Main Manuscript

Wandering albatross exert high take-off effort in weak wind with low wave conditions.

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Abstract

The relationship between the environment and the small-scaled behavior of marine animals is not fully understood. This is largely due to the difficulty in obtaining environmental datasets with a high spatiotemporal precision. The problem is particularly pertinent in assessing the influence of environmental factors in rapid high energy consuming behavior such as seabirds take-off. Here, to fill the gaps in existing database, we employed novel techniques using animal-borne sensors with motion records to estimate parameters on wind and ocean waves, and evaluated their influence on wandering albatrosses take-off. The measurement revealed that the wind speed and the wave height that the wandering albatrosses experienced during take-off ranged from 0.7 ~ 15.4 m/s and 1.6 ~ 6.4 m, respectively. The four indices that were measured (flapping number, frequency, running speed, and duration on the sea surface) also varied with the environmental conditions (i.e., flapping number varied from 0 to over 20). Importantly, taking-off was easier under higher wave condition in the constant wind speed, and take-off effort increased only when both wind and waves were gentle. Our data suggests that both ocean waves and winds play important roles in albatross take-off, and advances our current understanding of albatross flight mechanisms.

Impact statement: Winds and ocean waves condition experienced by albatrosses were estimated using animal-borne recorder and revealed that taking-off was easier under higher wave condition in the constant wind speed.

Keywords: Seabird, Biologging, ocean environment, Take-off

Introduction

Various oceanic environmental factors affect the ecology of marine animals. Predicted climate changes suggest increases in extreme climatic events (such as cyclones). Evaluating individual relationships between each environmental factor and marine animal behaviors is urgent for marine ecological conservation, especially for top predators that significantly impact the whole ecosystem. However, there are potential limitations: direct measures of empirical environmental data of marine animals is nearly impossible due to the spatiotemporal gaps in the observation network of the open ocean (Ardhuin et al., 2019; Villas Bôas et al., 2019). Various environmental parameters (such as ocean wind, waves, and sea surface temperature) are assumed to be important factors affecting the movement and foraging of flying seabirds (Adams and Navarro, 2005; Dunn, 1973; Haney et al., 1992; Nevitt et al., 2008; Suryan et al., 2008). Previous research has revealed many interesting seabird behaviors correlate with the ocean environment. However, the environmental data largely relies on ocean climatic modelling (Clairbaux et al., 2021; Clay et al., 2020; Padget et al., 2019; Weimerskirch and Prudor, 2019), as in situ observation data is limited and often collected a long distance from the bird. For example, records are collected at the colony island or using the nearest government observation point (Kogure et al., 2016; Yamamoto et al., 2017). Therefore, interpreting the data is difficult when doubts exist on whether the birds actually experienced the environmental conditions, making any conclusions conservative estimates only (Clairbaux et al., 2021; Clay et al., 2020). For example, although winter cyclones in the North Atlantic can induce mass seabird mortality, revealing the small-scale behavioral responses which lead to mortality is almost impossible with the spatiotemporal limits of thermodynamic modelling data (Clairbaux et al., 2021).

Seabird take-off may be affected by the surrounding environment (Clay et al., 2020) but has never been effectively investigated. Notably, behaviors with short timeframes (such as take-offs) require environmental data on spatiotemporally small scales, which is difficult to obtain, even using climatic models. Many procellariiformes have special flight techniques that use vertical wind shear, called dynamic soaring (Rayleigh, 1883; Richardson, 2011), and take-off requires a large amount of energy (Sakamoto et al., 2013) owing to vigorous flapping (Sakamoto et al., 2013; Sato et al., 2009) and sea surface running to reach the velocity to initiate take-off (Sato et al., 2009). Previous research revealed the heart rate of the largest seabird, wandering albatross (*Diomedea exulans*), drastically increases at the moment of take-off reaching 3 – 4 times the basal heart rate (Weimerskirch et al., 2000). After take-off, the tachycardia progressively decreases during flight (Weimerskirch et al., 2000), the flying

heart rate is close to the basal rate of a resting bird on the nest. Therefore, the highest proportion of the total energy expenditure of wandering albatross during the foraging trip is the take-off rate, not the duration or distance of the flight (Shaffer et al., 2001). Thus, take-off is one of the most important behaviors in the daily energy budget of flying seabirds in the open ocean. Understanding the relationship between take-off and the ocean environment is critical for estimating the future climate change effects on the life history of seabirds (Weimerskirch et al., 2012).

Previous research has partially identified the role of wind conditions on take-off when investigating general flight tactics of seabirds (Clay et al., 2020; Kogure et al., 2016). For example, the flapping effort of the European shag (*Gulosus aristotelis*) at take-off decreases as wind speed increases (Kogure et al., 2016). However, a comprehensive understanding of take-off has not been achieved as other environmental parameters, such as waves, have not been investigated. Ocean waves potentially affect take-off efforts because seabirds usually run on the ocean surface as they take-off (Norberg and Norberg, 1971; Sato et al., 2009). Additionally, the ocean surface slope is a key factor in creating complicated wind patterns immediately above the surface, which may affect the flight tactics of procellariiformes (Bousquet et al., 2017).

In this study, we devised a new approach to estimate the empirical environmental conditions using seabird dynamic motion records without the aid of either climate models or observational data. The recent development of animal-borne recorders has been remarkable (Wilmers et al., 2015). It is now possible to deploy various sensors on animal-borne recorders, to generate a new field of oceanography: ocean observations using animal-borne sensors (Harcourt et al., 2019; McMahon et al., 2021). Many studies have reported that marine environmental data can be collected using highly mobile marine animals such as pinnipeds, sea turtles, and seabirds (Charrassin et al., 2008, 2002; Doi et al., 2019; Roquet et al., 2014). Furthermore, unlike direct measurement by deploying sensors (e.g., thermometers), indirect techniques to observe the physical environment via the dynamic animal motion records (Goto et al., 2017; Sánchez-Román et al., 2019; Uesaka et al., 2022; Yoda et al., 2014; Yonehara et al., 2016) generated using the Global Navigation Satellite System (GNSS) have been developed recently. GNSS is now able to record their position and movement every second (or even in sub-second scales) using very small animal-borne recorders. These newly developed techniques using animal-borne recorders should compensate for previous observational gaps in oceanic data, especially in the open ocean and polar regions where our access and deployment of observation equipment is

complicated. The environmental variables obtained directly from animals provide the environmental conditions they experience. Seabirds are one of the most enthusiastically studied oceanic species because of their high mobility and adaptability to both air and water. Methods involving the observation of wind and waves, using GNSS data regarding the flight paths and floating motions of seabirds on the sea surface, are well-developed and have potential applicability in future studies (Goto et al., 2017; Uesaka et al., 2022; Yonehara et al., 2016).

Wandering albatrosses were investigated because their habitat includes the Subantarctic (30 °S – 60 °S), where the ocean is annually rough (Suryan et al., 2008) causing their flight style to be largely influenced by the ocean conditions (Richardson, 2011; Weimerskirch et al., 2012). Furthermore, previous studies have revealed the foraging area has annually shifted southward with the polar shift of the westerly wind pattern (Weimerskirch et al., 2012). Considering the enormous cost of take-off (Shaffer et al., 2001; Weimerskirch et al., 2000), studying their response to various environmental conditions is essential for us to estimate the impacts of climate change on the life history of seabirds. We aim to estimate the physical environmental conditions (ocean winds and wave heights) experienced by wandering albatross as they take-off by utilizing the dynamic motion records to evaluate the effects of wind and wave conditions on take-off dynamics (Fig. 1). Procellariiformes, like many seabird species, require extensive limb motion for take-off which is not limited to flapping behavior. Therefore, the evaluation of take-off effort involves both surface running and flapping behaviors. The wandering albatross individuals were tagged using recorders that include both GPS and acceleration sensors with high time resolutions.

Results

Trip data

We obtained 1477 h from 44 wandering albatross in 2019 (N = 21, 623 h) and 2020 (N = 23, 854 h). Two types of recorders with different battery sizes were used. The mean recording time of the trip data and the standard deviation (SD) was 9.5 ± 1.3 h for the small battery recorders and 59.7 ± 9.6 h for the large battery recorders. The albatross sex ratio was balanced between years and recorder type (Table. S1).

The absolute value of the GPS horizontal velocity revealed 703 take-offs from 1477 h of trips. A total of 453 out of 703 take-offs were followed by more than 5 min of flight. For each flight, the wind speed and direction were estimated using the flight path (Yonehara et al., 2016). A total of 299 take-offs occurred after more than 15 min of floating time. The wave height were estimated for each 299 take-offs using the floating motions (Uesaka et al., 2022). For 185 take-offs, we estimated the wind and wave conditions in combination.

Environmental conditions at the take-off moment

Of the 453 estimated wind parameters, 26 were unreliable based on the Akaike information criterion (AIC) comparison and were not included in the analysis. The remaining 427 results revealed wind speeds of 6 – 8 m/s were most frequently experienced by taking-off wandering albatross (Fig. S1A). Mean ± SD of the estimated wind speed was 6.5 ± 2.7 m/s, and the maximum and minimum wind speeds were 15.4 and 0.7 m/s, respectively. Winds blowing from west to east were frequently observed (Fig. S1B). This result is consistent with the prevalence of westerlies around the wandering albatross breeding colony (Nicholls et al., 1997; Weimerskirch et al., 2015).

Ocean waves were estimated using all 299 take-offs after more than 15 min of floating time to calculate the significant wave height. The most frequently experienced wave heights ranged from 2.5 ~ 3.0 m at the take-off moment (Fig. S1C) and the mean ± SD was 3.0 ± 0.8 m. The minimum and maximum wave heights were 1.6 and 6.4 m, respectively. Like wind direction, the wave direction (coming from) had a west bias due to the westerlies (Fig. S1D).

Take-off properties

To quantify the take-off effort, we calculated four parameters: running duration, running speed, flapping number, and flapping frequency from the acceleration records obtained at the moment of take-off. Mean ± SD running duration of wandering albatross was

5.1 ± 1.5 s with a range from 1.1 s to 11.7 s (Fig. S2A). The mean value for males was slightly lower than that for females (Fig. S3A), but the difference was not significant (M: 5.0 ± 1.5 s, F:5.2 ± 1.5 s, $p = 0.10$, Mann-Whitney U test). The albatross running speed mean value ± SD was 6.5 ± 1.6 m/s (Fig. S2B). Male birds had slightly higher speeds than females (M: 6.7 ± 1.5 m/s, F:6.3 ± 1.6, $p < 0.01$, Fig. S3B). Running duration and speed significantly correlated (Pearson's $r = 0.57$, $p < 0.01$). The linear regression slope (with a fixed intercept of zero) was 1.23 m/s^2 (Fig. S4). We interpret the slope as the acceleration of running wandering albatross.

The flapping number, i.e., the number of wing flaps after the running phase, was estimated using the dorsoventral acceleration. The mean flapping number was 4.3 times with a range from zero to over 20 times (Fig. S2C). Take-offs without flapping after the running phase were frequently observed (33.3%). Conversely, continuous flapping above 20 times were also occasionally observed, which corresponds to a long time flapping (8 s ~) after take-off considering the flapping frequency of wandering albatross (2.5 ~ 3.0 Hz). There was no significant difference in flapping number between the sexes ($p = 0.22$, Mann-Whitney U test, Fig. S3C). The mean ± SD flapping frequency was 2.55 ± 0.29 Hz, and most ranged from 2 to 3 Hz (Fig. S2D). However, some flapping frequency results were outside the detection range (1.8 ~ 4 Hz) and not included in our analysis. Therefore, the sample size of the flapping frequency used in our analysis was 669. There was no significant differences in flapping frequency between the sexes ($p = 0.18$, Mann-Whitney U test, Fig. S3D).

Environmental effects on take-off parameters

The take-off directions were compared with the wind direction estimated from the flight path after take-off. Wandering albatross tended to take-off with headwinds ($p < 0.01$, v-test) (Fig. 2). However, the cruising direction did not correlate with headwind direction, indicating that wandering albatrosses face the wind in take-off regardless of their destination. The mean ± SD air speed of wandering albatrosses at the end of the running phase (lift-off moment from the sea surface) calculated using the running speed, wind speed, and relative take-off direction was 12.2 ± 3.1 m/s.

The relationships between each take-off parameter (running duration, running speed, flapping number, and flapping frequency) with environmental conditions (wind speed and wave height) were tested using linear mixed models (LMMs). The running duration required for wandering albatross take-off significantly decreased as wind speed and wave height increased (Fig. 3). Similarly, the running speed was significantly lower under stronger wind

and higher wave conditions. Wandering albatross tend to flap fewer times under stronger wind conditions. Conversely, wandering albatross can flap over 20 times in weak wind conditions, although the flapping number in weak wind conditions varies greatly. There is also a declining trend in the flapping number with wave height. Albatross taking-offs in wave heights below 2 m always require flapping. The flapping frequency was lower as the wind speed and wave height increased, but the trend with higher wave heights remains unclear. The LMMs results are provided in Table S2 of the supplementary information.

