Black-tailed gulls alter their flight height and airspeed according to wind conditions during their coastal commuting trips

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ABSTRACT: Seabirds are expected to increase their flight height in tailwind and to increase their airspeed in headwind during goal-oriented flight to minimize their cost of transport. To understand how flapping birds respond to variability in wind speed and direction experienced during their commuting flights between their breeding colony and foraging areas, we measured the flight height and speed of black-tailed gulls *Larus crassirostris* using GPS loggers. We analyzed the relationships between these flight parameters and local wind speed and direction. Over the course of the 2016 to 2018 breeding seasons, we tagged 105 birds at 2 colonies in northern Hokkaido, Japan. A total of 90 flight track-lines within a 500 m radius of 5 coastal meteorological stations were analyzed. The median flight height ranged from 0 to 153.8 m, and the median ground speed and airspeed were between 18.6–82.1 and 19.5–93.0 km h^{-1}, respectively. Gulls flew higher with greater tailwind speed, supporting the hypothesis that birds utilize greater wind assistance at higher altitudes. Furthermore, gulls increased their airspeed under strong headwind conditions, suggesting they adjust airspeed to achieve the most cost-effective speed to reach their destination. Better understanding the drivers of seabird flight height is key to assessing the potential for collisions with wind turbines in coastal and offshore wind farms. These findings provide useful information to reduce collisions with coastal and offshore wind facilities.

KEY WORDS: *Larus crassirostris* · Airspeed · Collision · Flight height · GPS tracking · Wind turbine · Optimal flight theory · Wind conditions

1. INTRODUCTION

Wind is one of the major factors structuring fundamental processes of marine ecosystems (Mann & Lazier 2006). Wind can shape the life history traits and biogeography of marine organisms, which may use this force to assist their movements at or above the water surface (e.g. Woodcock 1993, Park & Choi 2010, Munro et al. 2019). However, both wind strength and direction are also extremely variable locally, and consequently the organisms relying on aeolian power to assist their movements may also need to be highly flexible in their behavior to accommodate such variability.

Especially in central place foraging marine animals such as seabirds, the organisms need to commute regularly between breeding and feeding sites and may thus greatly benefit from using wind power efficiently, to minimize their energy expenditure (Weimerskirch et al. 2000, Goto et al. 2017). Birds are thus assumed to regulate their flight behavior under variable environmental conditions to optimize energy expenditure

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and to minimize adverse effects of unfavorable environmental conditions (Elliott et al. 2014, Lane et al. 2019).

One mechanism through which seabirds may respond to varying local wind speed and direction is by adjusting their flight height (Liechti 2006). Field observations show that birds fly at higher altitudes with tailwinds during both short- and long-range movements (Krüger & Garthe 2001, Kahlert et al. 2012, Tarroux et al. 2016). Since wind speed increases with altitude (Arya 2001, Iwatani et al. 2005), flying higher in tailwind conditions may thus allow the birds to utilize greater wind support working in the direction of travel, which minimizes their energy expenditure (Liechti 2006). On the other hand, seabirds fly closer to the ocean surface in headwind conditions; they may then take advantage of wind shear (decreased wind speed with proximity to ocean surface/ground due to friction) to reduce movement costs. Birds flying close to the sea surface or the ground (altitude under 4 m) are expected to benefit energetically from the latter effect (Finn et al. 2012).

Another way seabirds may respond to local wind speed and direction is by adjusting their airspeed, i.e. the speed of the bird relative to the air flow surrounding it (Schnell & Hellack 1979, Bloch & Bruderer 1982, Hedenström et al. 2002). Optimal flight theory and wind tunnel experiments suggest a U-shaped relationship between airspeed and mechanical energy expenditure of a flying bird (Rayner 1999, Tobalske et al. 2003, Pennycuick 2008). Based on this, 2 flight-speed models are proposed: the minimum power speed (V_{mp}) and the maximum range speed (V_{mr}). The minimum power speed is the speed that requires the lowest metabolic power from the bird to keep flying. The maximum range speed, which is faster than minimum power speed, is the speed that allows the greatest air distance to be covered per unit of fuel-energy consumed (Pennycuick 1978). This maximum range speed allows the bird to minimize the cost of transport, defined as the energy cost (combining basal and activity-specific metabolic rates) per distance traveled (Schmidt-Nielsen 1972, Hedenström & Alerstam 1995), when undertaking a goal-oriented flight (Pennycuick 1978). While minimum power speed is predicted to be constant under varying wind speed and direction, maximum range speed is predicted to increase with headwind (Pennycuick 1978); the bird is expected to fly at faster airspeeds to overcome the adverse force caused by headwinds and gain distance (Videler 2005). Several mathematical models have been derived to predict power consumption as well as flight speed as a function of wind speed and bird morphology (e.g. Tucker 1975, Pennycuick 2008).

Studies that examined the effects of wind on flight height initially focused on migratory flights (e.g. Krüger & Garthe 2001, Erni et al. 2005, Kahlert et al. 2012). Recent studies have shifted to the breeding season using GPS tracking combined with wind data obtained from reanalysis products (McLaren et al. 2016, Lane et al. 2019). In the context of optimal flight theory, field studies showed that birds do adjust their airspeed, seemingly to optimize their cost of transport (Yoda et al. 2012a, Elliott et al. 2014, Kogure et al. 2016). However, to our knowledge, few studies have examined the effect of wind on flight height and airspeed using measured wind data combined with fine-scale flight data. Hence, the aim of our study was to quantify the relationship between wind conditions and flight behavior by combining hourly measured local weather data and fine-scale (1 s) GPS tracking.

