Strong winds reduce foraging success in albatrosses

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Highlights

- Albatrosses exploit wind for flight but seemingly avoid strongest winds in storms.
- We use multi-stream biologging data to relate albatross foraging to environment.
- Our two study species experience reduced foraging success in stormy conditions.
- Wandering albatross land repeatedly in very strong winds, possibly to avoid injury.

Summary

Knowledge of how animals respond to weather and changes in their physical environment is increasingly important given the higher frequency of extreme weather recorded in recent years and its forecasted increase globally [1,2]. Even species considered to be highly adapted to extremes of weather, as albatrosses are to strong winds [3–5], may be disadvantaged by shifts in those extremes. Tracked albatrosses were shown recently to avoid storms and the strongest associated winds [6]. The drivers of this response are so far unknown, though we hypothesise that turbulent storm conditions restrict foraging success, possibly by reducing the detectability or accessibility of food, and albatrosses divert towards more profitable

conditions where possible. We tested the impact of physical environment - wind speed, rainfall, water clarity, and time of day - on feeding activity and success of two species of albatrosses with contrasting foraging strategies. We tracked 33 wandering and 48 black-browed albatrosses from Bird Island (South Georgia) with GPS and immersion loggers, and 19 and 7 individuals respectively with stomach-temperature loggers to record ingestions, providing an in-depth picture of foraging behaviour. Reduced foraging profitability (probability of prey capture and overall mass) was associated with stormy conditions, specifically strong winds and heavy rain in surface-seizing wandering albatrosses, and probability of prey capture was reduced in strong winds in black-browed albatrosses. We show that even highly wind-adapted species may frequently encounter conditions that make foraging difficult, giving context to storm avoidance in albatrosses.

Keywords: animal behaviour, biologging, climate impacts, extreme weather, seabirds

Results

Tracked albatrosses covered a vast area of the Southern Ocean (figure 1A) and a wide range of environmental conditions. Black browed and wandering albatrosses experienced wind speeds up to 20 and 23 m/s, respectively (figures 1B and 1C).

The rate of landings of albatrosses (and other seabirds) during daylight is often used a proxy for prey capture attempts or foraging effort, although with the caveat that this cannot be verified without information on ingestions. Here we show how this rate is influenced by the local environment using generalised additive mixed-effects models (GAMMs). Both species landed more frequently in heavier rainfall (figure 2A & 2C). During the day, both albatross species landed more often in moderately clear waters (figure 2B & 2D), suggesting that visual cues may be important for detection of prey, or these conditions correlated with an increased availability of food within the diving depth of each species. The landing rate of wandering albatrosses was strongly influenced by wind, most notably that they landed far more frequently at wind speeds > 18 m/s than in slower wind speeds (figure 2E). In addition, landings in stronger winds were very short (median = 48s, IQR = 186s), suggesting they were not landing in order to rest on the water surface, and they instead repeatedly landed and took off during those conditions (Figure S1, Movie S1). Though the minority of tracking data co-occurred with such strong winds (figure 1C), this still represented > 52 hours of total time spent tracked by 9 individuals. Landing rates of black-browed albatrosses were not significantly correlated with wind strength, though they were not tracked in the same upper range of wind speeds (max < 20m/s, fewer than 0.3% track points > 18 m/s), although the overall distribution of encountered wind speeds were otherwise similar (figure 1B). Both species landed more frequently at night, when they are known to spend more time on the water [7].

Landings are often assumed to represent foraging attempts in albatrosses. However, our results so far show that wandering albatross land very frequently in very strong winds. To test whether landings were proportional to food intake, and to disentangle landings and prey capture attempts in certain conditions, we modelled probability of ingestion per landing as a response to environmental conditions. This was tested using GAMMs, which showed that probability of ingestion per landing varied with wind speed for both species (Table S1). For

wandering albatrosses, an inverted u-shaped relationship between wind speed and probability of ingestion showed that mid-high wind was associated with high likelihood of ingestion per landing, peaking at 17m/s (figure 3C). This peak around 17m/s corresponds to relatively low landing rates (figure 2E), suggesting that although wandering albatrosses were less likely to land in such conditions, they were more likely to acquire prey when they did. For black-browed albatrosses, the probability of ingestion per landing was consistent up to 10m/s, after which it began to drop (figure 3A). Ingestion probability was also lower for wandering albatrosses in heavier rainfall (figure 3D), and higher for black-browed albatrosses in clearer waters during daylight only (figure 3B). Probability of ingestion was also higher in daylight than darkness and increased with the length of time on the water following landings for both species. The model balanced accuracy was 68% and 72% for black-browed and wandering albatross respectively, signifying good model fit (Table S1).