Independent effect of wind and waves on take-off

Although some components of ocean waves are generated by ocean winds, the correlation between the wind speed and wave height is not consistent. Some of the albatross take-offs involved information on both wind speed and wave height. Therefore, we evaluated the respective effects of wind and waves on wandering albatross take-offs. The correlation between wind speed and wave height was not strong ($r = 0.27$, $p < 0.01$). Some take-offs were performed in weak winds but high wave conditions or the opposite conditions (Fig. 4A). The take-off conditions were divided into four environmental categories using the peak in the curve of the fitted probability density distribution, which were 6.0 m/s (wind speed) and 2.8 m (wave height) (wind speed: Weibull distribution (Carta et al., 2009), wave height: log normal distribution (Ferreira and Guedes Soares, 2000)). The categories comprised: 48 samples (weak wind low wave: WL), 33 samples (weak wind high wave: WH), 27 samples (strong wind low wave: SL), and 77 samples (strong wind high wave: SH). The running duration varied significantly between the four categories ($p < 0.01$, Kruskal-Wallis test). The mean running duration in the WL conditions was 6.0, which was the longest of the four categories (Fig. 4B). Relatively long running (of over 6 s) mainly occurred in WL conditions, and the running duration decreased with the wind speed or wave height (Fig. S5). Similar results were obtained for both running speed and flapping number. However, flapping frequency did not significantly vary between the four categories ($p = 0.06$). Take-offs involving over 30 flaps mainly occurred in WL conditions.

The variance inflation factor (VIF) of wind speed and wave height was 6.86, which did not exceed the general threshold of 10 (Dormann et al., 2013). The LMMs, models including wind speed, wave height, and the interaction used the smallest AIC for all take-off parameters (Table S3). However, the difference between the lowest and the second lowest AIC was below two for running speed, flapping number, and flapping frequency. The simulation of the running duration using the estimated coefficient shows that even under

weak wind conditions (2 m/s), the running duration decreases from 8 to 4 s as the wave height increases. Conversely, low values were maintained under strong wind conditions (8 m/s) regardless of the wave height (Fig. 5). Similarly, the running speed decreased from 9 to 6 m/s as the wave height increased, regardless of the wind strength. The flapping number followed the same trend. Conversely, the flapping frequency did not decrease as the wave height increased.

Discussion

Although observation networks in the ocean are under development and climate modelling accuracy is increasing, they remain unable to accurately estimate the surrounding environment of marine animals at small scales. We demonstrate the environmental variables estimated using individual animal recorders are highly valuable when the spatiotemporal scale and accuracy of climate models and observation networks are too broad for the research. We provide details on how seabird take-offs are affected by wind and waves.

Seabird take-offs using accelerometers

We quantified the running behavior of seabirds at the moment of take-off, which is the most energy-consuming behavior for soaring seabirds (Sakamoto et al., 2013; Shaffer et al., 2001; Weimerskirch et al., 2000). Previous studies have ascribed this large energy expenditure to the vigorous flapping required for take-off (Clay et al., 2020; Sato et al., 2009; Shaffer et al., 2001). Indeed, the continuous flapping behavior is rare in cruising flight and was even recorded after the running phase of take-off in this study. However, we suggest the running behavior is also a large cost in take-off because albatross have to reach a fast initial speed to lift off the sea surface by rapidly moving their hindlimbs for up to ~ 10 s in unfavorable conditions (as demonstrated in this study).

We provide a first attempt at detecting the running signal of taking-off seabirds and build a relatively simple algorithm (which can be easily applied to other species) using lateral acceleration. The running duration may increase or decrease by approximately 0.5 s depending on the configure of the algorithm, such as smoothing parameters and threshold values. However, we focused on the relative changes in the running behavior in association with wind speed and wave height, and the error of the absolute value is not a serious problem.

The flapping characteristics during the running phase were also researched. The dorsoventral acceleration signal fluctuates during the running phase making it difficult to identify each flapping signal, even after applying the band-pass filter. Therefore, counting the number of flaps immediately after the running phase was the only reliable parameter for evaluating flapping effort. It was difficult to confirm the frequency of the running phase was derived from flapping behavior. Sato et al. (2009) (Sato et al., 2009) reported that the flapping frequency of wandering albatrosses at the moment of take-off is higher (2.9 ~ 3.4 Hz) than that of cruising flight (2.5 ~ 2.7 Hz). In our study, the flapping frequency after the running phase was not as high as Sato et al. (2009) reported. Therefore, it is likely that the

wandering albatross undertake high frequency flapping only during the running phase, as they lift off the sea surface. After lift-off (i.e., the running phase is finished), the wandering albatross continue with a moderate flapping frequency until they reach a certain degree of flight stability. Simultaneous video records of flapping and running motions with acceleration records are required to separate the parameter estimates.

In-depth studies on seabird take-offs are just beginning with the aid of miniaturized animal-borne recorders with the main aim of understanding how seabirds flap their wings (12, 15). However, in land birds (e.g., finches and doves) take-off requires a large contribution by hindlimbs (Provini et al., 2012) and the role of the hindlimb in take-off kinematics is as important as that of the wing (Provini and Abourachid, 2018). Therefore, it is highly likely that seabird take-offs also require a great contribution by the hindlimbs. Further seabird hindlimb research is required. This study provides the basic characteristics of the running behavior of wandering albatross, running duration, and running speed.

Take-off effort with environmental conditions

The first finding is that wandering albatross can take-off in a variety of environmental conditions (wind speed: 0.7 ~ 15.4 m/s, wave height: 1.6 ~ 6.4 m). A previous study on wandering albatross identified the transition state from resting to flying tended to increase as the wind speed increased (Clay et al., 2020). Our results found some take-offs were performed under weak wind (2 – 4 m/s) conditions, suggesting wind speed is not the only parameter influencing flight decisions of wandering albatross, and wave height should be included in future studies.

The results showed that the running and flapping behavior tends to decrease as the wind or wave conditions increase. Running duration decreases as either the wind speed or the wave height increases and peaks when both the wind and waves are weak. The same trends existed in running speed and flapping number. Although optimum statistical models for each take-off parameter are determined using the AIC value, some models provide similar results to this model. For instance, the AIC variation in running speed between the best model and the second-lowest AIC model was only 0.27. However, both models contained wind speed and wave height as the explanatory variables, similar to the other take-off parameters, except flapping frequency. The purpose of building a linear model was to clarify whether the effects of wind and waves are independent. As long as both wind speed and wave height were included as explanatory variable in the model it reduced the volume of running and flapping behavior. Therefore, we can conclude that both strong winds

and high waves aid wandering albatross take-offs. The flapping frequency after the running phase was the only parameter that did not correlate with wave height (as identified using the LMMs model). However, we assume the flapping frequency during the running phase is more important. Future research needs to investigate the effects of wave height as wandering albatross need to climb up or run down the wave slope. Therefore, the flapping frequency during the running phase should be highly influenced by wave height.

Contribution of strong wind and high waves to seabird take-off

The reduced running behavior and flapping times under strong wind conditions is simply described by the mechanism of the lift force which has been predicted by previous studies (Clay et al., 2020; Kogure et al., 2016). Seabirds need to gain lift force before take-off, and the volume of force is proportional to the square of the relative speed of the wings to the surrounding air (air speed) (Vogel, 1983). It has been anecdotally suggested that seabirds take-off into the wind (i.e., headwind), and stronger winds can produce a sufficiently large lift even before the ground speed of the seabird reaches the value required for flight. As a partial demonstration of this theory, a study on the European shag (*Gulosus aristotelis*) (Kogure et al., 2016) found the take-off direction was significantly biased towards headwinds. Regarding soaring seabirds, only one study (Clay et al., 2020) on wandering albatrosses has confirmed a bias in take-off direction with wind direction. However, the authors acknowledge the limits in the climate model and GPS sampling resolutions and recognized the unreliability of small-scale responses to in situ variation in the atmosphere. Our study reveals wandering albatross significantly tend to take-off into the wind, using robust fine scale data estimated from the flight records of wandering albatross. Our data is reliable as the empirical value provided is actually experienced by the albatross. Furthermore, by quantitatively evaluating the flapping and running effort, we demonstrate the theory of effortless take-offs by soaring seabirds in stronger wind conditions.

The mean air speed of wandering albatrosses at the end of the running phase was close to the average flight speed (approximately 15 m/s) (Weimerskirch, 2002), indicating that wandering albatross gain sufficient lift at the end of the running phase and efficiently utilize ocean wind. Wind speed varies with altitude, therefore the wind blowing on the ocean surface must be smaller than the values estimated from the flight records of wandering albatross as albatross usually fly 3 – 12 m above the ocean surface (Pennycuick, 1982). Therefore, the calculated air speed is probably an overestimate when compared with the ocean surface. To compensate for the insufficient lift force gained during the running phase,

wandering albatross flap their wings several times after the running phase. Therefore, the flapping number in weak wind conditions can exceed dozens before reaching stable flight.

The most important finding of this study is that the take-off effort estimated by the running behavior and number of flaps decreased not only with stronger winds but also with higher waves. While the role of ocean wind on flying seabirds has been well described (Pennycuick, 2008), how ocean waves influence the flight of seabirds remains largely unknown. However, many studies have reported the characteristic flight of soaring seabirds by tracking the ocean wave surface over long distances (Pennycuick, 2008, 1982; Richardson, 2011; Stokes and Lucas, 2021), which even occurs in weak or no wind conditions. Seabirds seem to be aided by atmospheric forces above the slope-like wave topography, the flight method using the shape of waves is called wave-slope soaring (Richardson, 2011). It is well recognized that air flows occur above ocean waves (Bousquet et al., 2017; Buckley and Veron, 2016). Richardson (2011) (Richardson, 2011) described the theoretical model of wave-slope soaring, where the flight mechanism of albatross are a combination of both dynamic soaring, which uses vertical wind shear above the ocean surface (~ 15 m), and wave-slope soaring, which uses the updraft caused by the wave topography. Thus, seabirds can continue to soar in weak wind conditions. Further mathematical analysis reveal the wave-induced updraft (even in windless conditions) can provide 60% of the transportation cost of a brown pelican (*Pelecanus occidentalis*, 2 ~ 3 kg), which is a wave-slope soarer (Stokes and Lucas, 2021). Thus, it is possible that the take-off effort by wandering albatross is also reduced by high waves. While qualitative field observations and mathematical demonstrations provide the only previous research on the role of waves on soaring seabirds, we experimentally demonstrated that ocean waves aid the most energy-consuming behavior, take-off. This finding helps future discussions on the oceanic topography mechanisms affecting seabird flight.

The mechanism by which high waves aid wandering albatross take-off is not clear. It is difficult to conclude a certain updraft is producing additional lift for wandering albatrosses, it is possible there are other unresolved mechanisms. It is also possible that a rough topographic surface provides a favorable bump, like a slope or cliff to jump off into the air. Our results were restricted to wave height as the parameter of the ocean surface. Future research involving ocean surface steepness or wave frequency components will reveal the detailed mechanism of how waves make seabird take-off easier. In particular, ocean surface topography heavily relies on whether the dominant wave component is due to a swell (low-frequency waves propagated from a distance) or wind waves (high-frequency waves

generated by local wind); moreover, this topography affects the wind pattern on the sea surface.

We revealed how the take-off effort of wandering albatross change in various oceanic conditions. As take-off is one of the most energy-consuming behaviors that can dominate the total energy expenditure of a wandering albatross journey, this data will be a great help for considering how climate changes can alter the life of albatrosses. Future research, especially on albatross, should quantitatively evaluate the energy consumption of take-off with the wind and wave conditions. Currently, there is no major barrier to accomplishing this goal, it would require utilizing motion records to estimate the surrounding environment with additional methods to estimate energy consumption, such as cardiograms. Recognizing the negative effect of the changing oceanic environment on seabirds (Sydeman et al., 2015), revealing the direct small-scale mechanisms of environmental factors (such as wind, wave, tide, current, and sea surface temperature) effects on animal behavior, especially in take-off is urgently required. The concept of estimating the surrounding environment using motion records is a novel solution with great potential to unravel the small spatiotemporal uncertainties in seabird research.

Materials and Methods

Field experiment

The recorders, Ninja-scan (Little Leonardo, Tokyo, Japan), record triaxial acceleration at a very high time resolution (100 Hz). Ninja-scan also records 3D GPS positions (5 Hz), Doppler velocity (5 Hz), temperature (6 Hz), pressure (6 Hz), geomagnetism (6 Hz), and angular velocity (100 Hz). There are two types of Ninja-scans with different battery masses (Naruoka et al., 2021). Small Ninja-scans weighed 28 g, which is below 1% of the body mass of wandering albatross are expected to record for 7 h. Large Ninja-scans weighed 91 g, which corresponds to approximately 1% of the body mas of a wandering albatross are expected to record for 65 h.

Ninja scans were attached to breeding wandering albatross at Possession Island, Crozet archipelago (46°25 S, 51°44 E) in the South Indian Ocean in 2019 and 2020. In 2019, 12 small Ninja scans were attached (in tandem) to 6 individuals. On each bird, one recorder had a delay timer so that the recording period of the two recorders did not overlap. Additionally, 15 birds had individual Ninja-scans attached, of which 8 were small Ninja-scans and 7 were large Ninja scans. In 2020, 10 small Ninja-scans were attached in tandem to 5 individuals. Additionally, 19 birds had individual Ninja-scans attached, of which 7 were small Ninja-scans and 12 were large Ninja-scans. In summary, 21 and 24 wandering albatrosses were tagged in 2019 and 2020, respectively. All experiments were performed from late January to early March of each year, which corresponds to the incubation period of wandering albatross. Recorders were attached to the back of each bird with waterproof tape (Tesa, Hamburg, Germany) and glue (Loctite; Henkel, Dusseldorf, Germany). All recorders were retrieved within 35 days. One small Ninja-scan which had been attached in isolation in 2020 did not work correctly. The effects of the attached recorders on wandering albatross were previously assessed (Barbraud and Weimerskirch, 2012; Phillips et al., 2003) and revealed that small recorders (less than 3% of their body mass) do not negatively impact breeding or foraging behaviors. The experiment was conducted as part of Program 109 of the Institut Polaire Paul Emile Victor with permission from the Préfet des Terrs Australes et Antarctiques Françaises, France.

