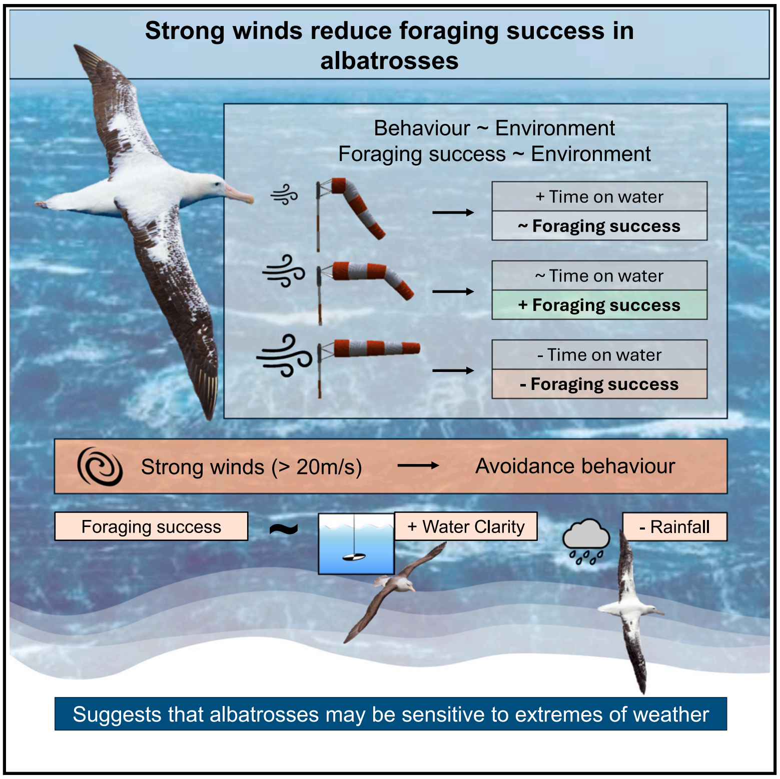
Report

Current Biology

Strong winds reduce foraging success in albatrosses

Graphical abstract



Highlights

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

Authors

Jamie Darby, Richard A. Phillips,
Henri Weimerskirch,
Ewan D. Wakefield, José C. Xavier,
Jorge M. Pereira, Samantha C. Patrick

Correspondence

jamie.darby@ucc.ie

In brief

Strong winds reduce the energy required for flight and takeoff in albatrosses; however, little is known about how wind impacts other behaviors, such as foraging. Darby et al. combined at-sea behavior and stomach-temperature data from two species of albatross to demonstrate the negative impact of stormy weather on foraging behavior and prey capture.

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Report

Strong winds reduce foraging success in albatrosses

Jamie Darby,[1,2,7,8,*] Richard A. Phillips,[3] Henri Weimerskirch,[4] Ewan D. Wakefield,[5] José C. Xavier,[3,6] Jorge M. Pereira,[6] and Samantha C. Patrick[1]
[1]School of Environmental Sciences, University of Liverpool, Liverpool L3 5DA, UK
[2]School of Biological, Environmental and Earth Sciences, University College Cork, Cork T23 N73K, Ireland
[3]British Antarctic Survey, Natural Environmental Research Council, Cambridge CB3 0ET, UK
[4]Centre d'Étude Biologique de Chizé, CNRS, La Rochelle Université, 79360 Villiers-en-Bois, France
[5]Department of Geography, Durham University, Durham DH1 3LE, UK
[6]University of Coimbra, MARE—Marine and Environmental Sciences Centre/ARNET—Aquatic Research Network, Department of Life Sciences, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
[7]X (formerly Twitter): @Jamie_Darby
[8]Lead contact
*Correspondence: jamie.darby@ucc.ie
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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 hypothesize that turbulent storm conditions restrict foraging success, possibly by reducing the detectability or accessibility of food, and albatrosses divert toward more profitable conditions where possible. We tested the impact of the 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 behavior. 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 the 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.

