



Migratory movements, distribution, habitat preference, and activity patterns of the endangered Abbott's booby *Papasula abbotti*

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ABSTRACT: The Abbott's booby *Papasula abbotti* is one of the most threatened seabirds in the world. The non-breeding behaviour and distribution of Abbott's boobies are largely unknown but evidence suggests they migrate between breeding attempts. This lack of information impedes the identification and quantification of the threats the birds are exposed to outside of their breeding season. We studied the migratory movements of Abbott's booby using geolocator–immersion loggers. A total of 22 adult birds were tracked between 2007 and 2014. Analysis of the 27 migratory trips revealed that birds migrated on average 2500 km east of Christmas Island to an area centred around the Banda Sea, Indonesia. The timing of Abbott's booby migration (from November–December to April) coincides with the Indonesian–Australian monsoon, a period characterised by reversing prevailing winds and decreased regional oceanic primary productivity. The birds' movements matched the pattern of reversal of the prevailing winds. No birds were recorded on migration between 17 May and 26 October, which suggests that the whole population of adult Abbott's boobies is on Christmas Island during that period. Migrating Abbott's boobies spent little time on the water during the day or at night (15%), and individuals preferred waters with a narrow range of sea surface salinity (32.5–34.5 PSU), rugged seafloor topography, and sea surface temperatures above ca. 28°C. Overall, these novel results identify the area within which potential threats, such as interactions with fisheries or effects of climate change on the species' marine habitats, should be investigated.

KEY WORDS: Migration · *Papasula abbotti* · Abbott's booby · Conservation · GLS · Bio-logging

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1. INTRODUCTION

Migration is a key movement behaviour for many species (Milner-Gulland et al. 2011). Individuals undertake seasonal round trips to find or follow food or water, as a response to environmental conditions, or to reproduce; for example, to encounter mating partners at a specific time and location (Shaw 2016). These movements are often crucial for individual survival (e.g. White et al. 2014, Alerstam & Backman 2018) or successful reproduction (e.g. Singh & Ericsson 2014, Fayet et al. 2017) and can affect species population dynamics.

Seabirds are one taxon that displays impressive migrations (Spear 2018). For many seabird species, migration during the non-breeding period is an essential part of their life cycle. Breeding imposes constraints on the foraging range, and seabird breeding colonies are often spatially restricted by the availability of terrestrial sites where the birds can successfully reproduce, which can lead to high levels of inter- and/or intraspecific competition for food (e.g. Pettex et al. 2019, Lee et al. 2021). Prey availability may also vary seasonally around breeding sites (e.g. McKnight et al. 2013, Takahashi et al. 2015), and seasonal variation of air and sea surface temperatures (SSTs) can

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affect costs of thermoregulation (Cook et al. 2020, Choy et al. 2021, Grunst et al. 2023). Additionally, at high latitudes, the seasonal decrease in daylength reduces the time available for diurnal foragers to feed (Hromádková et al. 2020). Outside the breeding season, birds can migrate and hence escape these pressures. Therefore, migration can be crucial for the birds' survival or successful reproduction; for example, to start their next breeding attempt in ideal body condition (Crossin et al. 2013, Jones & Ryan 2013).

Seabirds are, however, also one of the most threatened groups of birds (Croxall et al. 2012, Dias et al. 2019). At sea, they are predominantly threatened by fisheries bycatch and reduction in food availability due to overfishing or climate change and extreme weather conditions (Dias et al. 2019). During migration, these threats can increase mortality (e.g. Ramos et al. 2012, Felis et al. 2019) or have carryover effects on reproduction (e.g. Rolland et al. 2008, Desprez et al. 2018). Variation in migration paths among sexes, age groups, or failed and successful breeders may lead to differences in their spatio-temporal distribution and hence in the respective threats they encounter (e.g. Clay et al. 2016, Barrionuevo et al. 2020). Understanding why, when, and where seabirds migrate between breeding attempts is therefore crucial to develop effective conservation measures (Grémillet & Boulinier 2009, Croxall et al. 2012, Lascelles et al. 2016). While movements of seabirds of temperate zones have been extensively studied, less is known about the non-breeding movements of tropical species, and tropical sulids in particular (Croxall et al. 2012, Kohno et al. 2019, Almeida et al. 2021) and the migratory behaviour of tropical seabirds can vary considerably between and within species (e.g. Weimerskirch et al. 2017).

The Abbott's booby *Papasula abbotti* is one of the most threatened seabird species in the world. This tropical sulid is listed as Endangered on the IUCN Red List of Threatened Species (<https://datazone.birdlife.org/species/factsheet/22696649>; accessed 18 Nov 2021). It once had a wide distribution that ranged from the Mascarenes and Seychelles in the western Indian Ocean (Ridgway 1896, Gibson-Hill 1950, Bourne 1976, Nelson 1978, Cheke 2001, Hume 2023) to the Solomon Islands and possibly Vanuatu and the Marquesas Islands in the Pacific Ocean (Steadman et al. 1988, Steadman 2006). Today, Abbott's booby only breeds on Christmas Island in the eastern Indian Ocean, where the species nests in the top of emergent trees of primary rainforests (Nelson & Powell 1986).

On Christmas Island, decades of phosphate mining reduced the breeding habitat of Abbott's boobies by

one-third (Reville et al. 1990). In 1989, 62% of Christmas Island was declared a National Park with the original purpose to protect the breeding habitat of the Abbott's booby (James & McAllan 2014). The estimated population size on Christmas Island is 2500 pairs (Yorkston & Green 1997). While the population is considered to be stable (Morris-Pocock et al. 2012), the species is still vulnerable, as its breeding grounds remain limited to this island only. Thus, stochastic events, invasive alien species (e.g. yellow crazy ant *Anoplolepis gracilipes*), and mining activities could impact the species considerably (Department of the Environment and Heritage 2004).

Importantly, little is known about the at-sea threats faced by the Abbott's booby (Hennicke 2012). Tracking studies of adult Abbott's boobies during early chick rearing provided a first insight into the species foraging movements and behaviour. Breeding birds forage close to Christmas Island with a median maximum distance per trip of 56.8 km (range: 3.6–556.7 km), and the distance and duration of foraging trips increase with decreasing primary productivity (Hennicke & Weimerskirch 2014a,b). However, the species' non-breeding migration remains poorly known. Non-breeding birds are believed to travel to the Banda Sea (Cadée 1989, van Balen 1996), although individuals have been observed as far as the Mariana Islands (Pratt et al. 2009) and the Maldives (Anderson et al. 2016), suggesting a widespread at-sea distribution.

This study presents the first data describing the non-breeding migration of the Abbott's booby and is only the second investigation of the non-breeding behaviour of a tropical sulid (Kohno et al. 2019). Adult Abbott's boobies were tracked with light-level geolocator–immersion loggers across 7 yr to identify their (1) movements, (2) distribution, (3) habitat preference, and (4) activity patterns during their non-breeding migration.

2. MATERIALS AND METHODS

2.1. Study site and species

This study was carried out on the Australian territory of Christmas Island (10° 25' S, 105° 40' E) in the western Indian Ocean. Situated approximately 350 km off the south coast of Java, Indonesia, the 135 km² tropical island is the only known breeding location of the nearly monomorphic Abbott's booby (males weigh 94% of female weight; Nelson 1978).

The Abbott's booby breeding cycle is amongst the longest of any birds, spanning ca. 17 mo from pre-lay-

ing activities (e.g. nest building) to the final departure of juveniles (details in Nelson & Powell 1986). A single egg is laid between April and September, with an egg-laying peak between mid-May and mid-July. The egg is incubated for ca. 57 d and the chick reared for ca. 151 d. After fledging, adults keep feeding the juvenile around the nest for ca. 230 d, until the juvenile's final departure from the nest between June and November of the second year of the breeding cycle. Between November and April, adult Abbott's boobies are seemingly scarce on Christmas Island despite their protracted breeding cycle (Nelson & Powell 1986).

2.2. Deployment and retrieval of geolocators

Fieldwork took place annually, from 2007 to 2015, between late August and early October. Breeding adult Abbott's boobies were equipped with geolocator–immersion loggers (GLSs) from Biotrack/Lotek (models: Mk4, Mk7, Mk15, Mk3006; Table 1). All birds equipped were either on an egg or with a chick of approximately 2–6 wk of age. The birds were caught in 2 areas of high nest density, in the north-west and south-west of the island (see Hennicke & Weimerskirch 2014a). The nests were located in treetops between 12 and 40 m high and were accessed by tree climbing (see Hennicke & Weimerskirch 2014a). The birds were caught on the nest by hand or using a ca. 1 m noose pole and were lowered down to the ground in a bag. On the ground, GLS loggers were attached to metal rings from the Australian Bat and Bird Banding Scheme using cable ties. The devices weighted up to 2.5 g, i.e. 0.2% of the birds' body mass. After logger attachment, birds were put back into the bag, pulled up to the nest site

in the canopy and released on the nest. The procedure, from catch to release, lasted approximately 30 min.

During subsequent fieldwork seasons (i.e. August–October), nest sites were systematically checked at least once per season until the GLSs were retrieved, and information on the breeding status was recorded (e.g. chick still present at the nest, adult visible at the nest, new nest). To maximize the chances of recording migrations, GLS loggers were retrieved at least 2 yr after deployment or 1 yr if the birds had started a new breeding attempt. The GLSs were retrieved following the same capture and handling procedure as for deployments.