In this study, we focused on the flight response of black-tailed gulls *Larus crassirostris* breeding in northern Hokkaido, Japan (Fig. 1a), to local wind conditions. Importantly, one major foraging area used by this population is located to the east of Cape Soya (Kazama & Watanuki 2021; Fig. 1a). Black-tailed gulls use a 'commuting-type' foraging strategy, where they mostly exploit known and predictably good foraging areas, compared to other seabird species that use a more 'opportunistic' strategy to maximize their search distance while foraging (e.g. Ventura et al. 2020). Based on this characteristic, we can assume that flight portions occurring between the breeding colony and this feeding area for both outbound and inbound trips are relatively straight goal-oriented commuting flights. Furthermore, black-tailed gulls mostly use flapping flights during the commuting portion of their foraging trips; flapping flight accounted for 81% of flight behavior during commutes between foraging grounds and back (calculated from R. Ma et al. unpubl. data).

With the objective to relate wind speed and direction to the height and air speed of flapping flights in the realm of aerodynamics, we examined 2 hypotheses. First, since wind speed increases with height (Arya 2001, Iwatani et al. 2005), we hypothesized that the gulls would fly higher with tailwinds to utilize greater wind force in their travel direction and minimize their cost of travel (Liechti 2006). Hence, we predicted a positive correlation between wind speed (in the direction of the aimed goal) and flight height. Second, we assumed individuals would fly with maximum range speed during their commuting flights to minimize their cost of transport (Pennycuick 1978).
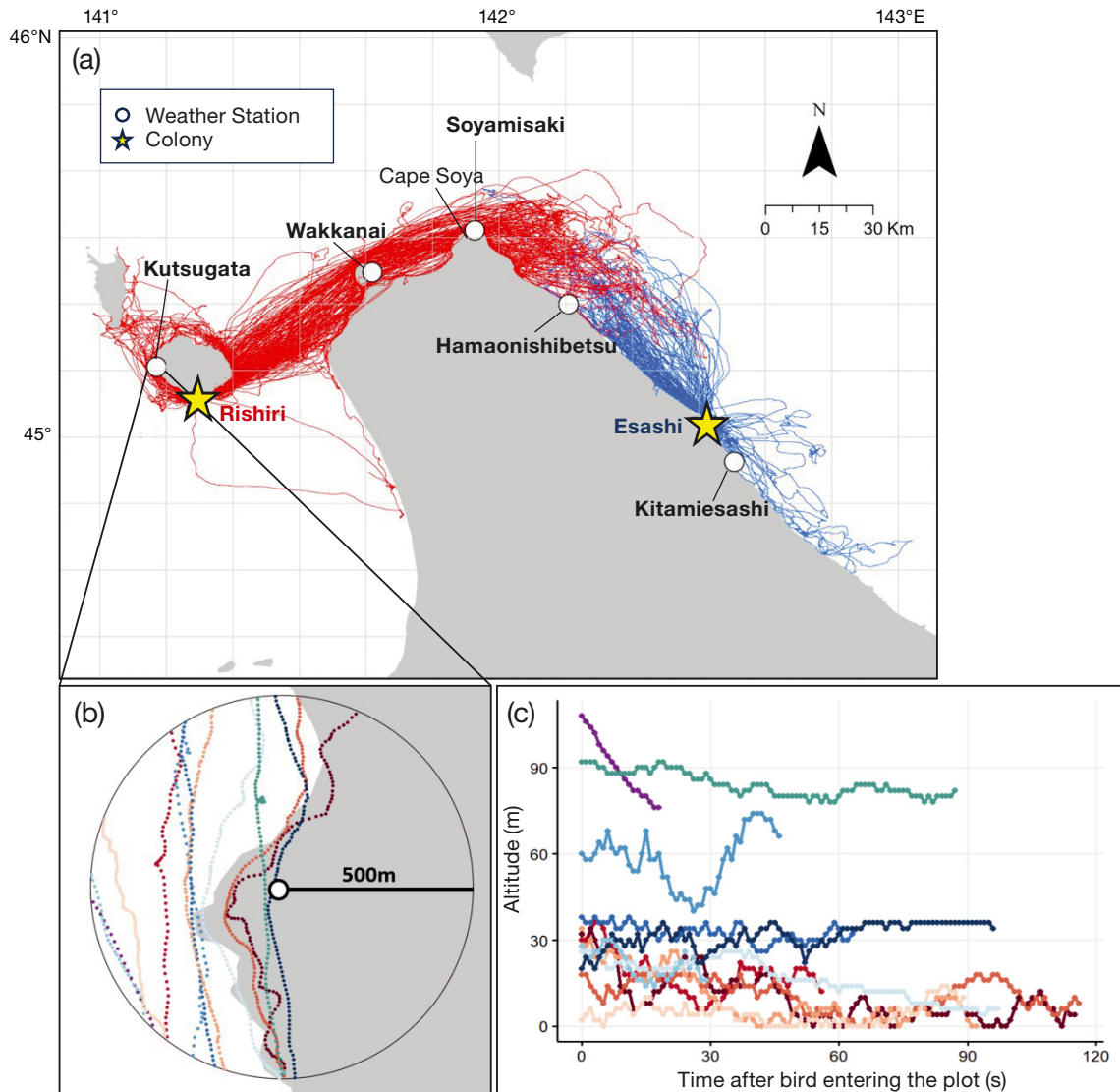
Fig. 1. Study area and track-lines. (a) Locations of the study colonies at Rishiri and Esashi (yellow stars) and weather stations (white circles) located in northern Hokkaido, Japan, and track-lines of 99 individual gulls tagged during 2016–2018. The red and blue lines represent tracks of birds tagged on Rishiri Island and in Esashi town, respectively. (b) GPS fixes extracted for analysis at Kutsugata weather station, comprising 12 track-lines. The weather station (white circle) is located at the center of the 500 m radius circle. (c) Change in the flight altitude recorded by the bird-borne GPS loggers, as the gulls entered and exited the 500 m radius around Kutsugata weather station. The same color code is used as in (b) to show the different individuals

