

 <p>Agreement on the Conservation of Albatrosses and Petrels</p>	<p>Joint Twelfth Meeting of the Seabird Bycatch Working Group and Eighth Meeting of the Population and Conservation Status Working Group</p> <p><i>Lima, Peru, 8 August 2024</i></p> <p>Rafting behaviour of albatrosses and petrels</p> <p><i>Eleanor Kowalska O'Neil, Caitlin. K. Frankish and Richard. A. Phillips</i></p>
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SUMMARY

Seabirds often spend time on the water in the vicinity of their breeding colonies at the start or end of foraging trips, which may be for bathing, social interaction, information transfer, or to reduce predation risk for small petrels that prefer to return to land in darkness. We used GPS and immersion data collected over multiple years to investigate rafting behaviour of Wandering, Black-browed, Grey-headed and Light-mantled Albatrosses and White-chinned Petrels. Nearly all tracked birds (89 %) landed within 10 km of the colony at the start of foraging trips for ~30 mins, whereas only 17% did so at the end, suggesting they likely use rafting mainly for plumage maintenance after extended breeding shifts on land. The duration, distance, and bearings of near-colony landings varied markedly according to species, wind speeds and period of the day (daylight vs. darkness), which may reflect differences in foraging direction, time constraints, degree of plumage soiling, diel activity patterns or the requirement for high wind speeds to depart from and return to the colony. Given that most individuals make extensive use of nearshore waters during the breeding season, effective marine spatial planning is required that eliminates or mitigates human risks around their colonies.

RECOMMENDATION

That the Seabird Bycatch and Population and Conservation Status Working Groups recommend Parties implement measures to reduce risks to rafting albatrosses and petrels, including reductions or prohibitions on shipping, carriage of heavy fuel oil, commercial or recreational fishing, and other activities that cause disturbance within 10km of breeding colonies.

Comportamiento de flotación en grupo de albatros y petreles

RESUMEN

Las aves marinas a menudo pasan tiempo en el agua en las cercanías de sus colonias de reproducción al comienzo o al final de los viajes de alimentación, que pueden dedicar a bañarse, interactuar socialmente, transmitir información o para reducir el riesgo de depredación de pequeños petreles que prefieren regresar a tierra en la oscuridad. Utilizamos datos de GPS e inmersión recopilados durante varios años para investigar el comportamiento de flotación en grupo de *Diomedea exulans*, *Thalassarche melanophris*, *Thalassarche chrysostoma* y *Phoebetria palpebrata* y *Procellaria aequinoctialis*. Casi todas las aves a las cuales se hizo seguimiento (89 %) aterrizaron a menos de 10 km de la colonia al comienzo de los viajes de alimentación durante aproximadamente 30 minutos, mientras que solo el 17 % lo hizo al final, lo que sugiere que probablemente usan la flotación en grupo principalmente para el mantenimiento del plumaje después de períodos de reproducción prolongados en tierra. La duración, la distancia y la orientación de los aterrizajes cercanos a las colonias variaron marcadamente según la especie, la velocidad del viento y el período del día (luz diurna vs. oscuridad). Esto puede reflejar diferencias en la dirección de búsqueda de alimentos, las limitaciones de tiempo, el grado de suciedad del plumaje, los patrones de actividad nocturnal o el requisito de altas velocidades del viento para salir de la colonia y regresar a ella. Dado que la mayoría de los individuos hacen un uso extensivo de las aguas cercanas a la costa durante la temporada de reproducción, se requiere una planificación espacial marina eficaz que elimine o mitigue los riesgos humanos alrededor de las colonias.

RECOMENDACIÓN

Que los Grupos de Trabajo sobre Captura Secundaria de Aves Marinas y Población y Estado de Conservación recomienden a las Partes que implementen medidas para reducir los riesgos para los albatros y petreles que practican la flotación en grupo, incluidas las reducciones o prohibiciones de la navegación, el transporte de fueloil pesado, la pesca comercial o recreativa y otras actividades que causen perturbaciones en un radio de 10 km de las colonias de reproducción.

Comportement de nage en groupe chez les albatros et les pétrels

RÉSUMÉ

Les oiseaux de mer passent souvent du temps sur l'eau à proximité de leurs colonies de reproduction au début ou à la fin des voyages de recherche de nourriture, pour se baigner, interagir socialement, partager des informations ou, dans le cas des petits pétrels qui préfèrent retourner à terre dans l'obscurité, pour réduire le risque de prédation. Nous avons utilisé les données GPS et d'immersion recueillies sur plusieurs années pour étudier le

comportement de nage en groupe (rafting) des *Diomedea exulans*, *Thalassarche melanophris*, *T. chrysostoma*, *Phoebetria palpebrata* et *Procellaria aequinoctialis*. Presque tous les oiseaux suivis (89 %) se sont posés pendant ~30 minutes à moins de 10 km de la colonie au début des voyages de recherche de nourriture, contre seulement 17 % à la fin, ce qui suggère que les moments de nage en groupe sont probablement surtout utilisés pour l'entretien du plumage après de longues périodes de reproduction sur terre. La durée, la distance et la localisation des moments passés à proximité de la colonie varient considérablement selon l'espèce, la vitesse du vent et la période de la journée (jour ou obscurité), ce qui peut refléter des différences dans la direction de l'alimentation, les contraintes temporelles, le degré de souillure du plumage, les profils d'activité quotidienne ou la nécessité d'une vitesse de vent élevée pour quitter la colonie et y revenir. Étant donné que la plupart des individus utilisent beaucoup les eaux littorales pendant la saison de reproduction, une planification spatiale marine efficace est nécessaire pour éliminer ou atténuer les risques anthropogéniques autour des colonies.