The model describing ingested mass per unit time for black-browed albatross performed poorly (Table S1), probably due to the small sample size (7 individuals) for this more complex analysis, despite a visible pattern in raw data that suggests ingested mass is reduced in stronger winds (figure 1D). For wandering albatrosses, ingested mass again had an inverted u-shape relationship with wind speed but with a more pronounced drop-off in high wind speeds and an earlier peak of ~ 10m/s (figure 3E), and was also lower in heavier rainfall (figure 3F).

Discussion

Animals are adapted to avoid or mitigate weather extremes that they naturally encounter, providing resilience that might buffer against the short-term impacts [8,9]. However, when such weather events become more commonplace and intense, avoidance or mitigation may be insufficient or impede regular function, and cumulative effects might be physiologically costly and, ultimately, reduce fitness [9–11]. Knowledge of how animals respond to current highs and lows of weather extremes allows us to understand how they may be impacted by future climate regimes, should their avoidance or mitigation strategies become too costly. Pelagic seabirds are particularly exposed to extremes of weather, spending most of their lives far from shore and away from shelter. To-date, response to extreme have varied by species, system, and context, with tubenose seabirds shown to avoid storms [6], avoid the strongest associated winds by flying toward lower winds in the storm's eye [12], follow storms to feed in the highly

mixed waters of their wakes [13], get caught up in storm tracks that relocate them [14], or starve and wash ashore [15].

Black-browed albatrosses at Bird Island feed on fish, krill, and squid [16] and wandering albatrosses predominantly on fish and squid [17,18]; these prey are captured at or within a few metres under the water surface [18–21]. Capture may involve dropping onto prey close to the surface from a low glide, sit-and-wait on the water, or in black-browed albatross, by pursuit dives powered by wing rows [20]. The probability of such food capture for both black-browed and wandering albatrosses was lower as wind speed increased towards the upper extreme. Strong winds might affect each method of prey capture in different ways: low glides might be difficult to maintain, and reduced visibility of prey in an agitated sea surface might make it challenging to locate from the air. We also show that strong winds are usually associated with reduced time spent on the water (Figure S2), so sit-and-wait tactics are also likely to be less viable in these conditions.

Higher average wind speeds over the breeding season (up to ~10m/s) were associated with shorter foraging trips and greater breeding success in wandering albatrosses in the Indian Ocean [22]. However, it was unclear in that study whether further increases in wind speeds due to climate change and increased storm frequency would continue to be beneficial. Our results suggest that foraging profitability starts to decline in hight wind speeds increase above 10-15 m/s, in heavy rain, and for black-browed albatross, in turbid water during the day. Global increases in wind speeds and frequency of severe storms are a consequence of climate change in past and coming decades [2]. According to our results, foraging profitability is impaired for both study species in conditions that they already encounter on a regular basis in the Southern Ocean, giving context to storm-avoidance behaviour of albatross species [6], and highlighting the negative impacts that more widespread storms may have on their ability to feed themselves and provision their chick.

Wandering albatrosses also showed reduced foraging profitability at very low windspeeds, which ties in with a recent study which concluded that the flight ability of wandering albatrosses was lowest in calm conditions, and the energetic cost of take-off was much higher [5]. Calm conditions are also associated with reduced travel speeds [23], and less prey searching behaviour [24]. The fishing success of smaller, lighter seabirds, such as terns, improves with windspeeds up to roughly 7m/s, as terns exploit headwinds to reduce ground speed when

positioning themselves for a prey-capture attempt [25]. Although the morphology and foraging strategies of albatrosses are very different to those of terns, our results highlight that similar principles may apply. Most albatross ingestions occur immediately after landing, suggesting locating and positioning over prey in the air prior to landing are important for successful prey capture. A study involving direct observations of feeding strategies of larger albatrosses reinforces this idea, as they can glide low to the water to search for and ambush prey from above, but only in winds greater than 8m/s [20]. Like terns, lower groundspeed while maintaining airspeed will likely facilitate this. Finer resolution biologging data may be used to verify whether albatrosses orientate into headwinds to maintain this low glide immediately preceding prey capture.

