias et al. 2019), the potential of substantially increasing the protected central Indian Ocean breeding populations to become a source of recruits for the tropical ocean, is appealing. These potential gains will not happen following rat-eradication as a single intervention on islands dominated by abandoned coconut plantations and restoration practitioners of such islands should heed this lesson (Carr et al. 2021b).

In the final analytical chapter, using the breeding seabird dataset I reviewed the two BirdLife International proposed seaward extension to breeding colony mIBAs and, explored for pelagic mIBAs using tracking data of breeding RfB. The key finding of this chapter's research was the interlinking of all mIBA boundaries that produced a proposed 'super' mIBA – that, crucially, lay completely within the MPA boundary. If designated, this mIBA would be the fourth largest in the Indian Ocean and 11th largest in the world (http://datazone.birdlife.org/site/results accessed 10 June 2021).

What are the Benefits of the BIOT MPA to Breeding Seabirds Based Upon These Findings?

Based upon this thesis, the CA, as a LSMPA that has designated all tIBAs as Strict Nature Reserves with severely restricted access (https://biot.gov.io/environment/terrestrial-protected-areas/ accessed 16 June 2021), offers full protection on land to > 90% of its 281,596 breeding pairs of tropical seabird (Carr et al. 2021a). As a no-take MPA, at sea it offers protection to the core foraging areas (mIBAs) of a vagile, top predator from bycatch - the greatest at sea threat to seabirds (Anderson et al. 2011, Dias et al. 2019). However, for the majority of tropical seabirds, bycatch is not a major threat due to the 'near-obligate association' with subsurface predators (Au and Pitman 1986). Unlike temperate and polar seabird populations, tropical seabirds cannot dive deep to catch prey and instead rely on subsurface predators such as tuna (Scombridae) to drive prey to the surface where they are caught. This means that in the case of tropical seabirds, removing subsurface top predators is a greater threat to survival than bycatch (Hays et al. 2020). Therefore an MPA that enforces a ‘no-take’ policy provides the greatest protection to tropical seabirds. For four species, Tropical Shearwater, RfB, Sooty Tern and Lesser Noddy, the breeding populations of the BIOT MPA are of global significance (Carr et al. 2021a – chapter 3).

Yet, the MPA could be vastly improved for seabirds and by proxy, biodiversity. In the MPA, there is 12 times more degraded terrestrial habitat unsuitable for most breeding seabirds than currently available. Restoring 1 km^2 of this degraded habitat could potentially more than double the number of breeding pairs of seabirds in the entire archipelago (Carr et al. 2021b).. Yet, seabird driven ecosystems (seabird islands – Mulder et al. 2011) have been proven to benefit associated marine ecosystems through nutrient transfer (Graham et al. 2018, Benkwitt et al. 2021). The ecological restoration of this degraded land could, theoretically, increase biodiversity at an ocean-basin scale due to the “biodiversity corridor / stepping-stone” role the BIOT MPA provides between the east and western Indian Ocean (Sheppard et al. 2013). With the ocean’s health (McCauley et al. 2015) and seabirds populations in decline (Croxall et al. 2021), BIOT MPA authorities could make a massive contribution to restoring declining biodiversity.

How Does This Contribute to the LSMPA Merits Debate?

O’Leary et al. (2018) addressed three themes of criticism of LSMPAs, placement, governance and management; political expediency and; social-ecological value and cost. One theme remains unresolved, that of size. Evidence presented for LSMPAs suggest they offer greater protection to oceanic migrants and highly mobile species (Lester et al. 2009, Fox et al. 2012, Hays et al. 2020), and that small, strategically placed no-take MPAs can be effective in protecting mobile species, for at least part of their annual cycle (Kerwath et al. 2009). Alternatively, there is an argument for not having no-take MPAs and use improved fisheries management to protect declining ocean biodiversity (Hilborn et al. 2004, Jones 2007). My research supports the premise that LSMPAs offer protection to highly mobile species, especially when they are under a no-take designation. The BIOT MPA offers undisturbed breeding grounds to seabirds and, as proven by tracking data, when in the early stages of breeding, RfB feed almost exclusively within the MPA boundary. As the MPA is ‘no-take’, for RfB and other near-obligate associate seabirds witnessed at multi-species feeding aggregations, the threat from fisheries operations, e.g. bycatch (Dias et al. 2019), should be negated.