Accordingly, we expected to see an increase in the tracked gulls' airspeed with stronger headwind speed.

2. MATERIALS AND METHODS

2.1. Study area and species

Gulls were studied at 2 breeding locations in northern Hokkaido: at Rishiri Island in 2016, 2017, and 2018, and at a breeding colony in the coastal town of Esashi in 2017 and 2018 (Fig. 1a). More than 20 000

and 3000 pairs of black-tailed gulls breed on Rishiri Island and Esashi, respectively (K. Kazama unpubl. data). A total of 105 birds were captured at their nests during the incubation period using a snare or box traps. GPS loggers (GipSy-5, Technosmart, L × W × H: 40 × 20 × 7 mm, 11 g) were attached to the central back feathers using TESA® tape as described by Mikami et al. (2022). The devices corresponded to ca. 1.6% of the gulls' average body mass (669.74 g), well below the 3% recommended threshold to minimize disturbance (Phillips et al. 2003). The loggers were programmed to record tridimensional location (lati-

tude, longitude, and altitude) every second, and were able to record for 70 h. Out of the 105 tagged gulls, 104 individuals were successfully recaptured 5–7 d after the deployment, and tracking data were available from 99 individuals.

We did not examine the relationship across entire foraging trips, but instead selected sections of the trips (500 m buffer regions around the weather stations) (Fig. 1a,b). We acknowledge that the birds' behavior during these sections of the tracks along the coast (near the weather station) may differ from other parts of the tracks when the birds are further offshore; however, the selected data conferred 2 advantages in our approach. First, it provided a unique opportunity to accurately examine our question using locally measured wind data, collected independently to our GPS data. Second, this apparent limitation also provided the advantage to rule out one potential confounding factor in the gulls' behavioral adjustment to variable wind conditions: the birds' movement direction. It is likely that the birds may use a combination of concurrent behavioral adjustments, including flight height, airspeed, travel direction, and wing shape and area, which may be difficult to measure accurately when taken all together. In our approach, we selected only the trip portions where the birds were traveling along a relatively straight line, toward a consistent destination that was un-changed for that period. This allowed us to minimize the influence of this potential confounding factor (changing flight direction) and provide the best possible measure of the other behavioral responses initiated.

2.2. Weather station and track-lines

The GPS fixes occurring within a 500 m radius from the 5 Automated Meteorological Data Acquisition System (AMeDAS) stations located along the study area coastline were extracted for analysis (Fig. 1a,b) using the GIS software ArcGIS Pro (ESRI 2018). The weather stations record both wind direction along 16 compass sectors and wind speed. These stations are located 30–250 m inland and 19.5–36 m above sea level. The GPS position and height of the birds were matched with the wind direction and speed recorded at the closest hour. A radius of 500 m was chosen based on the small difference between wind speed/direction measured at the coastline and that measured 400 m offshore (Shimada et al. 2018), as well as the small (<5%) change in expected wind speed within 500 m from the coastline (Barthelmie et al. 1996). Thus, in this study we assumed that wind

direction and speed recorded at the weather station were representative of the winds experienced by the birds flying within the study area.

In this study, we defined a track-line as a series of continuous GPS fixes passing within a 500 m radius of a weather station (Fig. 1b,c). A total of 94 track-lines were extracted from our GPS dataset, but 4 were excluded from further analysis because in those 4 track-lines, more than 50% of the GPS fixes indicated a speed under 15 km h^{-1}, which suggested that the bird had landed (Yoda et al. 2012b, Kazama et al. 2018).

2.3. Determining flight height

The GipSy-5 GPS loggers recorded altitude for each fix at a 1 s interval. These tags are accurate to 7.1 ± 6.0 and 6.9 ± 5.4 m (mean ± SD) when the loggers connect with 4 and 6 satellites, respectively (J. Okado & Y. Watanuki unpubl. data; see Text S1 in the Supplement at www.int-res.com/articles/suppl/m723p201_supp.pdf). Although more than 95% of the fixes were made when the logger was connected to 6 or more satellites, we used GPS fixes made with 4 or more satellites to minimize error range and maximize sample size.