Heavy rain was associated with higher probability of landing for both species, but led to reduced meal size for wandering albatrosses. We hypothesise that heavy rainfall reduces visibility of prey at or close to the water surface for the albatrosses. Increased landings may indicate that albatrosses avoid flight during heavy rain [26], and so remain on the water. For black-browed albatrosses, ingestion per landing was positively correlated with water clarity, which may impact the foraging behaviour of seabirds that can capture their food below the water surface [27]. Black-browed albatrosses breeding in the Falkland Islands regularly dive to depths of 10m and reaching a maximum of nearly 20m [28], whereas conspecifics tracked from Bird Island only made occasional shallow dives [19]. Our results confirm that both the frequency of foraging attempts and foraging success are higher in clearer waters for black-browed albatrosses during the day, even though our study population at Bird Island feeds predominantly on prey at or close to the surface. This is in contrast to the intuitive non-effect of underwater visibility on probability of ingestion of wandering albatrosses, as studies so far indicate that this species has very poor diving ability and captures most of its prey on or within reach of the water surface [19,20,29], so underwater cues of food availability are likely less important.

Perhaps the most surprising result was the high rate of landings in strong winds (> 20 m/s) for wandering albatrosses, despite the low associated profitability of feeding. After initial prey detection, high winds may impair manoeuvrability or cause the albatross to lose visual contact with its target, leading to multiple failed capture attempts. It seems unlikely, however, that an albatross would invest substantial energy and time attempting to feed in conditions that lead

to such low prey acquisition. Another explanation is that they are forced to land to avoid the mechanical stress on their wings in very windy conditions. Wandering albatross appear to limit their across-wind mean airspeed to 20m/s by reducing the turn angle of their dynamic soaring flight style, likely to ensure the aerodynamic force on their wings remains within the mechanical tolerance [30]. The upper limit of wind speeds encountered by albatrosses in that study was 20m/s, and it may be that if wind speeds above this limit cannot be avoided, wandering albatross experience severe turbulence in the shear layer just above the water surface, causing excess force to their wings, and must therefore land regularly to avoid injury. However, they also cannot remain on the water, as they will be rolled and submerged by breaking sea waves, posing considerable risk of injury and waterlogging to birds that remain at the water surface [31]. At this point, they must manage the risk associated with the most turbulent conditions in both the air and on the water. In practice, we see that as winds increase above 20 m/s, wandering albatross do this by alternating between sitting on the water and taking flight when one or the other becomes more favourable. A caveat in our study and others (e.g., Richardson & Wakefield [30]) is that they rely on modelled average wind speeds and relationships tested at spatial resolutions of several kilometres. Actual windspeeds experienced at finer scales will extend above and below the values that we use for reference, likely explaining the shift between one behaviour and another. Additionally, windspeeds tend to be underestimated in the widely available and commonly used ECMWF ERA5 climate reanalysis dataset, especially in storm conditions [32,33]. Therefore, this 20 m/s limit above which wandering albatrosses repeatedly land is very likely an underestimate of the upper range of wind speeds that they experienced.

Our results suggest that both albatross species in our study may struggle to find food in inclement weather. We showed that wandering albatross land and take off repeatedly in severe winds, perhaps out of necessity and likely at high energetic cost, even though strong winds are usually considered to facilitate take off [5]. Avoiding extremes of weather such as cyclones can be costly, as it reduces foraging success and requires seabirds to reroute [12,34]. Understanding why Southern Ocean albatrosses can detect [35] and avoid [6] storms highlights that there is an upper limit to the wind speed that can be tolerated, even for such well-adapted species, beyond which the cost of finding food must outweigh the relative profitability. As albatrosses are so well adapted for exploiting winds, there seemed little

reason to consider them to be disadvantaged by increasing storm frequency and intensity. However, our study paints a different picture, and shows that as storms become more widespread with climate change, albatrosses may need to endure conditions more frequently that inhibit foraging and may even prove dangerous, forcing them to land on the water surface to avoid damaging their wings. While they may also benefit energetically from cheaper commuting costs in higher winds, our study also suggests that this benefit plateaus in the strongest winds. Such information on species responses to environment, and the underlying mechanisms, is vital for understand the costs and benefits of an increasingly unpredictable environment.