Take-off identification

First, data recorded on the colony island was eliminated based on the GPS position. Then, take-off was determined using the absolute value of the GPS horizontal velocity. When wandering albatross float on the sea surface (i.e., before take-off), a relatively low speed which is generally below 2.5 m/s, is recorded, while the flying speed exceeds 5 m/s (Weimerskirch, 2002). Take-off was defined as the moment when the horizontal speed exceeds 4 m/s and rises to a higher speed. The soaring (flying) speed occasionally meets this criteria. Therefore, the horizontal speed was smoothed using the moving average (20 points : 0.4 s). If the horizontal speed crossed the 4 m/s line several times within a short period, they were classed as take-offs for very short flights and were not used in our investigation. Therefore, we selected only take-offs that included over 30 s of floating followed by over 30 s of flying.

Wind estimation

Yonehara et al. (2016) (Yonehara et al., 2016) proposed estimating the wind speed and direction of seabird flight paths using the sinusoidal curve relationship between the flight speed and flight direction. When seabirds fly in the air, their flight speed against the ground (ground speed) is mainly affected by the wind speed, which is maximized in tail winds and minimized in head winds. The maximum speed is the sum of the flight speed against air (air speed) and wind speed, whereas the minimum speed is the difference between the air speed and wind speed. The relationship between the flight speed (ground speed) and flight direction recorded by the GPS are fitted using a sinusoidal curve (Shimatani et al., 2012). We followed the methodology in Yonehara et al. (2016) to collate the flight speed V and flight direction θ data for 5 min after take-off and the curve was fitted using the following equation:

$$V = V_a + V_w \cos(\theta + \phi_w)$$

where V_a is the air speed, V_w is the wind speed, and ϕ_w is the wind direction. Ten seconds immediately after the take-off moment was not included in the estimation. Following Yonehara et al. (2016), the AIC of the sinusoidal fitting was compared to the linear fitting with a fixed slope of zero. When the AIC difference between the linear and sinusoidal fitting was below two, the estimated results were considered unreliable and discarded. Wind speeds and directions were not calculated when take-offs were not followed by over five minutes of flight. The sinusoidal curves were performed using Igor Pro version 8.04 (Wavemetrics, Portland, OR, USA).

Wave estimation

The ocean wave properties experienced by seabirds before take-off were estimated by analyzing the floating motion at the sea surface (Uesaka et al., 2022). The wave height was estimated from the vertical GPS displacement records before take-off. The estimate requires sufficiently long records of vertical displacement. Therefore, the wave height was not calculated for take-offs that did not follow a surface floating time of over 15 min. The sampling period of 15 min ensured the reliability of the wave statistics (Whitford et al., 2001) and provided a large volume of estimated wave data. The estimate did not include the ten seconds before the detected take-off moment. We followed the methodology of Uesaka et al. (2022) (Uesaka et al., 2022). The vertical GPS displacement records were high-pass filtered using a cutting-off frequency of 0.07 Hz to eliminate the GPS derived error (Olynik et al., 2002). We separated the time series record of the vertical displacement into individual waves by applying the zero-up-crossing method. The mean wave height of the highest third of all individual waves was calculated to provide the significant wave height, which is the most widely used statistical wave parameter (Whitford et al., 2001).

Sea surface running by seabirds

Many procellariiformes require a running phase before take-off from the sea surface (Sato et al., 2009). However, studies using accelerometers have not focused on the acceleration signal of this behavior. Surface running involves asymmetrical leg movements. Therefore, the lateral acceleration obtained from the recorder (attached to the back of the seabirds) provides signals derived from the running motion (Fig. 6). We confirmed that running signals appear in the lateral acceleration records at the moment of take-off by streaked shearwaters (*Calonectris leucomelas*), which are phylogenetically like wandering albatross (see Supplementary Information Text and Fig. S6).

To explore the running duration of wandering albatross, we built an algorithm to detect the running phase from the lateral acceleration around take-off. The lateral acceleration signal is composed of a dominant component (0.25 ~ 0.4 s) and a high-frequency fluctuation component (< 0.2 s period). Although the dominant component is the lateral movement derived from surface running, the flapping period of wandering albatross appears around this period (0.3 ~ 0.4 s). The flapping behavior is laterally

475 symmetrical and does not appear in the lateral acceleration records. However, this is not
476 always the case, when (occasionally) recorders are attached to the back of the seabird
477 in a slightly tilted position. To avoid confusion between running and flapping behavior, a
478 high-frequency fluctuation component in the lateral acceleration signal was used to
479 detect the running phase. A band-pass filter was designed to extract the high-frequency
480 fluctuation component from the acceleration records, and then the variance per unit time
481 (0.6 s) was calculated at each point. Running phase was defined as when the variance
482 of the acceleration exceeded the threshold value (2% of the peak value). This algorithm
483 reasonably detects the running phase regardless of the running duration. However, if
484 there is a signal gap in the middle of the running phase, the algorithm regards the gap as
485 the end of the running phase, underestimating the running duration. However, these
486 cases are rare, and we assume it does not affect our evaluation of the running
487 characteristics of wandering albatross. We also calculated the horizontal speed at the
488 end of the running phase and take-off direction using the GPS velocity. The take-off
489 direction was defined as the vectoral average direction during the running phase. We
490 also calculated the cruising direction which was defined as the moving direction 5 min
491 after take-off. All procedures were performed using Igor Pro version 8.04 (Wavemetrics,
492 Portland, OR, USA).
493
494 Flapping behavior after the running phase
495 Dorsoventral acceleration records include signals derived from seabird wing
496 flapping behavior (Fig. 6). The flapping signals during the running phase fluctuate, which
497 is assumed to be caused by the leg-derived dorsoventral motion. This caused the
498 flapping data to be unclear in identifying the flapping number and frequency. Therefore,
499 we only focused on the wing flapping signals after the running phase. A bandpass filter
500 extracted the clearest flapping signals (1.8 ~ 4.0 Hz). The number of continuous flapping
501 signals after the running phase were counted. The flapping period of the wandering
502 albatross is approximately 0.3 ~ 0.4 s, therefore we defined the end point when the
503 interval of the flapping exceeded 0.5 s. The flapping frequency after the running phase
504 was calculated using the spectral peak value of the continuous wavelet-transformed
505 dorsoventral acceleration. All procedures were performed using Igor Pro version 8.04
506 (Wavemetrics, Portland, OR, USA).
507

Comparison of the take-off parameters with environmental conditions

The wind directional bias of the take-off direction was tested using the v-test (modified Rayleigh test). The air speed V_a at the end of the running phase was estimated using the following equation based on the parameters obtained from this study:

$$V_a = V_r + V_w \cos(\theta_t - \phi_w)$$

Where V_r is the running speed at the end of the running phase, V_w is the wind speed, θ_t is the take-off direction, and ϕ_w is the wind direction. The effects of wind speed and wave height on each take-off parameter (running duration, running speed, flapping number, and flapping frequency) were evaluated using linear mixed models (LMMs) with individuals treated as random effects. To identify significance levels, the models were compared to null models based on the AIC value.

To evaluate the combined effect of wind and waves, we categorized take-off conditions into four groups, “WL conditions,” “WH conditions,” “SL conditions,” and “SH conditions”. The mean values of each take-off parameter were compared between the four groups. Furthermore, the independent effects of wind and waves on take-off parameters were evaluated using LMMs, including wind speed, wave height, and their interaction as explanatory parameters with individuals as random effects. VIF was also calculated before the LMMs analysis to assess whether the multicollinearity effect could be dismissed. The V-test was performed using Igor Pro version 8.04 (Wavemetrics, Portland, OR, USA). The LMMs calculations were performed using the PypeR package in Python 3.0.

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715 **Figures**

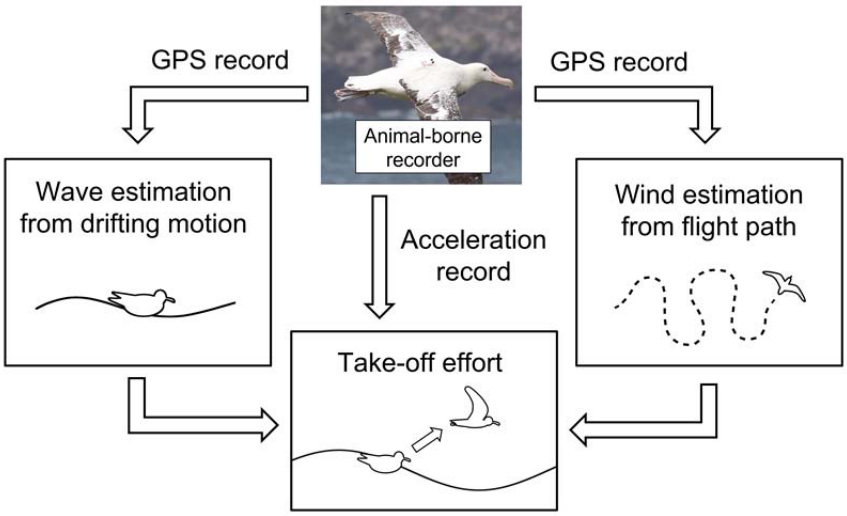

Fig. 1. Conceptual framework of the study estimating environmental condition experienced by studied individual.

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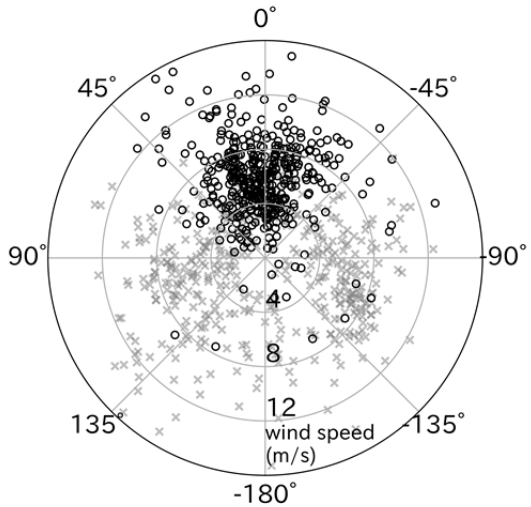

Fig. 2. Effect of wind direction on take-off of wandering albatrosses. Relative take-off direction to the wind direction (black circles, n = 427) significantly distributed around 0° (head-wind), whereas the cruising direction relative to the wind (gray x-mark, n = 427) is not. The radial axis represents the wind speed.

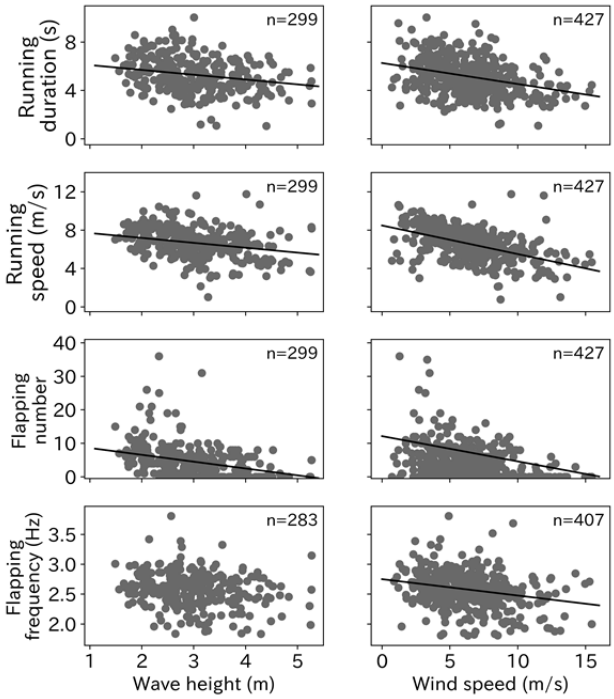

Fig. 3. Environmental effect on take-off. Effort for the take-off (Running duration, Running speed, Flapping number, and Flapping frequency) significantly decreased as wave height and wind speed increased ($p < 0.01$) except the relationship between flapping frequency and wave height ($p = 0.026$). Solid line shows the linear regression line determined from the LMMs and the number at the right top corner on each graphs shows the sample sizes.

719

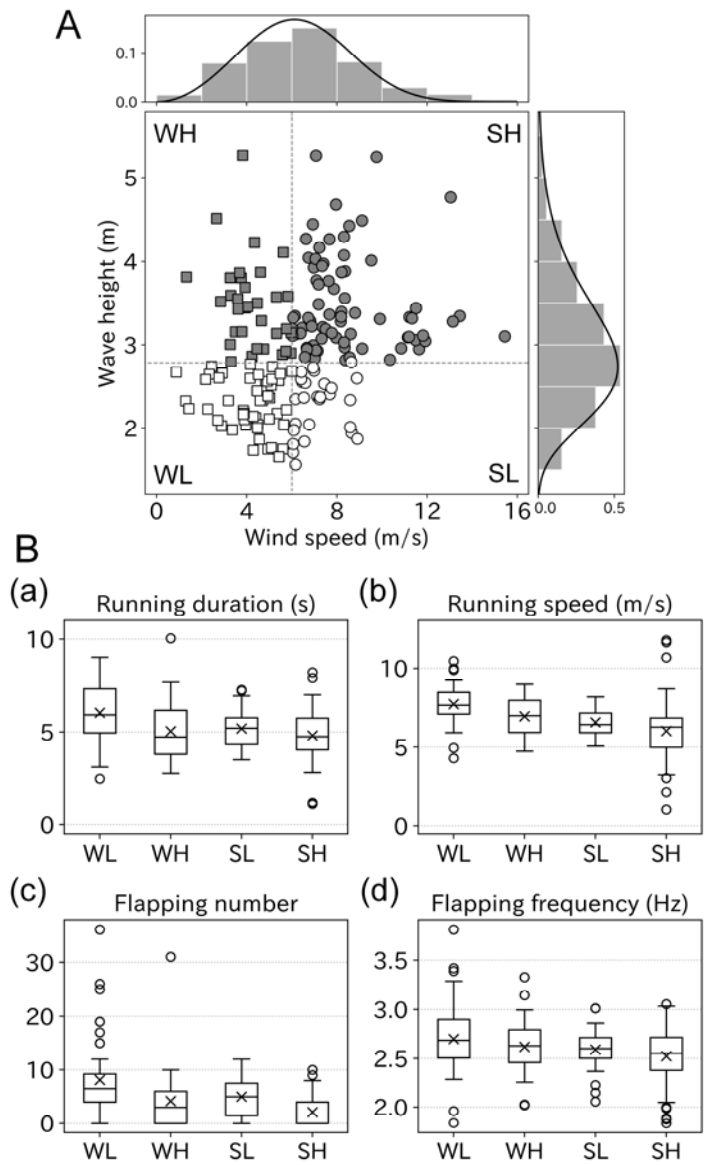

Fig. 4. (A) Correlation between wind speed and wave height was weak (r = 0.27, n = 185). Bar charts and solid lines written above and right of the scatter plot are normed histograms of wind speed and wave height and curve fitted lines. Based on the peak value of fitted lines scatter plots were divided into 4 groups, WL: weak wind low wave (open square), WH: weak wind high wave (filled square), SL: strong wind low wave (open circle), and SH: strong wind high wave (filled circle). (B) Take-off effort comparison among four groups (a: running duration, b: running speed, c: flapping number, and d: flapping frequency). Cross mark indicate the mean value.

