



Similar at-sea behaviour but different habitat use between failed and successful breeding albatrosses

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ABSTRACT: Breeding failure is expected to induce behavioural changes in central place foragers. Indeed, after a failed reproductive attempt, breeding individuals are relieved from having to return to their breeding site for reproductive duties and thus are less constrained than successful breeders in their movements during the remainder of the breeding season. Accordingly, they are expected to adjust their behaviour, travelling longer in distance and/or time to reach foraging grounds. They are also expected to use different foraging areas to decrease local intra-specific competition with successful breeders. We compared the at-sea behaviour and habitat use of successful and failed Indian yellow-nosed albatrosses nesting in Amsterdam Island, Southern Indian Ocean, during 2 chick-rearing seasons. Failed breeders exhibited the same at-sea foraging behaviour, travelling as far and as long as successful breeders. They also spent the same amount of time on their nest between at-sea trips. Nevertheless, habitat models revealed partial spatial segregation of failed breeders, which used specific foraging areas characterized by deeper and colder waters in addition to the areas they shared with successful breeders. Our study shows the importance of combining a range of analytical methods (spatial analysis, behavioural inferences with advanced movement models and habitat models) to infer the at-sea behaviour and habitat use of seabirds. It also stresses the importance of considering individual breeding status when aiming to understand the spatial distribution of individuals, especially when this information may have conservation implications.

KEY WORDS: Breeding failure · Behavioural state · Foraging behaviour · *Thalassarche carteri* · Procellariiformes · Habitat models · Inter-individual variability

1. INTRODUCTION

Seabirds are currently one of the most threatened groups of birds, with nearly 50% of all species showing a decline in population size in recent years (Croxall et al. 2012, Dias et al. 2019). Commercial fisheries are one of the greatest threats to seabirds through both competition with fisheries (Grémillet et al. 2018) and incidental mortality in fishing gear (Anderson et al. 2011, Phillips et al. 2016). Other threats include

pollution, pathogens, climate change and invasive predators, such as rats, mice and cats (Croxall et al. 2012, Phillips et al. 2016). Due to their extreme life history traits, Procellariiformes, which include albatrosses and petrels, are particularly vulnerable: they are long-lived, exhibit delayed sexual maturity and lay a single-egg clutch that cannot be replaced. Moreover, Procellariiformes are wide-ranging, and their foraging range frequently covers 100s to 1000s of km (e.g. Nicholls et al. 2002, Pinaud & Weimer-

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skirch 2007, Mackley et al. 2010, Gutowsky et al. 2014a), inevitably overlapping with fisheries (Phillips et al. 2016). Hence, understanding the spatial ecology of Procellariiformes is crucial for identifying potential threats they may face at sea.

In recent decades, the development of miniaturized tracking devices that record individual locations has provided detailed knowledge on the at-sea distribution and foraging ecology of numerous seabird species (Oppel et al. 2018). Notably, it has been shown that seabird at-sea distribution is largely driven by the distribution and abundance of prey, which is in turn determined by the biophysical environment (Weimerskirch 2007). However, at-sea distribution also strongly varies among species, populations of the same species and individuals of the same population (Phillips et al. 2017a). Intra-specific variation may depend on sex (Patrick & Weimerskirch 2014, Edwards et al. 2016), age (Lecomte et al. 2010, Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Gutowsky et al. 2014b, Weimerskirch et al. 2014) and/or other inter-individual differences (Gutowsky et al. 2015). One major factor likely to affect the at-sea distribution and foraging behaviour of seabirds is breeding status, namely whether an individual is currently succeeding or failing at reproduction (Phillips et al. 2017a). Indeed, during the breeding season, successful breeders may allocate the majority of their time to foraging for themselves and their offspring, making multiple trips between the colony and foraging areas, whereas failed breeders are not restricted in such a way and may be free to engage in longer and/or further at-sea trips (e.g. Fijn et al. 2014, Ponchon et al. 2017). Likewise, breeding failure may lead individuals to leave the colony earlier and use different wintering grounds, leading to spatial segregation during the non-breeding season (Phillips et al. 2005, Catry et al. 2013, Clay et al. 2016), with potential negative consequences on subsequent reproductive success (Desprez et al. 2018). Yet the short- and long-term consequences of breeding failure are still overlooked in movement studies because failed and non-breeders are generally more challenging to capture and track. Indeed, they are not as attached to their nesting site as successful breeders are and may leave their colony earlier (e.g. Catry et al. 2013, Ramos et al. 2018).

Identifying important seabird areas for prioritizing conservation efforts is usually based on tracking data collected from successful breeders (e.g. Delord et al. 2014, Lascelles et al. 2016, Soanes et al. 2016, Dias et al. 2017, Heerah et al. 2019), and it is only recently that other life stages have been tracked (Péron &

Grémillet 2013, Gutowsky et al. 2014b, Weimerskirch et al. 2014, de Grissac et al. 2016). However, there is still little information on at-sea movements of breeders that have failed at the egg or chick stage. In terrestrial ecosystems, several recent studies have demonstrated that conservation actions were more effective when inter-individual variation was taken into account. For example, accounting for individual differences in seasonal movement behaviours of African elephants *Loxodonta africana* resulted in the design of very different conservation corridors to enhance connectivity (Osipova et al. 2019). On the other side, accounting for individual breeding performance in noctule bats *Nyctalus noctula* (Mackie & Racey 2007) and sage grouse *Centrocercus urophasianus* (Smith et al. 2018) highlighted the need to protect distinct areas, as failed and successful breeders did not use the same habitats. Gaining information on the behaviour and habitat use of failed breeding individuals may thus help determine whether they use similar areas to successful breeders or whether they are spatially segregated and behave differently.

The Indian yellow-nosed albatross *Thalassarche carteri* inhabits the Southern Indian Ocean. On Amsterdam Island, failed breeders represent a large proportion of the population, which has been recurrently hit by avian cholera outbreaks (Weimerskirch 2004, Jaeger et al. 2018). The disease, caused by the bacterium *Pasteurella multocida*, appears to be responsible for the death of a large proportion of albatross chicks (Bourret et al. 2018, Jaeger et al. 2018, 2020). Introduced rodents likely also contribute to the low breeding success of the population (Micol & Jouventin 1995) as observed in other seabird populations worldwide (Cuthbert & Hilton 2004, Jones & Ryan 2010, Caravaggi et al. 2019, Holmes et al. 2019).