Acknowledgements

This project was supported by the Natural Environmental Research Council and National Science Foundation (under grants NERC-NSF GEO NE/V015036/1 and NSF GEO-NERC 1951500). José Xavier and Jorge Pereira were supported by Fundação para a Ciência e Tecnologia (FCT) under the project LA/P/0069/2020 granted to the Associate Laboratory ARNET, by the grant MARE-UIDB/04292/2020, PTDC/BIA-BDE/64539/2006, and SFRH/BD/64558/2009, and by the Portuguese Polar Program PROPOLAR. Thanks to Oliver Padget, Manon Clairbaux, and Natasha Gillies for support and direction in the writing stage of the manuscript. We thank the two anonymous reviewers for helpful and constructive feedback. We would like to dedicate this work to Mike Harris, whose guidance and enthusiastic encouragement were an inspiration to ourselves and to so many others in the seabird research community.

Author contributions

JD, SCP, RP, and HW created the concept. RP, JX, JP, and EW collected data. JD, RP, HW, JP, and EW analysed data. All authors contributed to writing the paper.

Declaration of interests

The authors declare no competing interests.

Inclusion and diversity

We support inclusive, diverse, and equitable conduct of research.

Supplemental Information

Figure S1: Movement metrics and behaviour in high wind speeds.

Tabel S1: Descriptions of each generalised additive mixed-effects model in this study.

Movie S1: Tracks and landing behaviour of 6 wandering albatrosses in a storm. Related to figure 2.

Figure S2: How wind impacts time spent on the water.