The models of GLS used in this study measured light levels; electrical conductance between 2 electrodes, a proxy for saltwater immersion and therefore for the at-sea activity of the birds; and temperature when immersed (see Text S1 in the Supplement at www.int-res.com/articles/suppl/m743p075_supp.pdf and Biotrack 2013 for details on the recording schedule). Prior to deployment, most GLSs were left for calibration (6–15 d) at the south point of Christmas Island in an open location to limit the effect of vegetation or topography on light levels recorded around twilight. To assist with calibration, one GLS (model Mk4) was left stationary for 10 mo at the calibration site.

In total, 55 GLS were deployed from 2007 to 2015 on 25 males and 19 females (Table 1); 9 birds were equipped with a GLS 2 times in different years. A total of 33 GLS were recovered after 12–37 mo, and the data were extracted using BASTrack software (Biotrack 2013). Eleven GLS malfunctioned or ran out of battery before retrieval and were sent back to the manufacturer for data extraction; useful data were recovered for 6 of these GLS. Due to their higher sampling frequency, the immersion data of all MK7 filled the available memory capacity before or soon after the beginning of non-breeding migrations and were therefore not used.

Table 1. Summary of Abbott's booby geolocator–immersion logger (GLS) deployment and retrieval. In brackets: number of males and females, respectively

Year	Model deployed	No. of GLS deployed	No. of GLS retrieved	No. of non-breeding migrations recorded
2007	Mk4	4 (2, 2)		
2008	Mk7	7 (4, 3)		5 (2, 3)
2009			4 (2, 2)	5 (3, 2)
2010	Mk15	9 (6, 3)	6 (4, 2)	8 (5 ^a , 3)
2011	1 Mk7, 2 Mk15	3 (1, 2)	1 (0, 1)	2 (1, 1)
2012	Mk3006	10 (7, 3)	7 (5, 2)	6 (2, 4)
2013	Mk3006	16 (8, 8)	8 (4, 4)	2 (2 ^a , 0)
2014	Mk3006	6 (3, 3)	5 (2, 3)	1 (1, 0)
2015			2 (1, 1)	
Total		55 (31, 24)	33 (18, 15)	29 (16, 13)

^aOne of the migrations was only partially recorded (i.e. GLS malfunctioned or ran out of battery before the bird returned to Christmas Island)

2.3. Processing of light data and estimation of locations

Location estimates were derived from light data using the threshold method (Lisovski et al. 2020). Two locations per day are calculated from the time at which pairs of consecutive twilights were recorded in relation to a reference time zone (e.g. Greenwich Mean Time). Latitude is estimated

from the time between 2 consecutive twilights, and longitude is derived from the times of local midday and midnight.

GLS data was decompressed using Decompressor software (BAStack software suite v.18; Biotrack). Clock drift was adjusted at decompression. All further processing of the light data was done in RStudio v.1.4.1717 (RStudio Team 2021) with R v.4.1.0 (R Core Team 2021). Twilight events were identified using the function 'preprocessLight' from the R package 'TwGeos' v.0.1.2 (Lisovski et al. 2016). Unreliable twilights associated with shading or artificial light (i.e. narrow light peak in an obvious night period) were removed, and 10 min was subtracted from the sunset times due to the GLS recording schedules (see Biotrack 2013).

The length of pre-deployment calibration was not long enough to reliably estimate the zenith angle corresponding to the chosen threshold (Lisovski et al. 2012b). Instead, zenith angles were determined using on-bird calibration whilst the birds were on Christmas Island (see Text S2 & S3 for details). The location estimates were then refined using the R package 'SGAT' v.0.1.3 (Sumner et al. 2009, Lisovski et al. 2012a), a Bayesian framework that uses prior information on the species' ecology to compute a posterior distribution of location estimates by Markov chain Monte Carlo (MCMC) (see Text S4 for details).

To identify the range of dates around the equinox when estimation of locations is not reliable, the latitude and longitude difference between location estimates (simple threshold method) and Christmas Island were plotted over time for the stationary GLS that was left for 10 mo on the island (Fig. S1). From visual inspection, at the latitude of Christmas Island, latitude estimation was considered unreliable within 21 d on either side of an equinox.

The estimated overall accuracy of the final location estimates, as calculated from the latitude and longitude standard deviation of the MCMC final run for each final location estimate, was 385 ± 68 km for latitude and 218 ± 33 km for longitude outside of an equinox period, and 668 ± 151 km for latitude and 176 ± 37 km for longitude around an equinox. The relative accuracy, calculated following Halpin et al. (2021), was 0.73 ± 0.10 outside of an equinox, and 0.84 ± 0.06 around an equinox.

2.4. Spatial analyses

Migrations were defined as periods when the birds were further than 500 km from Christmas Island (i.e. maximum known distance travelled by the adults dur-

ing early chick rearing; Hennenke & Weimerskirch 2014b) for more than 14 continuous days (i.e. based on the expected maximum duration between 2 attendances of the chick; Nelson & Powell 1986) (see Text S5 for details). Thus, the terms 'non-breeding range' or 'non-breeding distribution' that are used hereafter and the related analyses only refer to migrating birds, not non-breeding birds that might potentially stay on or around Christmas Island (see Sections 3 & 4). In total, 6906 location estimates were retained (242 ± 53 bird⁻¹ for full migrations) for a total of 27 full and 2 incomplete migrations.

The latitude of location estimates around an equinox was interpolated between the last location before the equinox period and the first one after (26% of all location estimates), using the recorded longitude for each location. If the return date was within an equinox period, then the retrieval site's latitude at the return date was used for the interpolation. The longitude was smoothed with a 5-point moving average using the same boundaries.

For a full migration, location estimates on land within the estimated accuracy were relocated to the nearest shoreline (5% of all location estimates). No location estimates were further inland than the estimated accuracy.

Migrations were divided into 3 different phenophases: the outbound migration (the period from the departure from Christmas Island to the arrival at the non-breeding range), the non-breeding range residency (the period when the birds are at their non-breeding range), and the return migration (the period from the departure from the non-breeding range to the return on Christmas Island). The phenophases were determined using the standard squared displacement method (Börger & Fryxell 2012), using the double-sigmoid model for the migration data (Bunnefeld et al. 2011) applied to mean squared displacement data (average per day) using non-linear mixed-effects models (Börger & Fryxell 2012), with Christmas Island as the Day 0 start point (see Text S6 for details). Two trips were incomplete, as the loggers stopped recording before the return trip. For these 2 trips, only the outbound migration was retained for analyses involving the phenophases.

The outcome of the breeding attempt preceding a migration was estimated primarily from the data on the breeding status recorded during annual field surveys using criteria based on the species' breeding biology (Nelson & Powell 1986); in particular, the stage at which the devices were deployed (i.e. on an egg or with a young chick) in relation to the length of the breeding cycle (see Text S7 for criteria).

2.4.1. Utilisation distributions

Utilisation distributions (UDs) were calculated using fixed kernel density estimation (Fieberg & Börger 2012, Horne et al. 2020) on a 50×50 km grid (Clay et al. 2017) with a bandwidth of 186 km (Lascelles et al. 2016) using the R package 'adehabitatHR' v.0.4.19 (Calenge 2006) (See Text S8 for details). The 99.9, 95, and 50% UD were used to quantify the full range (99.9%) and to derive measures as used in the standard seabird conservation mapping literature (95% home range and 50% 'core area') (e.g. Fromant et al. 2020, Hipfner et al. 2020, Börger 2021). To account for different trip durations and number of trips per bird for estimation of the population-level UD, UD were first calculated per trip, then averaged per individual for each grid cell, and finally averaged across individuals. The non-breeding range distance was calculated individually as the distance between the centroid of the 1% UD (calculated for the non-breeding range residency only) and Christmas Island (Ramos et al. 2017).

The 95 and 50% UD overlap between males and females, failed and successful breeders, and across years was calculated using Bhattacharyya's affinity index (BA; Fieberg & Kochanny 2005) in the R package 'adehabitatHR'. Only years with at least 5 migrations were retained (2008, $n = 5$; 2009, $n = 5$; 2010, $n = 7$; 2012, $n = 6$). The significance of the observed overlap was assessed using a randomisation procedure (Breed et al. 2006). Separately, sexes, breeding success, and years were randomly reassigned 1000 times, maintaining the observed ratios. For each reassignment, the 95 and 50% UD of each group were obtained following the method detailed above and the overlap was calculated. The p-value was calculated as the proportion of overlaps from the randomisation procedure that had a lower BA than the observed overlap.

2.4.2. Sightings away from Christmas Island

To complement the UD derived from the movement data, known sightings of the species made since 1980 that were more than 500 km away from Christmas Island were compiled from the literature, the community science database eBird (eBird 2023), and records obtained by bird or marine wildlife boat tour companies operating in Southeast Asia, where the species is suspected to migrate. Bird or marine wildlife boat tour companies were identified through a web search, then by asking each company for the contacts of similar companies known to them to operate in Southeast Asia. Each company was asked for sight-

ings of Abbott's boobies along with the most accurate date and location possible of the sightings. As it is virtually impossible to visually differentiate juveniles from males (Nelson 1978), the age class is rarely recorded; therefore, no attempt was made at differentiating sightings of juveniles or adults. For eBird data, sightings identified from their metadata as duplicates were removed. Only sightings from tour operators were retained in the case of duplicates between eBird and tour operators.