How Do Tropical LSMPAs Benefit Breeding Seabirds and Biodiversity Globally?

Including the recently reviewed CA IBAs, there are 49 tIBAs and 13 mIBAs within the 14 tropical LSMPAs that have a breeding seabird as the triggering species (Tables S1.1. and S1.2.). These 62 IBAs host in the region of 15 million breeding adult seabirds (http://datazone.birdlife.org/home accessed July 2021). There are a minimum of 42 seabird species (≈ 13% of all seabird species) breeding in the 14 tropical LSMPAs designated to date. Of these, virtually the entire global population of seven species nests entirely within them of which one is IUCN Red-Listed as Critically Endangered, three as Endangered, two as Vulnerable and three as Near Threatened (Table S1.1. and S1.2.). The total area covered by the 14 tropical LSMPAs is 6,537,788 km^2, of which ≈ 88% is no-take, fully protected ocean (Table 1.1.). Clearly, the 14 tropical LSMPAs are beneficial to breeding seabirds, especially the 88% no take LSMPAs that offer protection *per mare, per terram*.

Top predators are strong candidates to be umbrella species (Ozaki et al. 2006). Here, an umbrella species is defined as a species whose conservation confers protection to a large number of naturally co-occurring species (Roberge and Angelstam 2003). Thus, protecting an umbrella species should theoretically protect an entire suite of sympatric species with similar habitat requirements (Simberloff 1999). Many tropical seabirds are near-obligate associates of subsurface predators, particularly tuna and dolphin (Au and Pitman 1986). In the no-take LSMPAs and those that protect the feeding grounds of near-obligate associate seabirds, not only are sympatric seabirds being protected but, another suite of highly mobile predators in a different (underwater) dimension are also receiving protection.

In addition to ‘umbrella conservation’ benefitting biodiversity in LSMPAs, there is a growing body of evidence (much emanating from the BIOT MPA) that seabird islands (Mulder et al. 2011) offer cross-ecosystem benefits (Graham et al. 2018, Benkwitt et al. 2019, 2021a/b). Seabirds foraging often hundreds of kilometres from breeding islands in the pelagic realm bring back nutrients via captured prey to breeding and roosting islands. A portion of these nutrients is deposited on the island, often via guano but other transfer routes are possible e.g., dropped regurgitate. The deposited nutrients ‘run-off’ islands and enter nearshore ecosystems where they enrich the environment. This enrichment has been proven to enhance coral reef productivity and functioning (Graham et al. 2018), alter patterns of algal abundance and fish biomass on coral reefs (Benkwitt et al 2019) and alter demographic rates in coral-reef fish (Benkwitt et al. 2021a). Critically, these cross-ecosystem benefits are weakened on islands that have invasive predators (Graham et al. 2018, Benkwitt et al. 2021b). With seabirds populations declining at perilous rates globally (Croxall et al. 2012) and threats remaining dire both on land and at sea (Dias et al. 2019), LSMPAs that protect seabird populations at breeding colonies and on their feeding grounds offer an avenue of hope, especially in LSMPAs that are eradicating invasive predators and rehabilitating degraded breeding habitat.

Potential Applied Implications

Through this thesis, the CA has received an updated assessment of its terrestrial importance to breeding seabirds via the IBA programme. This has laid a foundation stone and is not an end point. IBA monitoring into the future is needed to assess the effectiveness of conservation measures (BirdLife International 2006). Specific to the CA, the health of the IBAs can be used as a measure of the success of the MPA (Lascelles et al. 2016). Further, seabirds offer unique insights into ecosystem status and change (Piatt et al. 2007). By monitoring the breeding seabird colonies in tIBAs over time using the data in this thesis as the baseline, the health of the BIOT MPA and surrounding ocean will be under constant surveillance.