As breeding failure is overlooked in tracking studies compared to other factors such as breeding stage within the breeding season (incubation vs. chick-rearing), we investigated the at-sea behaviour and habitat use of Indian yellow-nosed albatrosses nesting on Amsterdam Island based on their breeding status during 2 chick-rearing seasons: 2015–2016 and 2018–2019. We predicted that failed breeders would perform longer trips than successful breeders, as they do not need to regularly return to the colony to feed their chick. These may be longer trips in terms of maximum distance to the colony or total distance travelled and/or in terms of trip duration since failed breeders could spend more time foraging in areas closer to the colony rather than travelling further (Votier et al. 2017). Failed and successful breeders were also predicted to forage at least partly in dis-

tinct areas that may differ in oceanographic characteristics, with failed breeders being able to target areas of high productivity that may be too far away from the colony for successful breeders (Antolos et al. 2017). Failed and successful breeders were also predicted to exhibit different activity budgets, with failed breeders spending more time resting on the water and less time flying than successful breeders (Ponchon et al. 2019). Moreover, we expected failed breeders to spend more time on their nests compared to successful breeders in order to maintain pair bonds (Hedd & Gales 2005).

2. MATERIALS AND METHODS

2.1. Study area and species

The study was carried out in a colony of Indian yellow-nosed albatrosses on Amsterdam Island (37° 86' S, 77° 52' E) during 2 breeding seasons: December 2015–January 2016 and November 2018–January 2019 (hereafter 2015 and 2018 respectively). This population holds two-thirds of the world's population, with ca. 22 000 pairs breeding each year (Heerah et al. 2019). The species annually lays a single clutch of one egg in September–October that hatches in late November or early December. Chicks fledge in March–April. The average adult apparent annual survival rate is 0.90 (Gamble et al. 2019), the average annual breeding success is 0.16 (Jaeger et al. 2018) and chick survival rate varies annually between 0.08 and 0.58, with low chick survival being correlated with the occurrence of avian cholera outbreaks (Jaeger et al. 2020). The Indian yellow-nosed albatross is currently classified as Endangered on the IUCN Red List of Threatened Species, as the population has decreased by 86.6% between 1981 and 2016 (Jaeger et al. 2018).

2.2. GPS equipment

Each study year, 2 groups of adult Indian yellow-nosed albatrosses were tracked during the early chick-rearing period. One consisted of failed breeders which had lost their eggs or young chicks ($n = 30$) and the other consisted of successful breeders ($n = 18$). Failed breeders were equipped with solar-powered GPS-UHF loggers (Harrier-L or Uria; Ecostone) which were attached to the birds' back feathers with Tesa® tape after breeding failure. The devices were programmed with an initial acquisition fre-

quency of 15 min, but this could be modified to 5, 10 or 20 min, depending on battery charge and weather conditions. When the birds were in range, location data were automatically downloaded by an antenna placed at the edge of the study colony. Failed breeders were tracked between 9 December 2015 and 11 January 2016 and between 30 November 2018 and 19 January 2019. The loggers naturally fell off after some time for those birds that could not be recaptured to retrieve the loggers.

Because they could be more easily recaptured, successful breeders were equipped with GPS devices (i-GotU GT-600; MobileAction Technology) programmed with a fixed acquisition frequency of 5 min. The loggers were attached to the back feathers with Tesa® tape. Successful breeders were tracked between 5–20 December 2015 and 30 November–26 December 2018. In 2018, GPS devices had a duty cycle of 17 h on and 7 h off at night, providing locations from 05:00–22:00 h UTC (GMT+5). All individuals were recaptured to retrieve the loggers and access the data. We had no information on the age or sex of equipped individuals.

2.3. Data analysis

As only 3 failed breeders were tracked beyond 26 December over the 2 study years, these data were excluded from the analysis, and the study periods were bounded between 5–21 December 2015 and 30 November–26 December 2018 to match the tracking period of successful breeders. Moreover, because of the important time gaps due to duty cycles in successful breeders in 2018, 2 separate data sets were used.

2.3.1. Trip characteristics and colony attendance

The first data set included all complete trips, which were composed of a minimum number of 12 consecutive locations further than 1 km from the colony for a total duration of at least 2 h, regardless the duration of time gaps within trips. It was used to calculate the general trip characteristics (maximal distance to the colony, total trip duration and total distance travelled), to retain as much data as possible and avoid discarding the longest trips, which generally had the longest time gaps for failed breeders. Trip characteristics were calculated for each trip and then averaged for each individual and eventually averaged by breeding status and year for the summary presented in Table 1. Note that because of the presence of large

time gaps in successful breeders in 2018 and failed breeders in both years, the total distance travelled is likely underestimated. Time spent in the colony between 2 at-sea trips was averaged for each individual and then averaged for each group. As the minimum trip duration for successful breeders in 2018 was 30 h, it is unlikely that colony attendance was overestimated due to the non-detection of nocturnal trips occurring during the off period of the loggers.

Linear mixed models were used to test the effects of breeding status (fixed), year (fixed) and individuals (random) on trip characteristics and colony attendance, which were square-root-transformed to improve the normality of the residuals. Power analyses were conducted with the 'simR' package (Green & MacLeod 2016) to check the statistical power of the models. Additional *F*-tests were conducted to compare variances between failed and successful breeders.

2.3.2. Individual at-sea behaviour and distribution

A second data set was used to analyse individual distribution and at-sea behaviour. First, data from failed and successful breeders in 2015 as well as data from failed breeders in 2018 were filtered to remove all trips which had time gaps >5 h. Data from suc-

cessful breeders in 2018 were filtered with a different time threshold of 8 h, to avoid discarding all trips. Then all trips from the 4 groups were linearly interpolated to 15 min intervals to address the issue of uneven sampling in time intervals, using the R package 'pastecs' (Ibanez & Grosjean 2018).