Flight height was calculated by subtracting land elevation from bird flight altitude at each GPS fix. We downloaded land elevation data from the Geospatial Information Authority of Japan website (https://fgd.gsi.go.jp/download/menu.php, accessed on 30 Aug 2022). This GIS layer was composed of average elevation values calculated for each center point of a 0.2″ × 0.2″ (which approximates 5 × 5 m) grid which covered northern Hokkaido. If the closest elevation center point was more than 5 m away horizontally from the GPS fix, we assumed that the land elevation was 0 m, i.e. the GPS fix was over the sea. This GIS layer was not available for Hamaoni and Esashi. Thus, for the 7 track-lines occurring within Hamaoni and Esashi, we used a GIS layer with 5 m contour lines to estimate the land elevation at each GPS point. Most GPS fixes occurred above the sea, but 6 track-lines were partially over land. All GPS fixes above land fell between the coastline (0 m) and the 5 m contour line. Hence, we assigned a land elevation value of 5 m at all GPS points occurring over land.

2.4. Relative wind direction components

At each GPS point, the flight direction was calculated using the 'bearing' function in the package 'Geosphere' (v.1.5-14, Hijmans 2021). The ground

speed vector (v_g) was then derived based on the flight direction from the previous GPS fix and the ground speed. The wind vector (v_w) also consists of a direction and a speed component derived based on the measured wind speed and direction. The bird's airspeed vector (v_a) was then calculated by subtracting the wind vector from the ground speed vector ($v_a = v_g - v_w$). This airspeed vector indicated the self-propelled direction and speed. In a next step, at each GPS fix, the tailwind component (TWC) and adjusted tailwind component (ATWC) were calculated using the ground speed vector (v_g) and the wind vector (v_w) (Fig. 2a, modified from Kogure et al. 2016). Whereas TWC is the wind component blowing in the same direction as the groundspeed vector, ATWC is the wind component blowing in the same direction as the airspeed vector (Fig. 2a). In other words, TWC is the strength of wind working in/against the direction of the flight trajectory, and ATWC is the strength of wind force working directly in/against the bird's body axis (Fig. 2). Hence, negative ATWC values can also be considered as the strength of the wind that the bird has to overcome to gain distance. In our study, we calculated each wind component as:

$$TWC = v_w \times \cos\theta \qquad (1)$$

$$ATWC = v_w \times \cos\gamma \qquad (2)$$

where v_w is the wind vector, and θ is the angle between the ground vector and wind vector (Fig. 2a).

Flight height, airspeed, TWC, and ATWC calculated for each GPS fix were not independent from those calculated for the previous GPS fix, for a given track-line. Within-track-line variation in flight height was significantly smaller than between-track variation (1-way ANOVA, $F_{89\_7457} = 770.32$, $p < 0.001$). Hence, in this study, we used only the median value of flight height, flight direction, ground speed, airspeed, TWC, and ATWC per track-line. Moreover, the wind speed and direction data were measured only hourly, and it hence seemed adequate to match these discrete data with the single median height value retained for each track-line.

2.5. Statistics

We built linear mixed-effects models (LMMs) to examine the factors affecting median flight height and median airspeed. Bird individual IDs and plot locations were treated as random effects. For flight height, we included TWC, commuting direction (outbound to foraging area (0) / inbound to colony (1)), time of day (day (1) / night (0)), and sex of the individual as fixed effects. For median airspeed, we included ATWC, commuting direction, time of
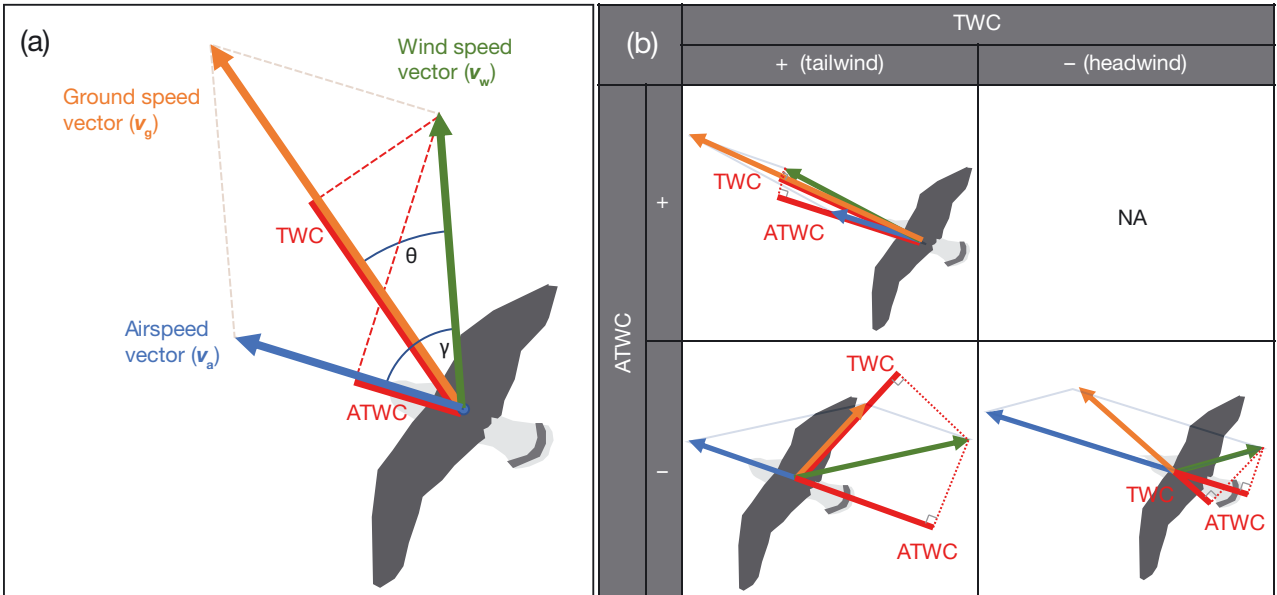