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 of 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 generalized additive mixed-effects models (GAMMs). Both species landed more frequently in heavier rainfall (Figures 2A and 2C). During the day, both albatross species landed more often in moderately clear waters (Figures 2B and 2D), suggesting that visual cues may be important for detection of prey or that 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 = 48 s, IQR = 186 s), suggesting they were not landing in order to rest on the water surface and, instead, they repeatedly landed and took off during those conditions (Figure S1; Video S1). Though the minority of tracking data co-occurred with such strong winds (Figure 1C), this still represented >52 h of total time spent tracked by 9 individuals. Landing rates of black-browed albatrosses were not significantly correlated with wind strength, and though they were not tracked in the same upper range of wind speeds (max < 20 m/s, fewer than 0.3% track points > 18 m/s), the overall distribution of encountered wind speeds was 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

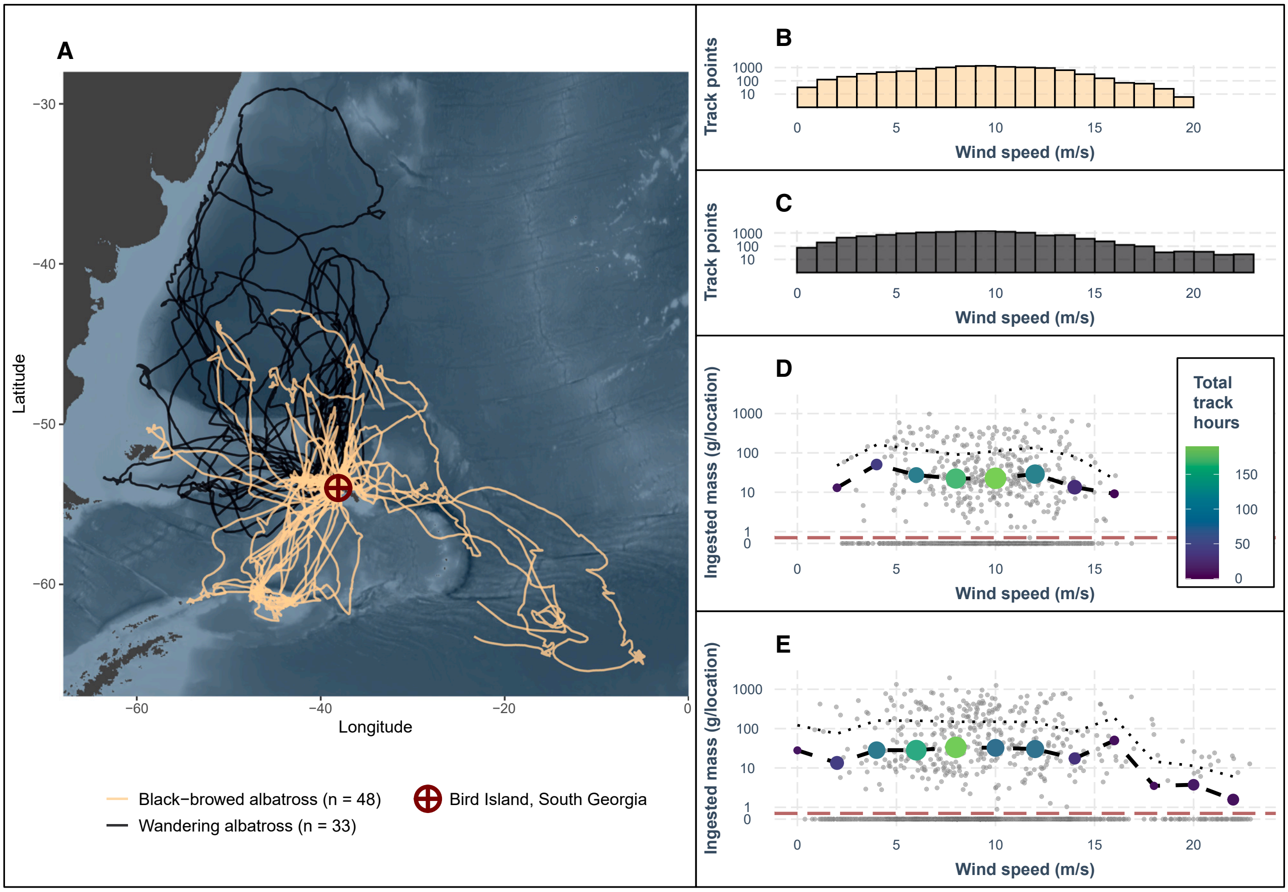

Figure 1. Tracking data

(A) 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.