The R package 'moveHMM' (Michelot et al. 2016) was used to fit a 3-state hidden Markov model (HMM) to the at-sea interpolated location data for each year separately. The states reflected 3 different activities at sea: (1) resting, characterised by a small step length and low turning angle, (2) travelling, characterised by a long step length and low turning angle and (3) foraging, characterised by an intermediate step length and a large turning angle (Grecian et al. 2018). A set of different initial parameters was used to ensure that the global minimum in negative log-likelihood had been reached. The model was validated with the visual inspection of pseudoresiduals. The Viterbi algorithm was used to classify the most likely behaviour at each time step (Fig. 1). Finally, all locations occurring between 22:00 and 05:00 h were excluded for all 4 groups to avoid overestimating resting and travelling activities due to linear interpolation. The proportion of time spent in each activity per trip and for periods between 05:00 and 22:00 h was calculated. Mixed effects logistic regressions

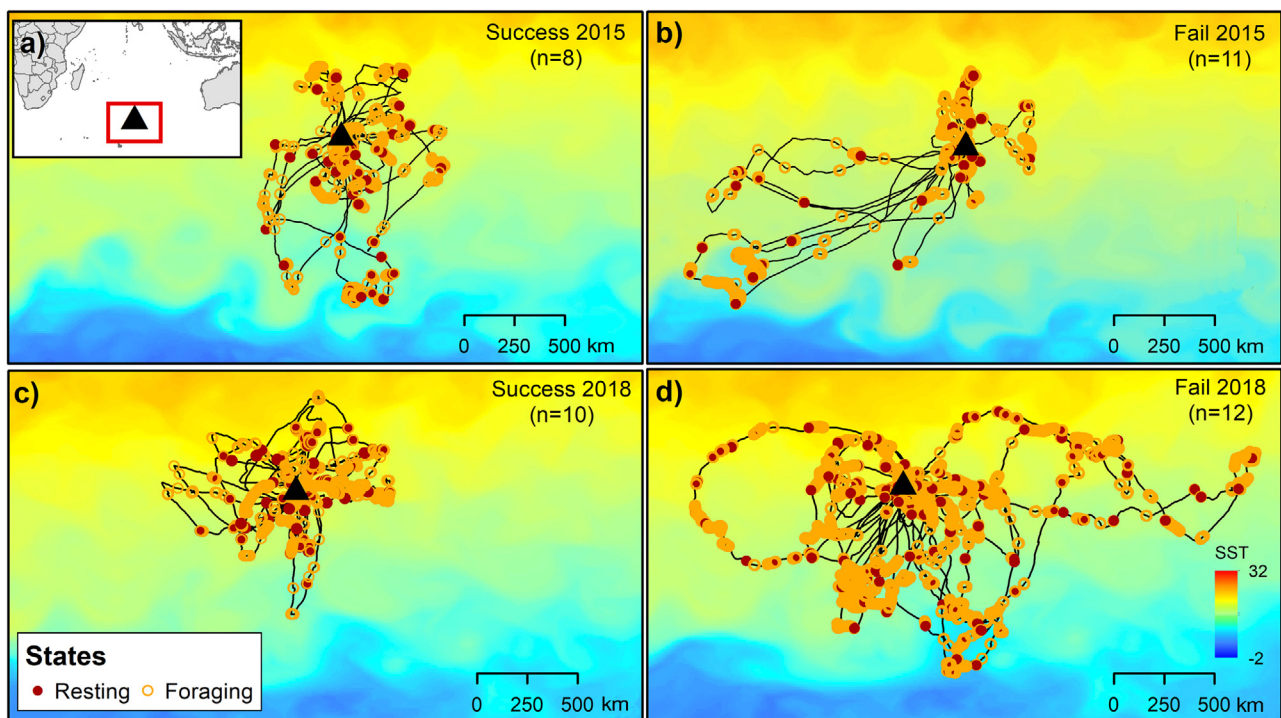


Fig. 1. At-sea locations between 05:00 and 22:00 h associated with foraging and resting states for (a,c) successful and (b,d) failed Indian yellow-nosed albatross breeders nesting on Amsterdam Island (black triangle) in 2015 and 2018. Tracks are superimposed with sea surface temperature (SST; °C)

were then used to test breeding status and year as fixed effects and individual identity as a random effect on the proportion of time spent in each of the 3 identified states.

2.3.3. Spatial analysis

At-sea distribution was inferred separately for successful and failed breeders and for each year from the calculation of the 50 and 90% utilization distribution (UD) contours, using the 'adehabitatHR' package (Calenge 2006) with a cell size of 500 m and a common smoothing factor, h , fixed at 70 km (rough average of h_{ref} values between status and year). A saturation plot showed that the tracking sample sizes for each group reached a plateau, suggesting sufficient representativeness of the different groups (see Appendix).

Spatial overlaps between the 50 and 90% UD of successful and failed breeders tracked the same year were estimated with a randomization procedure. An initial spatial overlap matrix was calculated with the 'kerneloverlap' function of the 'adehabitatHR' package, using the utilization distribution overlap index (UDOI; Calenge 2006) for each pair of individuals, regardless of their breeding performance for a given year. A second 'membership' matrix was built indicating whether a pair of individuals had the same breeding performance (coded 0) or a different breeding performance (coded 1). After removing diagonals from both matrices, a Pearson correlation coefficient (r_{obs}) was calculated between the 2 matrices. Then the distribution of each individual was randomly and independently rotated around the colony location. A new spatial overlap matrix and a new membership matrix were built, and a new Pearson's correlation coefficient (r_{rand}) was calculated. This randomization procedure was repeated 1000 times to obtain a distribution of r_{rand} representing the null hypothesis of no difference in the spatial distribution of the 2 groups (see Cecere et al. 2018 for the detailed procedure). All statistical analyses were carried out using R v.3.6.0 (R Core Team 2017).

2.4. Habitat modelling

Initially, 8 biological and oceanographic variables likely to affect seabird distribution were selected for the Southern Indian Ocean. Data for bathymetry, sea surface temperature (SST), chlorophyll a concentration (CHLA) and wind speed were obtained from

ERDDAP (<https://coastwatch.pfeg.noaa.gov/erddap>) while sea level anomalies (SLA) and eddy kinetic energy (EKE) were obtained from the Copernicus Marine Environment Monitoring Service (CMEMS; <http://marine.copernicus.eu/>). The environmental variables, which were available daily or weekly, were averaged for each of the 2 study periods (5–21 December 2015 and 30 November 2018–26 December 2018). SST and CHLA gradients (gSST and gCHLA respectively) were computed from the corresponding environmental layers using the 'terrain' function in the 'raster' package (Hijmans 2019). The final resolution of the layers was 0.1°. Prior to modelling, strongly correlated predictors were identified by estimating all pair-wise Spearman rank correlation coefficients. High correlation coefficients ($r > 0.7$) were found between SLA and SST in both 2015 and 2018 and between wind speed and SST in 2015. Therefore, SLA was excluded for 2018 and both SLA and wind speed were excluded for 2015. In 2018, gSST values were negligible (< 0.001) so this variable was also excluded. The remaining environmental layers were bathymetry, CHLA, gCHLA, SST, EKE and gSST for the 2015 models and bathymetry, CHLA, gCHLA, SST, EKE and wind speed for the 2018 models.