Fig. 2. (a) Conceptual diagram of wind vector (v_w), ground speed vector (v_g), airspeed vector (v_a), tailwind component (TWC), and adjusted TWC (ATWC) modified from Kogure et al. (2016). v_a is calculated by subtracting the wind vector from the ground speed vector. Note that we did not measure the heading of the bird directly. TWC is the wind component blowing in the direction of the overall flight trajectory, hence in the direction of v_g. ATWC is the wind component blowing in the direction of the birds' self-propelled power, hence the v_a. (b) Conceptual diagram of v_w, v_g, and v_a in different wind conditions

day, and sex. No strong collinearity was found between these factors (correlation ratio < |0.16| between all categorical and continuous variables, and phi coefficient < |0.25| between all categorical and categorical variables). Daytime and night-time were defined based on the local times of sunrise and sunset. The sunrise/sunset times for each day were calculated using the 'sunrise' and 'sunset' functions in the 'bioRad' R package (Dokter et al. 2019), at each of the 5 weather station locations. To determine whether the track-line occurred during the day or at night, we compared the sunrise and sunset times with the median time of each track-line. To run the models, we used the 'lmer' function in the 'LME4' package (Bates et al. 2015). All variables were rescaled to a value between 0 and 1. We then compared and ranked all possible LMMs for both flight height and airspeed respectively using Akaike's information criterion (AIC) in the 'MuMIn' package (Barton 2018). Models with delta AIC values <2 were considered equally plausible (Burnham & Anderson 2003), and models carrying the 95% cumulative model weight were selected as adequate models. All statistical analyses were performed using the open-source software R v.4.3.0 (R Core Team 2023). Values are reported as average ± SD.

2.6. Modeling maximum range speed and minimum power speed

Mathematical models can make predictions on how animals are expected to adjust their flight behavior (i.e. airspeed) to varying wind speed based on basic morphological measurements such as body mass, wingspan, and wing area (Pennycuick 2008, Klein Heerenbrink et al. 2015). To assess whether gull tracks showed characteristics of maximum range speed or minimum power speed models, predicted airspeed was modeled in each case and compared to the observed airspeeds. We used the 'afpt' package in R to model the maximum range speed and the minimum power speed of black-tailed gulls (Klein Heerenbrink 2023). This approach allows flight costs in seabirds to be estimated by implementing the aerodynamic power model described by Klein Heerenbrink et al. (2015). We used the following values for the parameters in the model: body mass = 672 g, wingspan = 1.18 m, wing area = 0.138 m^2, type = seabird. We used the mean body mass of the 48 individual gulls tracked in this study. The other values are taken from Watanuki (1987).

3. RESULTS

3.1. Track-line samples

The total 90 track-lines used in our study comprised 7547 GPS fixes from 26 female and 22 male birds (Table A1 in the Appendix; Text S1). Most track-lines were recorded during daytime (n = 69), whereas only 21 occurred at night. The gulls tended to fly closer to shore on their inbound flights compared to their outbound flights. Accordingly, most track-lines (within the 500 m radius of the coastal weather stations) were inbound trips (n = 75), with just 15 being outbound trips. The number of track-lines also largely differed among study sites: 12 were recorded at Kutsugata, 6 at Wakkanai, 65 at Soyamisaki, 1 at Esashi, and 6 at Hamaoni.

3.2. Flight height and TWC

The maximum flight height across all GPS tracks analyzed was 171.5 m (Table A2). The median flight height for each track-line ranged from 0 to 153.8 m with a grand median of 22.0 m (n = 90 track-lines, Table A3). The top 3 equally plausible models (delta AIC <2) explaining the median track-line flight height all included TWC and time of day as predictor variables (Table 1). All equally plausible models predicted a positive effect of TWC on flight height (parameter-estimate value of the best model: 0.537) and a negative effect of time of day (lower flight height during the day, parameter-estimate value of the best model: −0.128).