720

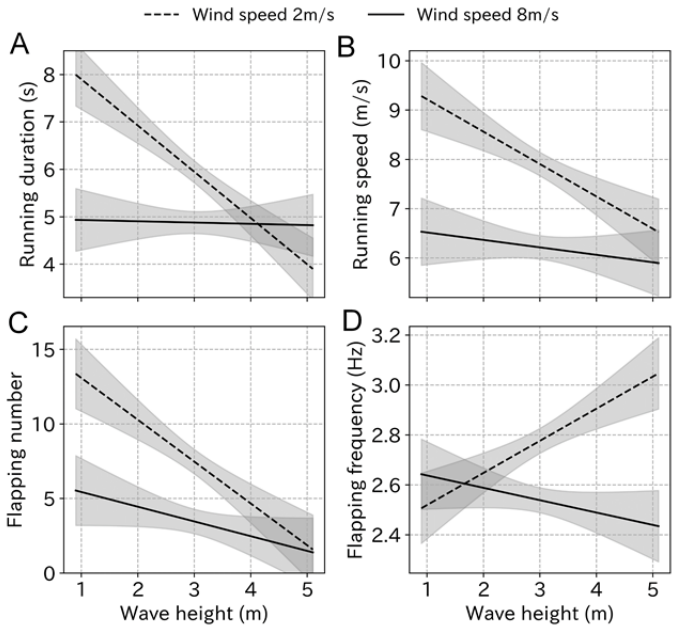

Fig. 5. (A) running duration, (B) running speed, (C) flapping number, and (D) flapping frequency in response to the wave height change under weak wind (dashed line, 2 m/s) and strong wind (solid line, 8 m/s) condition estimated from the result of LMMs. Gray area represents 99% CI.

721

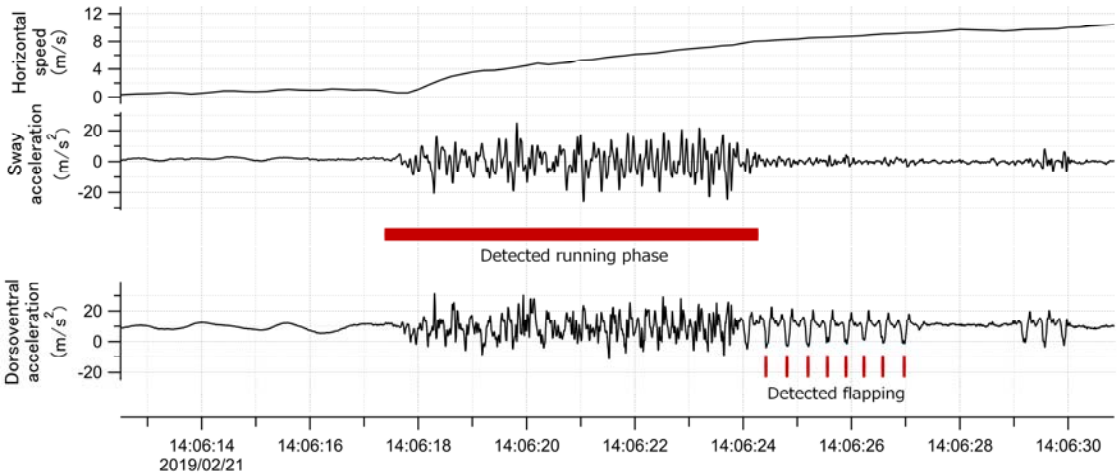

Fig. 6. Time series data of horizontal speed (top), lateral acceleration (middle), and dorsoventral acceleration (bottom) signals of the wandering albatross at the moment of taking off. Horizontal speed start increasing from the beginning of the take-off. Red square shows the detected running phase based on the variance of the lateral acceleration signal. Red bars show the detected flapping behavior after the running phase based on the dorsoventral acceleration signal. Dorsoventral signal during the running phase is fluctuated, probably due to the shaking body derived from the running motion, and thus it is not easy to judge the existence of flapping behavior.

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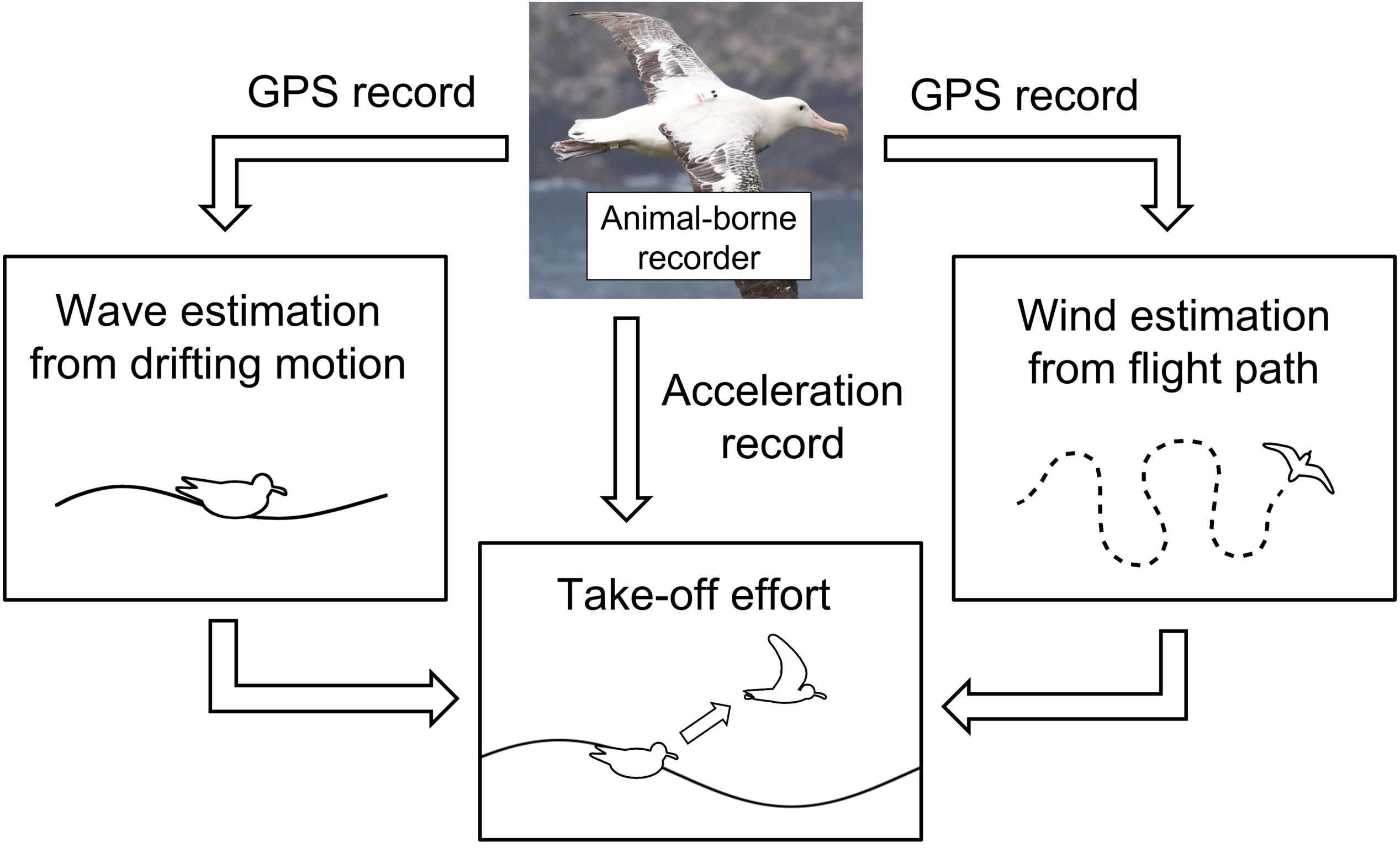
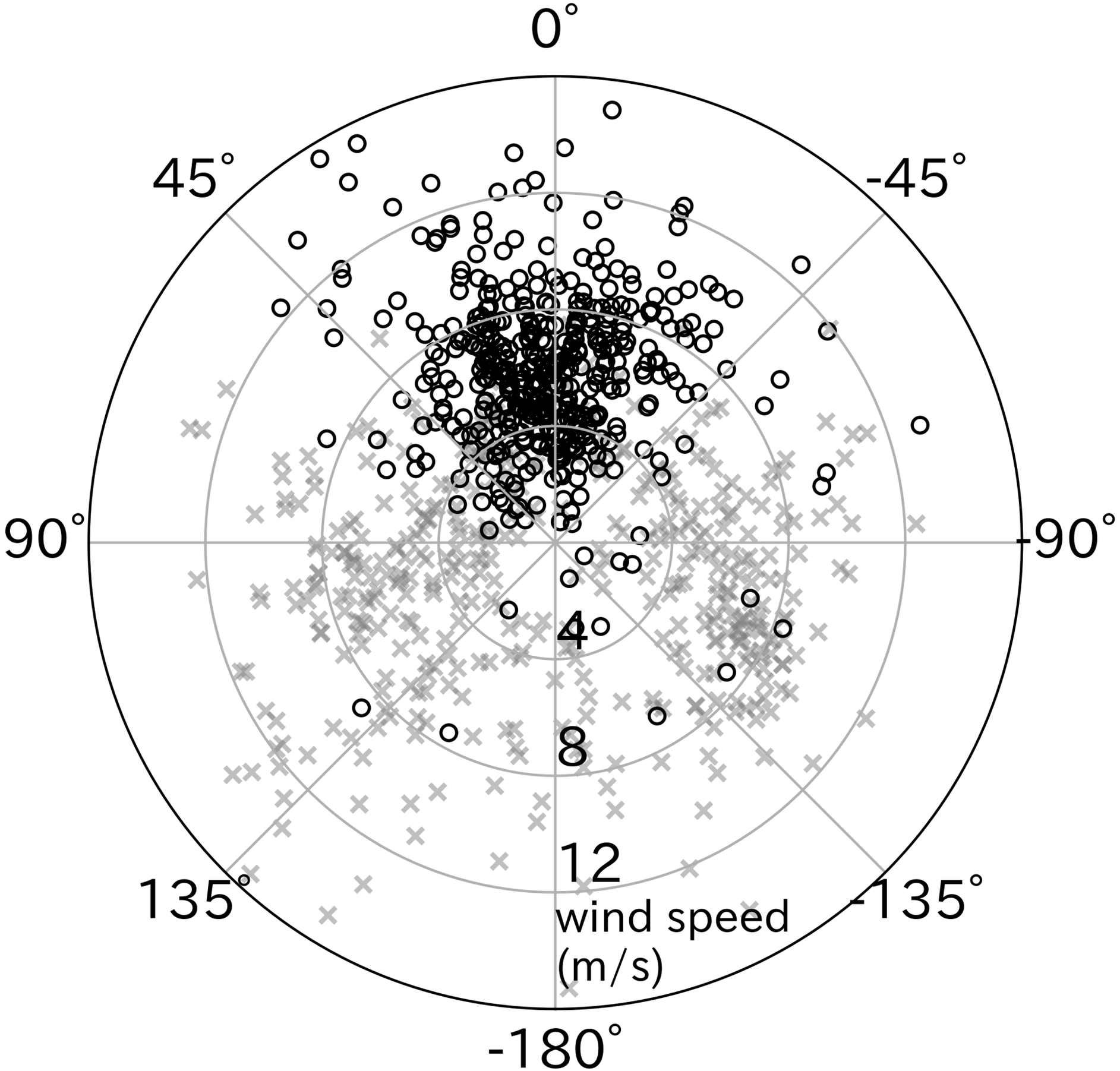
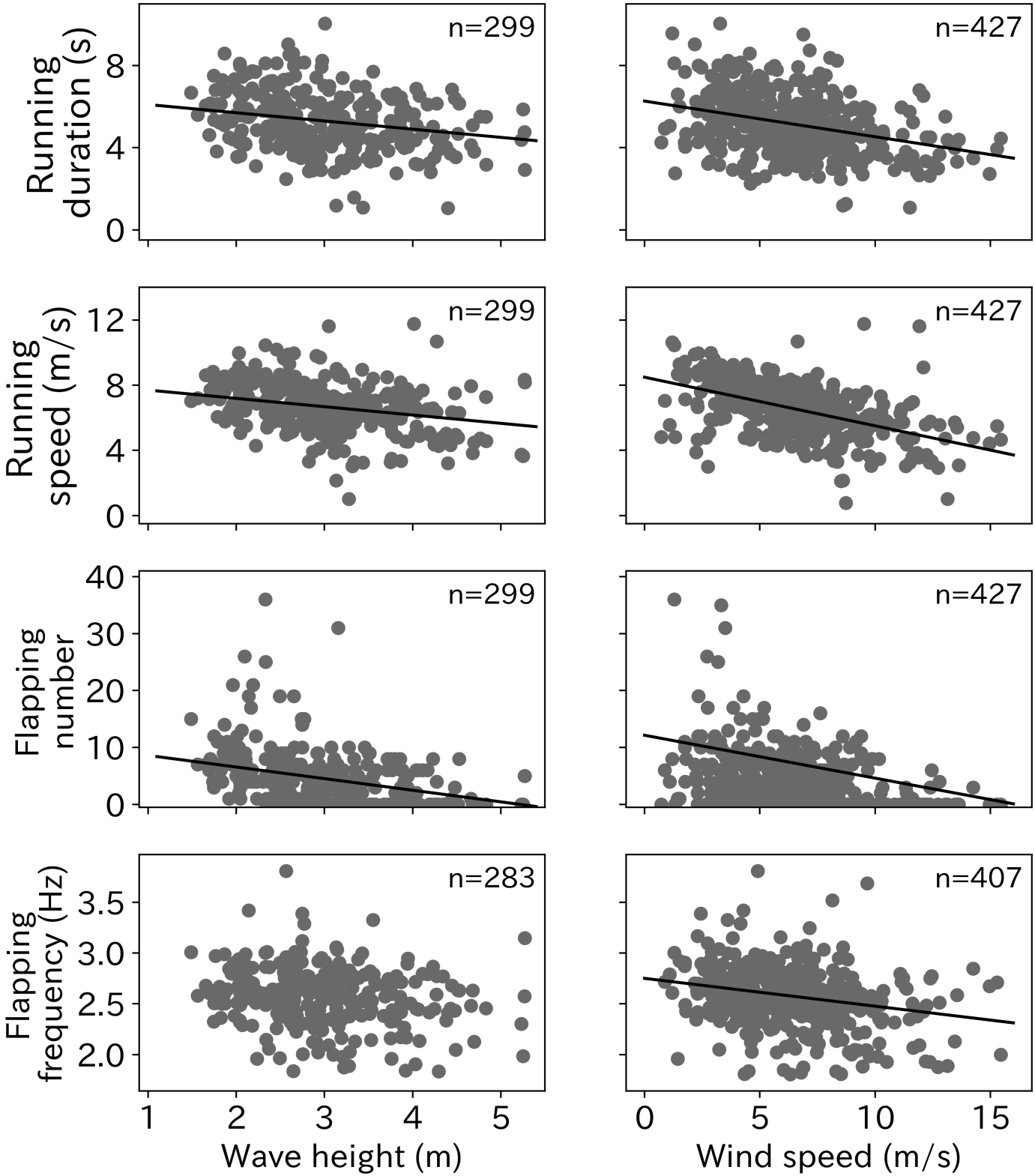
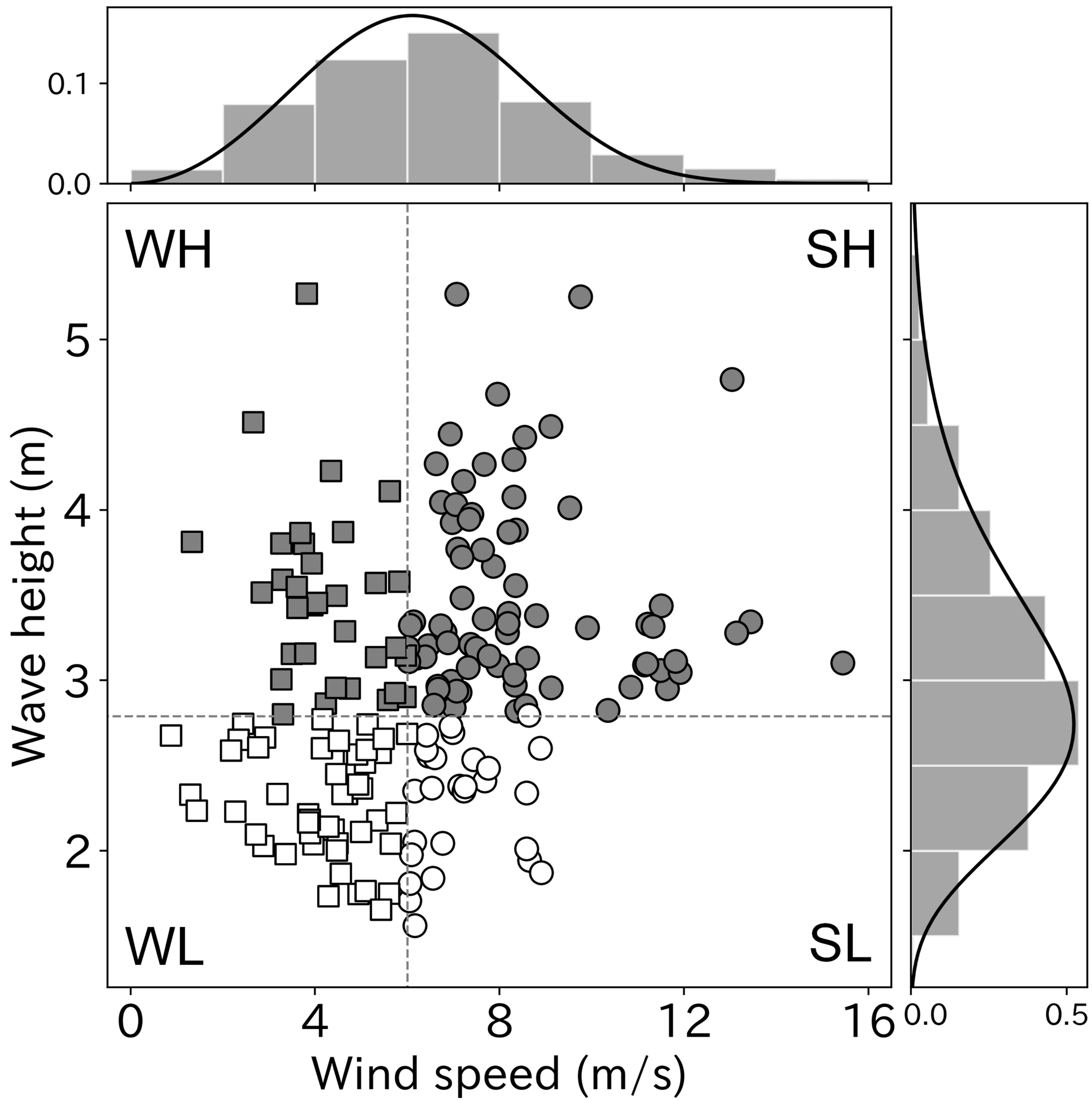