The presence probabilities were predicted separately for failed and successful breeders and separately for 2015 and 2018 using the software MaxEnt v.3.4.0 (Phillips et al. 2017b). Overall, 4 habitat models were built. Only locations associated with resting or foraging states were used. The 'spatially rarify occurrence data' tool in the python-based toolbox 'SDMtoolbox 2.0' for ArcGIS 10.6 (Brown et al. 2017) was used to filter the tracking data at 5 km to reduce spatial autocorrelation. Duplicated records were not removed to give more weight to cells used by several individuals. The models were replicated 50 times for each group and validated using bootstrap sampling. The predictive performance of the models was assessed using the area under the receiver operating characteristic curve (AUC), which evaluates how well model predictions discriminate locations where observations are present from background locations.

3. RESULTS

3.1. Trip characteristics and behaviour

Breeding failure was not associated with major individual behavioural changes, and this absence of change was consistent between the 2 years of tracking (Tables 1–3, Fig. 2). There was no significant dif-

Table 1. Sample size, at-sea trip characteristics and nest attendance of successful and failed Indian yellow-nosed albatross breeders in 2015 and 2018 based on the raw location data set. Results are shown as mean \pm SE (range)

	2015		2018	
	Success	Fail	Success	Fail
No. of individuals	8	13	9	14
Total no. of trips	24	29	19	42
Maximal distance from the colony (km)	340 \pm 40 (155–853)	470 \pm 70 (29–1230)	376 \pm 24 (233–631)	393 \pm 24 (24–1406)
Total distance travelled (km)	1099 \pm 141 (417–3253)	754 \pm 112 (58–2313)	1058 \pm 93 (578–2185)	1063 \pm 171 (59–4776)
Trip duration (h)	53 \pm 6 (17–171)	72 \pm 10 (4–175)	58 \pm 3 (31–89)	91 \pm 14 (5–413)
Time at nest between at-sea trips (h)	42 \pm 6 (14–116)	31 \pm 6 (1–100)	41 \pm 7 (5–76)	33 \pm 6 (0.3–115)

Table 2. Sample size and percentage of time spent in different behavioural states based on the reduced data set including locations occurring only between 05:00 and 22:00 h for successful and failed Indian yellow-nosed albatross breeders in 2015 and 2018. Results are shown as mean \pm SE

	2015		2018	
	Success	Fail	Success	Fail
Number of individuals	8	10	9	12
Number of trips	23	20	18	32
Time spent foraging per trip during day (%)	32.0 \pm 3.2	27.1 \pm 4.9	35.3 \pm 2.5	44.3 \pm 3.5
Time spent resting per trip during day (%)	20.5 \pm 3.0	25.0 \pm 3.3	25.5 \pm 5.9	25.9 \pm 2.2
Time spent travelling per trip (%)	55.6 \pm 4.1	65.3 \pm 3.8	56.7 \pm 5.8	47.8 \pm 1.8

ference between failed and successful breeders in terms of maximum distance to the colony or trip duration, although failed breeders presented greater inter-individual variability (F -test for max. distance to the colony: $F_{42,69} = 0.21$, $p < 0.001$; F -test for trip duration: $F_{42,69} = 0.10$, $p < 0.001$; Fig. 2). Note, nevertheless, that power calculation was $\leq 51\%$ for all 3 variables in 2015 and 2018, meaning that small significant differences may not have been detected.

The proportion of time spent foraging and resting between 05:00 and 22:00 h was similar (Table 2) as well as the time spent in the colony between at-sea trips (Table 1). Nonetheless, failed breeders tended to travel shorter total distances during a trip and both successful and failed breeders spent slightly more time flying in 2015 compared to 2018, although those differences were weakly significant ($p = 0.05$ and $p = 0.04$ respectively; Tables 1–3).

3.2. Observed at-sea distribution and predicted habitat use

Failed and successful breeders were not strongly spatially segregated, either in their 50 or 90% kernel UD (Fig. 3, Table 4); this

remained consistent between the 2 years of tracking (Table 4). Nevertheless, the bearing of the 2 groups when at sea was different. In 2015, successful breeders mainly used areas south of the colony, while failed breeders mainly used foraging grounds situated south-west of the colony (Figs. 1 & 3). In 2018,

Table 3. Results from the models testing the effects of Indian yellow-nosed albatross breeding status and year on trip characteristics (linear mixed models), nest attendance and time spent in 3 states (logistic regressions). Individual identity is included as a random effect. Significant results ($p < 0.05$) are in **bold**

Response variable	Explanatory variable	F or z	df	p
Maximal distance to the colony	Breeding status	0.03	110	0.86
	Year	0.31	110	0.58
Total distance travelled (km)	Breeding status	4.33	110	0.05
	Year	0.67	110	0.41
Trip duration (h)	Breeding status	1.18	110	0.28
	Year	0.73	110	0.40
Time at nest between trips (h)	Breeding status	3.23	29	0.08
	Year	0.09	58	0.77
Proportion of time spent foraging per trip	Breeding status	0.03	35	0.97
	Year	0.88	35	0.38
Proportion of time spent resting per trip	Breeding status	0	35	0.99
	Year	0	35	0.99
Proportion of time spent travelling per trip	Breeding status	0.12	34	0.90
	Year	-2.08	34	0.04

