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Main Manuscript for

Pelagic seabirds reduce risk by flying into the eye of the storm

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Abstract

Cyclones can cause mass mortality of seabirds, sometimes wrecking thousands of individuals. The few studies to track pelagic seabirds during cyclones show they tend to circumnavigate the strongest winds. We tracked adult shearwaters in the Sea of Japan over 11 years and find that the response to cyclones varied according to the wind speed and direction. In strong winds, birds that were sandwiched between the storm and mainland Japan flew away from land and towards the eye of the storm, flying within ≤ 30 km of the eye and tracking it for up to 8 hours. This exposed shearwaters to some of the highest wind speeds near the eye wall (≤ 21 m s^{-1}), but enabled them to avoid strong onshore winds in the storm's wake. Extreme winds may therefore become a threat when an inability to compensate for drift could lead to forced landings and collisions. Birds may need to know where land is in order to avoid it. This provides additional selective pressure for a map sense and could explain why juvenile shearwaters, which lack a map sense, instead navigating using a compass heading, are susceptible to being wrecked. We suggest that the ability to respond to storms is influenced by both flight and navigational capacities. This may become increasingly pertinent due to changes in extreme weather patterns.

Significance Statement

Cyclones can cause billions of dollars of damage and loss of human life. They can also cause mass mortality and strandings in seabirds. We used GPS tracking data from streaked shearwaters breeding in the world’s most active cyclone basin to understand how seabirds respond to these systems. Birds varied their response according to the wind speed and direction, generally flying towards the eye of the cyclone in strong winds. This surprising strategy enabled shearwaters to control their exposure to risky wind vectors that could drift them onshore. Nonetheless, birds may need to know where land is in order to avoid it. Juveniles lack this “map sense”, making them susceptible to wrecking in some scenarios.

Introduction

Cyclones can have devastating impacts, causing mass mortality of animals and disruption of entire ecosystems (1, 2). The intensity of these extreme events (also called hurricanes and typhoons depending on their location) is predicted to increase with climate change (3), while an increase in the frequency of the most intense storms is already being observed in regions prone to tropical cyclones (4). Little is known about the capacity of organisms to respond to these systems, including the extent to which mobile animals can avoid them, although a range of aquatic animals appear to move to deeper water (5, 6). Seabirds are particularly exposed to tropical cyclones because they develop over the ocean, and indeed, large numbers of seabirds can be wrecked after cyclones, numbering tens of thousands of individuals in the most extreme cases (7, 8).

A handful of studies have managed to track pelagic seabirds in 1–2 tropical cyclones, showing that adults circumnavigate the most intense parts of these systems, flying around or above them (9, 10). Indeed, red-footed boobies (*Sula sula*) and great frigatebirds (*Fregata minor*) have been known to fly 400–600 km from their routine foraging area during the passage of cyclones (10). Lower resolution movement data from black-naped terns (*Sterna sumatrana*) equipped with light-based geolocators showed these birds also moved away from cyclones that approached their breeding colony, although they did not always respond to cyclones during migration (11). It is also clear from widespread wrecks and inland strandings (9, 12, 13), that avoidance is not always possible. Indeed, one great frigatebird that was tracked 250 km from a cyclone and encountered winds > 100 km h^{-1} appeared to have been killed (10). It is therefore important to understand the fine-scale behavioural responses to cyclones in order to provide insight into the conditions that birds can, and cannot, tolerate.

Quantifying bird responses to extreme weather events remains challenging as they are, by definition, infrequent. Cyclones are also variable in terms of their intensity, spatial extent, movement speed and trajectory. Understanding the behavioural rules that birds employ in an attempt to mitigate storm detriment therefore requires animals to be tracked during multiple, rare events. We tracked 401 adult streaked shearwaters (*Calonectris leucomelas*) breeding on Awashima Island, Japan over 11 years. This region forms part of the Northwest Pacific cyclone belt, which is the world's most active cyclone basin and subject to large and extreme typhoons (14). Shearwaters breeding in this region therefore represent a model system to understand how pelagic birds respond to extreme wind speeds. Furthermore, storm systems enter the Sea of Japan from the southeast and can influence the whole region, from Japan in the East, to Russia, North and South Korea in the North and West (Fig. 1A), restricting the opportunities for circumnavigation. We quantified the behavioural responses of shearwaters to 10 tropical cyclones and storms (Fig. 1, Table S1) using a combination of statistical and agent-based modelling to assess how birds modify their flight direction in relation to both (i) the eye of the typhoon/ storm as it moved through the Sea of Japan and (ii) the nearest point on land. Overall, our aim was to provide novel insight into the capacity of seabirds to respond to the direct effects of extreme weather events.