(B and C) 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) The mass ingested per hour for black-browed and wandering albatrosses, respectively, with each gray point a raw data point. Intervals spent entirely in flight were excluded from these graphs, as they likely represent commuting behavior. The thick broken line is the trend of average ingested mass with wind speed, with the light dotted line is 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 wind speeds. 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.

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 modeled probability of ingestion per landing as a response to environmental conditions. This was tested using GAMMs, which showed that the 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 17 m/s (Figure 3C). This peak at around 17 m/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 10 m/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 of 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 ∼10 m/s (Figure 3E), and was also lower in heavier rainfall (Figure 3F).

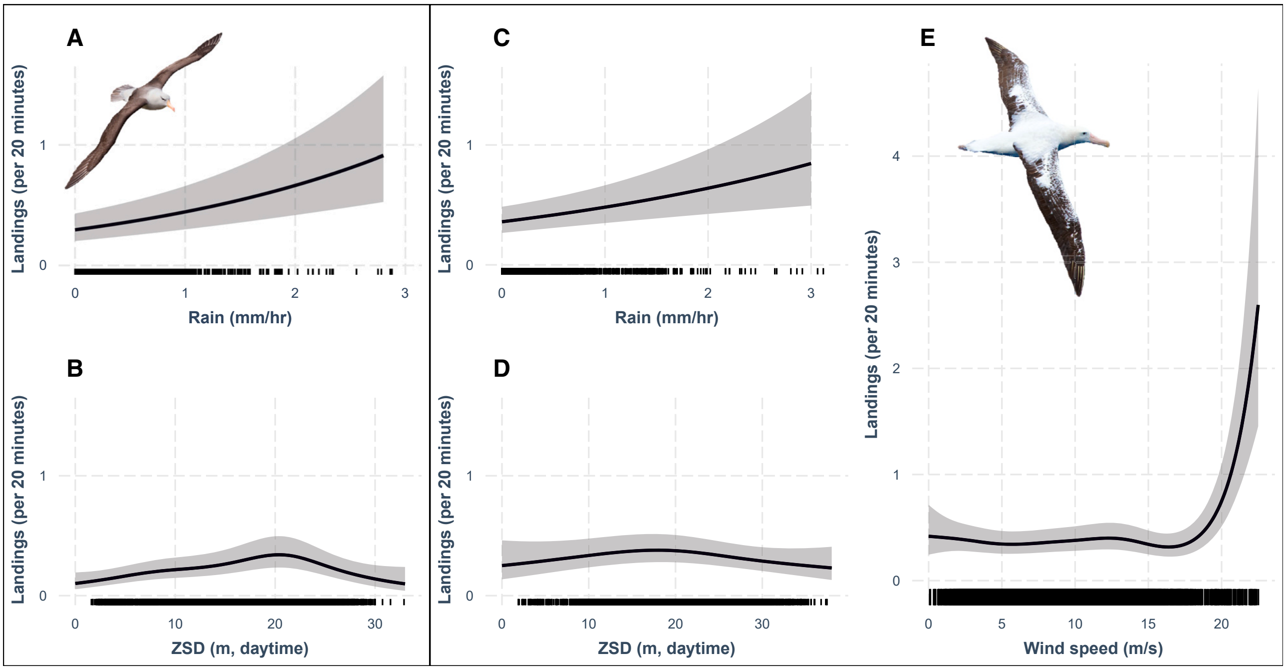

Figure 2. Albatross landing rates as a response to environmental conditions

Partial responses of landings per 20 min to environmental covariates from models for black-browed (A and 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 modeled from remote-sensing data and is an estimated measure of water clarity. The shaded area around each trend represents the 95% confidence interval. 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.
See also Figures S1 and S2, Video S1, and Table S1.