This thesis has clearly demonstrated the benefits to breeding seabirds of ecological restoration of degraded tropical islands and, through the IBA programme has identified the terrestrial areas of importance to breeding seabirds. By ‘clustering’ islands in the tIBA designations (Carr et al. 2021a), islands of low ecological importance (i.e., rat-infested and dominated by abandoned coconut plantations) lie inside the tIBA boundaries, e.g., degraded Eagle Island lays inside the Western Great Chagos Bank island group tIBA. Removing invasive predators aids the recovery of seabird populations (Hilton and Cuthbert 2010, Bedolla-Guzmán et al. 2019, Holmes et al. 2019), with rat eradication a priority not only for seabirds, but also for surrounding reef ecosystems (Graham et al. 2018, Savage 2019, Benkwitt et al. 2021). For conservation practitioners, including ecologically impoverished islands into a discrete cluster of IBA islands gives a focus to environmental rehabilitation projects. In the CA, ecological restoration of degraded islands offers the only hope for the recovery of the historically pauperised seabird populations (Bourne GC 1886, Bourne WRP 1971).

Protecting the ocean is a fundamental tenet of a no-take MPA (Wenzel et al. 2016). Despite the declaration of the BIOT no-take MPA in 2010, illegal, unregulated and unreported (IUU) fishing still occurs (Ferretti et al. 2018). Authorities of the BIOT MPA now have scientifically credible evidence of a marine biodiversity hotspot within the MPA, the 62,379 km^2 CA mIBA. This area should be a focus for enforcement against IUU, safeguarding seabirds against fishery operations and by proxy, protecting a suite of associated biodiversity.

Limitations

The CA is about as remote as possible in the Indian Ocean (Carr et al. 2013). It is difficult to access, expensive to operate in, seabird fieldwork at breeding colonies has to be expeditionary and it is logistically challenging due to a lack of commercial facilities. These factors dictate that time in the field to collect data will always be limited.

The CA breeding seabird dataset gathered over a decade (Carr et al. 2021a) underpins three of the four analytical chapters and is used to delineate both terrestrial (Carr et al. 2021a) and marine IBAs (Ch.6). Ideally, this dataset would have been collected from long-term monitoring, through censuses of every island conducted twice in a single year to catch periodic, episodic and asynchronous breeding species (Carr et al. 2021a), at a minimum of every four years to satisfy IBA monitoring guidelines and IUCN Red List review periodicity (BirdLife International 2006). Using a precautionary approach to conservation (Cooney and Dickson 2012), the CA breeding seabird populations are given as the maximum recorded in a single year over the decade-long recording period (Carr et al. 2021a). Had there been a systematic, funded seabird monitoring programme in place, more detailed analysis of population dynamics and trends could have been included as part of the status and distribution analysis. This is a serious limitation as the population trends since the northern atolls became uninhabited in the 20th Century for nearly all species are unknown, and this is after the catastrophic declines following man's colonisation in the late 18th Century (Bourne GC 1886, Bourne WRP 1971). Whilst population estimates are now published (Carr et al. 2021a), without systematic, funded population monitoring into the future, seabird population trends will remain uncertain at best, the health of IBAs unknown and the efficacy of the BIOT MPA unresolved.

The identification of marine biodiversity hotspots (mIBAs) in the BIOT MPA based upon tracking data is a valuable conservation asset and management tool, especially if these areas have their protection enforced to prevent IUU fishing. However, the delineation of pelagic mIBAs in the MPA are based upon a single seabird species. Marine biodiversity hotspots and mIBAs are better delineated using a suite of species, as opposed to one (BirdLife International 2010, Lascelles et al. 2016). Other marine biodiversity hotspots may exist that warrant recognition and enhanced protection and at present, these remain unknown.

Future Research Direction

The global significance of the BIOT MPA to breeding seabirds is now understood. However, due to the recent addition of B (regional) IBA qualifying criteria (http://datazone.birdlife.org/site/ibacritreg accessed 14 June 2021), there needs to be a further review of tIBAs. As part of this thesis, western Indian Ocean regional IBA thresholds for four species of seabird were calculated (Ch. 6). Future research should calculate regional IBA thresholds for the remaining seabird species in order for the CA IBAs (and other western Indian Ocean IBAs) to be assessed for their regional significance. Married to this regional research should be a systematic, funded, long-term breeding seabird monitoring programme.