Results

Isolating GPS tracks from the 75 shearwaters that were exposed to storms (Fig. 1B, C) showed that birds flew in all wind conditions, appearing no less likely to fly as wind speeds increased to typhoon strength (Fig. 2A). The maximum wind speed in the Sea of Japan was estimated to be 97 km h^{-1} (27 m s^{-1}) by ERA5, and 148 km h^{-1} (41 m s^{-1}) by IBTrACs (Table S1). In all scenarios, birds tended to fly with a strong crosswind component, consistent with their dynamic soaring flight style (Fig. 2B) (15).

We modelled how birds adjusted their flight direction in relation to the eye of the storm. We did this using two datasets, as the combination of the storm trajectories and maximum wind speeds meant that birds were not exposed to storm conditions in all systems (Fig. S1). In the first model, we used tracking data from birds operating in all ten storms. We then ran a second model using data from the strongest storms only, where 55 shearwaters flew in three typhoons and two severe tropical storms (Table S1), hereafter referred to as storms for simplicity. The second model enabled us to focus on bird responses to extreme events. The outputs of the two models were near identical in terms of the shape and significance of the partial effects (Fig. S2, Table S2) and the overall variance explained (Adj. $R^2 = 0.23$ in both cases).

Wind speed (estimated using ERA5 reanalysis data) was a good predictor of the birds' flight direction with respect to the eye of the storm, with birds flying away from the eye in winds < 10 m s^{-1} and being attracted to it in strong winds (Table S2, Fig. 3, Fig. S2). The interaction between wind speed and wind direction was also highly significant, with birds being more likely to fly towards the eye when they experienced strong southerly winds, and away from the eye in strong northerly and easterly winds (Fig. S2). This highlights that the birds' position with respect to the cyclonic circulation was important. This phenomenon was also evident in the GPS tracks, which showed that individuals flew towards the eye when they were positioned close to Honshu Island (Movies S1 and S2), whereas birds positioned at the outer reaches of the usual foraging area circumnavigated storm Talim (Movie S1).

Whether birds were ahead of- or behind the storm (considered from 0–180°), was also significant, although the shape of this response was very variable (EDF = 16 for 5 storms, Fig. S2). The main tendencies were for birds to fly away from the storm when they were almost directly ahead of it, and towards the storm when they were directly behind it (this may also relate to the wind direction they experience, as described above). Animations of the individual trajectories show several individuals tracking the storm path, for example, one bird "chased" the eye of storm Talim for > 4 h and two individuals chased typhoon Cimaron for > 8 h (Movies S1 and S2). Finally, storm identity also had a significant effect on flight direction (GAMM Table S2).

We developed an agent-based model to assess whether the shearwater's response to the wind field around the strongest storms represented a specific tendency to fly towards the storm eye. Agents were programmed with the GAMM output of flight direction in relation to the five strongest storms (described above), placed in a random grid in the core foraging area, and exposed to the wind field of the five strongest storms. Overall, agents were attracted to storms that came within 60–170 km of the core foraging area (typhoon Cimaron, storm Talim, typhoon Jebi, mean flight direction ≤ 70°), but did not respond to storms that were further away (e.g. typhoon Goni, which was 330 km away at the closest point) (Table S3).

Of the agents that were capable of reaching the eye (based on distance, agent speed and simulation time), 28–66% came within 60 km of the central point of the storm, for all storms except Goni where no agents came this close, but few came within 30 km (apart from storm Talim, where this figure reached 34%) (Table S3). Similar proximities were observed in our GPS data as one quarter of the birds (13 of 55) came within 60 km of the central point of the five strongest storms, and four individuals came within 30 km (Movies S1 and S2).

Overall, the primary determinant of flight direction with respect to the eye of the storm was the wind field. Adding distance to land to our GAMM of flight direction in relation to the storm eye did not improve the AIC or deviance explained. Nonetheless, a separate GAMM of flight direction with respect to land during all 10 storms showed a positive and almost linear effect of wind strength on the tendency to fly towards land, with shearwaters flying away from land as wind speeds increased (Table S4, Fig. 3, Fig. S3).