3.3. Airspeed and ATWC

The maximum ground speed and airspeed across all recorded GPS data were 102.0 and 126.1 km h^{-1}, respectively (Table A2). The median ground speed of track-lines ranged between 18.6 and 82.1 km h^{-1}, while the median airspeed of track-lines ranged between 19.5 and 93.0 km h^{-1} (Table A3). The top 5 equally plausible models explaining median air speed of track-lines all included ATWC as a predictor variable (Table 2). All equally plausible models predicted a negative effect of ATWC on airspeed (parameter-estimate value of the best model: −0.16), reflecting that the birds generally increased their airspeed under negative ATWC. The expected airspeed predicted by the model of Klein Heerenbrink (2023) showed a negative relationship with ATWC

Table 1. Summary of fixed effect parameters for best-fit models explaining the median track-line (flight) height ranked by Akaike's information criterion (AIC) scores. **Bold** indicates equally plausible models (delta AIC <2), and adequate models carrying the 95% cumulative model weight are listed. Tailwind component (TWC), commuting direction (Outward/Inward), time of day (Daylight), and sex of the individual (Sex) were included as fixed effects in the global model. Bird individual IDs and plot locations were treated as random effects

Model rank	Model	df	AIC	Delta	Weight
1	**Flight height ~ TWC + Daylight**	**6**	**−58.6**	**0.00**	**0.468**
2	**Flight height ~ TWC + Daylight + Sex**	**7**	**−57.4**	**1.24**	**0.251**
3	**Flight height ~ TWC + Daylight + Outward/Inward**	**7**	**−56.6**	**1.98**	**0.174**
4	Flight height ~ TWC + Daylight + Sex + Outward/Inward	8	−55.3	3.24	0.093
5	Flight height ~ TWC	5	−50.0	8.65	0.006

Table 2. Summary table of fixed effect parameters for best-fit models explaining the median track-line airspeed ranked by Akaike's information criterion (AIC) scores. **Bold** indicates equally plausible models (delta AIC <2), and adequate models carrying the 95% cumulative model weight are listed. Adjusted tailwind component (ATWC), commuting direction (Outward/Inward), time of day (Daylight), and sex of the individual (Sex) were included as fixed effects in the global model. Bird individual IDs and plot locations were treated as random effects

Model rank	Model	df	AIC	Delta	Weight
1	**Airspeed ~ ATWC**	**5**	**−85.0**	**0.00**	**0.242**
2	**Airspeed ~ ATWC + Outward/Inward**	**6**	**−84.3**	**0.70**	**0.413**
3	**Airspeed ~ ATWC + Daylight**	**6**	**−83.5**	**1.47**	**0.529**
4	**Airspeed ~ ATWC + Sex**	**6**	**−83.5**	**1.53**	**0.642**
5	**Airspeed ~ ATWC + Outward/Inward + Daylight**	**7**	**−83.3**	**1.98**	**0.732**
6	Airspeed ~ ATWC + Outward/Inward + Sex	7	−82.5	2.48	0.802
7	Airspeed ~ ATWC + Daylight + Sex	7	−82.0	2.90	0.858
8	Airspeed ~ ATWC + Outward/Inward + Daylight + Sex	8	−81.2	3.71	0.897
9	Airspeed ~	4	− 81.0	4.04	0.929
10	Airspeed ~ Outward/Inward	5	−80.0	5.31	0.946

when a bird was flying at its maximum range speed, indicated as the solid red line in Fig. 3. The expected airspeed under minimum power speed was predicted to be 36.0 km h^{-1}.

4. DISCUSSION

4.1. Effect of wind on height

We confirmed that tailwinds affected flight height of black-tailed gulls (Table 1, Fig. 4). High-resolution GPS-derived data showed that the tracked gulls flew higher under stronger TWC, thus supporting the hypothesis that birds use wind assistance while commuting (Liechti 2006). A similar effect of tailwind on seabird flight height was reported in both breeding and non-breeding lesser black-backed gulls *Larus fuscus* (McLaren et al. 2016, Serres et al. 2019), breeding northern gannets *Morus bassanus* (Lane et al. 2019), and Antarctic petrels *Thalassoica antarctica* (Tarroux et al. 2016).

However, flight height of gulls was much more variable when TWC was positive (Fig. 4), possibly due to the effects of location-specific updrafts/ downdrafts and turbulence. These effects are complex, and irregular fine-scale gusts of air may affect flight height, especially in birds such as raptors which utilize vertical air flows to gain altitude (Bohrer et al. 2012, Poessel et al. 2018, Scacco et al. 2019). We did not find a significant site-specific difference in turbulence that would lead to biases in vertical wind movement between study sites (Text S2); however, there may be finer-scale turbulence causing increased within-site variability. The stronger correlation between altitude and TWC when TWC was negative could be due to wind shear effects. The birds may be facing a greater need to minimize adverse effects of strong headwinds by flying close to the surface (Finn et al. 2012, Tarroux et al. 2016) in contrast to birds flying in tailwinds (positive values of TWC).