The use of tracking data to identify pelagic mIBAs for the first time in the CA was a ground-breaking step in the central Indian Ocean. Yet, it was only a first step. One assumption made in this thesis via tracking data was that RfB is an adequate umbrella species. It is argued that there is little evidence that single species umbrellas selected only on the basis of their large area requirements are useful and that multi-species umbrellas offer promising conservation avenues (Roberge and Angelstam 2003). The pelagic mIBAs identified in the CA for RfB are scientifically delineated core feeding areas of a near-obligate associate, not simply areas of occurrence (Ch. 6). Therefore, these areas should ‘umbrella’ sympatric species core-feeding areas, especially other near-obligate associates of sub-surface predators. However, further tracking of breeding seabirds is required in the CA, especially the IBA qualifying pelagic species of Sooty Tern and Tropical Shearwater. This would produce comparative results from which to assess RfB as a single umbrella species and, would assist in informing the single versus multi-umbrella species debate. In addition to the umbrella species debate, this would also inform if there are other pelagic areas of IBA quality within and/or out-with the BIOT MPA and would inform the ‘size of MPA’ debate (Toonen et al. 2013).

Further tracking is required of RfB on Nelson’s and Danger Island to gather data from the monsoon season not tracked to date for comparison with the results from the Diego Garcia colony. The Diego Garcia colony showed very strong overlap in seasonal foraging areas (Ch. 6), it would be of conservation interest to know if this seasonal overlap of foraging areas is consistent throughout the CA RfB colonies.

Within the CA, tracking data of other highly mobile, top predators other than seabirds is available (sea turtles – Hays et al. 2014, sharks – Curnick et al. 2020, mantas – Andrzejaczek et al. 2020). Marine scientists and conservationists operating in the CA have the opportunity to produce a crosstaxon publication demonstrating the benefits of LSMPAs to more than avifauna. Layering of tracks from differing taxon could demonstrate what key species, populations or life history stages are actually protected by a LSMPA of a politically determined size and shape, and at what times. This could highlight what, where and even how in the BIOT MPA additional conservation measures are required to protect, conserve and rehabilitate species.

The environmental benefits of rehabilitating ecologically degraded islands through eradicating invasive predators is well researched (Mulder et al. 2011). The benefits of eradicating invasive predators from degraded tropical seabird islands coupled with seabird breeding habitat management is a science in it’s infancy. This thesis has empirically demonstrated the potential benefits to breeding seabird populations of this dual intervention strategy (Carr et al. 2021b). Scientists and restoration practitioners in the CA have the opportunity (if funded) of testing the benefits of predator eradication coupled with habitat management. Results from such an experiment could impact and influence ecological restoration planning and funding throughout the Tropics.

Conclusion

This thesis, using the IBA programme has demonstrated that the CA has provided an undisturbed sanctuary for breeding seabirds, especially on islands with native habitat and no introduced predators and, at sea, the no-take LSMPA has proven large enough to protect the entire foraging areas of a top predator, at least through the incubation and chick-rearing phase of breeding (Chs. 3 and 6). However, it is a sanctuary that has been transformed by man through the clearance of native habitats and the introduction of invasive species that have historically decimated seabird populations and continue to limit species recovery. I have shown that ecological restoration of degraded islands, involving eradicating introduced rats and managing vegetation, could potentially produce a huge increase in breeding seabird numbers (Ch. 5).

Linking this BIOT MPA research to LSMPAs globally, by demonstrating that the core feeding areas of a vagile, highly mobile top predator that forages over impoverished ocean are all within the boundary of the LSMPA brings hope.