Discussion

We show that shearwaters flew towards the eye of multiple typhoons, a behaviour that was more likely as wind speed increased, with birds even moving towards the eye of the strongest typhoon in the study period (Fig. 3, Table S1). This strategy exposed birds to some of the strongest wind strengths, as speeds increase towards the eye wall and only decrease within the eye itself. Given that storm eyes have a diameter of 20–50 km (16), it is clear that the four birds that came within 30 km of the eye were operating in or close to the eye wall. These results are surprising given that almost all other seabirds tracked in relation to storms have avoided the strongest winds, either by remaining on or close to land in the case of pelicans, juvenile frigatebirds and boobies (10, 17), or by circumnavigating the storm system (10, 17), in agreement with optimal navigation theory (18).

Shearwaters differ from almost all other species tracked in storms to date through their use of dynamic soaring flight, which enables them to extract energy from the vertical wind gradient and fly at low metabolic cost (19-21). As a result, procellariformes are able to exploit strong winds, as evident by the example of one gray-headed albatross (*Thalassarche chrysostoma*) that flew along the edge of a deep depression in the southern ocean (achieving groundspeeds > 35 m s^{-1} (22)). Streaked shearwaters are relatively small, weighing some 580 g, and typically fly with airspeeds up to ~14 m s^{-1} (23), yet here we find that adults flew in winds up to 21 m s^{-1}. The actual wind speeds experienced by shearwaters is likely to have been even greater, as ERA5 tends to underestimate wind 10 m above the surface by 5–20 m s^{-1}, depending on the storm intensity and its stage of evolution (24). Nonetheless, this will be tempered by the tendency to fly close to the water surface for most of the dynamic soaring cycle (25), where wind speeds are lower (e.g. wind speeds are predicted to drop from 21 to 18.5 m s^{-1} between 10 and 5 m (26)). Variation in flight height may therefore provide a way for shearwaters to modulate their exposure to the strongest winds, while still extracting energy from them.

But flight style cannot, in itself, explain the shearwaters’ response to typhoons, because shearwaters only flew towards the eye of the storm when this took them away from the mainland and when they were experiencing strong winds (*cf.* (22)). The context-dependency of this behaviour also means it is unlikely that birds moved towards the eye to exploit temporary increases in productivity (27). Instead, we suggest that birds fly towards the storm, and sometimes track its path, to avoid the strong onshore winds that occur in the wake of storms as they move north through our study area. Shearwaters are well-adapted to flight close to land in moderate winds. For instance, Awashima shearwaters fly along the coastline on a daily basis as they move northward to forage, and partly pass through a narrow strait (the Tsugaru Strait) at the north of the Sea of Japan (Fig. S4) (28). Streaked shearwaters at another colony also head towards the coast and fly along it in normal wind conditions (~10 m s^{-1}), using the coastline as a navigational cue (25).

The tendency to fly away from the mainland, which we observe in association with strong winds, therefore appears to be a particular strategy for storms, when their ability to compensate for drift may be compromised. In such circumstances, land can represent a range of threats for shearwaters, from the direct risk of collision and uncontrolled landings in extreme winds (as reported for procellariiformes during a 1984 storm in South Africa (13)), to the limited capacity to take-off once grounded, and their susceptibility to predators, including crows and raptors (28, 29).

The instances when shearwaters did circumnavigate a storm suggests that they have an active and flexible response to storm systems (*cf.* (11)), which varies with their location and the wind direction they experience. Circumnavigation is unlikely to be feasible when birds are in their core foraging area close to Honshu Island, as storms approach from the southwest, typically sandwiching birds between the storm path and the land (Fig. 3, 4). Clockwise circumnavigation would require birds to fly with strong headwinds that could also drift them towards Honshu Island (Fig. 4). Anticlockwise circumnavigation from the core foraging area would require birds to sustain groundspeeds greater than the storm speed for hundreds of kilometres as they fly north and west towards Russia and Korea, before exiting south of a storm. This seems untenable given that storms in our study reached translation speeds > 20 m s^{-1}. The individuals that circumnavigated a storm did adopt this strategy, but crucially, they were already northwest of the storm's path, reducing the distance required for circumnavigation.