All 3 equally plausible models (Table 1) predicted a negative effect of daylight on flight height of black-
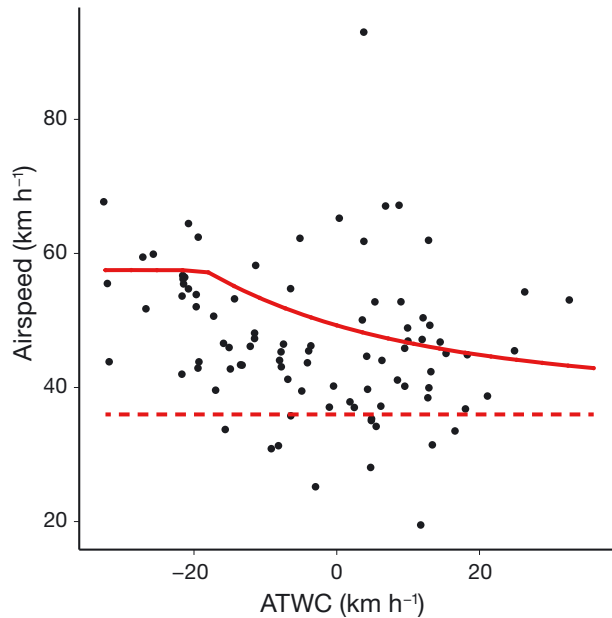
Fig. 3. Relationship between median airspeed and median adjusted tailwind component (ATWC) (n = 90 track-lines). Negative correlation is predicted by the model of Klein Heerenbrink (2023) (R package 'afpt'). The solid red line shows the predicted airspeed at maximum range speed for black-tailed gulls with 672 g body mass. The expected airspeed plateaus at large negative ATWC due to the maximum available power determined by the muscle properties of the bird. The dotted red line shows the predicted airspeed at minimum power speed (36.0 km h^{-1})
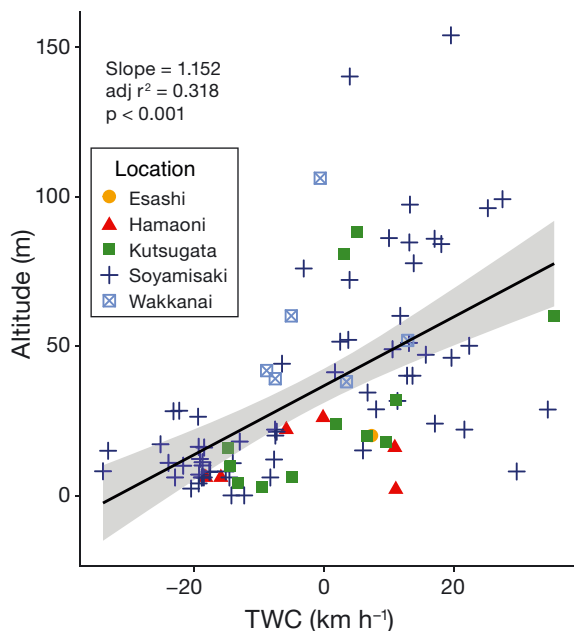
Fig. 4. Relationship between median flight height and tailwind component (TWC) (n = 90 track-lines). Straight line shows the linear regression ($y = 1.15x + 36.65$, r^2 = 0.318, p < 0.001, $F_{1,88}$ = 42.44), and the light gray shading indicates the 95% confidence interval. Different symbols represent the 5 weather stations (see Fig. 1)

tailed gulls (estimated coefficient ranging between −0.128 and −0.125). In contrast, flights of lesser black-backed gulls, including both tortuous prey-searching flights and relatively straight commuting flights, were found to be higher during daytime (Corman & Garthe 2014, Ross-Smith et al. 2016). Gulls being visual animals, they may fly at higher altitudes during the day than at night because of the increased visibility (Corman & Garthe 2014). Time of the day may also indirectly affect flight height through changing local wind direction, such as creating sea breeze during the day and land breeze during the night (Trujillo & Thurman 2020), but the wind direction at the 5 weather stations did not differ markedly between day and night in our study (Fig. 5). There may be other factors driving the flight height to be lower during the day, but the mechanism was unclear from our study.

4.2. Effect of wind on airspeed

ATWC had a negative effect on airspeed, meaning that tagged gulls were flying at faster airspeeds, reflecting an increase in self-propelled locomotion, when facing greater wind force against their body axis. In general, a bird is expected to increase power for self-propulsion to overcome air flow resistance and move forward towards its goal when flying at the maximum range speed, as indicated with the red line in Fig. 3. Hence, the negative relationship found between airspeed and ATWC suggests that the tracked gulls were approaching their maximum range speed. This result, the increased airspeed under increased headwind speeds, fits nicely with previous observations on other seabird species, including gulls and other taxa (black-legged kittiwakes *Rissa tridactyla* and European shags *Phalacrocorax aristotelis*; Elliott et al. 2014, Kogure et al. 2016). Furthermore, most of the observed points were above the minimum power speed predicted by the model of Klein Heerenbrink (2023) (Fig. 3). Therefore, we conclude here that black-tailed gulls may be minimizing their cost of transport by adjusting their airspeed.