Figures

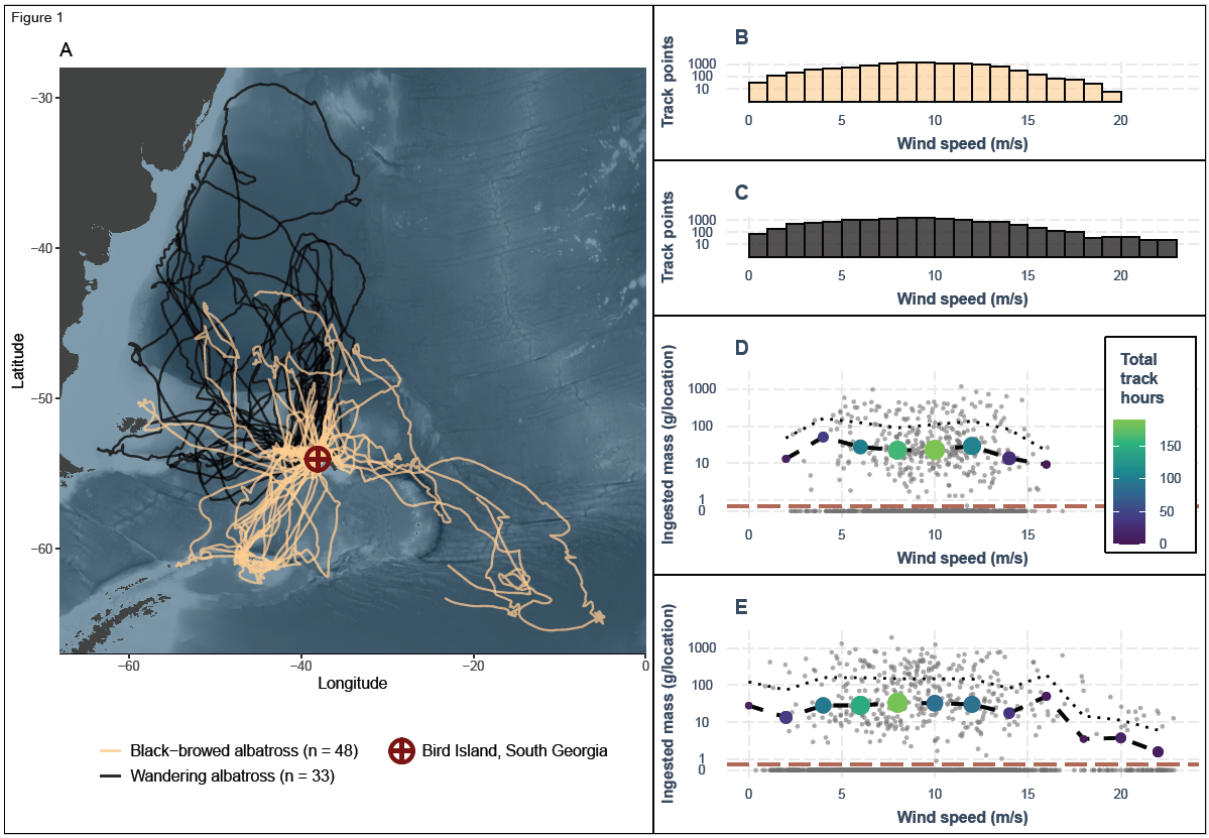

Figure 1. Tracking data. Tracks of black-browed and wandering albatrosses from Bird Island (South Georgia, 54°00'S, 38°03'W) during the chick-rearing period in 2008 and 2009, respectively (A). B and C show the range of wind conditions experienced by tracked black-browed and wandering albatross, respectively, with y-axis log transformed to facilitate viewing. D and E show the mass ingested per hour for black-browed and wandering albatrosses, respectively, with each grey point a raw data point. Intervals spent entirely in flight were excluded from these graphs, as they likely represent commuting behaviour. The thick broken line is the trend of average ingested mass with windspeed, with the light dotted

line the upper standard deviation of this relationship. The size of the points along this trend corresponds to the number of landings in each range of windspeeds. The y-axes of these plots are log transformed, as the distribution of ingested masses was heavily right skewed. 0 values are included below the red broken line, as these are not retained by the log transformation.