2.4.3. Statistical analyses

The effects of sex and breeding success on the timing and the duration of the phenophases, total duration of the trips, non-breeding range distance and individual full range, home range, and core area were assessed with linear mixed-effect models using the R package 'nlme' v.3.1.152 (Pinheiro et al. 2021). Sex and breeding success were set as fixed effects and year as a random effect. Bird identity was not used as a random effect as only 4 of them had more than one value per metric. The normality of residuals was checked with QQ plots and Shapiro-Wilk tests. Heteroscedasticity was checked by plotting the residuals against the fitted values. Best-fittings models were selected using Akaike's information criterion adjusted for small sample size (AIC_C). For model comparison, the models were fitted using maximum likelihood, and the estimates of the best-fitting model were computed using restricted maximum likelihood. When several models were competing (i.e. $\Delta AIC_C < 2$), the most parsimonious model was selected, and when the models had the same number of parameters, both models were inspected. All competing models that fell into this category did not show any significant effect of the predictor variables considered in these models, so there was no need to refine the selection process for these models.

2.5. Habitat modelling

Habitat preferences were assessed by comparing environmental variables at used and available locations using generalised additive mixed models (GAMMs, package 'mgcv'; Wood 2017), with bird identity as a random effect (Clay et al. 2017, Bonnet-Lebrun et al. 2020, Raine et al. 2021). Used locations (i.e. GLS location estimates for the non-breeding range residency) and available locations (i.e. marine pseudo-absence locations selected within the 99.9% UD calculated

from all tracks) were set as a binomial response variable with a logit link function. Location estimates around an equinox period or those that were relocated from land to sea were excluded from this analysis (33% of non-breeding range residency locations). Pseudo-absence locations were sampled using correlated random walks (see Text S9 for details). For each used location, 80 random locations were sampled and given the timestamp and bird identity of the used location (Text S9).

Nine environmental variables known to affect pelagic seabirds and fish distributions were used as candidate predictors to describe the marine habitats (e.g. Carneiro et al. 2016, Clay et al. 2017, Ben Abdallah et al. 2018, Bonnet-Lebrun et al. 2020, Maynou et al. 2020) (Table 2): (1) SST ($^{\circ}\text{C}$); (2) the SST gradient, a proxy for thermal fronts, which was calculated as the standard deviation of SST in a 200 km radius around the location (Carneiro et al. 2016, Clay et al. 2017); (3) sea surface salinity (SSS; PSU); (4) chlorophyll *a* concentration (chl *a*; mg m^{-3}); (5) mixed layer thickness (m); (6) barrier layer thickness (m), calculated as the difference between

the depth of the top of the thermocline and the potential density mixed layer depth (Yuan et al. 2020); (7) eddie kinetic energy (EKE), calculated using the equation $\text{EKE} = 1 / 2(u^2 + v^2)$ (Zhang et al. 2021), where *u* and *v* are the zonal and meridional geostrophic velocities anomalies, respectively; (8) depth (m) at 15 arc second spatial resolution resampled at 0.1° resolution for ease of computation; and (9) the standard deviation of depth in a 200 km radius of a location, a proxy for sea floor topography (Carneiro et al. 2016, Clay et al. 2017). Locations for which data of an environmental variable was missing were excluded from the analysis (2% of total locations, used and available). Collinearity between variables was checked using Spearman's rank correlation test, and correlated variables ($|\rho| > 0.5$) were not included in the same model. Variables were smoothed in the GAMMs using cubic regression splines with shrinkage. The number of basis functions was set to 4 to avoid model over-fitting (Arrizabalaga et al. 2015, Carneiro et al. 2016) and was increased if it did not give enough flexibility for the curve to match the data (Clay et al. 2017).

Table 2. Environmental variables considered for the analyses of habitat preference of adult Abbott's boobies during migration. NA: not available

Variable	Unit	Spatial resolution	Temporal resolution	Dataset	Source
Sea surface temperature (SST)	$^{\circ}\text{C}$	$0.25^{\circ} \times 0.25^{\circ}$	Daily mean	NOAA OI SST V2 High Resolution Dataset	https://psl.noaa.gov (accessed 21 Dec 2021)
Standard deviation of SST (SST gradient)	$^{\circ}\text{C}$	$0.25^{\circ} \times 0.25^{\circ}$; 200 km radius	Daily mean	NOAA OI SST V2 High Resolution Dataset	https://psl.noaa.gov (accessed 21 Dec 2021)
Sea surface salinity	PSU	$0.25^{\circ} \times 0.25^{\circ}$	Daily mean	Copernicus Global Ocean Ensemble Physics Reanalysis	https://doi.org/10.48670/moi-00024 (accessed 18 Jun 2022)
Chlorophyll <i>a</i> concentration	mg m^{-3}	$0.25^{\circ} \times 0.25^{\circ}$	Daily mean	Copernicus Global Ocean Biochemistry Hindcast	https://doi.org/10.48670/moi-00019 (accessed 10 Feb 2022)
Mixed layer thickness	m	$0.25^{\circ} \times 0.25^{\circ}$	Daily mean	Copernicus Global Ocean Ensemble Physics Reanalysis	https://doi.org/10.48670/moi-00024 (accessed 18 Jun 2022)
Barrier layer thickness	m	$0.5^{\circ} \times 0.5^{\circ}$	5 day mean	SODA v3	https://apdrc.soest.hawaii.edu/erddap (accessed 24 May 2023)
Eddie kinetic energy	$\text{cm}^2 \text{s}^{-2}$	$0.25^{\circ} \times 0.25^{\circ}$	Daily instantaneous	Copernicus Global Ocean Gridded L4 Sea Surface Heights and Derived Variables	https://doi.org/10.48670/moi-00145 (accessed 20 Jan 2022)
Depth	m	$0.1^{\circ} \times 0.1^{\circ}$	NA	GEBCO Gridded Bathymetry Data	https://www.gebco.net (accessed 10 Feb 2022)
Standard deviation of depth	m	$0.1^{\circ} \times 0.1^{\circ}$; 200 km radius	NA	GEBCO Gridded Bathymetry Data	https://www.gebco.net (accessed 10 Feb 2022)

The best predictive model was selected using a forward k -fold cross-validation process, with birds set as folds (Carneiro et al. 2016). Each model was trained using all birds but one and then tested on the remaining one; this process was repeated for all birds. At each iteration, the area under the receiver operator characteristic curve (AUC) was calculated (package 'pROC'; Robin et al. 2011), and the mean AUC of all iterations was used to determine the performance of the model. AUC scores from 0.5–0.7, 0.7–0.8, 0.8–0.9, and >0.9 are commonly interpreted as poor, acceptable, excellent, and outstanding model performances, respectively (Hosmer et al. 2013). Variables were first modelled separately. The model with the highest mean AUC was selected and the remaining variables were iteratively added to the selected model. The process was repeated until adding any other variable did not result in a significant increase in mean AUC. The significance of the mean AUC increase was assessed using a paired t -test.

2.6. Analyses of immersion data — proportion of time spent on water

The immersion data was processed using the online tool Actave.net (Mattern et al. 2015). The output provides 1 value d^{-1} for several metrics ($n_{\text{data}} = 2030$). The proportion of time the loggers were immersed (i.e. the birds were on or in the water) was calculated per period of the day (i.e. dawn, daylight, dusk, night). Actave.net uses nautical dawn and dusk, i.e. the time between sunrise and sunset and the beginning and end of the nautical twilight (when the sun is 12° below the horizon). The proportion of time spent on water was used over the raw time spent on water to account for seasonal variation in the duration of periods of the day.

To assess the influence of sex, breeding success, phenophase, and their interactions, Bayesian zero-one-inflated beta regressions with a logit link function from the R package 'brms' v.2.16.0 (Bürkner 2017, 2018) were used for the proportion metrics, with years and bird identities as random effects. The best predictive models were selected by leave-one-out cross-validation, which computed the expected log-predictive density (elpd) (R package 'loo' v.2.4.1; Vehtari et al. 2017, 2020). The model with the lowest elpd was selected. When models were competing (i.e. the $\text{elpd} \pm \text{SE}$ of a model intersected the elpd of the best-fitting model), the most parsimonious model was selected. All model estimates reported were back-transformed.

Most codes used in this study are available on GitHub at https://github.com/JoChambon/ABBO_migration.

3. RESULTS

3.1. Migration movements and distribution

A total of 33 GLS tags ($n = 22$ birds) were recovered, from which 27 full non-breeding migration paths and 2 partial paths (81 and 147 days) were reconstructed. The birds migrated predominantly (89%, 24 out of 27 paths) east of Christmas Island (Fig. 1) to the waters around the Lesser Sunda Islands and in the Banda Sea, where the 50% UD ($\sim 1\,317\,500\text{ km}^2$) is centred (Figs. 2 & 3). Several paths (9%, 5 out of 27) continued north and northeast of the Banda Sea into the Celebes Sea ($n = 1$) or the Pacific Ocean ($n = 4$), while one went southwest of Christmas Island and 2 extended northwest along Sumatra. This resulted in a widespread total non-breeding distribution (99.9% UD: $\sim 18\,257\,500\text{ km}^2$; Fig. 2).