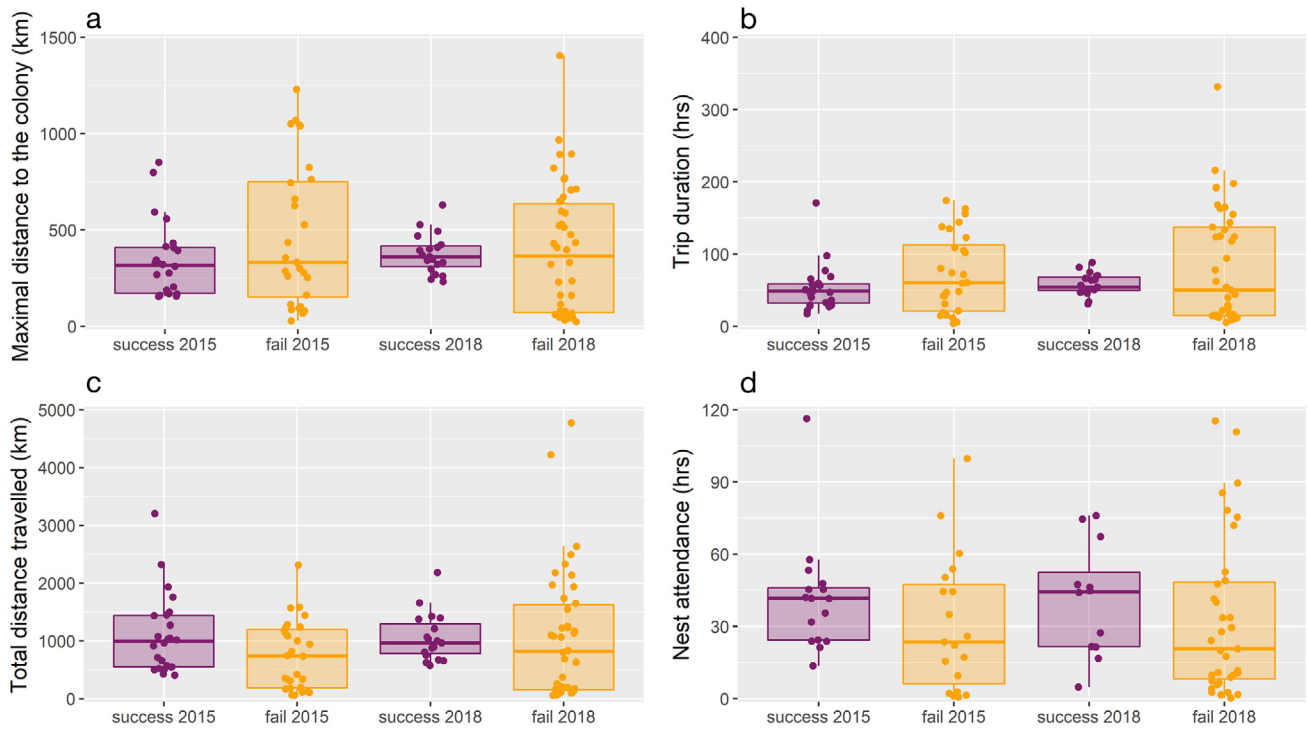


Fig. 2. Boxplots of the trip characteristics of Indian yellow-nosed albatrosses by breeding status and year. Boxplots represent the 25th to 75th percentile, while the bold line represents the median. Each dot represents a trip. (a) Maximal distance to the colony, (b) trip duration, (c) total distance travelled and (d) nest attendance

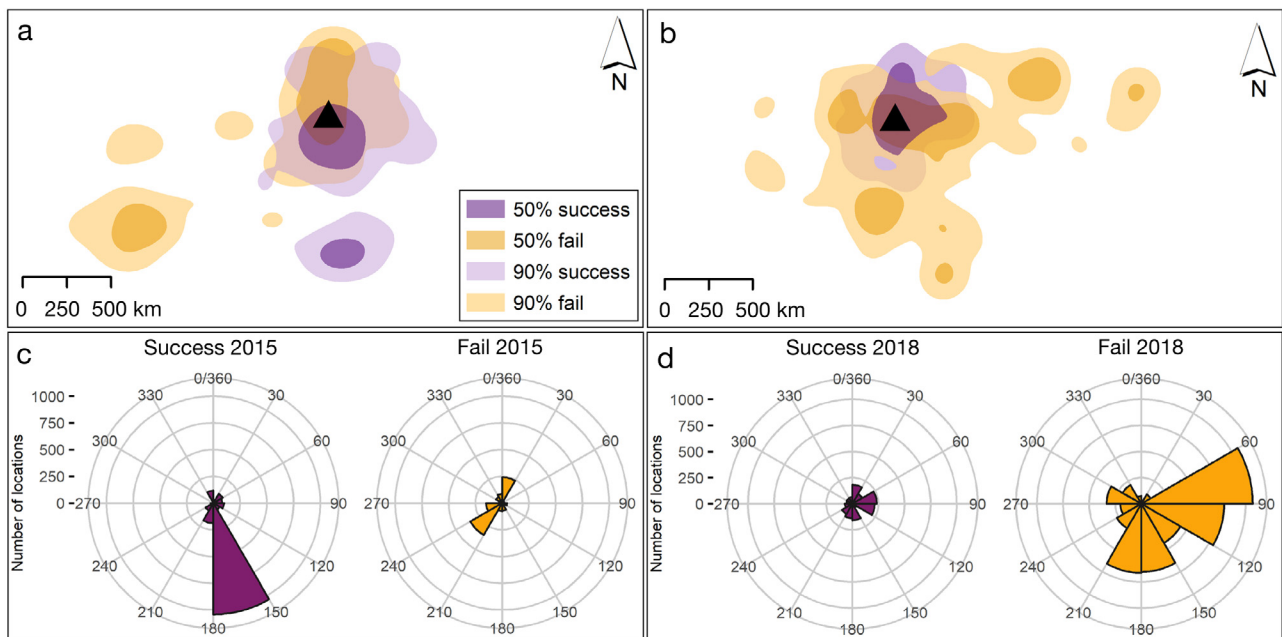


Fig. 3. (a,b) Kernel uniform distribution of foraging and resting areas used between 05:00 and 22:00 h by successful and failed Indian yellow-nosed albatross breeders nesting on Amsterdam Island (black triangle) in 2015 and 2018. (c,d) Rose diagram showing the directions of foraging and resting locations between 05:00 and 22:00 h for successful and failed breeders in 2015 and 2018. The center of each rose diagram represents the colony location, and length of each wedge reflects the number of locations in that direction. All rose diagrams have a consistent scale, with each ring representing 250 points

Table 4. Observed and randomized overlap (utilization distribution overlap index [UDOI] method) of 50 and 90 % UD between failed and successful breeders tracked the same year or between individuals with the same breeding status tracked in different years. All comparisons were non-significant ($p > 0.05$), indicating no spatial segregation between the 2 groups tested

	50% UD			90% UD		
	r_{obs}	r_{rand}	p	r_{obs}	r_{rand}	p
Success vs. failed in 2015	-0.14	-0.08 ± 0.06	0.18	-0.14	-0.10 ± 0.04	0.22
Success vs. failed in 2018	-0.07	-0.09 ± 0.06	0.67	-0.03	-0.09 ± 0.04	0.92
Success 2015 vs. success 2018	-0.07	-0.08 ± 0.08	0.53	-0.60	-0.06 ± 0.06	0.49
Failed 2015 vs. failed 2018	-0.20	-0.13 ± 0.05	0.08	-0.19	-0.17 ± 0.04	0.34

successful breeders used habitats east of the colony while failed breeders had a more variable bearing, mostly directed east and south (Figs. 1 & 3).