Knowing that the predator is a near-obligate associate of subsurface predators and a strong contender as an umbrella species, increases hope exponentially. Accepting that there will be differences in foraging strategies intra and interspecies throughout the tropical LSMPAs and this thesis only relates to breeding birds, does not detract from the benefits bestowed by tropical LSMPAs globally; housing 15 million + breeding birds of some 13% of all seabird species of which nine are listed as threatened to a degree is benefit alone. The knowledge that the BIOT MPA is large enough to encompass the feeding grounds of its most mobile Sulid is a strong indicator that all tropical LSMPAs will offer similar benefits. These benefits will be only be reaped in LSMPAs when the seabird species within them are fully protected *per mare, per terram*.

MANAGEMENT RECOMMENDATIONS

As a result of this thesis, the following management recommendations are made:

- BIOTA: Implement and fund a long term monitoring programme of the breeding seabirds of the BIOT MPA.
- BIOTA: Commence ecological restoration of the degraded islands of the BIOT MPA, focusing on those contained within the tIBAs.
- BirdLife International: That the CA mIBA be formally designated.

REFERENCES

Anderson OR, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O and Black A. 2011. Global seabird bycatch in longline fisheries. Endangered Species Research 14(2): 91-106.

Andrzejaczek S, Chapple TK, Curnick DJ, Carlisle AB, Castleton M, Jacoby DM, Peel LR, Schallert RJ, Tickler DM and Block BA. 2020. Individual variation in residency and regional movements of reef manta rays Mobula alfredi in a large marine protected area. Marine Ecology Progress Series 639: 137-153.

Au DW and Pitman RL. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. The Condor 88(3): 304-317.

Bedolla-Guzmán Y, Méndez-Sánchez F, Aguirre-Muñoz A, Félix-Lizárraga M, Fabila-Blanco A, Bravo-Hernández E, Hernández-Ríos A, Corrales-Sauceda M, Aguilar-Vargas A, Aztorga-Ornelas A, Solís-Carlos F, Torres-García F, Luna-Mendoza L, Ortiz-Alcaraz A, Hernández-Montoya J, Latofski-Robles M, Rojas-Mayoral E and Cárdenas-Tapia A. 2019. Recovery and current status of seabirds on the Baja California Pacific Islands, Mexico, following restoration actions. Pages 531-538 in: CR Veitch, MN Clout, AR Martin, JC Russell and CJ West. (Eds.). Proceedings of the Island Invasives 2017 Conference. Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

Benkwitt CE, Wilson SK and Graham NA. 2019. Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Global Change Biology 25(8): 2619-2632.

Benkwitt CE, Taylor BM, Meekan MG and Graham NA. 2021a. Natural nutrient subsidies alter demographic rates in a functionally important coral-reef fish. Scientific Reports 11(1): 1-13.

Benkwitt CE, Gunn RL, Le Corre M, Carr P and Graham NA. 2021b. Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. Current Biology, in press.

BirdLife International. 2006. Monitoring Important Bird Areas: a global framework. Cambridge, UK. BirdLife International. Version 1.2.

BirdLife International. 2010. Marine Important Bird Areas toolkit: standardised techniques for identifying priority sites for the conservation of seabirds at sea. BirdLife International, Cambridge UK. Version 1.2: February 2011.

Bourne GC. 1886. General Observations on the fauna of Diego Garcia. Proceedings of the Zoological Society of London 1886: 331-334.

Bourne WRP. 1971. The Birds of the Chagos Group, Indian Ocean. Atoll Research Bulletin 149: 175-207.

Carr P, Hillman JC, Seaward MR, Vogt S and Sheppard CR. 2013. Coral Islands of the British Indian Ocean Territory (Chagos Archipelago). Pages 271-282 in: Sheppard CRC. (Ed.). Coral Reefs of the United Kingdom Overseas Territories. Springer, Dordrecht.

Carr P, Votier S, Koldewey HJ, Godley B, Wood H and Nicoll MAC. 2021a. Status and phenology of breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory. Bird Conservation International 31(1): 14-34.

Carr P, Trevail A, Bárrios S, Clubbe C, Freeman R, Koldewey HJ, Votier SC, Wilkinson T and Nicoll MAC. 2021b. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. Restoration Ecology p.e13386.