Most birds (93%, 25 out of 27 tracks) used similar routes for their outbound and return migration (Figs. 1 & 4). Of the birds for which 2 non-breeding migrations were recorded ($n = 5$), only one did not migrate in the same direction from one year to another (i.e. one migration to the Banda Sea, the other along the coast of Sumatra). One bird visited the same general area in the Banda Sea in both years, but in one year, after spending time in the Banda Sea, it continued to an area in the Pacific Ocean, reaching the maximum recorded distance for all birds with a location estimate in the waters of Micronesia, about 5680 km from Christmas Island (Fig. 1).

The location estimates ranged from $24.18 \pm 4.69^\circ\text{ S}$ to $12.50 \pm 6.07^\circ\text{ N}$ and $89.29 \pm 2.98^\circ\text{ E}$ to $155.34 \pm 2.31^\circ\text{ E}$. The individual non-breeding range distance of the tagged Abbott's boobies was on average $2531 \pm 600\text{ km}$ away from Christmas Island and the individual core area size was $548\,000 \pm 185\,000\text{ km}^2$ (Table S1). Estimates from the best-fitting models indicate that neither the non-breeding range distance nor the core area size were affected by sex or breeding success (Table 3). There were no significant differences in the UD spatial coverage between males and females (50% UD BA: 0.33, $p = 0.15$; 95% UD BA: 0.81, $p = 0.75$) (Fig. S2A) or between failed and successful breeders (50% UD BA: 0.31, $p = 0.13$; 95% UD BA: 0.77, $p = 0.24$) (Fig. S2B). The spatial coverage of the UDs did not differ across years (for all pairwise comparisons of 50% and 95% UD, $p > 0.16$) (Figs. S3 & S4).

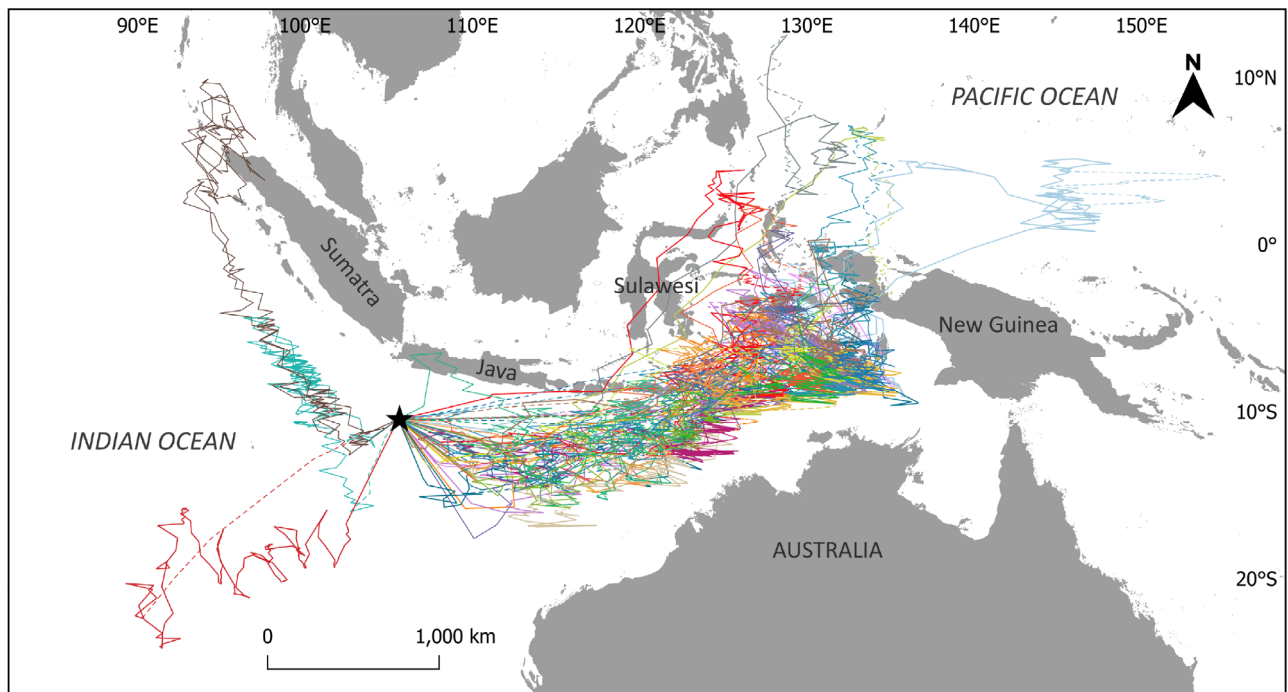


Fig. 1. Individual migration paths of adult Abbott's boobies ($n = 27$). Dashed lines: portion of path around an equinox (± 21 d) with interpolated latitude. Star: Christmas Island

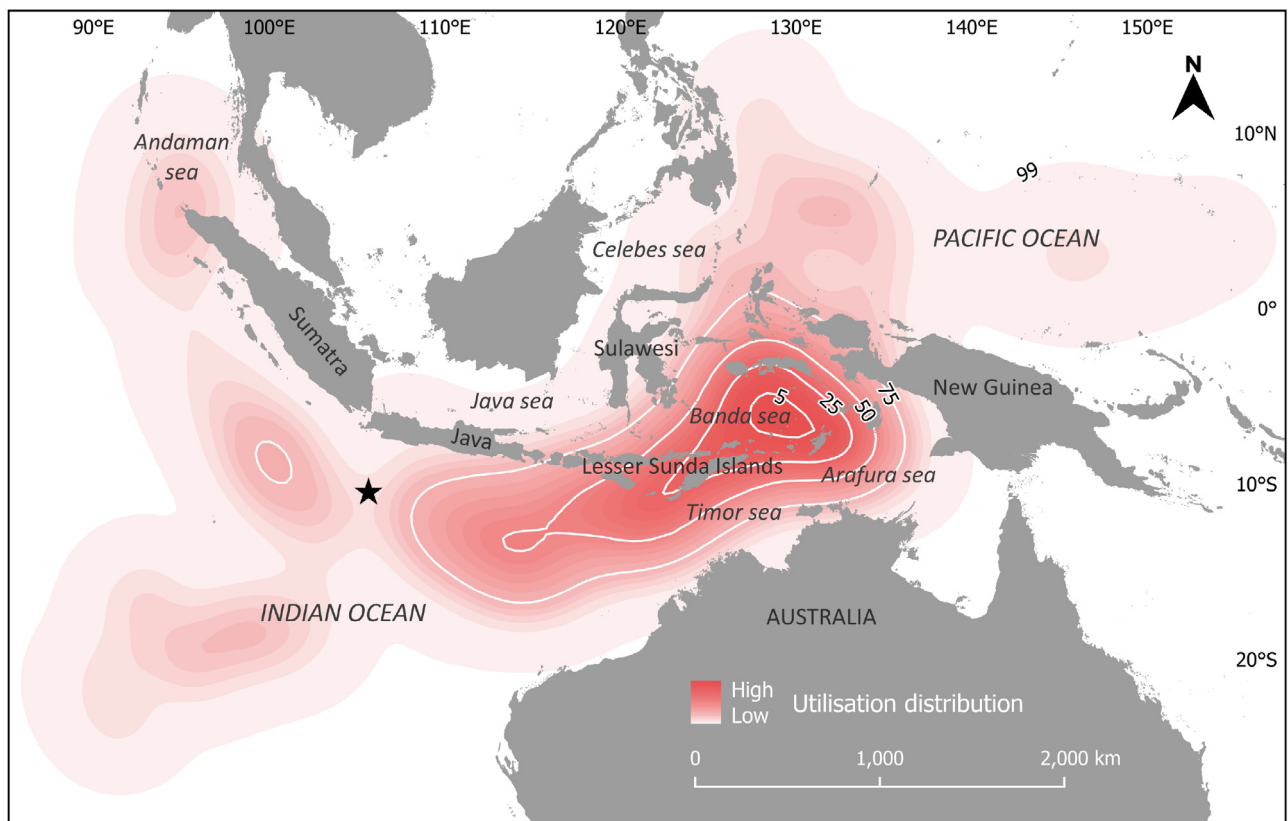


Fig. 2. Utilisation distributions of adult Abbott's boobies during non-breeding migration (5 to 99.9%). Years, sex, and breeding success pooled across 27 tags on 22 birds with full migration data. Star: Christmas Island



Fig. 3. Abbott's booby 50% utilisation distribution during migration with marine BirdLife International's Important Bird and Biodiversity Areas (IBAs; only 2 significant marine IBAs in the region: around Ashmore Reef and in the West of Borneo), Marine Protected Areas (MPAs), the Sunda Banda Seascape (SBS), the Exclusive Economic Zones (EEZ) boundaries, the 6 major Indonesian seabird colonies (de Korte & Silvius 1994, de Jong 2011), and Ashmore reef, an important Australian seabird breeding site within Abbott's booby 50% utilisation distribution (Clarke et al. 2011)

The mean total duration of the non-breeding migration was 121 ± 26 d (range: 71–167 d, $n = 27$; Table S2). On average, the birds started their outbound migration on 7 December ± 27 d and travelled for 33 ± 18 d, reaching their non-breeding range on 9 January ± 32 d (Table S3) where they spent 65 ± 40 d on average. They started their return migration on 15 March ± 32 d, travelling for 23 ± 17 d before reaching Christmas Island on 7 April ± 25 d.