RECOMMANDATION

Que les groupes de travail sur les captures accessoires et sur l'état de la population et de la conservation recommandent aux Parties de mettre en œuvre des mesures pour réduire les risques pour les albatros et les pétrels lors des moments de nage en groupe, notamment par le biais de réductions ou d'interdictions de la navigation, du transport de mazout lourd, de la pêche commerciale ou récréative et d'autres activités sources de perturbations à moins de 10 km des colonies de reproduction.



Rafting behaviour of albatrosses and petrels at South Georgia

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Abstract

Seabirds often spend time on the water in the vicinity of their breeding colonies at the start or end of foraging trips, which may be for bathing, social interaction, information transfer, or to reduce predation risk for small petrels that prefer to return to land in darkness. Although such behaviour (hereafter rafting) is common, there are few data on variation in its incidence or timing across species, or analyses of relationships with intrinsic or extrinsic factors such as breeding stage (reflecting central-place foraging constraints) or weather. Here, we use GPS and immersion data collected over multiple years at Bird Island, South Georgia, to investigate rafting behaviour of four albatross and one burrow-nesting petrel species. Nearly all tracked birds (89%) landed within 10 km of the colony at the start of foraging trips for ~ 30 min, whereas only 17% did so at the end, suggesting they likely use rafting mainly for plumage maintenance after extended breeding shifts on land. Rafting duration, distance and bearing from the colony varied markedly according to species, wind speeds and period of the day (daylight vs. darkness), which may reflect differences in foraging direction, time constraints, degree of plumage soiling, diel activity patterns, or the requirement for high wind speeds for efficient flight. Given that all the study populations are decreasing, and most individuals make extensive use of nearshore waters during the breeding season, effective marine spatial planning is required that eliminates or mitigates human risks around their colonies.

Keywords Seabird • Tracking • Behaviour • Rafting

Introduction

Many seabird species are known to spend time on the sea surface in the vicinity of their breeding colonies either at the start or end of foraging trips. This behaviour is usually considered to serve one or more of the following functions: bathing, social interaction, information transfer, or reducing predation risk (Wilson et al. 2009; Weimerskirch et al. 2010; Carter et al. 2016; Granadeiro et al. 2018; Richards et al. 2019). As seabirds often breed in dense colonies where their plumage can become soiled from nest or burrow maintenance, guano from neighbours, windblown particles, etc.,

bathing before the commute to foraging grounds allows individuals to clean their feathers, maintaining waterproofing and improving flight efficiency (Granadeiro et al. 2018; Sánchez-Román et al. 2019). Birds may have been at the colony for days without access to water, and so may also land on the sea straight after departure to drink and rehydrate (Weimerskirch et al. 2010; Granadeiro et al. 2018). According to the Information Centre Hypothesis (Ward and Zahavi 1973), aggregations of rafting birds may serve as sources of social information, helping individuals to find mates (Daniels et al. 1994), make decisions about where to recruit (Halley et al. 1995), or signal the direction of profitable patches of prey (Weimerskirch et al. 2010).

Rafting on the colony at the end of the foraging trip is likely to serve different functions. According to the Self-Herd Principle (Hamilton 1971), temporary animal aggregations which are not the consequence of aggregated resources such as food should provide adaptive benefits to individuals. Most small petrels prefer to return to land in darkness to reduce predation risk, and it is logical that a bird which returns close to the colony towards the end of the day should raft there until after twilight has ended. Indeed, Scopoli's

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shearwater *Calonectris diomedea* extend the duration of their incoming rafting bouts to delay return to their burrows until after the moon has set (Rubolini et al. 2015). Regardless of whether it is daylight or darkness, rafting would also be adaptive if it improves coordination of return onto land by waves of individuals, leading to swamping of predators or kleptoparasites (Le Corre and Jouventin 1997; Wilson et al. 2008).

As a very large proportion of birds from a seabird population may engage in rafting (Granadeiro et al. 2018), waters close to the colony may be of high conservation value and require stringent management regimes to reduce anthropogenic risks. Seabirds are among the most threatened groups of birds due to their extreme life histories, colonial breeding habits and extensive at-sea distributions, all of which expose them to numerous hazards, including invasive alien species, incidental mortality (bycatch) in fisheries, climate change and disease (Dias et al. 2019; Phillips et al. 2022). Tracking of seabirds has been key to identifying areas of intensive use at sea that require protection (Le Corre et al. 2012; Lascelles et al. 2016; Hays et al. 2019; Beal et al. 2021). However, these efforts have largely focussed on detecting where seabirds forage, which can be at considerable distances from colonies, even during the breeding season (Frankish et al. 2020a; Fayet et al. 2021; Soanes et al. 2021). Determining the proportion of a population that rafts, where and for how long, is thus a priority for identifying key areas for birds, and for informing spatial planning such as the implementation of marine extensions to Specially Protected Areas (Wilson et al. 2009).