GPS record
Animal-borne recorder
GPS record
Wave estimation from drifting motion
Acceleration record
Wind estimation from flight path
Take-off effort


0°
45°
-45°
90°
-90°
135°
-135°
-180°
4
8
12
wind speed
(m/s)

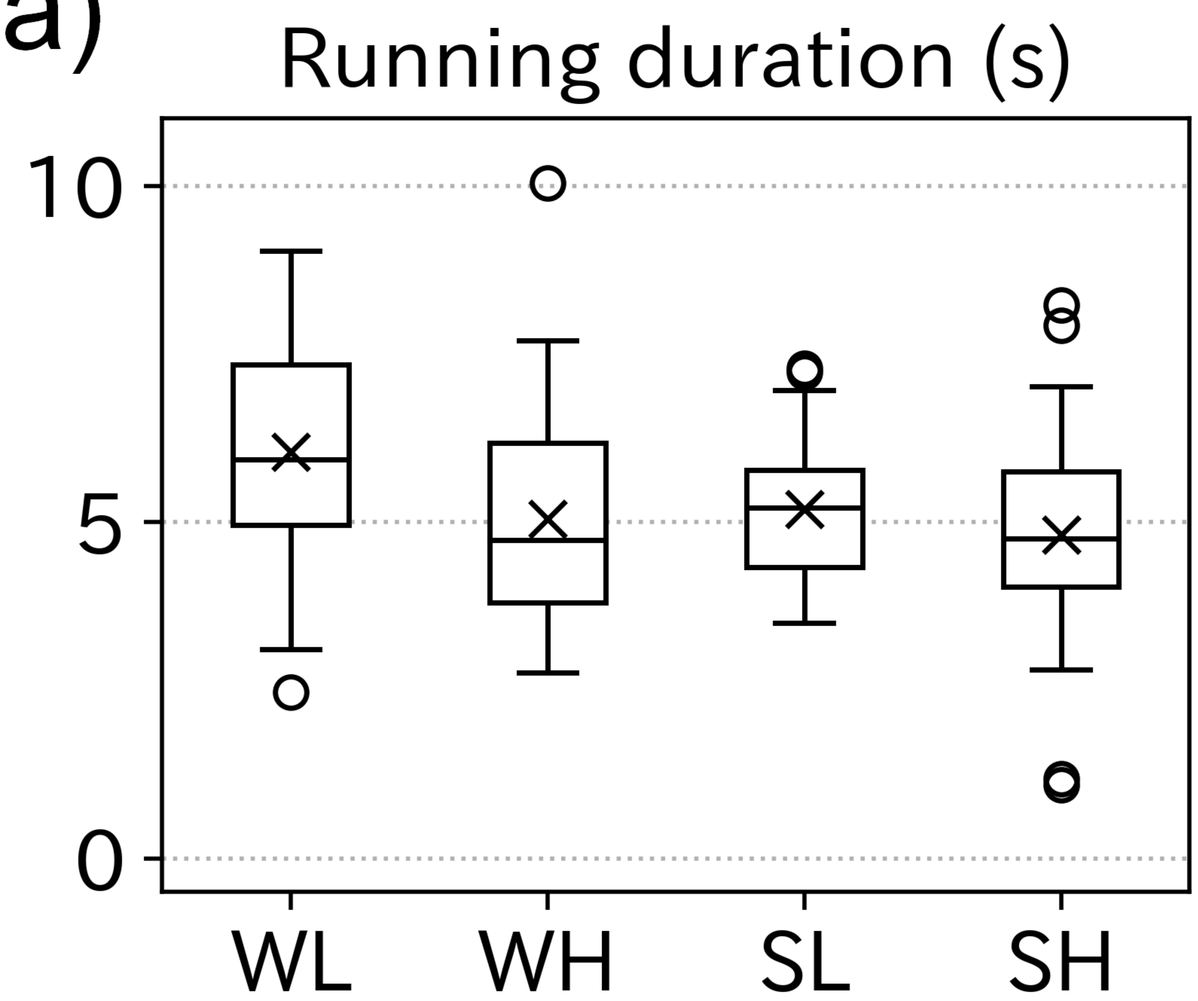

Running duration (s)
n=299
n=427
Running speed (m/s)
n=299
n=427
Flapping number
n=299
n=427
Flapping frequency (Hz)
n=283
n=407
Wave height (m)
Wind speed (m/s)

A

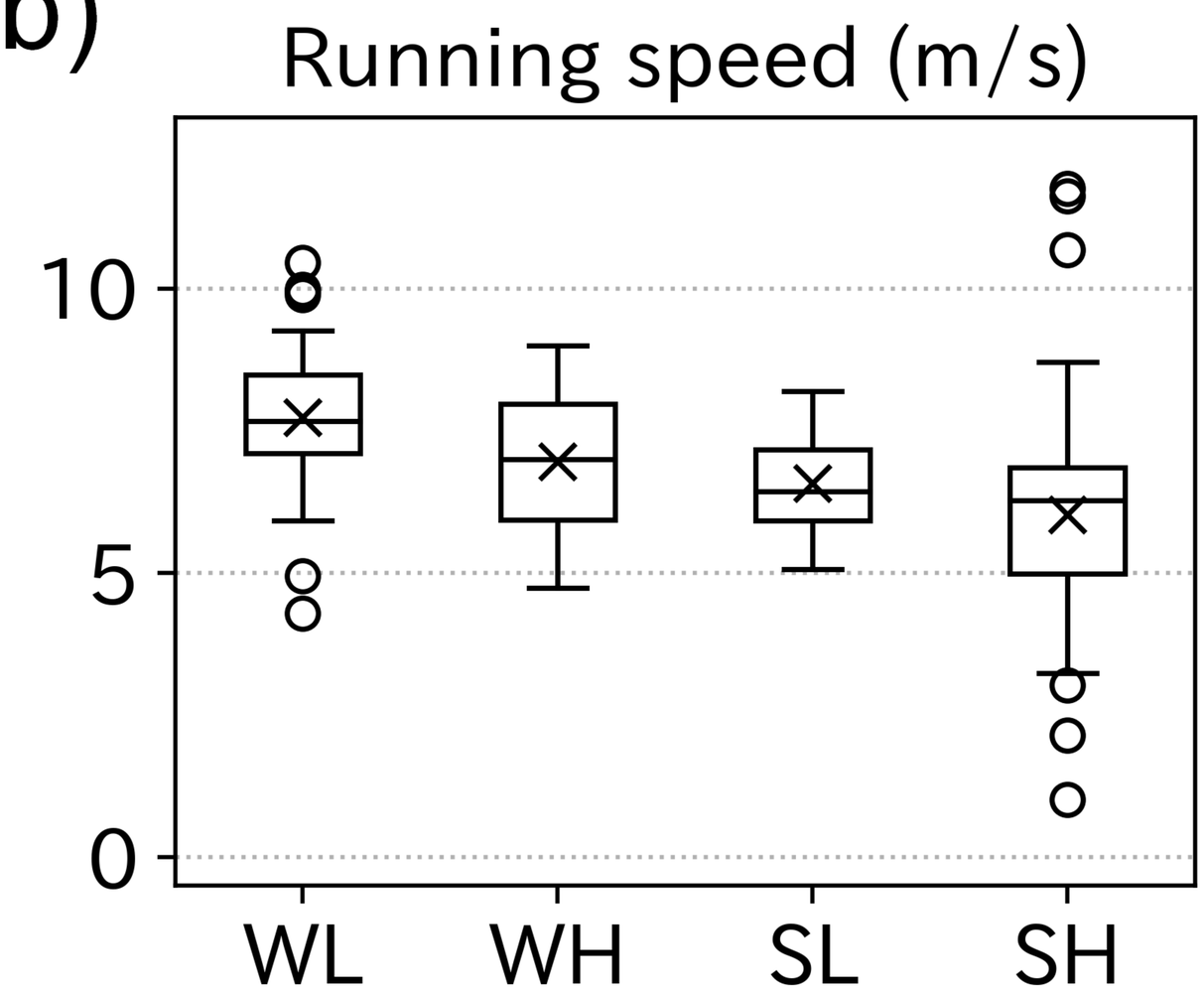

0.1
0.0
WH
SH
WL
SL
5
4
3
2
Wave height (m)
0
4
8
12
16
0.0
0.5
Wind speed (m/s)