Most failed breeders migrated within the first year of deployment ($n = 13$ out of 18), 1 yr before successful ones. Estimates from the best-fitting model showed that breeding success had a significant effect on the seasonal timing (day of the year) of the different phenophases of migration but not on the duration of these phases (Tables 4 & 5). Within a given year, successful breeders left Christmas Island (16 November ± 11 d, $p = 0.01$, $n = 7$), reached their non-breeding range (8 January ± 13 d, $p = 0.01$, $n = 7$), and started their return migration (15 February ± 13 d, $p = 0.03$, $n = 7$) earlier than failed breeders (17 December ± 6 d, $n = 18$; 9 February ± 10 d, $n = 16$; and 18 March ± 10 d, $n = 16$). Sex did not affect the start of the outbound migration, but the outbound migration of the males was

twice as fast (23 ± 6 d, $p = 0.002$, $n = 16$) as that of the females (46 ± 5 d, $n = 13$), resulting in an earlier arrival in their non-breeding range (end of outbound migration: 6 January ± 12 d, $p = 0.03$, $n = 16$ for males; 9 February ± 10 d, $n = 13$ for females). The non-breeding range residency was shorter for females (43 ± 11 d, $p = 0.03$, $n = 13$) than males (75 ± 14 d, $n = 14$). There was no difference between sexes in the timing and duration of the return migration. Models of the movement metrics did not provide evidence of any interactive effects between sex and breeding success in the timing and duration of the phenophases, i.e. models with interactions did not receive support (Tables 4 & 5). However, this might be a result of the unbalanced data groups once these variables were combined (e.g. only 2 successful males; Tables S2 & S3).

3.2. Sightings away from Christmas Island

A total of 72 sightings of Abbott's boobies more than 500 km away from Christmas Island since 1980 were found in the literature and from observational data (Fig. 5, Table S4; eBird 2023, R. Clarke unpubl.

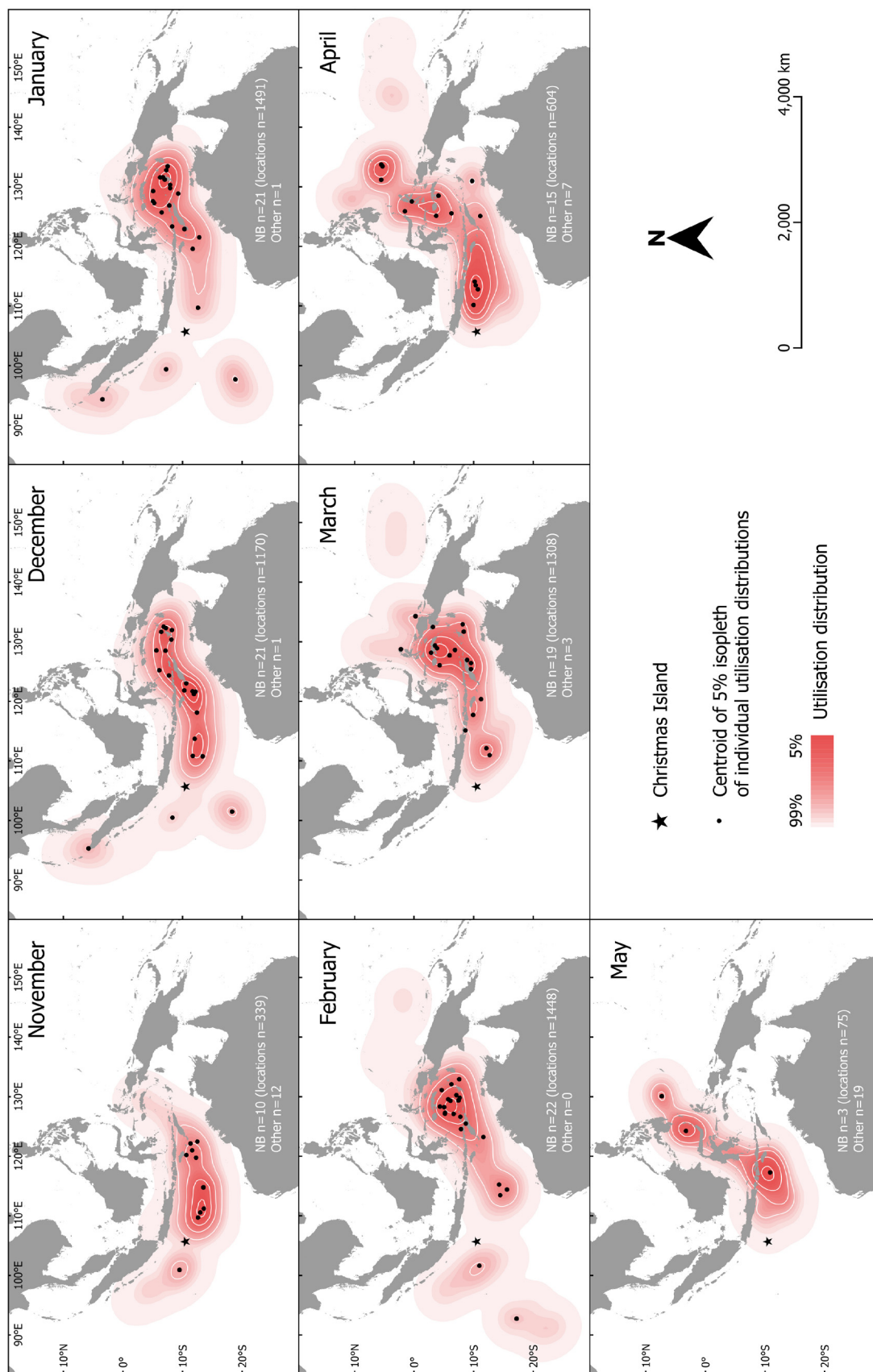


Fig. 4. Monthly utilisation distributions of Abbott's booby non-breeding migration. Only non-breeding migration locations were used for the calculation of the utilisation distributions and years were pooled together. NB: number of tracked birds at least partially in their migration during the month; 'other': number of tracked birds that had not yet started their migration by the end of the month or were already back from their migration by the beginning of the month

Table 3. Model selection and best-fitting model estimates (with 95% confidence intervals) of the non-breeding range distance (km) and individual utilisation distribution (UD) areas (10^5 km²) of Abbott's booby non-breeding migration. Only best-fitting models (difference in Akaike's information criterion corrected for small sample size [ΔAIC_C] < 2) plus next best-fitting model are displayed. **Bold** model: best-fitting models. (†) indicates competing best-fitting model with same number of parameters and no significant fixed effect ($p > 0.4$). BR: breeding success

Variable	Model	ΔAIC_C	AIC_C weight	Estimate (95% CI)	<i>t</i> -value	<i>p</i>
Non-breeding range distance	BR	0	0.47	Failed: 2656 (2394–2918)	19.85	0
	Sex [†]	0.20	0.42	Successful: 2527 (2037–3017)	19.34	0.62
	Sex + BR	3.25	0.09			
	Null	25.48	0			
Individual 99.9% UD area	Sex	0	0.46	Female: 52.66 (46.22–59.10)	16.16	0
	BR [†]	0.14	0.43	Male: 54.79 (45.86–63.70)	16.63	0.64
	Sex + BR	3.28	0.09			
	Null	18.97	0			
Individual 95% UD area	Sex	0	0.45	Female: 27.16 (23.34–30.99)	13.91	0
	BR [†]	0	0.45	Male: 27.35 (22.05–32.65)	13.98	0.95
	Sex + BR	3.31	0.09			
	Null	16.11	0			
Individual 50% UD area	Sex	0	0.59	Female: 6.17 (5.16–7.17)	12.02	0
	BR [†]	1.57	0.27	Male: 5.14 (3.75–6.53)	10.58	0.17
	Sex + BR	3.29	0.12			
	Null	14.24	0			

Table 4. Model selection and best-fitting model estimates of timing of phenophases of Abbott's booby non-breeding migration (day of year; adjusted for start and end of outbound migration, i.e. added 365 to day of year for dates between January and July). Only best-fitting models ($\Delta AIC_C < 2$), next best-fitting model and null model are displayed. **Bold** model: best-fitting model, or most parsimonious of competing best-fitting models. **Bold** estimate: 95% CI of estimate does not intersect the estimate of at least one other group. BR: breeding success

Variable	Model	ΔAIC_C	AIC_C weight	Estimate (95% CI)	<i>t</i> -value	<i>p</i>
Start of outbound migration	BR	0	0.59	Failed: 350.33 (337.48–363.17)	53.46	0
	BR + Sex	1.49	0.28	Successful: 319.30 (298.41–340.19)	50.55	0.01
	BR × Sex	3.65	0.10			
	Null	48.15	0			
End of outbound migration	BR + Sex	0	0.66	Failed: 404.49 (384.00–424.98)	38.69	0
	Sex	2.90	0.15	Successful: 371.61 (345.39–397.84)	36.24	0.01
	Null	124.27	0	Female: 404.49 (384.00–424.98)	38.69	0
				Male: 369.84 (346.12–393.56)	35.83	0.03
Start of return migration	BR	0	0.76	Failed: 75.89 (54.88–96.90)	7.08	0
	BR + Sex	3.30	0.15	Successful: 45.12 (20.09–70.16)	4.67	0.03
	Null	41.07	0			
End of return migration	BR	0	0.68	Failed: 101.19 (89.71–112.67)	17.27	0
	Sex	2.95	0.16	Successful: 81.86 (61.05–102.67)	15.45	0.09
	Null	26.3	0			

data). Most of them ($n = 46$) were recorded in an area encompassing the Banda Sea, the Lesser Sunda Islands, and Ashmore and Scott reefs and are included in our estimates of the migratory non-breeding distribution obtained using data loggers (Fig. 5). Sightings were regularly recorded on Rota Island in the Northern Mariana Islands between 2007 and 2012 ($n = 6$), and

more recently between 2020 and 2023 ($n = 16$). Two birds were found in the north of mainland Australia following a cyclone and a tropical storm. One sighting was recorded in the Maldives and one in the easternmost part of Papua New Guinea. Most sightings (74%) were recorded during the migration period, between November and April.