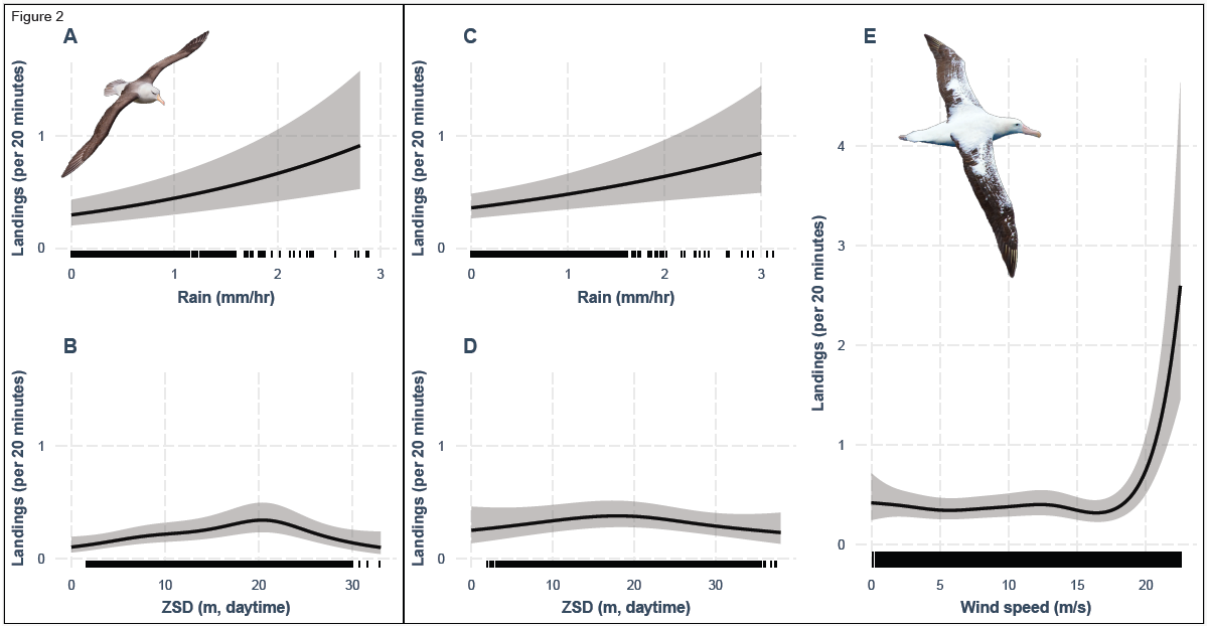

Figure 2. Albatross landing rates as a response to environmental conditions. Partial responses of landings per 20 minutes to environmental covariates from models for black-browed (A, B) and wandering (C-E) albatrosses tracked during chick-rearing from Bird Island (South Georgia) in 2008 and 2009, respectively. Secchi disk depth (ZSD) is modelled from remote-sensing data and is an estimated measure of water clarity. Rug plots at the base of each plot correspond to the range of values available for those covariates. Y-axes are on the same scale, except for E, which required a much broader response range.

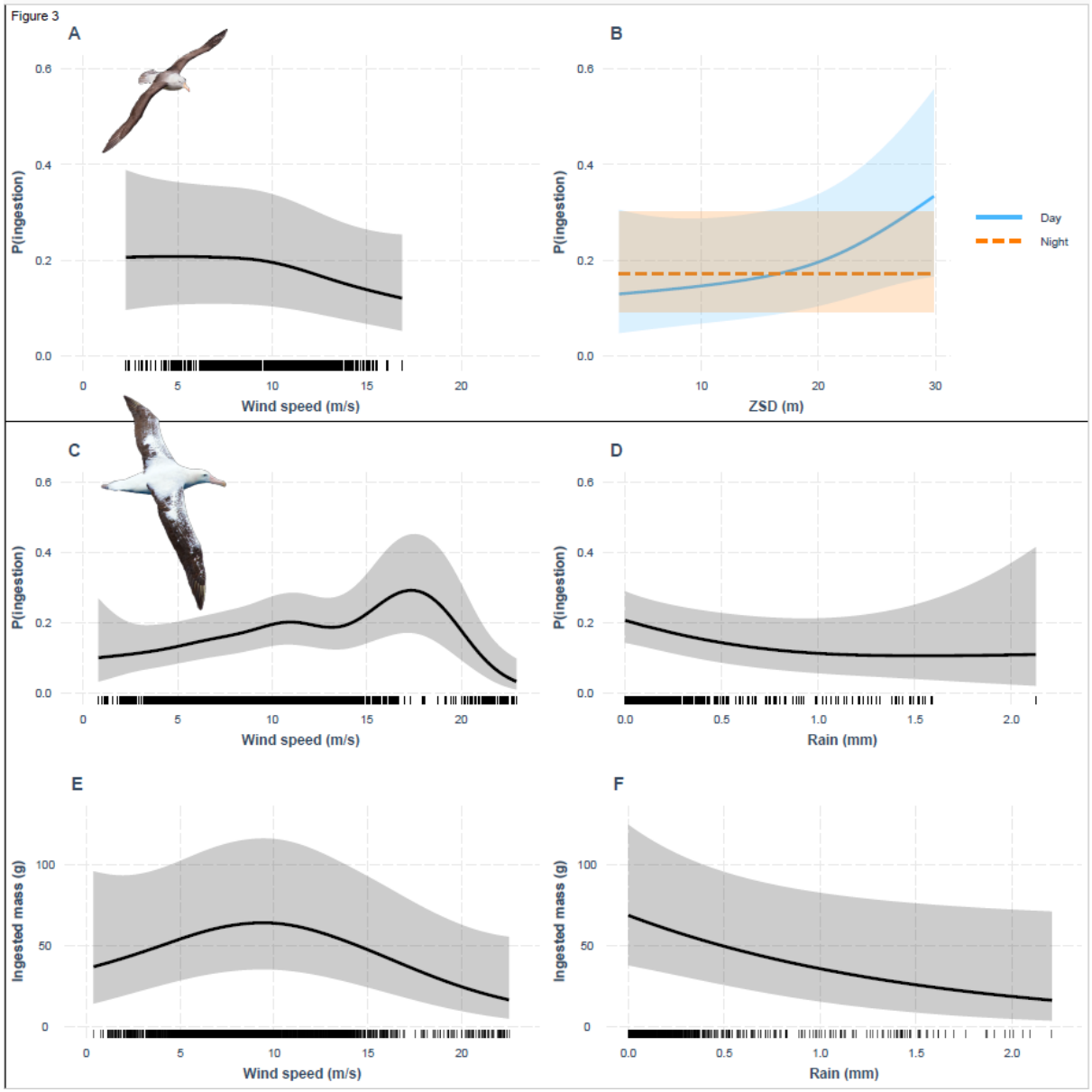

Figure 3. Albatross foraging success as a response to environment. Partial responses of probability of ingestion per landing event (A, B, C, D), or ingested mass per unit time (E, F) to environmental covariates. Secchi disk depth is modelled from remote sensing data and is an estimated measure of water clarity. Rug plots at the base of each panel correspond to the range of values available for those covariates.