B

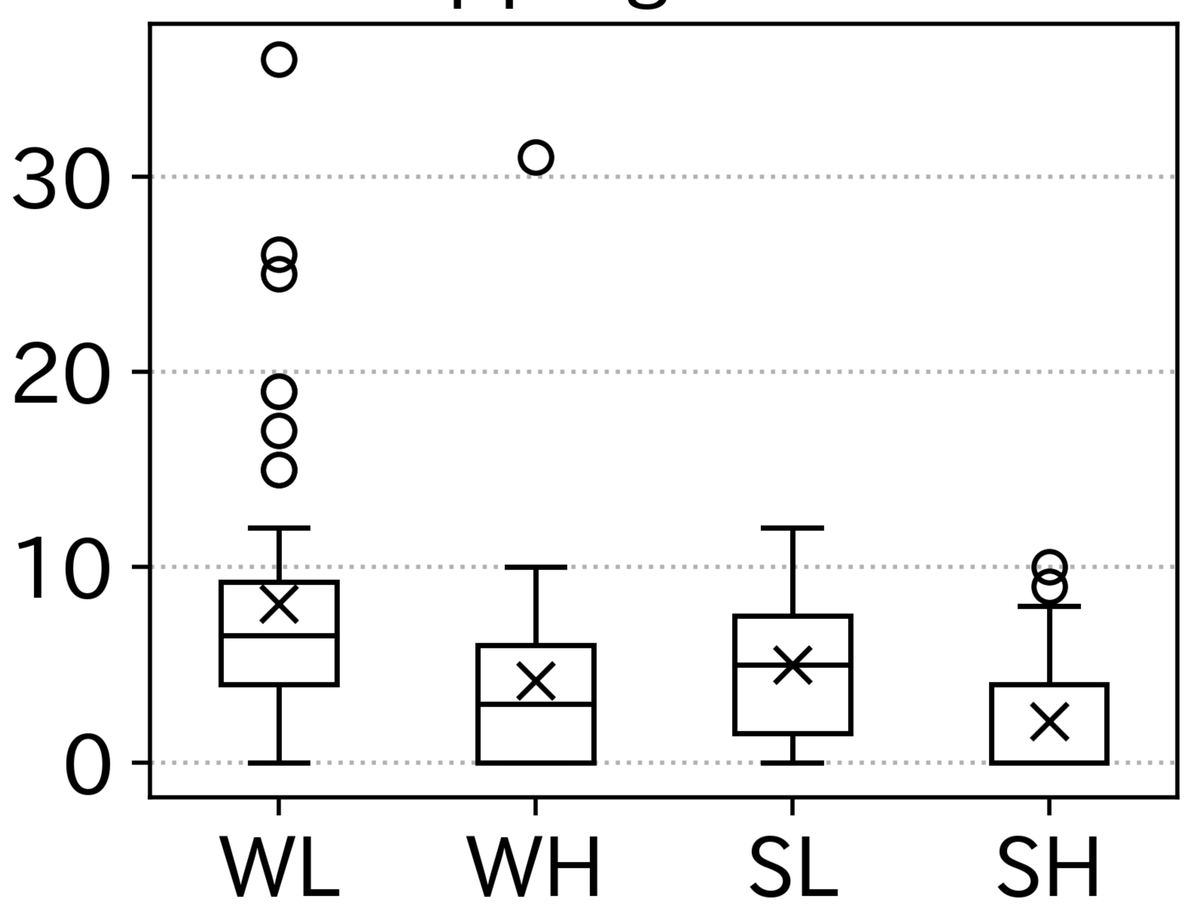
(a)


Running duration (s)
10
5
0
WL
WH
SL
SH

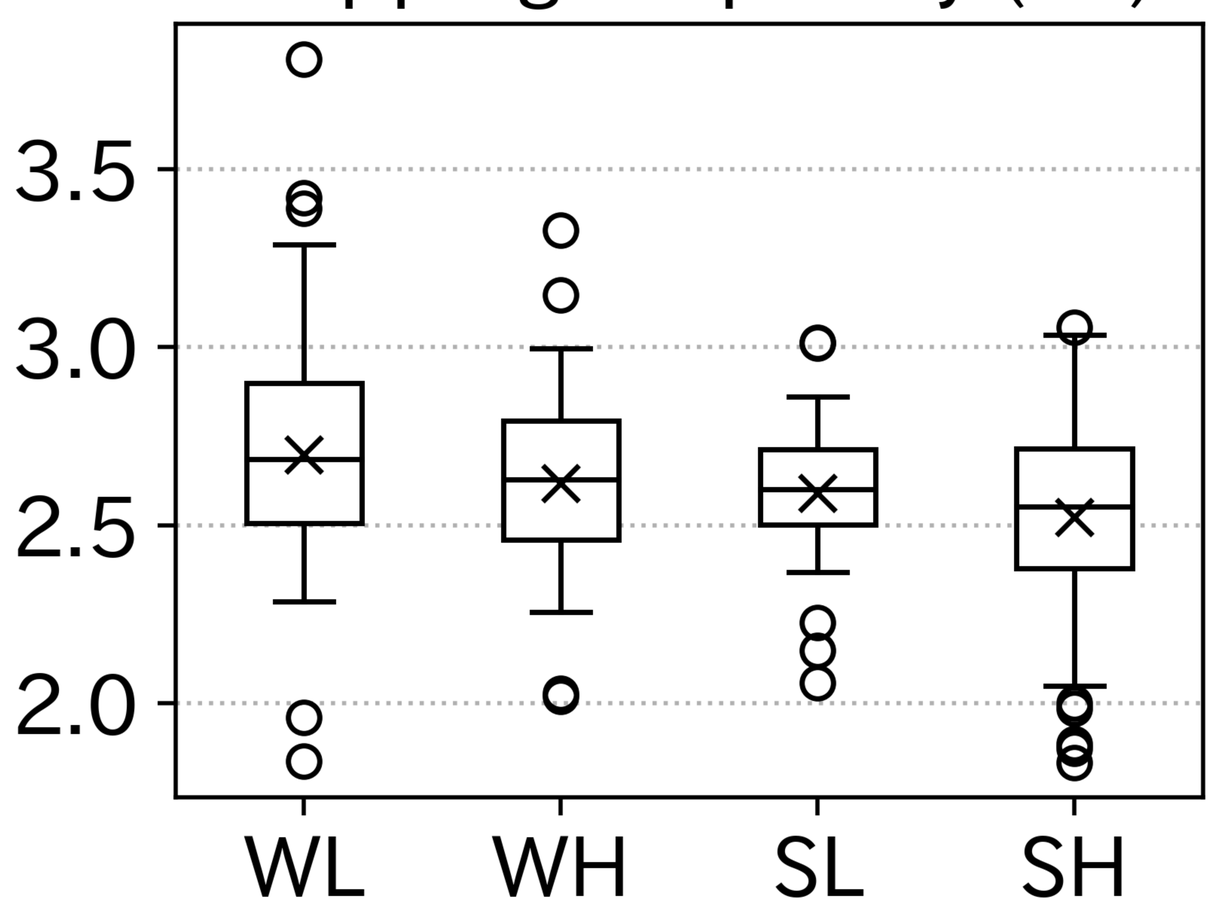
(b)