In this study, we investigated rafting behaviour in four surface-nesting albatrosses and one large, burrow-nesting petrel species breeding at South Georgia: wandering albatross (*Diomedea exulans*), black-browed albatross (*Thalassarche melanophris*), grey-headed albatross (*Thalassarche chrysostoma*), light-mantled albatross (*Phoebastria palpebrata*) and white-chinned petrel (*Procellaria aequinoctialis*). This island group supports globally important populations of all these species (12–50% of breeding pairs, worldwide; Phillips et al. 2016). All these populations have large foraging ranges during the breeding and non-breeding seasons, and have undergone major declines since the 1980s largely because of bycatch in fisheries, and to a lesser extent oceanographic change (Berrow et al. 2000; Pardo et al. 2017; Poncet et al. 2017). To date, rafting behaviour in these species has only been characterised in black-browed albatrosses at the Falkland Islands (Granadeiro et al. 2018). However, albatrosses, petrels and other seabirds often show extensive variability in their at-sea behaviour according to intrinsic and extrinsic variables (for a review see Phillips et al. 2017). We used GPS and immersion data from tracking of breeding birds from 2008 to 2019 to identify the first and last periods spent on the sea surface during foraging trips, and

determine how the characteristics (duration, distance and bearing from the colony) of these rafting periods varied with species, breeding stage, sex, year and time of day. In addition, as these species are reliant on wind for efficient flight (Weimerskirch et al. 2000; Wake et al. 2009; Clay et al. 2020), we investigated potential effects of wind speeds on the duration of rafting bouts, hypothesising that low wind speeds, i.e. sub-optimal flight conditions, lead birds to raft for longer.

Methods

Data collection

Fieldwork was carried out at Bird Island, South Georgia (54°00 S, 38°03 W) on wandering albatrosses (January–March 2012, March–April 2015 and March 2019), black-browed albatrosses (January–March 2008, January 2010, December 2014–January 2015 and January 2019), grey-headed albatrosses (December 2009–January 2010), light-mantled albatrosses (December 2009–January 2010 and December 2014–January 2015) and white-chinned petrels (December 2014–January 2015). Typically, 8–40 birds in each breeding stage (incubation, brood-guard or post-guard chick-rearing) and year were fitted with a GPS logger (i-gotU GT-120, Mobile Action Technology Inc., New Taipei City, Taiwan, or MiniGPSlog or MicroGPSlog, earth & Ocean Technology, Kiel, Germany), attached with Tesa fi tape to mantle feathers, and a combined Global Location Sensor (GLS)-immersion logger (Intigeo C250; Migrate Technology Lt, Cambridge, UK) fitted with cable-ties to a plastic ring on the tarsus. The GPS loggers were programmed with a 5–30-min sampling regime, and the GLS-immersion loggers tested for saltwater immersion every 3 s and recorded the time of transition between wet/dry states that lasted ≤ 6 s. Attachment of devices took < 12 min. Instrument loads (0.2–2.0% of body mass) were well below the threshold where deleterious effects might be expected, and there was no indication that mean foraging trip durations or chick meal mass was affected (Phillips et al. 2003, 2005). For further details see Wake et al. 2012, Scales et al. 2016, Clay et al. 2019, 2020; Frankish et al. 2020a, b.

Foraging trip departure and arrival times were estimated to be halfway between the time of the first or last GPS fix at sea, and the previous or subsequent GPS fix at the colony, as appropriate. Occasionally, an adult in the brood-guard or post-guard periods would feed the chick, depart, then return and feed again within the course of a few hours. During this time, the bird was probably close to the colony but not actively foraging, and we therefore only considered absences of > 6 h as foraging trips (following Weimerskirch et al. 1997; Phillips et al. 2003). GPS data were run with

an iterative forward/backward averaging filter to remove any locations which required sustained flight speeds above 90 km.h^{-1} (McConnell et al. 1992), and then linearly interpolated to 1-s intervals and matched with the immersion data to determine where birds had landed on the water surface.

Identification of rafting behaviour

To characterise potential rafting behaviour, we extracted the timings and locations of the first and last major landing event to occur during the outgoing and incoming portion of individual foraging trips. Following Edwards et al. (2007), a landing event (or wet bout) was considered to start when an immersion logger was wet for $> 30 \text{ s}$ (to exclude instances when the leg might have been immersed briefly during flight) and to end before a dry period that lasted $> 30 \text{ s}$ (to exclude brief flights). The duration, distance and bearing from the colony of the first and last wet bouts were calculated for every foraging trip. Bearing was calculated using function `earth.bear` in R package `fossil` (Vavrek and Vavrek 2020). Every bout was also assigned from the start time to daylight (day) or darkness (night) using function `crepuscule` in R package `maptools` package to determine the timing of civil twilight (when the sun is 6 degrees below the horizon; Bivand and Lewis-Koh 2017).

Outliers in terms of distance and duration of wet bouts from the colony were removed from the dataset if they had a z-score > 3 (Benhadi-Marín 2018). Five tracks which had incomplete GPS data because of battery or other device failure were also removed. Some birds were tracked for multiple trips, and so to avoid pseudoreplication a single trip was selected at random using the `slice_sample` function in R package `dplyr` (Wickham and Muller 2018). Although there was some variation in GPS sampling interval, degrading the fixes collected more frequently to a 30-min interval made no significant difference to the mean values for distance, duration and bearing of wet bouts relative to the original dataset, suggesting that GPS sampling resolution had minimal effect on our results (see section S1 in Online Resource 1).