Table 5. Model selection and best-fitting model estimates of duration of the Abbott's booby non-breeding migration and the different phenophases (days). Only best-fitting models ($\Delta AIC_C < 2$), next best-fitting model and null model are displayed. **Bold** model: best-fitting model, or most parsimonious of competing best-fitting models. (†) indicates competing best-fitting model with same number of parameters and no significant fixed effect ($p > 0.3$). **Bold** estimate: 95% CI of estimate does not intersect the estimate of at least one other group. BR: breeding success

Variable	Model	ΔAIC_C	AIC_C weight	Estimate (95% CI)	<i>t</i> -value	<i>p</i>
Outbound migration	Sex	0	0.79	Female: 46.20 (35.65–56.76)	8.58	0
	Sex + BR	3.09	0.17	Male: 23.04 (11.08–35.00)	4.78	0.001
	Null	42.83	0			
Non breeding range residency	Sex	0	0.74	Female: 42.62 (20.63–64.61)	3.80	0.002
	Sex + BR	3.20	0.15	Male: 74.62 (48.12–101.12)	6.17	0.03
	Null	30.48	0			
Return migration	Sex	0	0.53	Female: 33.68 (14.46–52.90)	3.43	0.004
	BR†	0.94	0.33	Male: 27.59 (18.38–36.80)	2.14	0.21
	Sex + BR	3.20	0.11			
	Null	26.44	0			
Total duration of non-breeding migration	Sex	0	0.40	Female: 114.36 (100.72–128.01)	16.42	0
	BR†	0.04	0.39	Male: 122.92 (104.02–141.81)	17.31	0.39
	Sex + BR	1.66	0.18			
	Sex × BR	5.17	0.03			
	Null	72.63	0			

3.3. Habitat preference

The habitat model, as selected with forward *k*-fold cross-validation, included (in order of addition to the model) SSS, the standard deviation of depth, and

SST (Fig. 6). Although this model explained only 17% of the deviance, it had a mean AUC of 0.83, reflecting 'excellent' predictive power (Hosmer et al. 2013). As SST and the SST gradient were correlated ($\rho = -0.53$) and SST gradient is a product of SST, the addition of

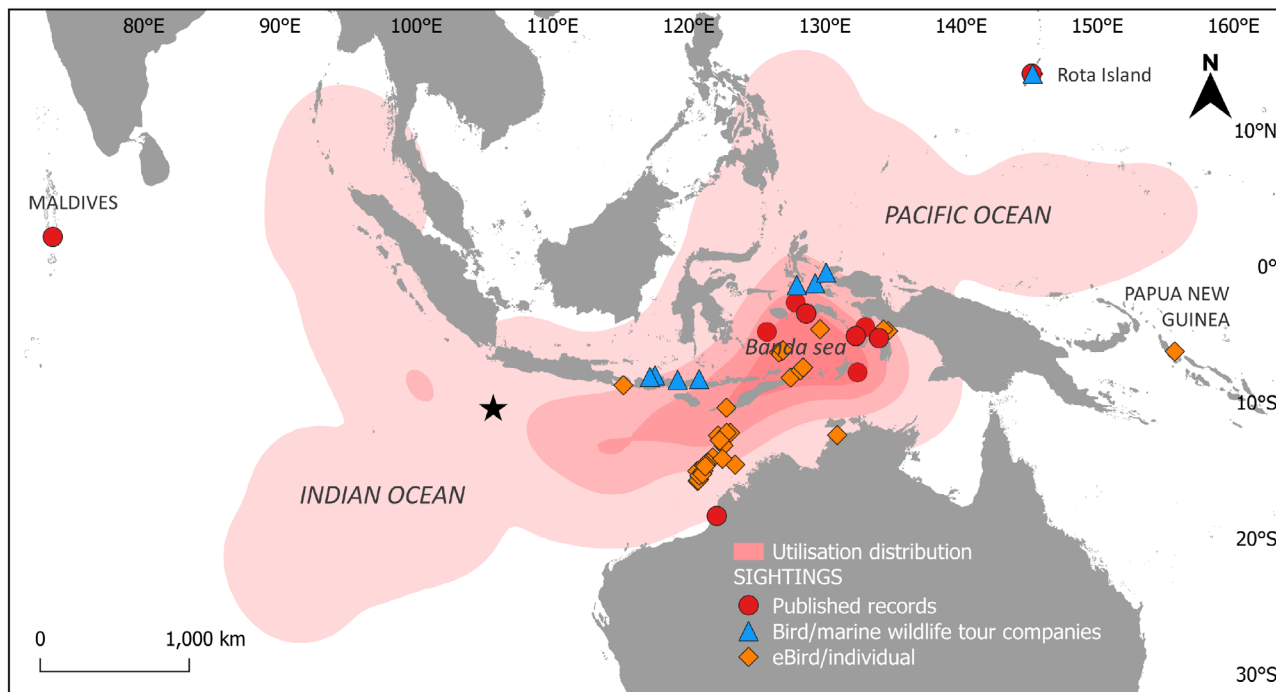


Fig. 5. Distribution of known sightings of Abbott's boobies more than 500 km away from Christmas Island since 1980 ($n = 72$) with overlaid 99.9, 75, 50, and 25% utilisation distribution contour lines from this study (derived from the logger data). Star: Christmas Island

SST gradient to this model was not tested. Within the species' 99.9% UD, the probability of occurrence of Abbott's boobies was higher in waters with a SSS between ca. 32.5 and 34.5 PSU (Fig. 6A) and a standard deviation of depth within a radius of 200 km of ca. 1700 m (Fig. 6B). Overall, Abbott's boobies made little use of the continental shelves of the Timor, Arafura, and Java seas or the abyssal plains of the Indian

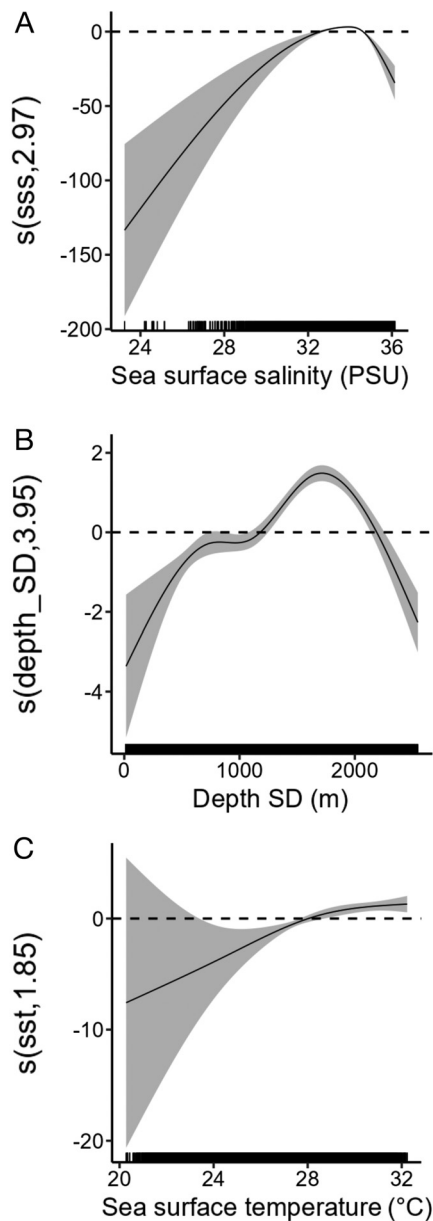


Fig. 6. Response curves for the predictors retained in the most parsimonious generalised additive mixed model for Abbott's booby habitat preference during migration. The y-axis represents the smooth function with the effective degrees of freedom indicated in brackets. Depth SD corresponds to the standard deviation of depth in a 200 km radius from a location. Grey shading: 95% CI; rug plot: data values

Ocean (Fig. S5). They showed a preference for waters with surface temperatures above ca. 28°C (Fig. 6C).

3.4. Activity patterns

Abbott's boobies spent little time per day in contact with water during their non-breeding migration (median proportion of time spent on water: 0.16; IQR: 0.09–0.30; range: 0.01–0.69 $n = 2030$; parameters calculated per individual first then averaged across individuals). One outlier individual was on the water 70% of the time (median proportion during the day: 0.56; at night: 0.98). Overall, the proportion of time spent on water was similar at dawn (median: 0.08; IQR: 0.05–0.23; range: 0.00–0.90; $n = 1962$), during daylight (0.15; 0.08–0.26; 0.01–0.59), at dusk (0.12; 0.05–0.52; 0.00–0.84), and at night (0.15; 0.07–0.36; 0.00–0.98) (Table S5). The proportion of time spent on water at dawn and dusk was not affected by sex, breeding success, or phenophase, i.e. the predictive power of best models did not improve significantly from the null model ($\Delta\text{elpd} \pm \text{SE}$ of the null model was -1.0 ± 2.0 for dawn; -1.9 ± 2.4 for dusk). There was no significant difference in time spent on water during daylight and at night between sexes, breeding success, or the different phenophases (Table 6).