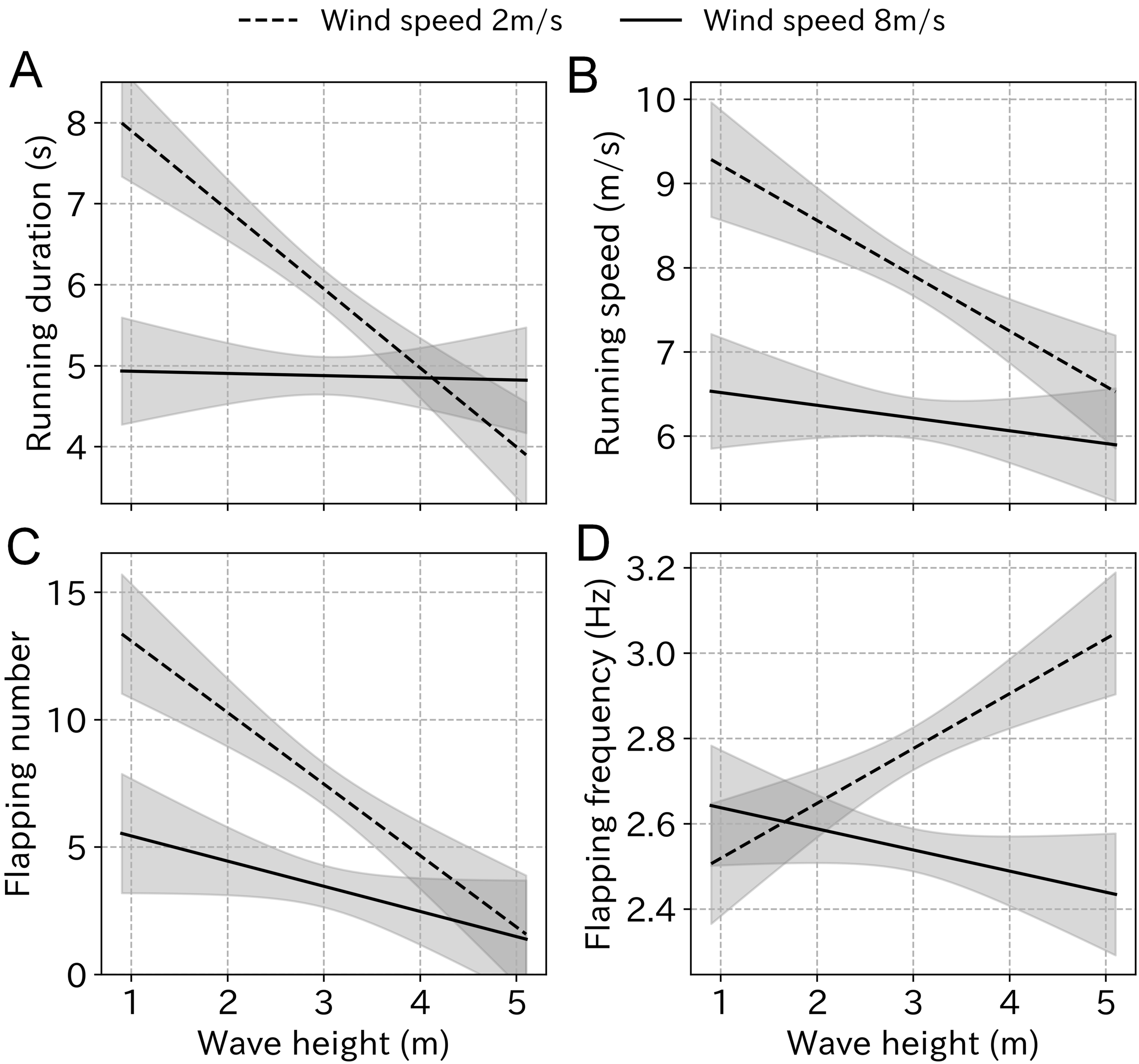

Running speed (m/s)
10
5
0
WL
WH
SL
SH

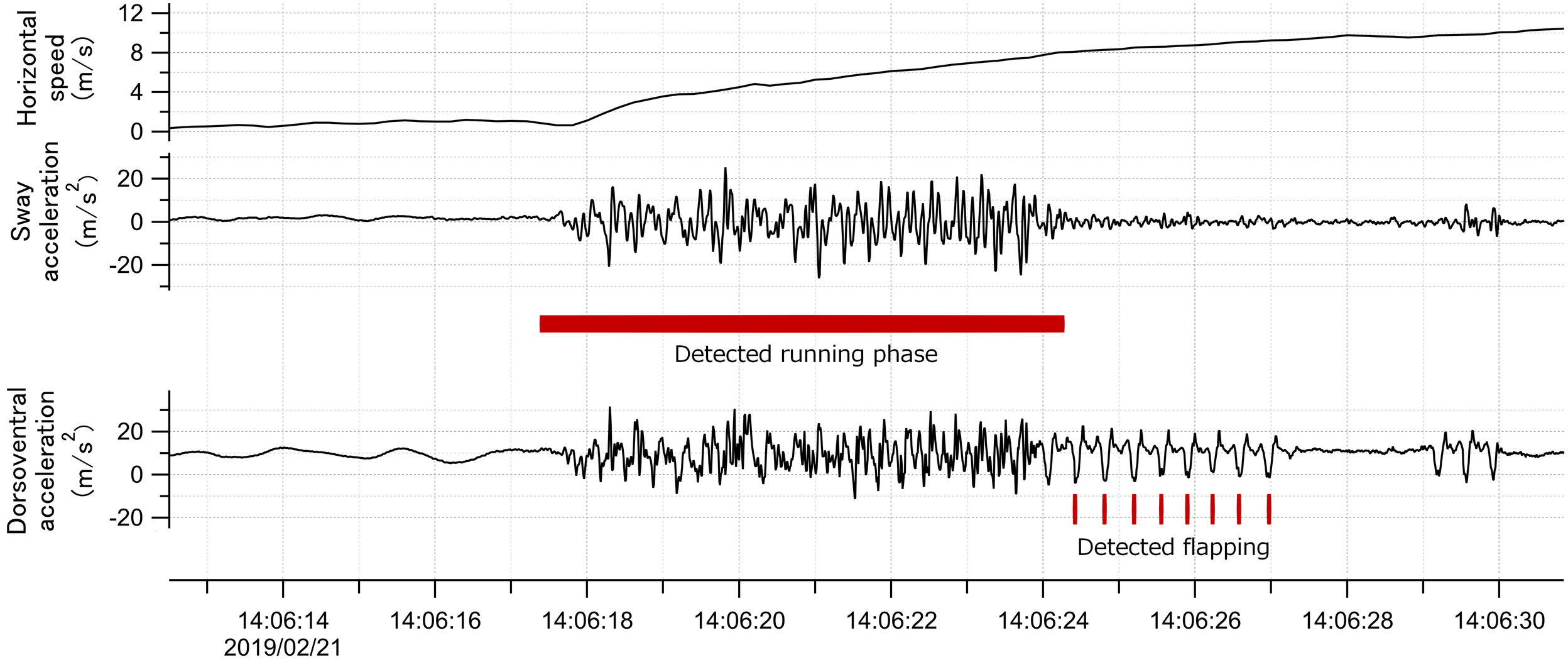
(c)

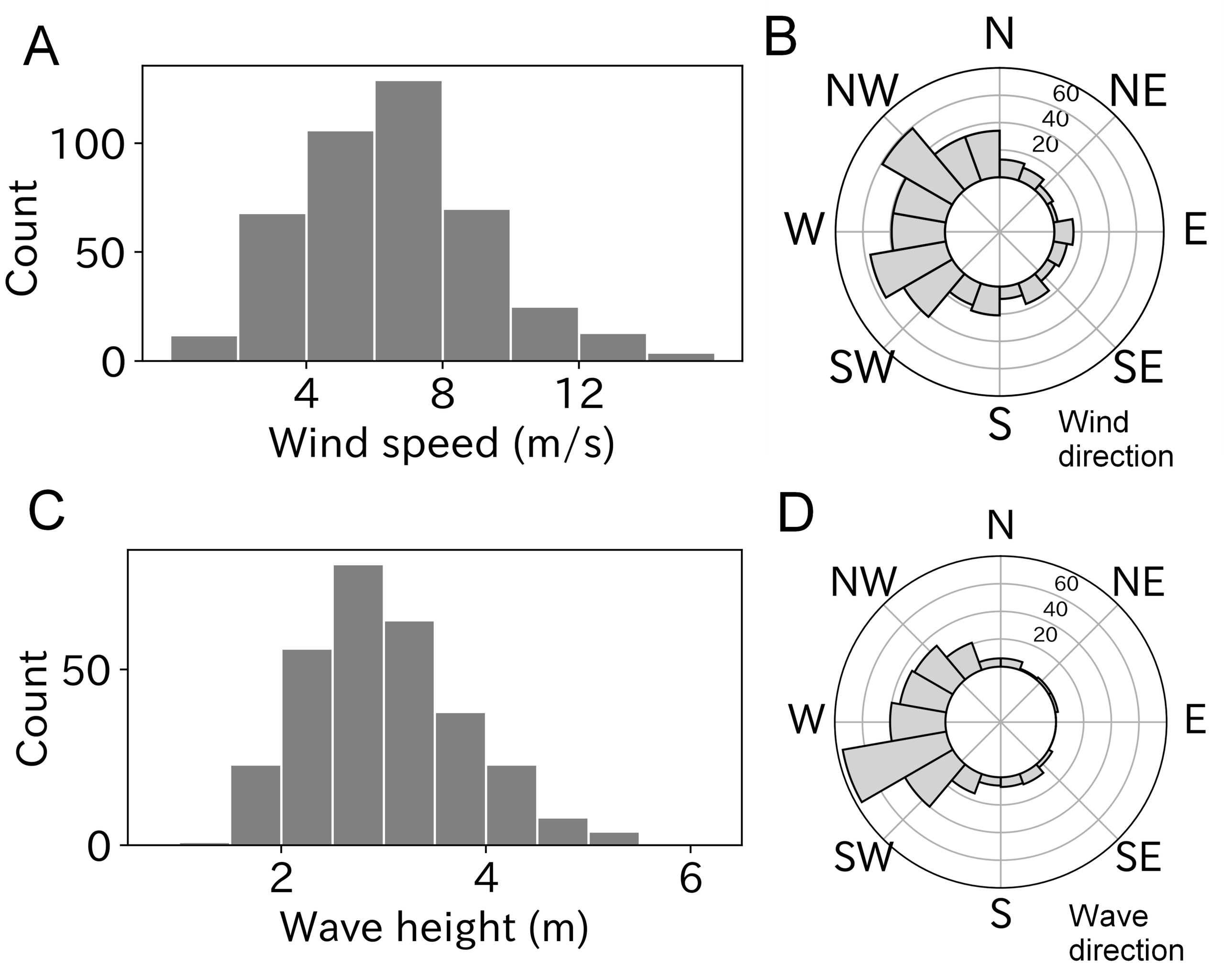

Flapping number
30
20
10
0
WL
WH
SL
SH

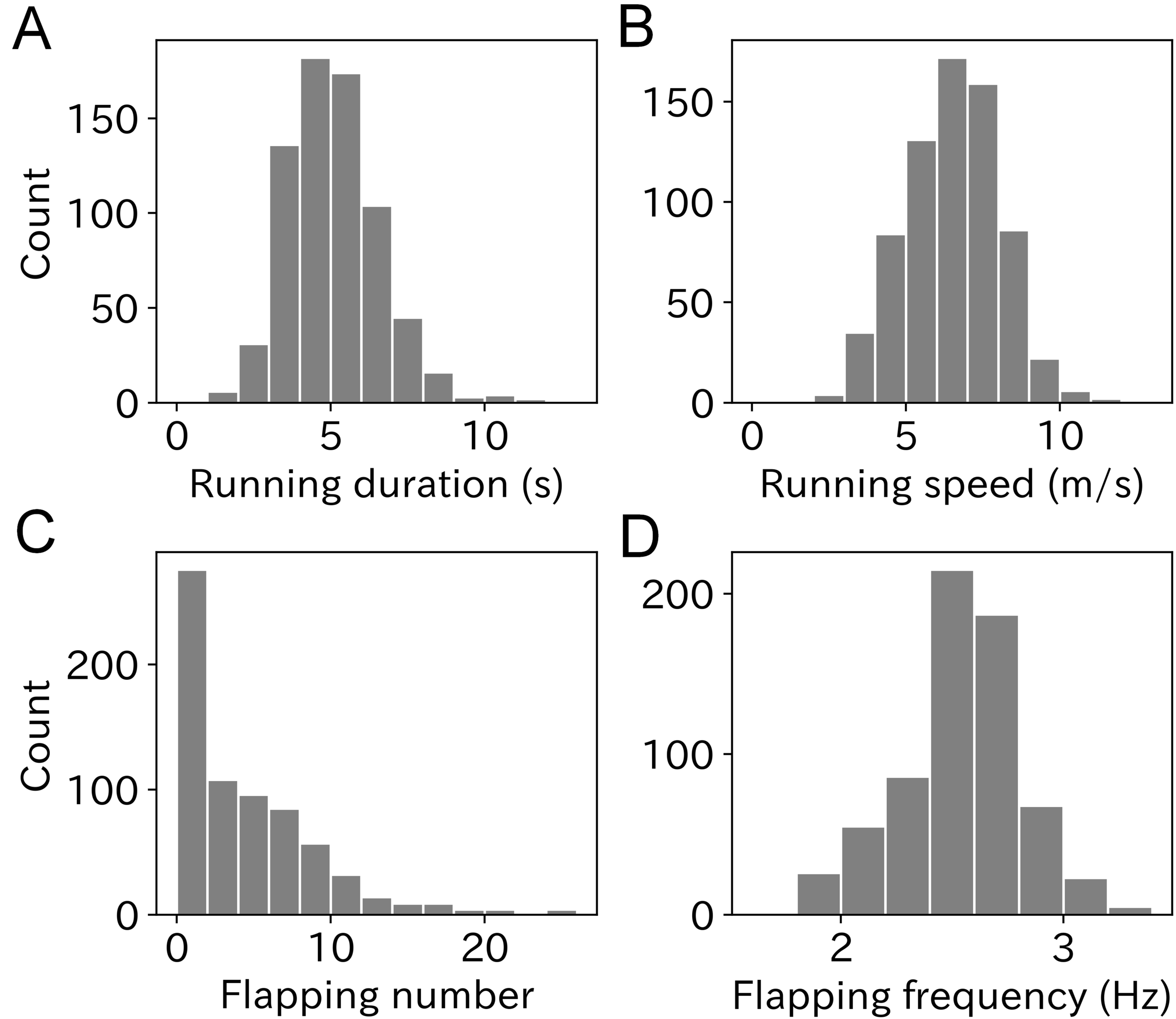
(d)