The 4 habitat models built from the foraging and resting locations of failed and successful breeders achieved AUC values >0.93 , indicating excellent model predictive abilities. They showed that failed and successful breeders had different habitat preferences (Fig. 4, Table 5). Failed breeders differed from successful breeders, especially in 2015, when 3 individuals used habitats with colder SST (around 10°C) that successful breeders and failed breeders in 2018

did not use (Fig. 4a). Failed breeders in 2015 also generally used habitats characterised by deeper waters (2700 and 4500 m deep), when other groups favoured depths of 1500 m (Fig. 4b). Both successful and failed breeders used habitats characterized by higher CHLA values in 2018 (Fig. 4c). While bathymetry was the most important variable for successful breeders in 2015, SST was still significant. On the contrary,

the 2 most important variables for failed breeders were SST and CHLA (Table 5); gSST and gCHLA, EKE and wind speed contributed $<10\%$ to individual distribution (Table 5).

The predictions obtained from the habitat models showed that failed and successful breeders were likely to be encountered in different areas (Fig. 5). In 2015, while successful breeders were predicted to be found mostly east of the colony (up to 1200 km but also in a 300 km range around the colony except west; Fig. 5a), failed breeders were predicted to substantially favour areas up to 300 km north-east of the

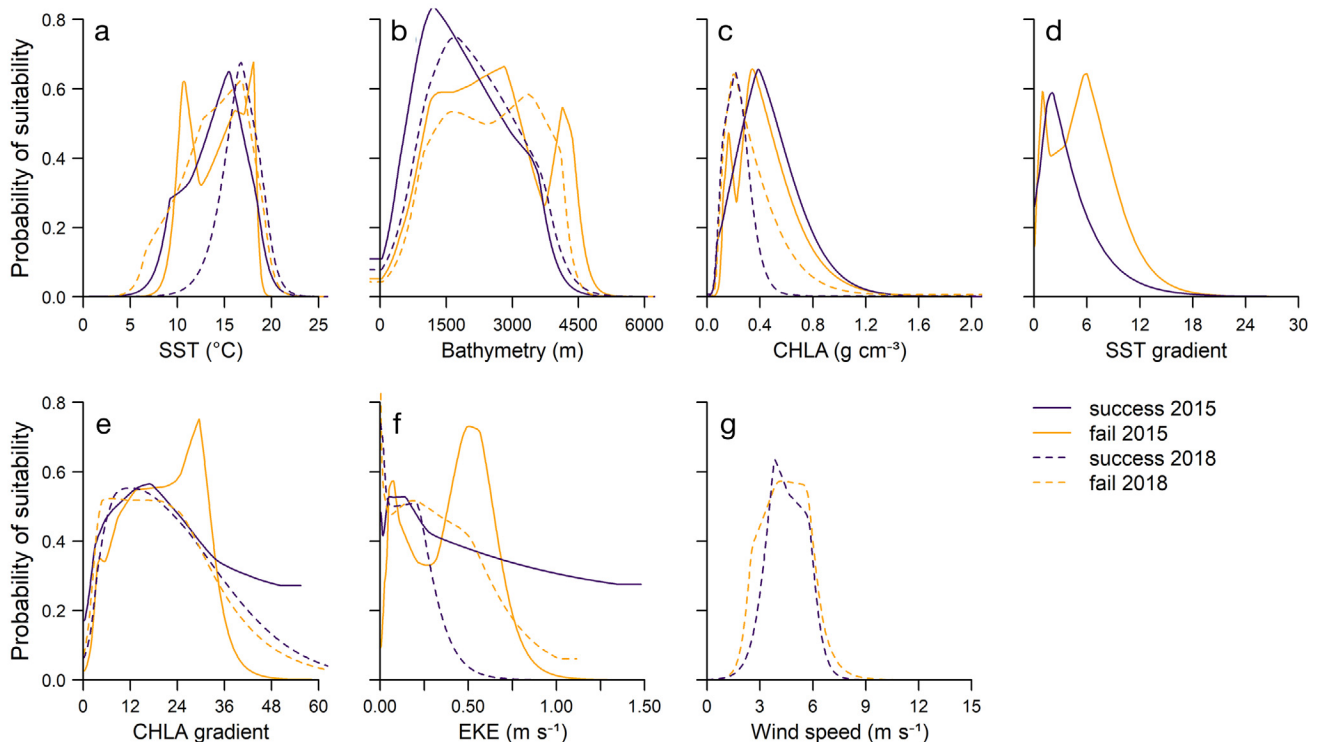


Fig. 4. Response curves obtained from the habitat models for each environmental variable for successful and failed Indian yellow-nosed albatross breeders in 2015 and 2018. Models were built from resting and foraging locations between 05:00 and 22:00 h. (a) Sea surface temperature (SST), (b) bathymetry, (c) concentration of chlorophyll a (CHLA), (d) SST gradient, (e) CHLA gradient, (f) eddy kinetic energy (EKE) and (g) wind speed

Table 5. Relative contribution (in %) of each environmental variable in individual distribution from 05:00–22:00 h based on resting and foraging locations obtained from a jackknife resampling. SST: sea surface temperature; CHLA: chlorophyll *a* concentration; gCHLA and gSST: gradient of CHLA and SST respectively; EKE: eddy kinetic energy. The most important variable for each group is indicated in **bold**

	—2015—		—2018—	
	Successful	Failed	Successful	Failed
SST	26.8	30.1	40.5	32.9
CHLA	18.5	28.5	20.8	30
Bathym	48.4	21.6	30.6	20.1
Wind speed	–	–	6.6	15.2
gCHLA	1.7	8.3	0.5	0.6
gSST	2.4	6.4	–	–
EKE	2.2	5.2	1	1.2

colony, as well as areas west and south-west of the colony, up to 1200 km (Fig. 5b). In 2018, successful breeders were still predicted to use areas east and north-east of the colony but presence probabilities were slightly lower (Fig. 5c). On the contrary, failed breeders were predicted to be found in a larger area than in 2015 but with lower probabilities (Fig. 5d). Nevertheless, they were still predicted to visit the

same area 1200 km south-west of the colony, an area that was never used by successful breeders.