To determine whether wind conditions influenced the durations of first and last wet bouts, wind speeds were computed from hourly zonal and meridional wind speed components downloaded from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis dataset (<https://doi.org/10.24381/cds.adbb2d47>; accessed June 2020). This variable was available at a 0.25° spatial resolution, corresponding to around $15\text{--}25 \text{ km}$ at the latitudes used by tracked birds, and was projected using a Lambert azimuthal equal-area projection centred at 90°S and 38°W . Covariate values were then extracted at each wet bout location.

Statistical analysis

Durations and distances of first and last wet bouts were non-normal in distribution (Shapiro–Wilk normality tests: $n = 258$, 265 , $0.12 < W < 0.69$, all $p < 0.0001$), and therefore non-parametric statistics were used to investigate differences in these variables between species, daylight vs. darkness, breeding stages (within species), sex and year. A paired Wilcoxon signed-rank test was used to determine whether the duration and distance to Bird Island of first wet bouts differed from those of last wet bouts within individual foraging trips, and a Moore's test for paired circular data was used to compare the mean bearings (Moore 1980). Those analyses were only conducted for birds for which characteristics of first and last wet bouts were available ($n = 252$). Kruskal–Wallis non-parametric analysis of variance tests, followed by post hoc multiple comparison tests were used to test for effects of daylight vs. darkness, species, breeding stage (within species), sex and year on the durations and distances of first and last wet bouts from land, and Watson's non-parametric homogeneity of means test was used to test for effects of these variables on bout bearings (Pewsey et al. 2013). As sample sizes for the comparison of wet bouts in daylight vs. darkness were low (see Table 1), an equal number in each group per species was selected at random using function `slice_sample` (Wickham and Muller 2018), and then data were pooled across species for statistical analysis. Differences in rafting characteristics among species were investigated using data from the incubation and brood-guard periods as post-guard data were only available for black-browed albatrosses. Effects of breeding stage were investigated in the three species for which sufficient data were available (black-browed, light-mantled and wandering albatrosses). Effects of sex were tested for species-stage combinations with $n \geq 5$ for each sex, and effects of year were investigated using tracking data from black-browed albatrosses during the brood-guard stage, as this was the only species-stage combination with > 2 years of data (2008, 2010, 2015 and 2019).

Linear models were used to determine whether wind speed affected the durations of first and last wet bouts. Species was included as a predictor variable, as was the two-way interaction between wind speed and species, and wet bout duration was log transformed to improve data spread. Model selection was carried out by ranking all possible combinations of predictors according to Akaike Information Criterion (AIC), where the most supported model(s) were considered to be those within $2 \Delta \text{AIC}$ of the top model (Burnham & Anderson, 2004). Candidate models were excluded from this set if there were simpler nested versions with lower AIC values (Arnold, 2010).

All data processing and analyses were carried out in R, version 4.1.1 (www.r-project.org).

Table 1 Characteristics of foraging trips and rafting behaviours of seabirds tracked from Bird Island (BI), South Georgia, between 2008 and 2019 during the incubation (INC), brood-guard (BR) and post-guard (PB) breeding stages

Species	BBA		GHA		LMA		WA		WCP	
	INC, BR, PB	2008, 2010, 2015, 2019	BR	2010	INC, BR	2010, 2015	INC, BR	2012, 2015, 2019	INC	2015
Breeding stages	INC, BR, PB		BR		INC, BR		INC, BR		INC	
Years	2008, 2010, 2015, 2019		2010		2010, 2015		2012, 2015, 2019		2015	
First/last landing	First Last	Last	First Last	First Last	First Last	First Last	First Last	First Last	First Last	First Last
Sample size	127 (122 day, 5 night)	126 (111 day, 15 night)	12 (10 day, 2 night)	11 (9 day, 2 night)	19 (17 day, 2 night)	16 (11 day, 5 night)	95 (86 day, 9 night)	93 (78 day, 15 night)	12 (4 day, 8 night)	12 (12 day, 0 night)
Mean trip duration (days)	4.08		3.02		8.53		6.56		12.01	
Maximum range (km)	1087 (INC), 319 (BR), 769 (PB)		817 (BR)		1370 (INC), 747 (BR)		1546 (INC), 423 (BR)		1681 (IN)	
Distance to wet bout (km)	7.52–18.37	45.04–73.38	10.03–9.33	115.73–131.91	10.69–8.74	182.34–149.74	11.27–49.24	67.36–80.63	5.31–0.90	67.39–51.18
Prop landing < 10 km of BI	0.94	0.34	0.75	0.18	0.63	0.60	0.89	0.19	1.00	0.80
Duration of wet bout (mins)	29.55–34.89	27.77–71.79	20.66–9.54	33.78–87.49	10.74–8.53	8.30–9.79	35.31–63.66	90.20–163.78	38.54–32.76	9.00–698.67
	Within-individual		Diurnal		Daylight		Darkness			
First/last landing?	First	Last	First	Last	First	Last	First	Last	First	Last
Sample size	252	252	22	22	37	37	10.80–10.60	105.00–101.00		
Distance to wet bout (km)	9.28–33.00	65.50–91.30	6.91–5.38	79.80–123.00			0.86			
Prop landing < 10 km of BI	0.89	0.26	0.73	0.35						
Duration of wet bouts (mins)	30.20–46.50	46.70–114.00	30.90–24.20	17.90–24.60			64.50–128.00		161.00–197.00	
	Stage		Sex							
INC	BR		PB		M		F			
First/last landing?	First	Last	First	Last	First	Last	First	Last	First	Last
Sample size	91	86	148	113	26	25	90	91	60	54