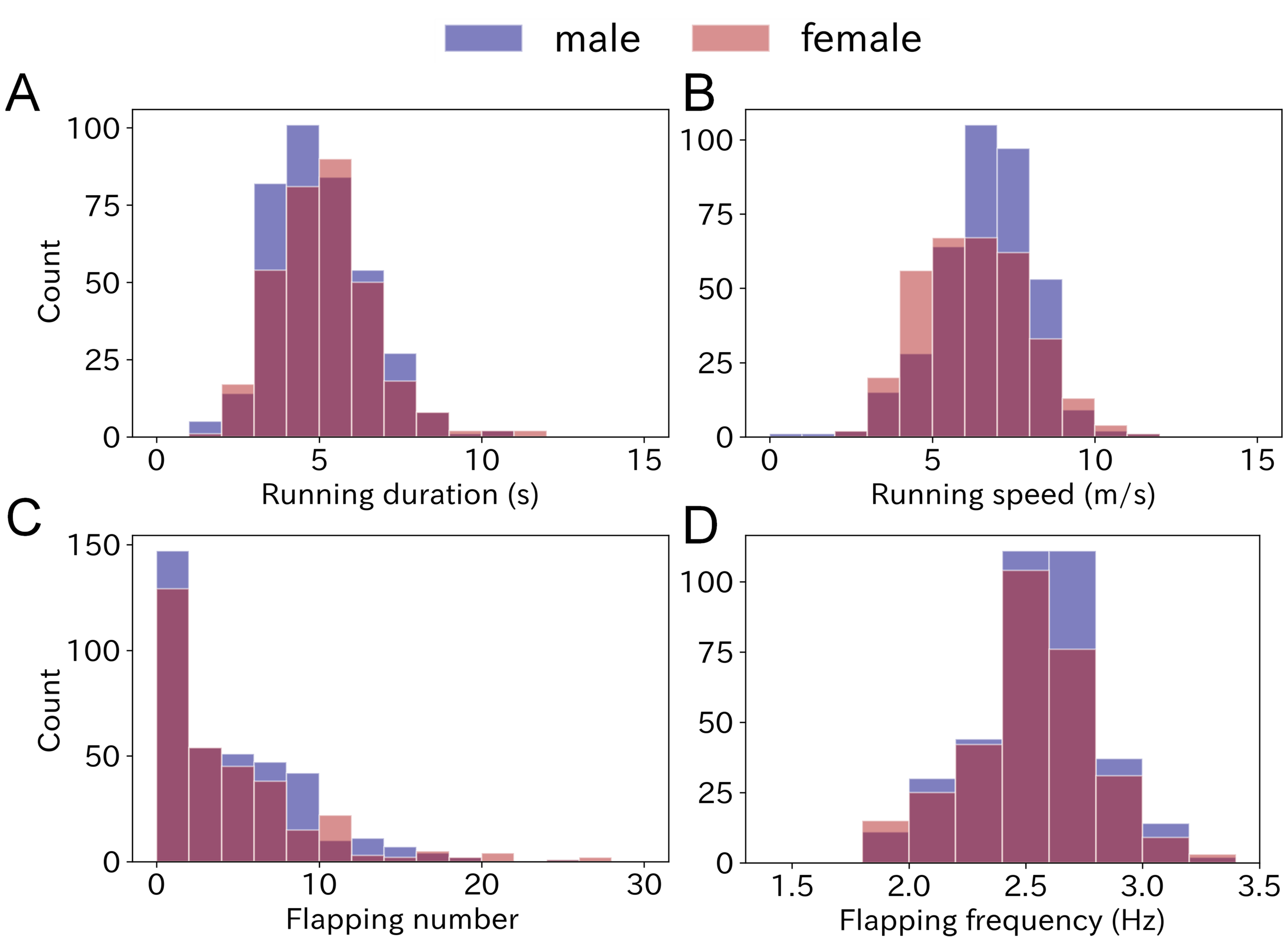

Flapping frequency (Hz)
3.5
3.0
2.5
2.0
WL
WH
SL
SH

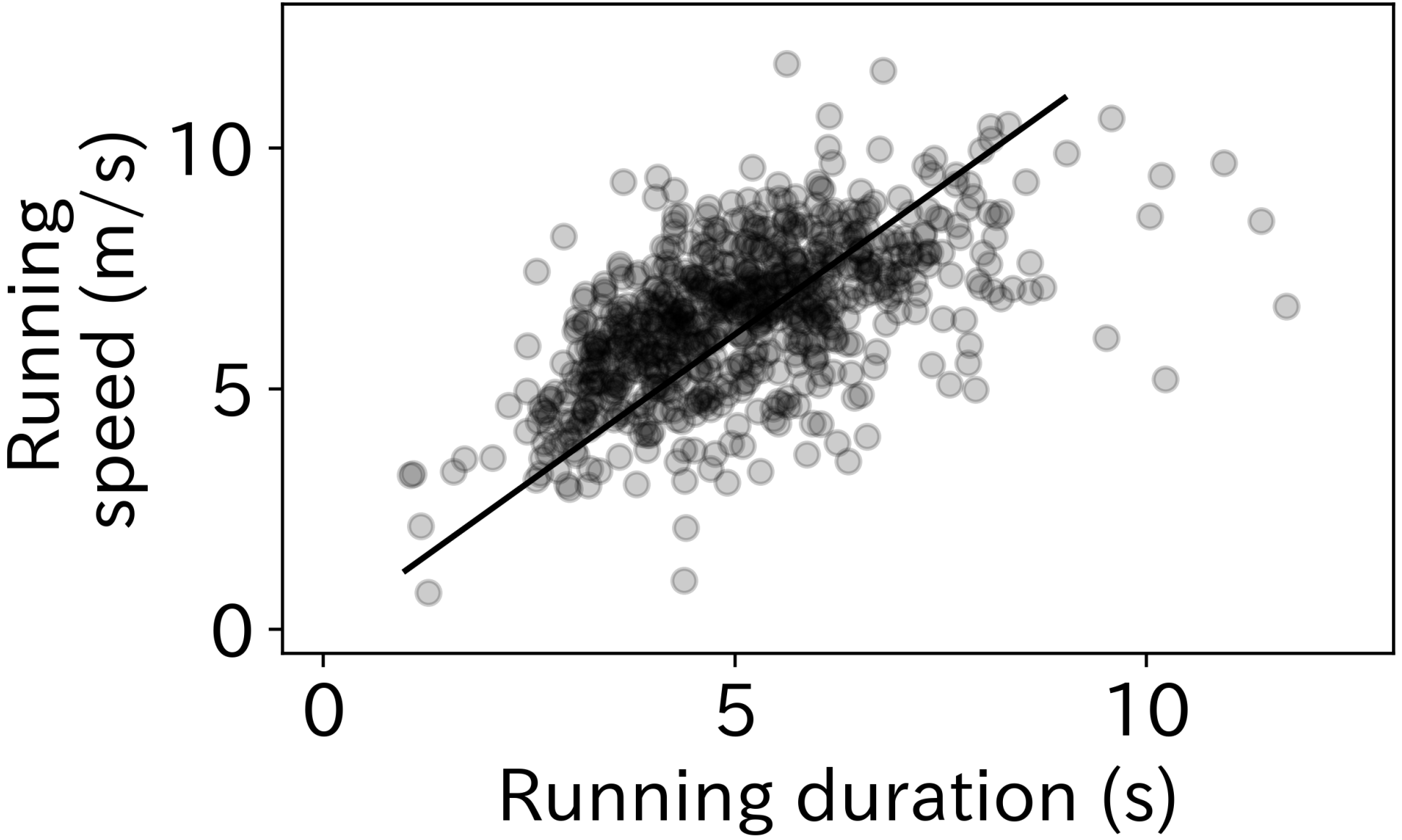

Wind speed 2m/s
Wind speed 8m/s
A
Running duration (s)
B
Running speed (m/s)
C
Flapping number
D
Flapping frequency (Hz)
Wave height (m)
Wave height (m)

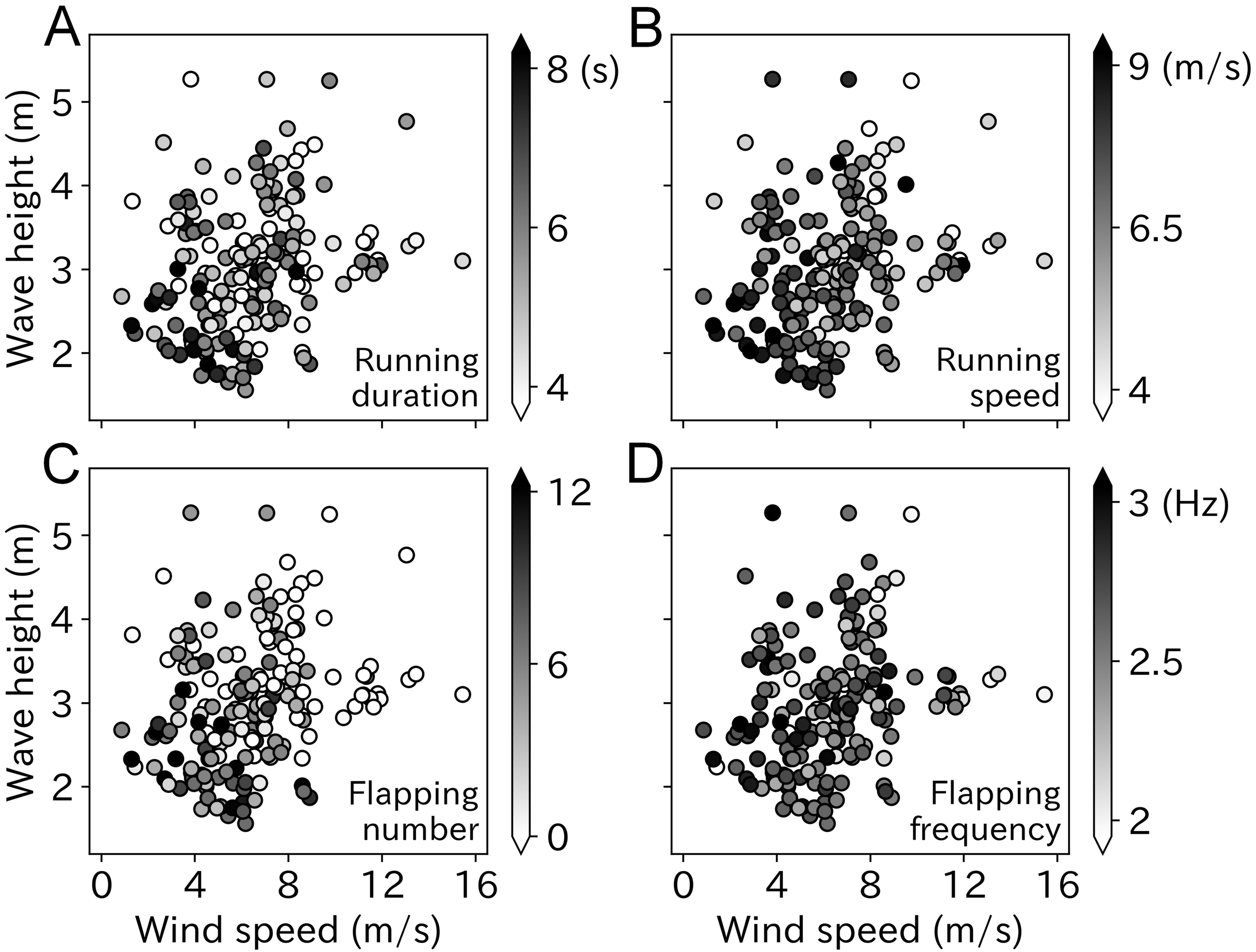

Horizontal speed (m/s)
12
8
4
0
Sway acceleration (m/s2)
20
0
-20
Detected running phase
Dorsoventral acceleration (m/s2)
20
0
-20
Detected flapping
14:06:14
2019/02/21
14:06:16
14:06:18
14:06:20
14:06:22
14:06:24
14:06:26
14:06:28
14:06:30

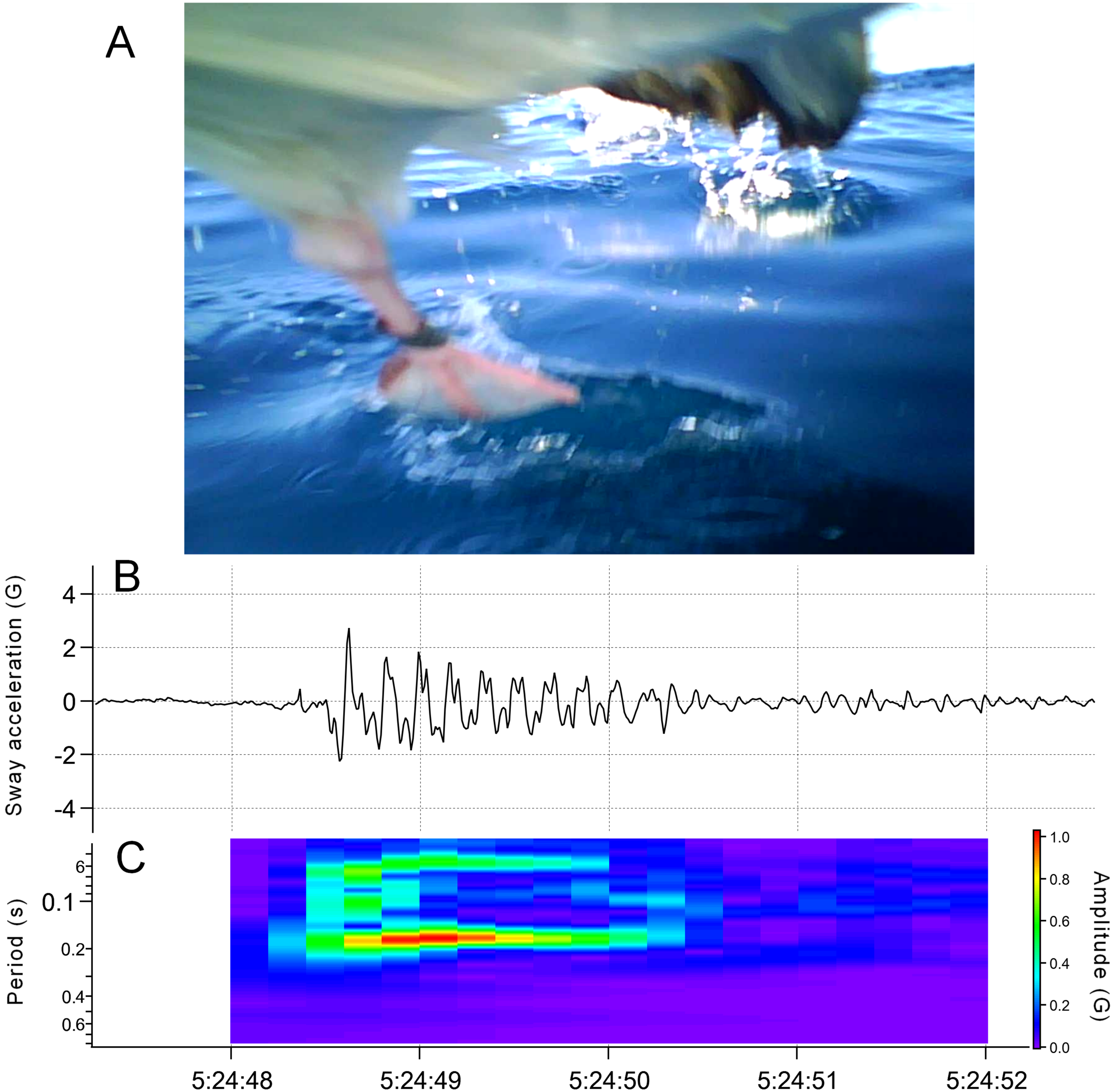

A
Count
100
50
0
4
8
12
Wind speed (m/s)
B
N
NE
E
SE
S
SW
W
NW
60
40
20
Wind direction
C
Count
50
0
2
4
6
Wave height (m)
D
N
NE
E
SE
S
SW
W
NW
60
40
20
Wave direction


A
Count
150
100
50
0
0
5
10
Running duration (s)
B
150
100
50
0
0
5
10
Running speed (m/s)
C
Count
200
100
0
0
10
20
Flapping number
D
200
100
0
2
3
Flapping frequency (Hz)


male
female
A
B
C
D
Count
Running duration (s)
Running speed (m/s)
Flapping number
Flapping frequency (Hz)
0
25
50
75
100
150
0
5
10
15
20
30
1.5
2.0
2.5
3.0
3.5


Running speed (m/s)
10
5
0
0
5
10
Running duration (s)


A
B
C
D
Wave height (m)
Wind speed (m/s)
Running duration
Running speed
Flapping number
Flapping frequency
8 (s)
6
4
9 (m/s)
6.5
4
12
6
0
3 (Hz)
2.5
2
0
4
8
12
16
2
3
4
5


A
B
Sway acceleration (G)
4
2
0
-2
-4
C
Period (s)
6
0.1
0.2
0.4
0.6
Amplitude (G)
1.0
0.8
0.6
0.4
0.2
0.0
5:24:48
5:24:49
5:24:50
5:24:51
5:24:52