4.3. Implications for collision risk with wind turbines

Areas around Hokkaido Island including our study sites have favorable wind conditions for coastal wind-generating facilities (Japan Wind Power Association 2017). Some areas of coastal Hokkaido are
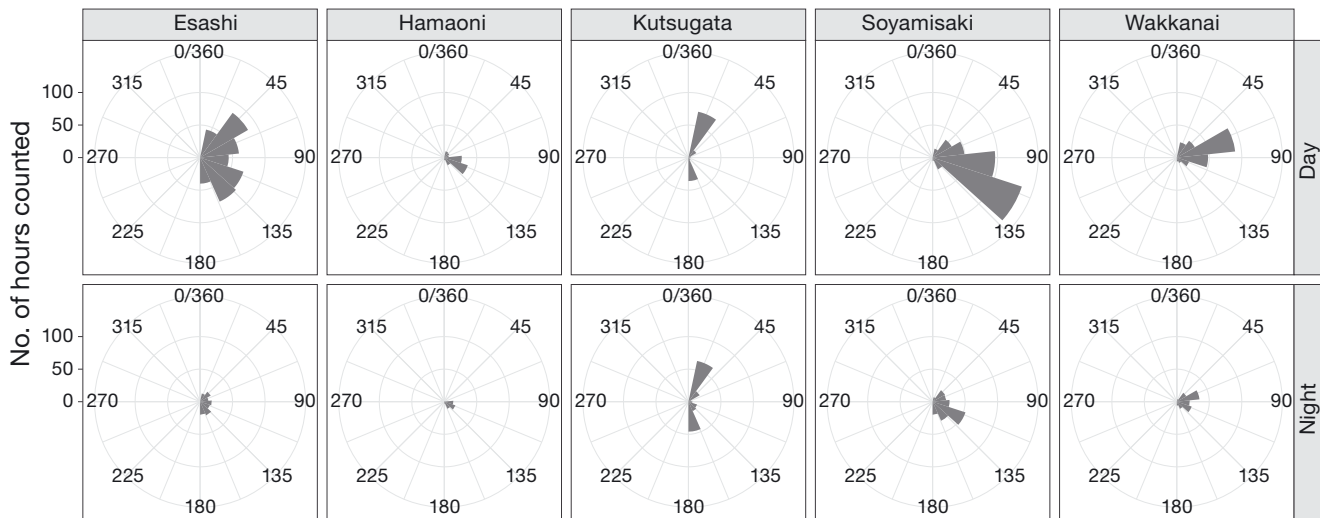
Fig. 5. Windscape at the 5 weather station locations during the period of logger deployment. Note that the *x*-axis indicates the number of occurrences and not intensity of the wind. Here, day was determined as 04:00–19:59 h (16 h of each day, n = 2773) and night was 20:00–03:59 h (8 h of each day, n = 1408)

designated as areas promoted for 'development and use of marine renewable energy' (https://www.mlit. go.jp/report/press/port06_hh_000269.html; accessed 21 Aug 2023). Coastal wind farms have high potential as renewable energy sources, but the increased collision risk they cause for seabirds is a concern (Drewitt & Langston 2006, Everaert & Stienen 2007). One important factor influencing collision risk is a bird's flight height in relation to the turbine blade height (Garthe & Hüppop 2004, Masden & Cook 2016, Ross-Smith et. al 2016).

In this study, we found that gulls adjusted their flight height according to the wind conditions they experienced. If we assume the turbine blade height to be at 20–120 m above sea level (Cook et al. 2018), the adjustments in flight behavior, especially the increased flight height under tailwinds, may result in an increased risk of collision (Fig. 4). Given that wind is an important factor in flight height, we suggest that local wind information, as well as locations of where prevailing wind may align with major commuting paths of birds, be incorporated in the environmental impact assessment of future coastal wind farm projects.

4.4. Conclusions

Based on high-resolution GPS tracking data and concomitant, locally recorded wind conditions, we found that gulls adjusted their flight height and airspeed according to wind conditions, presumably to optimize their cost of transport. However, the adjustments in flight behavior, especially the increased flight height under tailwinds, may increase the birds' collision risk with wind turbines. Under the increased promotion of windfarm implementation, we hope our research provides novel information on flight ability of seabirds to be incorporated in the environmental impact assessments and operation of future coastal wind farm projects.

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Appendix.

Table A1. Summary of field sites and number of individuals captured

Location	Year	Tagged individuals (n)	Recaptures (n)	Recaptures with retrievable data (n)	Mean logger deployment days	Success rate
Rishiri	2016	14	14	12	5.17	0.86
Rishiri	2017	33	32	31	4.52	0.94
Esashi	2017	12	12	11	6.55	0.92
Rishiri	2018	33	33	33	4.94	1.00
Esashi	2018	13	13	12	3.25	0.92

Table A2. Summary of parameter values calculated using 7547 GPS fixes

Parameter	Max	Min	Mean	Median	SD
Ground speed (km h^{-1})	102.0	1.1	41.7	39.7	13.7
Airspeed (km h^{-1})	126.1	3.2	45.4	45.4	13.1
Altitude (m)	182	0	33.5	22	33.0
Flight height (m)	171.5	−10.9	29.5	18.4	31.5
Wind speed (km h^{-1})	41.0	2.2	19.0	19.4	8.9
Tailwind component	41.0	−39.2	−5.6	−8.1	15.4
Adjusted tailwind component	40.0	−41.0	−6.4	−7.8	14.8
Adjusted cross wind component	11.4	0.0	3.1	2.8	2.1
Satellite	8	4	6.7	7	0.9

Table A3. Summary of parameter values calculated using 90 track-line medians

Parameter	Max	Min	Mean	Median	SD
Ground speed (km h^{-1})	82.1	18.6	45.6	41.5	13.1
Airspeed (km h^{-1})	93.0	19.5	47.0	45.7	11.0
Altitude (m)	162	0	38.0	25	34.1
Flight height (m)	153.8	0	34.4	22.0	32.6
Wind speed (km h^{-1})	41.0	2.2	18.6	16.7	9.0
Tailwind component	35.4	−34.0	−1.9	−4.0	16.2
Adjusted tailwind component	32.6	−32.6	−3.2	−3.6	14.9
Satellite	8	5	6.6	7	0.7