Results

Characteristics of rafting behaviour

Overall, 89% of the first wet bouts (100% for white-chinned petrels and 63–94% for other species) occurred within 10 km of Bird Island [range: 5.3–0.9 to 11.3–49.2 km, depending on species and breeding stage] (Table 1 and Figs. 1b and 2a), i.e. the great majority of tracked birds of all species landed on the water within close range of the colony on the outgoing portion of their foraging trips. By comparison, the average distances from the colony of final wet bouts on the return portion of foraging trips were considerably longer, more variable across species and more dispersed in terms of location; only 26% (34% of black-browed albatrosses and 8–18% of other species) of last wet bouts occurred within 10 km of Bird Island [range: 45.0–73.4 to 182.3–149.7 km, depending on species and breeding stage] (Table 1 and Figs. 1b and 2b). The durations of first and last landings also varied greatly among species (range: 10.7–8.5 to 38.5–32.8 min vs. 8.3–9.8 and 90.2–163.8 min; Table 1), and mostly occurred during daylight (only 10 and 14% of first and last wet bouts, respectively, were in darkness). White-chinned petrels were more likely than the albatross species to depart and return from their foraging trips during darkness (Fig. S1) and 67% of their outgoing wet bouts occurred during darkness (Fig. S2). Only wandering albatrosses conducted final wet bouts during darkness (11% of last wet bouts; Fig. S2), and then usually returned to the colony in the following daylight period (67% of foraging trips).

Differences in rafting behaviour at the start and end of foraging trips were also compared within individuals (Table 1). Compared to the first wet bouts, the last wet bouts were significantly longer in duration (Wilcoxon paired signed-rank test: $n = 252$, $V = 19,297$, $p = 0.0037$), further from the colony (Wilcoxon paired signed-rank test: $n = 252$, $V = 1960$, $p < 0.0001$), and more to the northwest (Moore's test: $n = 252$, $t = 3.84$, $p = 0.0001$).

Diurnal differences in rafting behaviour

There were no differences between daylight and darkness in the duration (Kruskal Wallis test: $n = 44$, $H = 0.23$, $p = 0.6304$), distance (Kruskal Wallis test: $n = 44$, $H = 1.92$, $p = 0.1661$) and bearing from the colony (Watson's non-parametric homogeneity of means test: $n = 44$, $p = 0.5889$) of the first wet bouts on foraging trips. However, on the return, wet bouts during darkness were significantly longer (Kruskal Wallis test: $n = 74$, $H = 18.28$, $p < 0.0001$) and further from the colony (Kruskal Wallis test: $n = 74$, $H = 10.48$, $p = 0.0012$), but did not differ in mean bearings

(Watson's non-parametric homogeneity of means test: $n = 74$, $p = 0.1243$) from those in daylight.

Inter-specific variation in rafting behaviour

There were significant differences between species in the mean distances and durations of their first (distance: Kruskal Wallis test, $n = 239$, $H = 22.76$, $p < 0.0001$ and duration: Kruskal Wallis test, $n = 239$, $H = 29.41$, $p < 0.0001$) and last (distance: Kruskal Wallis test, $n = 233$, $H = 31.72$, $p < 0.0001$ and duration: Kruskal Wallis test, $n = 233$, $H = 40.53$, $p < 0.0001$) wet bouts from the colony. Based on multiple comparison tests, on the outgoing portions of trips, light-mantled albatrosses landed significantly further from the colony than black-browed and wandering albatrosses (Figs. 1b and 3a) but spent significantly less time on the water than any other species (Fig. 3b). On the return portion, light-mantled albatrosses landed significantly further from the colony than black-browed and wandering albatrosses (Figs. 1b and 3c), and wandering albatrosses spent significantly longer on the water than black-browed and light-mantled albatrosses, and white-chinned petrels (Fig. 3d). Differences between species in bearing from Bird Island were only significant for the first wet bout (Watson's non-parametric homogeneity of means test: $n = 239$, $p = 0.0165$; Fig. 3e). Grey-headed and wandering albatrosses landed predominantly to the west ($\sim 270^\circ$), black-browed and light-mantled albatrosses slightly more south (~ 265 and $\sim 230^\circ$, respectively) and white-chinned petrels slightly more north ($\sim 275^\circ$).

Effects of wind on rafting behaviour

The top supported model included the additive effects of hourly wind speeds and species as predictor variables on the durations of first and last wet bouts during foraging trips (Table 2); mean bout durations were longer for all species when wind speeds were lower (Fig. 4).