Birds may well be able to detect approaching storms through changes in barometric pressure, which typically declines before a storm's arrival, or infrasound , which could also provide information on storm strength and location (10, 11, 30). Indeed, an early detection system may facilitate the selection of an appropriate response to the wind field. Beyond this, birds may also need to know where land is in order to avoid it. For instance, in our agent-based model, agents were programmed without any knowledge of, or response to, the location of land, and 91% of agents were "wrecked" on land in response to storm Komapsu (Table S3). Adult shearwaters do appear to have a map sense (25), which would be required for knowledge of the distance and direction to land, whether that is Japan to the East, or China, Russia to the West. The need to respond to typhoons could provide additional selective pressure for the development of such navigational capacities. If this were the case, juveniles should be less well equipped to respond to storms, as fledgling shearwaters lack a map sense, and instead use an innate compass bearing to migrate (28). In support of this, young shearwaters (not tracked here) appear to be particularly susceptible to being wrecked after storms, both within our study area and beyond (31-33), although the exact cause of wrecking and/ or mortality is unclear.

Overall therefore, the ability to respond to cyclones over the open ocean appears to be influenced both by flight capacity and navigational capacity. While boobies and frigatebirds circumnavigated cyclones in a manner determined by their soaring strategies (i.e. with frigatebirds gaining altitude in clouds to over-fly the systems (10), the fast, low-cost, dynamic soaring flight of shearwaters enables them to adopt an alternative strategy: Flight into the eye of the storm. This demonstrates that extreme winds only appear to become costly or risky in certain scenarios, such as when shearwaters might be drifted onto land. Nonetheless, the risk of wrecking may well be relevant for a range of procellariiformes, as many species distribute themselves in areas of cyclonic activity and often forage near continents or between continent and islands (34), probably due to the high productivity (35). Indeed, anecdotal examples of two other procellariiformes tracking the eye of a storm in the Southern Ocean (36) suggest this strategy could even function as a general mechanism to prevent unfavourable drift e.g. away from productive areas and/ or their breeding grounds, even when they are not operating in water bodies encircled by land. Extreme conditions have therefore selected for extreme responses in wind-adapted species. The question is the extent to which these will be sufficient as typhoon intensity, as well as potentially size and duration, increase.

Materials and Methods

Data collection

Streaked shearwaters breeding on Awashima Island (38° 27.102'N, 139° 14.363'E) were equipped with GPS loggers from 2008 to 2018, as described in (29, 37, 38), providing movement data from 401 individuals. In summary, birds were instrumented with Gipsy 2 & 4 GPS loggers in 2008–2016 and AxyTrek loggers (Technosmart, Rome, Italy) in 2017–2018. Loggers were attached to the back of each bird with waterproof tape (Tesa, Hamburg, Germany) and cyanoacrylate glue. The logger and tape represented <5 % of bird body mass. Ethical permissions for tagging were granted by the Animal Experimental Committee of Nagoya University (GSES). The experimental procedure was approved by the Ministry of the Environment Government of Japan.

GPS tracks were then selected for analysis according to whether they coincided with storm activity in the Sea of Japan. This resulted in 2,319 hours of observations from 75 individuals over 5 years (2010, 2014, 2015, 2017 and 2018), which were used for initial data exploration, where all birds were tracked during at least one storm. Flight was distinguished from drifting on the sea surface using a groundspeed threshold of 4.1 m s^{-1} following (39). We also applied a speed filter to remove positions that gave groundspeeds > 25 m s^{-1} to account for GPS location errors. This filtering threshold was identified using the cut-off point in groundspeed frequencies. Filters were applied to raw data, which were recorded at frequencies of 1 Hz to 1 minute depending on the year. This resulted in the removal of < 0.1% of GPS locations for the storms Talim, Jebi and Cimaron, and < 5.2% for the storms Kompasu and Goni (the five strongest storms). This did not result in any notable change in the distribution of step lengths between filtered and unfiltered data (Fig. S5), suggesting that we were not removing meaningful biological responses to high wind speed scenarios. In fact, the main determinant of the amount of data that was removed was the generation of GPS logger that was used, with older devices apparently giving more frequent erroneous locations.

Wind estimates were obtained from ERA5 global reanalysis models (Fig. 1A, Copernicus Climate Change Service (C3S) (40, 41), for all bird locations. Global reanalyses combine real observations with forecast general circulation models to provide observation-constrained grids of the wind field that are capable of representing most tropical storms (42). The two horizontal wind vectors (u, v) at 10 m from the surface were converted to horizontal wind speed and direction with a temporal resolution of one hour and a spatial resolution of 0.1°.