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 extremes has 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 feed predominantly on fish and squid[17,18]; these prey are captured at or within a few meters 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 toward 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 ∼10 m/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 high wind speeds that 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 behavior of albatross species[6] and highlighting the negative impacts that more widespread storms may have on their ability to feed themselves and provision their chicks.

Wandering albatrosses also showed reduced foraging profitability at very low wind speeds, 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 takeoff

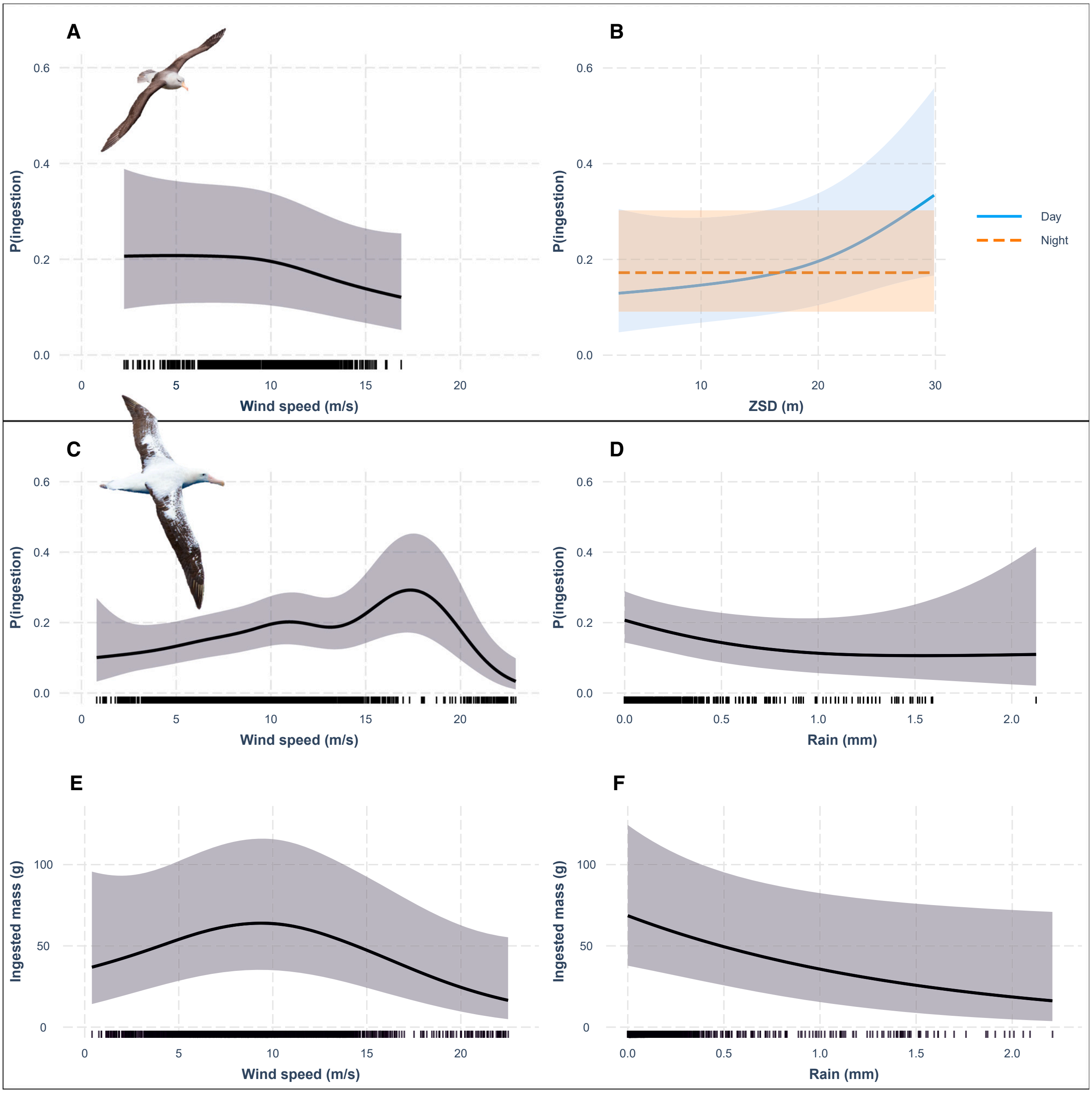

Figure 3. Albatross foraging success as a response to environment

Partial responses of probability of ingestion per landing event (A–D) or ingested mass per unit time (E and F) to environmental covariates. Secchi disk depth is modeled from remote-sensing data and is an estimated measure of water clarity. The shaded area around each trend represents the 95% confidence interval. Rug plots at the base of each panel correspond to the range of values available for those covariates.

See also Table S1.

was much higher.[5] Calm conditions are also associated with reduced travel speeds[23] and less prey searching behavior.[24] The fishing success of smaller, lighter seabirds, such as terns, improves with wind speeds up to roughly 7 m/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 that 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 8 m/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 hypothesize 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 behavior 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 10 m and reach a maximum of nearly 20 m,[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 maneuverability 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 20 m/s by reducing the turn angle of their dynamic soaring flight style, likely to ensure that 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 20 m/s, and it may be that if wind speeds above this limit cannot be avoided, wandering albatrosses 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 stay 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 albatrosses do this by alternating between sitting on the water and taking flight when one or the other becomes more favorable. A caveat in our study and others (e.g., Richardson and Wakefield[30]) is that they rely on modeled average wind