Effects of breeding stage on rafting behaviour

There were no significant differences between breeding stages in the duration (Kruskal Wallis tests, $19 < n < = 101$, $0.14 < H < = 2.49$, all $p > = 0.1149$) distance (Kruskal Wallis tests, $19 < n < = 101$, $0.38 < H < = 1.69$, all $p > = 0.1936$) and bearing (Watson's non-parametric homogeneity of means tests: $19 < n < = 101$, all $p > = 0.0846$) of the first and last wet bouts from Bird Island of black-browed, wandering and light-mantled albatrosses. In the only species for which data were available for all three stages (black-browed albatross), there were significant differences in the distances (Kruskal Wallis test: $n = 127$, $H = 27.42$, $p < 0.0001$)

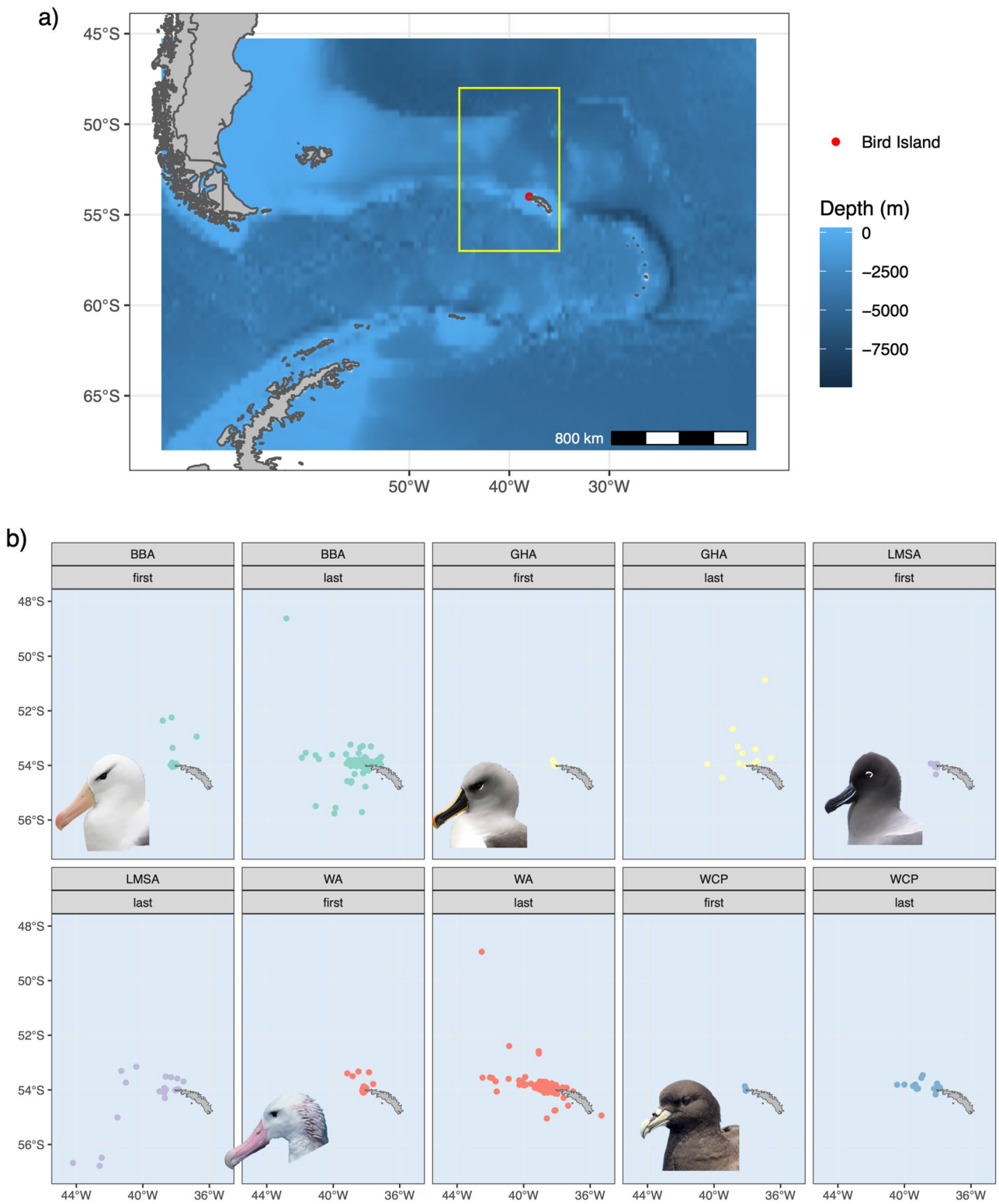


Fig. 1 a Location of the study site: Bird Island, South Georgia. The yellow rectangle shows the location and extent of plots shown in the lower panes. b Location of first and last landings (wet bouts) during the foraging trips of seabirds tracked between 2008 and 2019 during the incubation (INC), brood-guard (BR) and post-guard (PB)

breeding stages. BBA black-browed albatross (*Thalassarche melanophris*), GHA grey-headed albatross (*Thalassarche chrysostoma*), LMA light-mantled albatross (*Phoebastria palpebrata*), WA wandering albatross (*Diomedea exulans*) and WCP white-chinned petrel (*Procellaria aequinoctialis*)