Converse JD, Hoogstraal H, Moussa MI, Feare CJ and Kaiser MN. 1975. Soldado virus (Hughes group) from *Ornithodoros* (*Alectorobius*) *capensis* (Ixodoidea: Argasidae) infesting sooty tern colonies in the Seychelles, Indian Ocean. The American Journal of Tropical Medicine and Hygiene 24(6): 1010-1018.

Cooney R. and Dickson B. (Eds.). 2012. Biodiversity and the precautionary principle: risk, uncertainty and practice in conservation and sustainable use. Earthscan from Routledge, Oxon. UK.

Croxall JP, Butchart SH, Lascelles BEN, Stattersfield AJ, Sullivan BEN, Symes A and Taylor PHIL. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22(1): 1-34.

Curnick DJ, Andrzejaczek S, Jacoby DM, Coffey DM, Carlisle AB, Chapple TK, Ferretti F, Schallert RJ, White T, Block BA and Koldewey HJ, 2020. Behavior and ecology of silky sharks around the Chagos Archipelago and evidence of Indian Ocean wide movement. Frontiers in Marine Science 7: 1045.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG and Croxall JP. 2019. Threats to seabirds: a global assessment. Biological Conservation 237: 525-537.

Feare CJ. 1976. Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus-infected ticks. Ibis 118(1): 112-115.

Ferretti F, Curnick D, Liu K, Romanov EV and Block BA. 2018. Shark baselines and the conservation role of remote coral reef ecosystems. Science Advances 4(3): eaaq0333.

Fox HE, Mascia MB, Basurto X, Costa A, Glew L, Heinemann D, Karrer LB, Lester SE, Lombana AV, Pomeroy RS and Recchia CA. 2012. Re-examining the science of marine protected areas: linking knowledge to action. Conservation Letters 5(1): 1-10.

Graham NA, Wilson SK, Carr P, Hoey AS, Jennings S and MacNeil MA. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559(7713): 250-253.

Hays GC, Mortimer JA, Ierodiaconou D and Esteban N. 2014. Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. Conservation Biology 28(6): 1636-1644.

Hays GC, Koldewey HJ, Andrzejaczek S, Attrill MJ, Barley S, Bayley DTI, Benkwitt CE, Block B, Schallert RJ, Carlisle AB, Carr P, Chapple TK, Collins C, Diaz C, Dunn N, Dunbar RB, Eager DS, Engel J, Embling CB, Esteban N, Ferretti F, Foster NL, Freeman R, Gollock M, Graham NAJ, Harris JL, Head CEI, Hosegood P, Howell KL, Hussey NE, Jacoby DMP, Jones R, Pilly SS, Lange ID, Letessier TB, Levy E, Lindhart M, McDevitt-Irwin JM, Meekan M, Meeuwig JJ, Micheli F, Mogg AOM, Mortimer JA, Mucciarone DA, Nicoll MAC, Nuno A, Perry CT, Preston SG, Rattray AJ, Robinson E, Roche RC, Schiele M, Sheehan EV, Sheppard A, Sheppard CRC, Smith AL, Soule B, Spalding M, Stevens GMW, Steyaert M, Stiffel S, Taylor BM, Tickler D, Trevail AM, Trueba P, Turner J, Votier SC, Wilson B, Williams GJ, Williamson BJ, Williamson MJ, Wood H and Curnick DJ. 2020. A review of a decade of lessons from one of the world’s largest MPAs: conservation gains and key challenges. Marine Biology 167(11): 1-22.

Hilton GM and Cuthbert RJ. 2010. The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. Ibis 152: 443-458.

Hilborn R, Stokes K, Maguire JJ, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J and Cochrane KL. 2004. When can marine reserves improve fisheries management? Ocean & Coastal Management 47(3-4): 197-205.