4. DISCUSSION

4.1. At-sea behaviour

Contrary to our predictions, we did not find any major difference in the at-sea behaviour between failed and successful breeders, neither in 2015 nor in 2018. The tracked failed individuals shared the same trip characteristics and the same amount of time foraging, travelling or resting on the water as successful breeders. A recent study on black-browed albatrosses *Thalassarche melanophris* reported a difference in the time spent in foraging, resting and flying activities between successful and failed breeders when at sea, especially during daylight (Ponchon et al. 2019). However, this difference appeared later in the breeding season in that species, when the chicks were >3 mo old. Here, our tracking period mostly covered the early chick-rearing period, while chicks were <2 mo old. This suggests that during our study period, breeding individuals may not yet have paid a

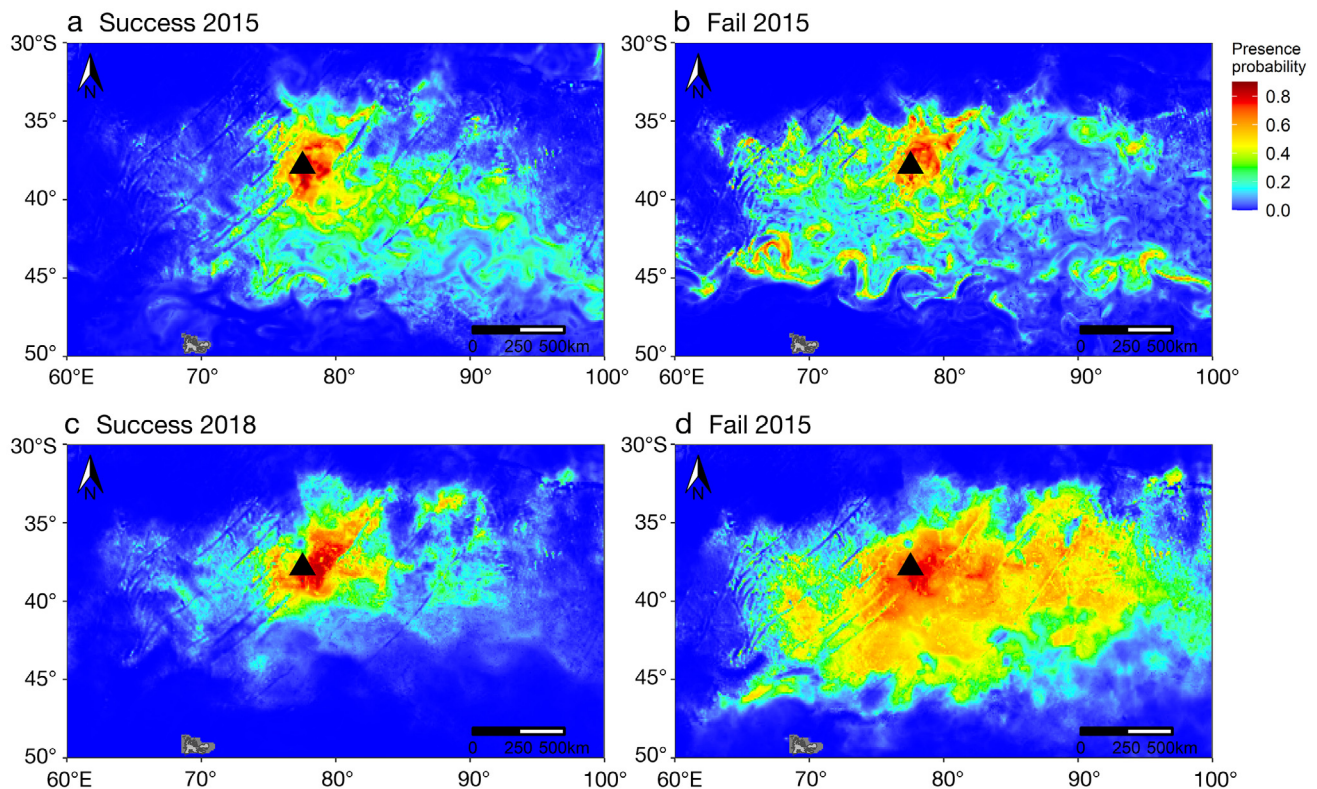


Fig. 5. Predictions of foraging and resting habitat suitability obtained from the habitat models built for successful and failed Indian yellow-nosed albatross breeders in 2015 and 2018. Black triangle: the nesting colony on Amsterdam Island

strong cost for reproduction and thus they did not have to forage more than failed breeders to be able to both feed their chick and maintain their own body condition. Alternatively, the foraging conditions were potentially good enough to prevent detecting any effect of reproductive cost on the variables we measured at that time of the breeding season.

Moreover, we had expected failed breeders to spend more time at sea, resting on the water or exploring foraging areas situated further away from their colony. But they did not. They travelled only slightly shorter total distances over a trip, although this is likely an underestimation due to the presence of long gaps that have been interpolated. Although they did not have to invest in reproduction any further, failed breeders did not change their at-sea behaviour, spending the same amount of time at sea as successful breeders. Nevertheless, they tended to go to sea more frequently than successful breeders and spent 28% less time on their nest between trips on average. Maintaining some nest attendance even after breeding failure shows that the birds are still attached to their nesting site, possibly due to the necessity of maintaining a pair bond with their mate.

4.2. Spatial distribution and habitat use

Failed and successful breeders were not significantly spatially segregated in either year. All the tracked birds mostly foraged in the same areas, on average 300–500 km away from the colony. This range is more restricted than that measured during incubation in successful breeders (Pinaud & Weimerskirch 2007, Antolos et al. 2017), but range contraction is frequent among albatrosses between incubation and chick-rearing (Weimerskirch et al. 1993, Awkerman et al. 2005, Heerah et al. 2019). Habitat models nevertheless revealed differences in the habitat preferences, and thus the predicted at-sea distribution, between failed and successful breeders. Although the tracked birds shared most of their foraging areas, failed breeders had a larger predicted distribution. In particular, failed individuals in 2015 differed from the 3 other groups as they used foraging areas characterized by colder and deeper waters, possibly associated with the Subtropical and Subantarctic Fronts (Pinaud et al. 2005). Successful breeders mainly foraged in habitat of $\sim 15^{\circ}\text{C}$, which aligns with the findings of a previous study that tracked individuals from the same colony (Antolos et al. 2017). Likewise, depth, SST and CHLA showed the strongest correlation with Indian yellow-nosed

albatross at-sea distribution during the chick-rearing season, as in successful Indian yellow-nosed albatrosses breeding in Prince Edward Island (Makhado et al. 2018). On the contrary, EKE, gSST and gCHLA, which are generally used as proxies for indicating the presence of fronts and eddies (Bost et al. 2009), were weakly correlated. This suggests that the birds were not specifically attracted by areas showing such oceanographic features, assumed to be important for marine top predators (Bost et al. 2009, Scales et al. 2014).