Storms were classified according to the maximum wind speed measured in the Sea of Japan by meteorological agencies, and recorded in the International Best Track Archive for Climate Stewardship (IBTrACS, http://ibtracs.unca.edu/index.php (43, 44)). IBTrACS provides the most comprehensive record of all major storms globally and it is ideal for detecting storm systems and for quantifying their tracks. Furthermore, wind speeds reported by meteorological agencies are not subject to the underestimation inherent in reanalysis models (24). We classified storms according to their wind speed using the Japanese meteorological agency categorization (JMA, https://www.jma.go.jp/jma/en/Activities/forecast.html#typh) (Table S1).

All storms in IBTrACS that passed through the Sea of Japan at times for which we had shearwater GPS data were included in the analysis. Storm tracks were retrieved from IBTrACS, http://ibtracs.unca.edu/index.php (43, 44)), which provided the coordinates of the eyes of all major storms with a temporal resolution of six hours. Each storm track was interpolated to one hour temporal resolution to match that of ERA5. Interpolations were run using the move package (version 4.0.0, (45)) in R (version 4.0.1, (46)) and the great circle method.

Statistical analysis

First we modelled the direction that birds flew with respect to the eye of a storm, where the storm was that closest to each GPS location. We used generalized additive mixed effect models (GAMMs, Table S2), as these models allow for complex, non-linear responses. We built one model that included flight data from all ten storms, including the weaker storms where birds experienced low to moderate wind speeds (Fig. S1), and a second model that included only the data from the severe tropical storms and typhoons (five storms, Table S1), to test whether birds demonstrated a distinct response to extreme events. This resulted in 690 hours of observation from 55 birds flying in the five strongest storms and 1,618 hours from 73 birds in all ten storms (after removing hours with non-flight data and when the storm eye was located over land and was inaccessible to birds). All attributes relating to bird movement represent hourly averages of each term estimated using the raw GPS locations, in order to match the resolution of the bird movement paths to the ERA5 reanalysis data.

The global model included wind speed, wind direction and bird position with respect to the storm eye. For the latter, values of 0^{o} indicated that a bird was ahead of the storm i.e. the eye was moving straight towards the bird, and 180^{o} directly behind it i.e. the storm was moving away from the bird. While wind direction was an indicator of the geographical location of a bird (e.g., birds are expected to experience southerly winds when East of a cyclone, Fig. 4), the bird's position in relation to the eye allowed us to test for difference in response according to whether the storm was travelling towards or away from a bird (as this was related to the storm's direction of travel, and was not an indicator of the bird's geographical location). The model also included interactions between wind speed and direction, and wind speed and bird position with respect to the storm, as each individual member term of the interaction was retained in the first stages of model selection. Storm ID was included as a random effect. We then extended this model to test if proximity to land improved the model fit. The same interactions were included as for global model 1, with an additional interaction between wind speed and distance to land.

In a final model, we tested whether the flight direction with respect to land varied with wind speed and direction during all ten storms, with the expectation that birds would be less likely to fly towards land in strong winds. The global model was the same as the previous models.

Model selection was performed using the smoothing shrinkage method (47). First, simple predictors were added using the "s( )" smoothing and the penalised thin plate regression spline ("ts") as smooth basis (but "re" for random effects) to form the global model. Each pair of terms was then assessed for concurvity using the mgcv package (48). Less significant terms in pairs with "worst" case concurvity > 0.8 were removed from further analysis. Second, the smoothed effect of each predictor was evaluated and terms where the effect shrank to zero were removed. Evaluation and exclusion of zero effects was repeated by the addition of the interaction terms using the tensor product smoothing "ti ()" with a simultaneous assessment of whether the removal of an interaction from the model resulted in significant reduction in AIC (≤ 2). In the refined model that included all remaining single predictors and interactions, the smoothing basis was set to thin plate regression spline ("tp") for continuous predictors and cyclic cubic regression spline ("cc") for the circular wind direction. Finally, the base dimension (k) of each term was assessed using the gam.check function of mgcv (48) and increased appropriately where needed.

In each model, the number of GPS fixes averaged per hour was used as a weight, normalized by the mean number of fixes in the modelled dataset. To account for temporal and spatial autocorrelation, all models included the date/ hour and the hourly interpolated coordinates for each set of GPS coordinates within each hour, using the corARMA and corSpatial functions from the nlme package, respectively (49). The final models were evaluated for outliers, uniformity, over/ under-dispersion and spatial/ temporal autocorrelation using the DHARMa package (50), with the test of under-dispersion being significant for all models. Significant outliers detected in the standardized residuals of the models of ten storms were removed when their value was outside the central 97% of the residual distribution (see https://rdrr.io/cran/DHARMa/man/outliers.html) and the models were refitted with the filtered datasets (e.g. 51). This procedure improved the model fit but did not change the significance level of terms or the predicted trends (shape of partial effects).