speeds and relationships tested at spatial resolutions of several kilometers. Actual wind speeds experienced at finer scales will extend above and below the values that we use for reference, likely explaining the shift between one behavior and another. Additionally, wind speeds 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 albatrosses 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 takeoff.[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 the notion 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 more frequently need to endure conditions that inhibit foraging and may even prove dangerous, forcing them to land on the water surface to avoid damaging their wings. Although they may 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 the environment, and the underlying mechanisms, is vital for understanding the costs and benefits of an increasingly unpredictable environment.

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: 1387, 1537, and are publicly available as of the date of publication.
- All stomach temperature and immersion data have been deposited at Zenodo and are publicly available at https://doi.org/10.5281/zenodo.13881532 as of the date of publication.
- All original code has been deposited at Zenodo at https://doi.org/10.5281/zenodo.13881532 and is publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

J.D., S.C.P., R.A.P., and H.W. created the concept. R.A.P., J.C.X., J.M.P., and E.D.W. collected data. J.D., R.A.P., H.W., J.M.P., and E.D.W. analyzed data. All authors contributed to writing the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.10.018.

A video abstract is available at https://doi.org/10.1016/j.cub.2024.10.018#mmc4.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Wandering albatross (*Diomedea exulans*)	Seabird tracking dataset (BirdLife)	Seabird Tracking Database:1387
Black-browed albatross (*Thalassarche melanophris*)	Seabird Tracking dataset (BirdLife)	Seabird Tracking Database: 1537
Deposited data		
Code to complete all statistical analyses	This study	https://doi.org/10.5281/zenodo.13881532
Software and algorithms		
R software version 4.1.2	www.r-project.org	N/A

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 categorized 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 color 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 centered on the location timestamp.

Stomach temperature was recorded every 20 seconds and analyzed 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 modeled 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.

Generalized 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.