STAR Methods

Key resource table

RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		

Wandering albatross (*Diomedea exulans*)	Seabird tracking dataset (BirdLife)	Accession number 1387
Black-browed albatross (*Thalassarche melanophris*)	Seabird Tracking dataset (BirdLife)	Accession number 1537
Deposited data		
Code to complete all statistical analyses	This study	doi.org/10.5281/zenodo.13881532
Software and algorithms		
R software version 4.1.2	www.r-project.org	N/A

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Jamie Darby (Jamie.Darby@ucc.ie).

Materials availability

This study did not generate new unique reagents.

Data and code availability

All tracking data have been deposited at Seabird Tracking Database (www.seabirdtracking.org) and are publicly available as of the date of publication. Accession numbers are listed in the key resources table. All other data (stomach temperature and immersion) and all code used in these analyses have been deposited on www.zenodo.org and are publicly available as of the date of publication. The DOI is listed in the key resources table. Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

Experimental model and subject details

All catching, handling, and tagging was carried out under permit at Bird Island, South Georgia (54°00'S, 38°03'W). Breeding black-browed albatrosses were captured and equipped with GPS and geolocator-immersion loggers (n = 48), with a subset also fitted with a stomach-temperature logger (n = 7), between January and March 2008 (for full deployment details, see Wakefield *et al*. [36]). Breeding wandering albatrosses were captured and equipped with GPS and geolocator-immersion loggers (n = 33), again with a subset fitted with stomach-temperature loggers (n = 19), between May and October 2009 (for full deployment details,

see Pereira *et al*. [17]). Individuals were recaptured, and devices retrieved after they had completed at least one foraging trip. GPS devices were back-mounted with Tesa® tape and set to record location at 30- and 20-minute intervals for black-browed and wandering albatrosses, respectively. Geolocator-immersion loggers were leg-mounted and tested for saltwater immersion every 3 seconds. Birds were induced to swallow stomach-temperature loggers, which recorded temperature at 0.1°C and 20s resolution. The loggers had a spring at the base that was set in gelatine at deployment and, once the gelatine dissolved, opened in the proventriculus to aid device retention. Loggers were retrieved by water offloading using a tube with a strong magnet that was attracted to a magnet on the top of the logger. Total device weight was always less than or equal to 3% of adult body weight [17,36], which is the threshold above which deleterious effects tend to be detected in albatrosses [37].

Method details

All data processing and analyses were conducted using R statistical software version 4.3.2 (www.R-project.org). GPS tracks were interpolated to generate locations at regular 30- and 20-minute intervals for black-browed and wandering albatrosses, respectively. Wind and rain data were sourced from the ECMWF ERA5 datasets (climate.copernicus.eu) and appended to track locations using bilinear interpolation in the MoveBank EnvAppend service [38]. These data were provided at hourly temporal and 0.25-degree spatial resolution. Solar elevation angle was appended to each track point using the *oce* package [39] and categorised as day or night based on the timing of civil twilight (solar angle of -6°). Secchi disk depth (ZSD), a measurement of water clarity, was sourced as a modelled estimate from MODIS satellite ocean colour data at daily 4 x 4km resolution from Copernicus Marine Service (marine.copernicus.eu). Activity data were recorded as either wet or dry every 3 seconds, with a switch from dry to wet taken as a landing event. The number of landing events was appended to each location timewise, within 20- or 30-minute segments depending on track point interval and centred on the location timestamp.