Holmes N, Spatz DR, Oppel S, Tershy B, Croll DA, Keitt B, Genovesi P, Burfield IJ, Will DJ, Bond AL, Wegmann A, Aguirre-Muñoz A, Raine AF, Knapp CR, Hung C-H, Wingate D, Hagen E, Méndez-Sánchez F, Rocamora G, Yuan H-W, Fric J, Millett J, Russell J, Liske-Clark J, Vidal E, Jourdan H, Campbell K, Springer K, Swinnerton K, Gibbons-Decherong L, Langrand O, Brooke, MdL, McMinn M, Bunbury N, Oliveira N, Sposimo P, Geraldes P, McClelland P, Hodum P, Ryan PG, Borroto-Páez R, Pierce R, Griffiths R, Fisher RN, Wanless R, Pasachnik SA, Cranwell S, Micol T and Butchart SHM. 2019. Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. PLoS ONE 14: e0212128.

Jones PJ. 2007. Point-of-view: arguments for conventional fisheries management and against no-take marine protected areas: only half of the story? Reviews in Fish Biology and Fisheries 17(1): 31-43.

Kerwath SE, Thorstad EB, Naesje TF, Cowley PD, Økland F, Wilke C and Attwood CG. 2009. Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon Marine Protected Area as a harvest refuge for a migratory fish species in South Africa. Conservation Biology 23(3): 653-661.

Lascelles BG, Taylor PR, Miller MGR, Dias MP, Oppel S, Torres L, Hedd A, Le Corre M, Phillips RA, Shaffer SA and Weimerskirch H. 2016. Applying global criteria to tracking data to define important areas for marine conservation. Diversity and Distributions 22(4): 422-431.

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S and Warner RR. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384: 33-46.

McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH and Warner RR. 2015. Marine defaunation: Animal loss in the global ocean. Science 347(6219).

Mulder CPH, Anderson WB, Towns DR and Bellingham PJ. (Eds.). 2011. Seabird islands: ecology, invasion, and restoration. Oxford University Press, Oxford, UK.

O'Leary BC, Ban NC, Fernandez M, Friedlander AM, García-Borboroglu P, Golbuu Y, Guidetti P, Harris JM, Hawkins JP, Langlois T and McCauley DJ. 2018. Addressing criticisms of large-scale marine protected areas. Bioscience 68(5): 359-370.

Ozaki K, Isono M, Kawahara T, Iida S, Kudo T and Fukuyama K. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conservation Biology 20(5): 1507-1515.

Piatt JF, Sydeman WJ and Browman HI. 2007. Seabirds as indicators of marine ecosystems. Marine Ecology Progress Series 352: 199-204.

Roberge J-M and Angelstam P. 2003. Usefulness of the Umbrella Species Concept as a Conservation Tool. Conservation Biology 18(1): 76-85.

Savage C. 2019. Seabird nutrients are assimilated by corals and enhance coral growth rates. Scientific Reports 9(1): 1-10.

Schreiber EA, Feare CJ, Harrington BA, Murray Jr BG, Robertson Jr WB, Robertson MJ and Woolfenden GE. 2020. Sooty Tern (Onychoprion fuscatus), version 1.0. In, Billerman SM. (Ed.). Birds of the World Cornell Lab of Ornithology, Ithaca, NY, USA.

Sheppard CR, Bowen BW, Chen AC, Craig MT, Eble J, Fitzsimmons N, Gan CH, Gaither MR, Gollock M, Keshavmurthy S and Koldewey H. 2013. British Indian Ocean Territory (the Chagos Archipelago): setting, connections and the marine protected area. Pages 223-240 in, Sheppard CR. (Ed.). Coral reefs of the United Kingdom Overseas Territories. Springer, Dordrecht.

Simberloff D. 1999. The role of science in the preservation of forest biodiversity. Forest Ecology and Management 115(2-3): 101-111.

Toonen RJ, Wilhelm TA, Maxwell SM, Wagner D, Bowen BW, Sheppard CR, Taei SM, Teroroko T, Moffitt R, Gaymer CF and Morgan L. 2013. One size does not fit all: the emerging frontier in large-scale marine conservation. Marine Pollution Bulletin 77(1-2): 7-10.

Wenzel L, Laffoley D, Caillaud A and Zuccarino-Crowe C. 2016. Protecting the World's Ocean - The Promise of Sydney. Aquatic Conservation: Marine and Freshwater Ecosystems 26(Suppl. 2): 251–255.