Agent based modelling

An agent-based model was developed to resolve (1) whether the response to the wind field resulted in birds flying towards the eye of the storm and (2) how often the predictions from model 1 resulted in birds being “wrecked” i.e. flying onto land. In both scenarios ten simulations of 400 agents were run, with agent starting points distributed randomly within the 70% kernel density contour of space use at-sea, determined across the five years of study (Fig. 1B). We used the output of model 1 (flight direction with respect to storm eye for the 5 strongest storms) to drive each agent’s heading at any time step (one hour). The output from model 1 was converted from the predicted 0–180^o to 0–360^o using a binomial GAMM predicting whether the agent should fly right or left in relation to the storm. Agent flight speed was fixed as the mean hourly groundspeed of the observations collected during each storm (~ 8–9 m s^{-1}) or set to 9.3 m s^{-1} (~ 33 km h^{-1}) when the mean ground speed exceeded this threshold. As each cell in ERA5 covered an area of ~ 11 km^2, each agent was set to make three steps per hour (~11 km each to complete a movement of ~ 33 km), to guarantee that each cell was taken into account. Agents started moving when the distance between the storm eye and the agent was ≤ 500 km. Movement was paused whenever this threshold was exceeded or the storm eye reached land. An agent was considered to reach the eye of a storm when its distance from the eye location was ≤ 30 km (the mean radius of 62 storm eyes as identified by (16). We ran simulations for the five storms classified as severe tropical storms and typhoons (Table S3, movies S3–S7).

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Data and materials availability: All data and code needed to evaluate the conclusions in the paper are available on the Dryad Digital Repository: https://datadryad.org/stash/share/q1_vXhtjR9quMdGI-kuC0odsxb40MO5X6Eeed1thuY8 with doi: https://doi.org/10.5061/dryad.2z34tmppj and will be publicly available upon acceptance for publication.

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Figures and Tables

Figure 1. Distribution of streaked shearwaters and storms in the Sea of Japan. (A) The area affected during the passage of tropical cyclone Goni (26/08/2015 04:00:00 (UTC)). The black star indicates the location of the colony near the Honshu Island. The right panels show the 70% density contour of hourly interpolated GPS locations during the 10 storms (upper panel) and the tracks of storms that passed through the Sea of Japan when at least one tagged bird was at sea (lower panel). The five strongest cyclones are given in the first row of the legend.

Figure 2. Bird behavior according to the wind field and land. (A) Hours of flight and non-flight behavior (n= 2,318 h) according to wind strength when birds were at sea during the 10 storms. (B) Kernel density of hourly mean flight direction in relation to wind direction during the 10 storms (n= 1,618 h), highlighting the selection of crosswinds. (C) Flight direction in relation to the eye of the five strongest storms, derived from the raw GPS estimates, showing birds were more likely to respond to storms that passed closer to them. The colors indicate the distance between the eye and tracked birds (90% quantile of bird – storm distance) with proximity increasing from blue to red. (D) The normalized kernel density of hourly mean flight direction in relation to the closest point on land (n= 1,618 h), during the 10 storms, showing birds only flew towards the eye when this took them away from land.

Figure 3. Bird responses to tropical cyclone Cimaron. (A) As Cimaron entered the Sea of Japan (black track), 32 birds were located within the 70% utilization area. (B) When the eye was at its closest to the birds, three birds had already flown towards and chased the eye (dark red and green), two more had initiated flight towards it (bright green) and the majority of birds located

within a layer of weaker winds, remained sheltered near the shore. In the same hour another storm can be observed to the west.

Figure 4. Responses to a hypothetical tropical cyclone travelling from south to north, for birds located within the core utilization area near the Awashima colony (marked with a star). (A) Anticlockwise circumnavigation with wind support, suggested by optimal navigation theory (18), becomes feasible when birds are positioned to the north and west of the eye (blue shade) and can benefit from tailwind assistance. This response was observed in our results. (B) Clockwise circumnavigation would require flight into headwinds that could also drift birds onshore. This response was not observed. (C) Flight towards the eye from this location (observed in our results) enables birds to benefit from crosswinds, takes birds away from land and avoids onshore winds that follow behind the eye. (D) Birds foraged close to shore when winds were relatively weak.