4. DISCUSSION

4.1. Migratory movements and distribution

The present study provides the first detailed and systematically collected information on the migratory behaviour and non-breeding distribution of Abbott's boobies. Given the paucity of sightings of Abbott's boobies away from Christmas Island (since 1980, $n = 72$), results from the present tracking study significantly improve our understanding of the species' migration. Migrating adult Abbott's boobies predominantly flew east to the Banda Sea and the waters around the Lesser Sunda Islands. They left Christmas Island in November–December and were back on the island in April. Most of the known sightings of Abbott's boobies more than 500 km away from Christmas Island since the 1980s were recorded in or near the estimated 75% UD of the present study, further supporting the importance of the area for the migration of this species. Additionally, 74% of the sightings were also recorded during the migration period, between November and April.

Table 6. Model selection and estimates (with 95% credible intervals) from the best predictive model for the proportion of time spent in contact with water by Abbott's boobies during non-breeding migration. Only best predictive models ($\Delta\text{elpd} \pm \text{SE}$ intercepts 0), next best predictive model, and null model are displayed. **Bold** model: best predictive model, or most parsimonious of competing best predictive models. BR: breeding success; Out: outbound migration; NB: non-breeding range residency; Ret: return migration; elpd: expected log-predictive density

Variable	Model	Δelpd	Estimate (with 95% CrI)
Immersion during daylight	Phenophase × Sex	0	Out:Female: 0.19 (0.10–0.35)
	Phenophase × Sex × BR	-0.7 ± 2.9	Out:Male: 0.19 (0.10–0.35)
	Phenophase + Sex + BR	-14.2 ± 6.7	NB:Female: 0.21 (0.11–0.38)
	Null	-24.3 ± 8.1	NB:Male: 0.17 (0.09–0.32) Ret:Female: 0.29 (0.16–0.49) Ret:Male: 0.16 (0.08–0.31)
Immersion at night	Phenophase × BR	0	Out: 0.28 (0.15–0.48)
	Phenophase × Sex × BR	-0.9 ± 2.0	NB: 0.26 (0.14–0.46)
	Phenophase + BR	-1.3 ± 2.4	Ret: 0.36 (0.20–0.56)
	Phenophase	-1.3 ± 2.4	
	Phenophase + Sex + BR	-1.4 ± 2.4	
	Phenophase + Sex	-1.4 ± 2.4	
	Phenophase × Sex	-1.7 ± 3.3	
	Sex × BR	-14.8 ± 5.5	
	Null	-15.1 ± 5.5	

Abbott's boobies showed high inter-individual consistency in the direction of migration. In the Indian Ocean, this is a trait shared with the bridled terns *Onychoprion anaethetus* from the west coast of Australia (Surman et al. 2018) and, to some extent, Barau's petrel *Pterodroma barau* (Pinet et al. 2011), although the latter displays higher variation in return migration paths. Other migratory seabird species breeding in the area have more diffused inter-individual migrations (Cтры et al. 2009, Le Corre et al. 2012, Jaeger et al. 2017, Surman et al. 2018, Franklin et al. 2022) that are often hypothesised to result from the unpredictability of prey distribution in the oligotrophic tropical waters (Weimerskirch 2007, Cтры et al. 2009, Jaeger et al. 2017). It may suggest that Abbott's boobies migrate to an area with a relatively predictable distribution of prey (Sutton et al. 2019).

The direction of the prevailing winds might be a key factor affecting the direction and timing of Abbott's boobies during non-breeding migration. In the austral summer at the longitudes of Indonesia, the Intertropical Convergence Zone moves south of the equator, resulting in the Indonesian–Australian monsoon (Wheeler & McBride 2005). During this period, the regional lower tropospheric prevailing winds shift from easterlies to westerlies (Wheeler & McBride 2005). This shift in the direction of prevailing winds around November–December coincides with the peak of the species' departure from Christmas Island to their non-breeding range in the east. Conversely, Abbott's boobies start their migration back west to Christmas

Island in February, at the end of the monsoon season, when the prevailing winds reverse to easterlies. The Abbott's booby individual that migrated northwest of Christmas Island to the northern point of Sumatra departed in late October, before the onset of the monsoon, and started its return migration in January, the peak of the monsoon. The 2 other birds that flew west of Christmas Island left later, in December, and probably faced the westerlies, which could explain why the maximum distances they reached were among the shortest recorded (1221 and 2137 km, against a species mean of 3001 ± 802 km). Interestingly, wedge-tailed shearwaters *Ardenna pacifica* breeding off the west coast of Australia, southeast of Christmas Island, migrate predominantly to the northwest between late April and mid-November when the prevailing winds are easterlies (Surman et al. 2018), i.e. the opposite of Abbott's booby's direction and period of migration. Our results suggest a strong relationship between the seasonal reversal of the prevailing winds and Abbott's booby migration, where birds might benefit from the wind direction to reach and come back from their non-breeding range (Thorne et al. 2023), and which requires further investigation (e.g. Adams & Flora 2010, Gibb et al. 2017, Hromádková et al. 2020, Nourani et al. 2023).

Although most failed breeders migrated 1 yr before successful breeders, the timing (day of the year) of the different phases of the migration varied little considering the species' protracted breeding cycle (ca. 17 mo). This suggests that if a breeding attempt fails

too long after the general departure date (i.e. on average, 18 November for successful breeders; Table S3), the birds remain on Christmas Island, possibly to start another breeding attempt or wait until environmental conditions are suitable for the next migration; for example, until the next favourable shift in wind directions (see above). However, information on when exactly the breeding attempts failed is not available to confirm this hypothesis.

Males reached their non-breeding range significantly faster than females but started their return migration and were back on Christmas Island at similar times. Overall, the duration of males' outbound migration was similar to their return migration. As the duration of the return migration is similar for both sexes, it seems unlikely that the slight sexual dimorphism would be the cause of the variation in duration of the outbound migration. However, differences in labour partitioning between males and females during chick rearing or post-fledging care could result in biased body mass decrease between sexes and, thus, different foraging strategies on the outbound migration, as one parent may need to recover more than the other from its breeding effort (Lormée et al. 2003, Weimerskirch et al. 2009a,b, Cornioley et al. 2016). There is little information on Abbott's booby parental roles during late chick-rearing or post fledging, but as females are slower on their outbound migrations, they may be more involved in providing for the chick during that period. Improved body condition from foraging within the non-breeding range could then explain the similar duration of return migration between males and females. Foraging parameters and body condition between male and female Abbott's boobies during early chick rearing do not differ significantly (Hennicke & Weimerskirch 2014a). However, the decline in body condition of breeding red-footed boobies *Sula sula* only differs between sexes during late chick rearing (Lormée et al. 2003), a period for which body condition data from adult Abbott's boobies is missing. Alternatively, as the spatial distribution of core areas used by males and females does not differ, temporal niche partitioning could have evolved to reduce intraspecific competition (Huffeldt et al. 2021).

No birds were recorded on migration between 17 May and 26 October, which suggests that the whole population of adult Abbott's boobies, regardless of their breeding status, is on Christmas Island during that period. This implies that population surveys conducted between these dates would estimate the entire population of adult Abbott's boobies. Accordingly, no sightings were recorded more than 500 km from

Christmas Island between 27 May and 15 September (Table S4; eBird 2023, R. Clarke unpubl. data).

Fine-scale movements of breeding Abbott's boobies during the monsoon remain unknown. From preliminary inspection of the GLS data for the birds that did not undertake a migration during that period, Abbott's boobies did not forage far enough to ascertain any difference from early chick-rearing foraging trips (max. distance recorded: 556.7 km; Hennicke & Weimerskirch 2014b) given the accuracy of geolocation (Halpin et al. 2021). The spatial scale of these movements limits further analyses with GLS data.

4.2. Habitat preference

During their migration (November–December to April), adult Abbott's boobies showed a preference for waters with a narrow range of SSS (ca. 32.5–34.5 PSU), rugged seafloor topography, and SST above ca. 28°C. This differs slightly from the oceanographic conditions in the species' breeding foraging range around Christmas Island during early chick-rearing (August–October), when birds forage in waters with an average surface temperature of 26°C (Hennicke & Weimerskirch 2014a).

Marine habitats around Christmas Island experience marked seasonal changes. During the monsoon season (November–April), landward Ekman transport resulting from the monsoon westerlies induces downwelling along the south shore of Java (Gordon 2005), which reduces the productivity of the surface water south of Java, including waters around Christmas Island (Subarna 2018, Mandal et al. 2022). In that period, the concentration of chl *a* (a proxy for marine productivity; i.e. density of phytoplankton) decreases, as does the catch of pelagic fish south of Java (Hendiarti et al. 2005, Hennicke et al. 2015, Subarna 2018, Mandal et al. 2022). This seasonal drop in marine productivity in Abbott's booby's breeding foraging range coincides with the non-breeding migration (November–April). Moreover, foraging trips of breeding Abbott's boobies during early chick rearing (August–October) are affected by variations in marine productivity, with longer and farther trips recorded when waters around Christmas Island are warmer and less productive (Hennicke & Weimerskirch 2014a). Therefore, the significant decrease in primary productivity around Christmas Island during the monsoon might be a key driver of Abbott's booby migration.