Stomach temperature was recorded every 20 seconds and analysed to identify and measure putative ingestions as Precipitous Drop, Exponential Rise (PDER) events [40], working on the assumption that sudden temperature drops correspond to ingestions, and the degree of the temperature drop and the recovery time correlate with amount of mass ingested. PDERs were identified using MTTemp from Jensen Software Systems, and the integral of the PDER curve,

along with estimated prey temperature and specific heat capacity, were used to estimate the mass of ingested prey. Where subsequent ingestions occurred before the stomach temperature had time to recover to an asymptote (internal body temperature), these were aggregated into a single meal, and the overall meal mass was estimated [41]. Each ingestion was matched in time to the preceding landing event. In the cases where ingestions occurred when the immersion data indicated the logger was dry, ingestion was assumed to have occurred when the bird was last on the water and the ingestion time was adjusted accordingly. This shift was always less than 2 minutes and presumed to relate to small offsets in the logger clocks, or ingestions that took place as or shortly after the bird took off. This limit covered the difference between all ingestions and landings for black-browed albatrosses. For wandering albatrosses, ~95% of ingestions were within this limit from the nearest time on the water, with the remaining 5% of ingestions far greater than 2 minutes from the nearest time on water. These were discarded as they could not be reliably assigned to a landing event, and to our knowledge, this species has not been documented to ingest prey without landing [20].

Quantification and statistical analysis

To model the at-sea activity of each species, for each track point interval not spent entirely on the water surface, number of landings was modelled as a response to wind speed, day/night, ZSD, rain, and location using a negative binomial error structure with a log link. Landings of < 15 seconds were removed from this analysis to omit occasions when birds were pattering on the water surface or loggers being splashed by spindrift in high winds, although this did not meaningfully change the model outputs. Albatrosses tuck their legs into waterproof contour plumage during sustained flight, so it's unlikely that rain or spindrift would confound the immersion reading on these tags in any case. To further understand how time spent on the water was influenced by environment, the period of time subsequently spent on the water following landing was then modelled as a response to wind speed, day/night, rainfall, and presence/absence of an ingestion during that time. This was again modelled using a negative binomial error structure with a log link.

To better understand how landings scaled with prey ingestion in varying conditions, presence or absence of ingestion for each landing event was modelled as a response to wind speed, day/night, ZSD, rain, and location, while time spent on the water after landing was also included to account for increased probability of prey consumption with greater time spent on

the water surface. This model was fitted with a binomial error structure with a logit link. Finally, foraging profitability was modelled as ingested mass per unit time, 20 minutes for wandering albatrosses, and 30 minutes for black-browed albatrosses, i.e. the track point interval for both. Sections of the track fully in the air were removed as these were likely commuting phases of trips. The descriptors for this model were wind speed, ZSD, rain, and location. The responses for these models were continuous with a high zero mass (black-browed: 70.5%, wandering: 80.1%, Table S1), so the models were fitted using a Tweedie distribution with a flexible power parameter (p) and a log link.

Generalised Additive Mixed Models (GAMMs) were fitted using the *mgcv* package [42] with individual identity as a random effect to account for individual differences in the rate of each modelled response. A 2-dimensional thin-plate spline term of latitude and longitude was included in each model to account for unexplained spatial variation, i.e. from differences in habitat and prey availability that we could not account for. All other model terms were included as thin plate regression splines with shrinkage, which return the simplest effective spline without arbitrarily constraining complexity. ZSD covariates were split by day and night, as water clarity and associated visual cues are likely more important during daylight. An autocorrelation function (ACF) plot was used to explore serial autocorrelation of residuals, which once verified (> 0.1), was modelled using a first order autoregressive function. Whole model selection was performed based on term shrinkage and *mgcv*'s inbuilt selection function. Multicollinearity between model splines was identified using a concurvity threshold of 0.8 [43]. The only covariate exceeding this threshold was rain, in the models describing landing rates of both black-browed and wandering albatrosses. Limited covariance was identified when plotting rain against other environmental covariates of interest, so the term was retained in the models. Issues of overfitting were buffered against in models with large sample sizes by including an increased null-space penalty using the *gamma* parameter in *mgcv*. Conformity of the final model to assumptions was verified via diagnostic plots produced using the *DHARMa* package [44]. For binomial models, balanced accuracy was used as a performance metric, as area under receiver operating characteristic curve (AUC) is often inflated for models with imbalanced responses. The deviance explained was calculated for all models.

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