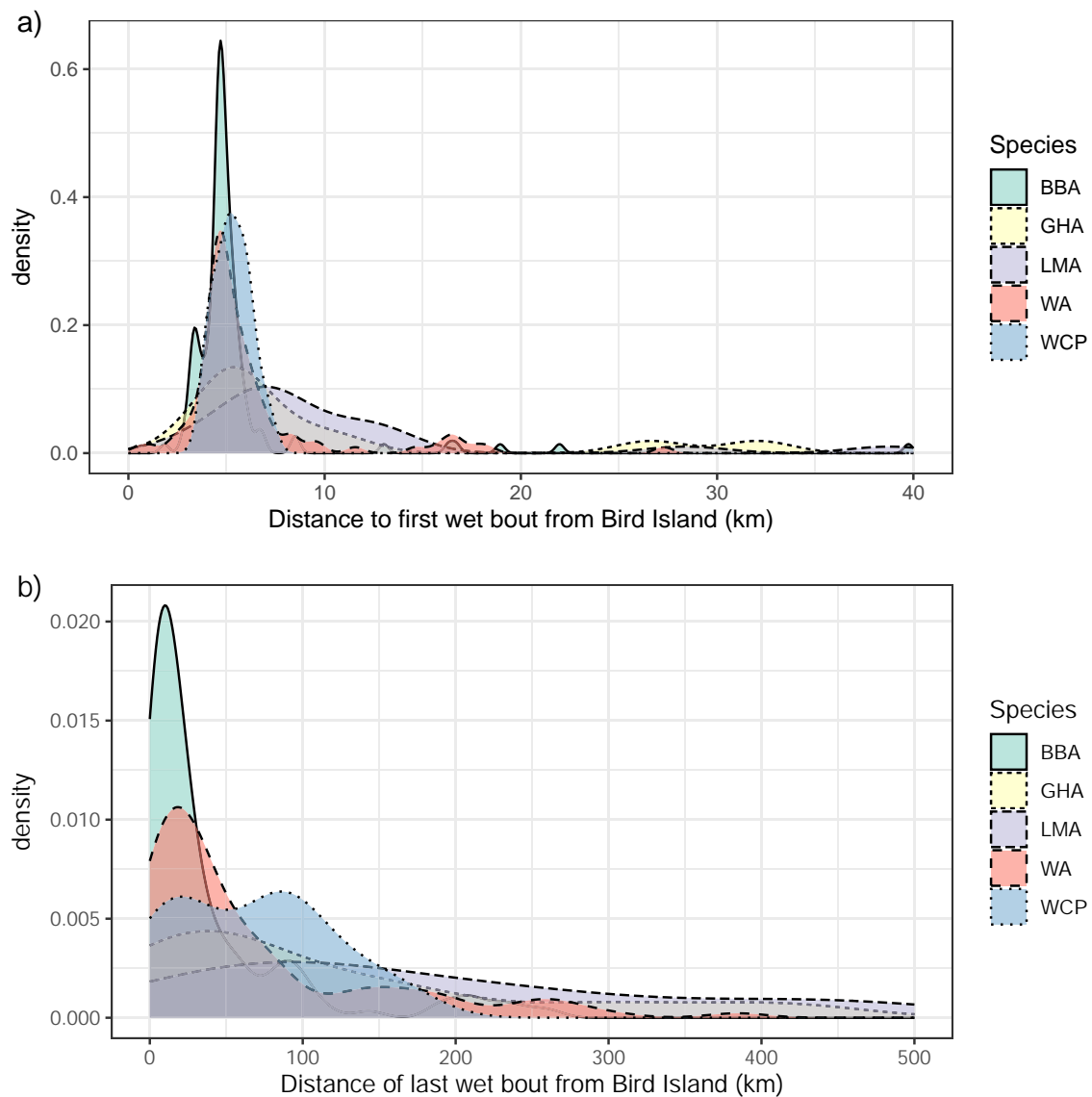


Fig. 2 Density plots of distance between Bird Island, South Georgia, and a the first wet bouts, and b the last wet bouts during the foraging trips of seabirds tracked using GPS between 2008 and 2019 during the incubation (INC), brood-guard (BR) and post-guard (PB) breeding stages. BBA black-browed albatross (*Thalassarche mel-*

anophris), GHA grey-headed albatross (*Thalassarche chrystostoma*), LMA light-mantled sooty albatross (*Phoebastria palpebrata*), WA wandering albatross (*Diomedea exulans*) and WCP white-chinned petrel (*Procellaria aequinoctialis*)

and durations (Kruskal Wallis test: $n = 127$, $H = 21.94$, $p < 0.0001$) of their first wet bouts, and the bearings of their last wet bouts from the colony (Watson's non-parametric homogeneity of means tests, $n = 127$, $p = 0.0142$). During the post-guard stage, black-browed albatrosses landed significantly closer to Bird Island ($n = 127$, $p < 0.05$) and spent significantly longer on the water ($n = 127$, $p < 0.05$) than during the incubation and brood-guard stages. Finally, the last wet bout during incubation, brood-guard and post-guard were northwest, directly west and southwest of the colony, respectively. These directions closely resemble directions

taken to forage, rather than wind directions upon return to Bird Island (Fig. S3).