Non-breeding birds are not bound to Christmas Island; thus, they could fly to more productive waters during the monsoon. However, in that period, overall

primary productivity decreases throughout Indonesian waters (Pusparini et al. 2017, Subarna 2018, Wijaya et al. 2020), and chl *a* concentration was not found to be a predictor of migrating Abbott's booby distribution. Given that Abbott's boobies feed higher up the food chain than organisms directly benefiting from the phytoplankton blooms (Hennicke & Weimerskirch 2014a), there could be a lag or a spatial mismatch between the increase in chl *a* concentration and that of prey abundance (Grémillet et al. 2008, Chande et al. 2021, de la Cruz et al. 2021). For example, Bali sardinella *Sardinella lemuru* abundance in the Bali Strait increases 3 mo after increasing chl *a* concentrations (Sartimbul et al. 2010). Also, pigmy blue whales *Balaenoptera musculus brevicauda*, feeding lower on the food chain and migrating from the south of Australia, stay around the Banda Sea from June to September, closer to the peak of chl *a* concentration in the Banda Sea (Thums et al. 2022).

The preference of migrating Abbott's boobies for a narrow SSS range (i.e. between ca. 32.5 and 34.5 PSU), the most predictive factor of the species' migratory distribution, and for high SST (i.e. above 28°C) is likely linked to the distribution of its main prey species. During early chick rearing, the only period for which the species' diet has been well studied, Abbott's boobies feed primarily on flying fish (81% of total prey biomass) (Hennicke & Weimerskirch 2014a). The distribution of many marine organisms, including several flying fish species, is influenced by salinity. For example, the distribution of the 2 flying fish species *Cypselurus poecilopterus* and *C. callopterus* is separated by the isohaline 35 PSU (Shakhovskoy 2018), close to the upper boundary of Abbott's booby migratory habitat. The main prey species of Abbott's booby during early chick-rearing is *Exocoetus volitans* (37.5% of flying fish diet), which the birds catch in waters with SSTs averaging 26°C (Hennicke & Weimerskirch 2014a). The distribution of *E. volitans* is highly dependent on SST, with their range corresponding roughly with the 25°C isotherm (Shakhovskoy 2018). Accordingly, *E. volitans* are mainly present around Christmas Island and in the Abbott's booby migratory range during September–November (i.e. during Abbott's booby early chick rearing) and is scarce in these areas the rest of the year (Shakhovskoy 2018). As several other species of flying fish are found in and around the Banda Sea (Syahailatua & Rijoly 2021), including during the monsoon (Rehatta et al. 2021, Tuapetel & Tupan 2021), this type of prey may still form a large part of Abbott's booby's diet during migration, although the composition of prey species very likely varies from early chick rearing.

Abbott's boobies did not show a preference for deep or shallow waters but did so for rugged seafloor topography. The Banda Sea is deep, with a maximum depth of 7.2 km (Pownall et al. 2016), but is surrounded by many islands and shelf breaks. While the southern coast of Java experiences a downwelling during the monsoon, the significant number of smaller islands around the Banda Sea and the shelf breaks, situated in the Indonesian Throughflow, may locally facilitate vertical mixing of nutrients (Tai et al. 2020, Tsutsumi et al. 2020), thus improving productivity and prey abundance and/or the predictability of their distribution.

4.3. Activity patterns

Abbott's boobies spent little time in contact with water at any time of the day (i.e. dawn, daylight, dusk, and night) during their migration, with no significant differences between phenophases or sexes. They spent more time in contact with water throughout the day during their migration (median: 15%) than in their foraging trips during early chick rearing (5.9%; GPS tracking with temperature–depth recorders; Hennicke & Weimerskirch 2014a). Conversely, the proportion of time spent on water at night was lower during migration (15%) than in overnight stays at sea during early chick rearing (ca. 50%, flying the rest of the time without dives; Hennicke & Weimerskirch 2014a). Although it is not possible to distinguish time flying from resting on land with GLS data, the behaviour recorded from GPS tracking during early chick rearing suggests that migrating adult Abbott's boobies might spend a significant part of the 'dry' time at night flying.

This study is only the second to investigate the at-sea non-breeding activity of a tropical sulid (Kohn et al. 2019). Overall, the small proportion of time spent on water by Abbott's booby is comparable to that observed for non-breeding brown boobies *Sula leucogaster* (mean \pm SD: 11.1 \pm 8.2%; Kohn et al. 2019). However, results differed significantly from temperate sulids, in particular at night (e.g. more than 90% of the time on water at night for migrating northern gannets *Morus bassanus*; Garthe et al. 2012). In some populations of breeding red-footed boobies, birds occasionally raft at sea overnight, but the proportion of time has not been reported (Austin et al. 2021). The only other species of tropical sulid known to regularly overnight at sea when breeding is the Nazca booby, which spends more than 99% of the night on water (Zavalaga et al. 2012). For the out-

bound and return migrations, the small amount of time spent on water by Abbott's boobies is comparable to many species of migratory seabirds from other families (see review in Bonnet-Lebrun et al. 2021). However, most of these species spend significantly more time on water while in their non-breeding range, a pattern not observed in Abbott's boobies.

When resting on water, seabirds are susceptible to predation by subsurface predators such as sharks (Randall et al. 1988); notably, by the tiger shark *Galeocerdo cuvier* (Brooke et al. 1976), which is present in Indonesian waters (Jatmiko & Nugroho 2020). Several seabird species display behavioural adaptations to the presence of these predators. For example, pied cormorants *Phalacrocorax varius* adjust their foraging distribution in response to tiger shark density (Heithaus 2005, Heithaus et al. 2009), and Cape gannets *Morus capensis* sleeping on water at night move further offshore to avoid high densities of Cape fur seals *Arctocephalus pusillus* (Courbin et al. 2022). Nazca boobies, which spend most of the night at sea resting on water (McKee et al. 2023), present more scars on their feet than other sulid species that spend less time on water, suggesting a higher risk of predation by subsurface predators (Zavalaga et al. 2012). As chick-rearing Abbott's boobies do not forage at night (Hennicke & Weimerskirch 2014a), the little time spent on water at night by non-breeding birds could be a behavioural adaptation to avoid subsurface predators.

Abbott's boobies may also rest on land in their non-breeding distribution. If non-breeding Abbott's boobies do not forage at night, flying for 85% of the night would have a high energetic cost (Weimerskirch et al. 2003). The energetic requirements outside of the breeding period are likely to be much lower than when breeding; thus, non-breeders can spend less time foraging. It was hypothesized that the low proportion of time spent on water at night by migrating brown boobies might result from the birds resting on islands (Kohn et al. 2019). Furthermore, some populations of red-footed boobies are known to visit islands in their non-breeding distribution (Almeida et al. 2021). Abbott's boobies have been regularly observed in forested areas of Rota Island in the western Pacific Ocean, an island that supports breeding populations of brown boobies and red-footed boobies (Pratt et al. 2009, eBird 2023). Whether these observations are of immature Abbott's boobies, birds that dispersed to Rota Island, or adults from Christmas Island that only visit during their migration is not known, although the latter is within the species' capacity (cf. the maximum distance recorded in this study), and several recent sightings on Rota mention a bird carry-

ing twigs, which could be nesting material indicative of a breeding attempt (eBird 2023). If these records are of visiting adults, it would suggest that Abbott's boobies use islands in the Banda Sea and surrounding waters to rest in their non-breeding distribution. Additionally, Abbott's boobies have been observed perching on floating marine debris (van Balen 1996, eBird 2023, S. Mustoe pers. comm.), a behaviour that may result in long 'dry' periods.

4.4. Conservation implications

Results from this study identified the core area used by Abbott's booby during its migration, a key step for the identification of threats the species may be facing during this period. The core area (50% UD) during migration spreads over 3 countries (including Exclusive Economic Zones), with the majority in Indonesia (89%) followed by Timor-Leste (6%) and Australia (2%), and only a small part in international waters (3%) (Fig. 3). Most of the core area (74%) is in the Sunda Banda Seascape, an Indonesian conservation priority area at the centre of one of the world's richest marine biodiversity hotspots (Ramírez et al. 2017, Setyawan et al. 2018), 4% is in marine protected areas, and less than 1% overlaps with confirmed marine Important Bird and Biodiversity Areas.

Unlike many seabird species that migrate to remote areas of the high seas, Abbott's boobies migrate to a populated archipelago inhabited by human communities that depend highly on marine resources (Suharsono et al. 2021). This may result in high levels of harmful interaction with human activities such as competition with fisheries (Suharsono et al. 2021), incidental bycatch (Zainudin et al. 2017), and also targeted capture of Abbott's boobies (Hennicke 2012). These findings require further investigation to evaluate, and ideally quantify, the actual impact of human interactions with Abbott's boobies during migration. In addition, as their migration seems to be linked to the monsoon, climate change might affect the species' migratory movements and distribution. For example, the Indonesian–Australian monsoon is influenced by El Niño–Southern Oscillation (ENSO, D'Arrigo et al. 2006, Setiawan et al. 2017), notably by disturbing the seasonal pattern of prevailing winds (Putri et al. 2021, Iskandar et al. 2022), and climate change is predicted to increase the intensity of ENSO events (Haszpra et al. 2020, Cai et al. 2022). Hence, further research is also required to assess the impact of climate change on Abbott's booby to safeguard the long-term survival of this endangered species.

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