Overall, the at-sea distribution and behaviour of Indian yellow-nosed albatrosses nesting on Amsterdam Island were consistent between years. An absence of clear spatial segregation suggested that the marine habitats used by Indian yellow-nosed albatrosses were productive enough to provide food for the whole colony, regardless of their breeding status, and that individuals favoured foraging areas close to their colony (Pinaud et al. 2005). Nevertheless, failed breeders showed some flexibility, as they also used areas that successful breeders did not reach. Interestingly, those areas are not farther away from the colony so they would presumably still be accessible to successful breeders. At the same time, as the levels of breeding failure are high in our study colony, most successful breeders become failed breeders over the breeding season, thereby decreasing competition between successful and failed breeders. Further information on diet, i.e. through stable isotopes, should be investigated to determine whether failed and successful breeders use different habitats but feed on the same prey species or whether each breeding group partly segregate both in space and diet.

Although we did not initially find any major difference in the at-sea behaviour or distribution between failed and successful breeders, we did find a difference in habitat preferences, revealed by the habitat models. Failed breeders were predicted to have larger distributions compared to successful breeders because they could use additional foraging areas characterized by deeper and colder waters. Those results show the importance of combining a range of analytical methods (spatial analysis, behavioural inferences with advanced movement models, habitat models) to infer the at-sea behaviour and habitat use of seabirds. Here, habitat models brought crucial additional information that behavioural and statistical analyses alone would have not highlighted.

Our study presents some limitations, however, that future studies might seek to address. Apart from the 7 h time gaps in the data for successful breeders in 2018 due to the duty cycles, data in failed breeders

also had several long time gaps. We limited biases by removing all trips containing gaps longer than 5 h. Nevertheless, fitting a movement model on interpolated data can lead to overestimations in resting or travelling, as interpolated trajectories are straighter than non-interpolated data. Moreover, the distributions presented here correspond to areas used mostly during daylight, between 05:00 and 22:00 h, so some foraging and resting areas might have been overlooked. Nevertheless, the UD kernels and the predicted distributions are relatively homogeneous, suggesting that the identified areas are likely used as much at night as during the day. Another limitation is that we do not have information on the exact age or sex of the tracked individuals, except that they are sexually mature and actually breed. It is thus theoretically possible that the small differences observed in the predicted distribution obtained from habitat models might be due to another factor such as age or sex. However, to date, no study has shown that sex or age lead to partial spatial segregation in Indian yellow-nosed albatrosses (Pinaud et al. 2005, Antolos et al. 2017, Makhado et al. 2018), so breeding failure is a likely factor to explain the observed patterns.

4.3. Conservation implications

In the present study, we only investigated the effects of breeding status during early chick-rearing, when individuals are still bound to their colony. Further studies are needed to determine whether breeding failure has longer-term effects on individual behaviour and habitat use, especially regarding carry-over effects on the subsequent non-breeding season and future reproductive performance. So far, some studies have concurrently tracked failed and successful breeding procellariiforms over winter, and each has provided contrasting results both in terms of spatial distribution and at-sea behaviour (Phillips et al. 2005, Catry et al. 2013, Clay et al. 2016, Desprez et al. 2018, Ramos et al. 2018, Ponchon et al. 2019). This poses major challenges in terms of conservation given the spatial scales procellariiforms are able to cover during the non-breeding season (Lascelles et al. 2016, Carneiro et al. 2020). Moreover, breeding failure is very common in our study population, and the proportion of failed breeders can rapidly increase over the breeding season, sometimes leading to complete breeding failure in the colony (Jaeger et al. 2018). Food shortage, major climatic extreme events and disease outbreaks can episodically lead seabird populations to massive breeding

failures (Ponchon et al. 2014, Barbraud et al. 2015, Jaeger et al. 2018, Ropert-Coudert et al. 2018, Piatt et al. 2020). Punctual breeding failures may not directly affect population persistence. Nevertheless, in the long term, several consecutive breeding failures may modify individual at-sea behaviour and distribution, which may expose individuals to greater threats encountered at sea (Heerah et al. 2019). It may also induce carry-over effects that may ultimately affect population dynamics and viability through reduced productivity and annual survival. This is why there is a pressing need to more thoroughly address inter-individual variability by including individual breeding status—in addition to breeding stage (juveniles, immatures or adults) or sex—in tracking studies to better predict individual spatial distribution and at-sea behaviour and ultimately mitigate threats to the entire population.

Data availability. GPS data are deposited on the Movebank website (program ECOPATH, Indian yellow-nosed albatross, managed by T. Boulonier), and all statistical analyses can be found on the GitHub repository (https://github.com/auponchon/yna_15_18_analysis).

Acknowledgements. We are grateful to Nicolas Giraud, Augustin Clessin, Marine Quintin, Hélène Le Berre and Vincent Bourret for their help in the field and Marine Bély for her help in designing the study. We also thank Vilma I. Ahtiainen for her preliminary analyses on the tracks 2015. Finally, we thank the work of 3 anonymous reviewers who provided constructive comments to improve the analyses and manuscript. This work was supported by the French Polar Institute (IPEV) programs ECOPATH-1151 and ORNI-THOECO-109, Réserve Nationale des Terres Australes Françaises, Zone Atelier Antarctique et Terres Australes and OSU OREME. The experimental design was approved by the Comité de l'Environnement Polaire and the French Ministry of Research (04939.03). This paper is a contribution of the Plan National d'Action Albatros d'Amsterdam. A.P. benefited from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No. 753420 (EcoEvoProspectS project).

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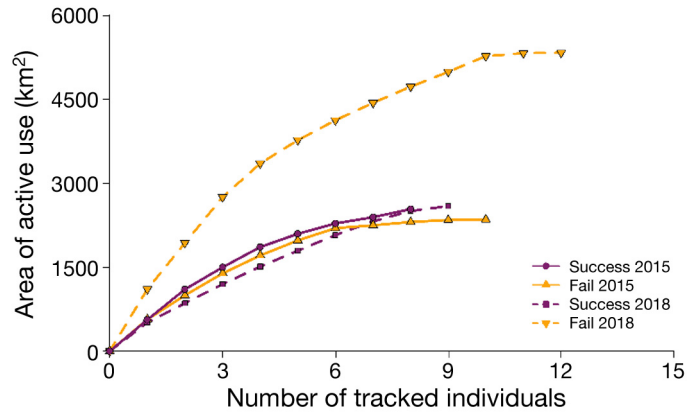
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Appendix.

Representativeness of the number of tracked Indian yellow-nosed albatross individuals used to calculate utilization distribution kernels. This sample size is based on an interpolated data set which contains locations recorded only between 05:00 and 22:00 h



*Editorial responsibility: Rory Wilson,
Swansea, UK
Reviewed by: 3 anonymous referees*

*Submitted: March 4, 2021
Accepted: August 30, 2021
Proofs received from author(s): November 6, 2021*