Sex differences in rafting behaviour

There were no significant differences between sexes in either distance from the colony (Kruskal Wallis tests first: $n = 24 - 65$, $0.01 < H < 1.67$, all $p > 0.1959$; last: $n = 24 - 64$, $0.01 < H < 1.22$, all $p > 0.2700$) or duration of first and last wet bouts on foraging trips (Kruskal Wallis tests first: $n = 24 - 65$, $0.01 < H < 0.89$, all $p > 0.3450$; last: $n = 24 - 64$, $0.01 < H < 3.06$, all $p > 0.0802$). Nor did

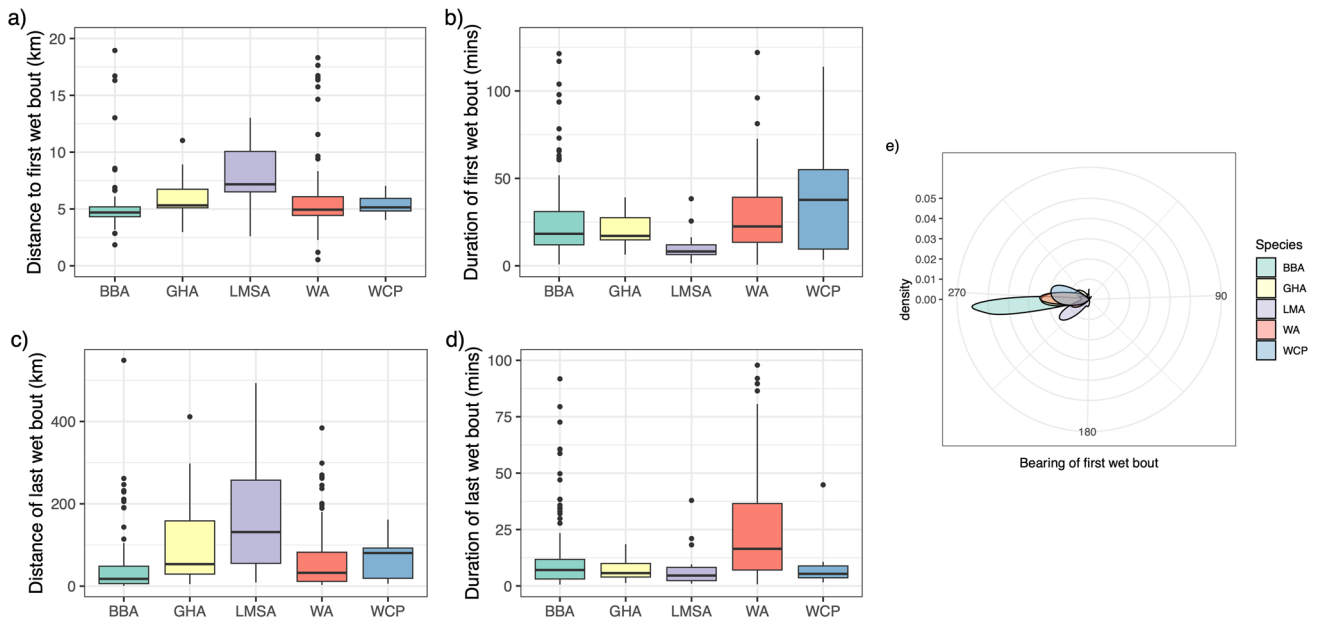


Fig. 3 Boxplots showing (a) distances between Bird Island, South Georgia, and the first wet bouts conducted during the foraging trips of seabirds tracked from Bird Island (South Georgia) using GPS between 2008 and 2019 during the incubation (INC) and brood-guard (BR) breeding stages. b Species-specific durations of the same wet bouts, c distances and durations of the last wet bouts con-

ducted by the same birds and e density plot of bearings of the first wet bouts. BBA black-browed albatross (*Thalassarche melanophris*), GHA grey-headed albatross (*Thalassarche chrysostoma*), LMA light-mantled sooty albatross (*Phoebastria palpebrata*), WA wandering albatross (*Diomedea exulans*) and WCP white-chinned petrel (*Procellaria aequinoctialis*)

Table 2 Effects of wind speed (m.s⁻¹), species and two-way interactions of wind speed and species on the durations of the first and last wet bouts conducted by seabirds during their foraging trips using linear models

Response variable	n	Predictor variables				df	AIC	Delta	Weight
		Intercept	Wind speed	Species	Species*Wind speed				
First wet bout duration (mins)	265	×	×	×		7	770.8	0	0.865
		×		×		6	774.9	4.12	0.110
		×	×	×	×	11	777.9	7.14	0.024
		×				2	816.7	45.90	0.000
		×	×			3	817.6	46.88	0.000
Last wet bout duration (mins)	265	×	×			7	986.2	0	0.784
		×	×	×	×	11	971.6	3.43	0.141
		×		×		6	972.9	4.72	0.074
		×	×			3	1009.6	41.46	0.000
		×				2	1011.1	42.88	0.000

Seabirds were tracked from Bird Island, South Georgia, using GPS between 2008 and 2019 during the incubation, brood-guard and post-guard breeding stages. Models including all possible combinations of the predictor variables were considered and ranked according to Akaike information criterion (AIC). Models within < 2 (Delta) of the best model were considered to be the best. × predictor variables retained in the different models; df the degrees of freedom; Weight the AIC weight, the relative probability that a given model is the best model

bearings differ between sexes (Watson’s non-parametric homogeneity of means test first: n = 24/65, all p > 0.1190; last: n = 24/64, all p > 0.07), except for wandering albatrosses during incubation (n = 34, p = 0.0067) in which the males landed to the northwest on the outgoing portion, and females were more varied in bearings.

Effects of year on rafting behaviour

In black-browed albatrosses during brood-guard, the durations of first and last wet bouts (Kruskal–Wallis test first: n = 73, H = 10.35, p = 0.0158, last: n = 72, H = 10.51, p = 0.0147), and distances of first wet bouts only

