Groping in the fog: soaring migrants exhibit wider scatter and do not properly adjust their flight in response to wind under low visibility conditions

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Abstract

Atmospheric conditions are known to affect flight propensity, behaviour during flight, and migration route in birds. Yet, the effects of fog have only been rarely studied, although they could disrupt orientation and hamper the accomplishment of the journey. Soaring migrants modulate their flight speed and direction in relation to the wind vector to optimize the cost of transport. Fog could limit the visibility of migrating birds such that they might not be able to detect landmarks that guide them during their journey. Consequently, landmark-based orientation, as well as adjustments of flight speed and direction in relation to wind conditions, could be jeopardized when flying in fog. Using a radar system that operated in a migration bottleneck (Strait of Messina, Italy), we studied the behaviour of soaring birds under variable wind and fog conditions over two consecutive springs (2016 and 2017), discovering that migrating birds exhibited a wider scatter of flight directions and responded differently to wind conditions under fog conditions. Birds flying through fog deviated more from the mean migration direction and increased their speed with increasing crosswinds. In addition, airspeed and groundspeed increased in the direction of the crosswind, causing a lateral drift of the individuals. Furthermore, the response to tailwind was opposite to that predicted by optimal migration theory. Our findings represent the first quantitative empirical evidence of flight behaviour changes when birds migrate through fog and explain why low visibility conditions could risk their migration journey.

Keywords: attenuating medium, bird migration, flight behaviour, Honey Buzzard, movement ecology, radar aeroecology, Strait of Messina

Introduction

Atmospheric conditions are known to affect flight propensity, behaviour during flight, and migration route in birds [1–3]. Migration routes can be several thousand kilometres long, across many different ecosystems, landscapes, and climatic regions. Migratory birds are adapted to fly under different weather conditions but in general they prefer to fly in favourable atmospheric conditions. For instance, massive nocturnal migration in North America is triggered by mild temperatures [4], and flight over ecological barriers is facilitated by tailwinds or weak headwinds and is avoided under strong headwinds [5–9].Fog and low clouds may lower the visibility of landmarks and hamper orientation [3, 10, 11]. Fog usually occurs in calm weather conditions (e.g., weak or no winds) near ground level, and its presence might be associated with otherwise good conditions for migration [12].Although birds may benefit from such weather, the low visibility associated with fog may cause disorientation and consequently avoidance of travelling [13, 14]. Bird flight behavior and movement path could be consequently affected by fog. For example, tracks of Sandhill Cranes (*Grus canadensis*) recorded on a foggy day with a marine radar were more tortuous and circuitous than on days with good visibility [15]. If the fog extends over a large area, birds could find themselves tens or even hundreds of kilometres away from their intended migratory routes and may become exhausted, as recorded for a flock of Turkey Vultures (*Cathartes aura*) flying over a fog-covered sea where the birds eventually alighted on a boat [16]. Fog may even cause mass-mortality events of migrating birds [17] and may postpone their departure from stopover sites as they wait for better weather conditions. In some cases, birds may even undertake reverse migration when visibility is poor [10, 13, 18, 19]. Indeed, fog was found to delay the arrival of birds at an offshore island in California [20]. These, mostly anecdotical, findings also highlight the difficulty in studying how fog influences bird behaviour. Yet, more comprehensive studies regarding the effects of fog on wildlife can be made in areas where

fog prevails during long time periods. For example, Panuccio et al. (2019)[14], which used radar to study soaring migrants in a migratory bottleneck in Southern Italy, documented substantial decrease in migration intensity under foggy conditions, likely indicating avoidance behaviour. Wind conditions may hamper or facilitate bird migration [3, 5, 21, 22]. Specifically, due to the benefits of flying with favourable wind, tailwind assistance could induce a decision to depart, resulting in high migration traffic rate [23–25]. To reduce their flight cost and migration duration [26–28] flying migrants should continuously adjust their flight behaviour in response to changes in wind speed and direction as predicted by the optimal migration flight theory [29, 30]. Consequently, their air- and groundspeed can change in a predictable manner [28]. Several studies have shown that both flapping and soaring birds reduce their airspeed under tailwinds and increase it under headwinds [29–31] and that the migrants' ground speed is also affected by tailwinds, headwind and crosswinds [28, 32–34]. In soaring migrants, the reduction of airspeed under tailwinds during gliding allows birds to cover larger distances in a short time by reducing the time-consuming thermal circling phase of the flight [32] and decreases the risk to switch to energy-expensive flapping flight [35, 36]. The aim of this study was to examine the effects of fog on orientation and response to wind in soaring migrants tracked by a marine radar over a migration bottleneck, The study was carried out at the Strait of Messina in Southern Italy, where Honey buzzards (*Pernis apivorous*) compose approximately 95% of the tracked migrants [28, 37]. We analysed the distribution of flight directions and the effects of wind conditions (speed and direction) on bird ground and airspeed under fog conditions. We predict a larger scatter of flight directions and an altered response to wind compared with clear sky conditions. Although, to the best of our knowledge, no theory exists for flight behaviour in fog and no previous study has quantitatively estimated how flight may change under these conditions, we predict that fog will affect bird response to the wind. In general, bird airspeed and flight direction are expected to change in predictable ways in relation to wind speed and direction to optimize the cost of transport [29, 38]. Whether birds will behave optimally also in fog is unknown and may depend on the information available to them under these conditions. If they rely on landmarks for optimizing their movement, and these landmarks are not visible in fog, the birds will behave in a non-optimal manner simply due to lack of information required to assess their movement.

Methods

Study area and data collection

Data collection took place during the spring of 2016 (24th March – 7th May) and 2017 (22nd March – 23rd May) near the edge of a flat highland frequently exposed to fog [14] in the Aspromonte Mountains, Calabria (38°23' N, 15°79' E – 1030 m a.s.l.), about 7 km inland from the Strait of Messina in southern Italy (see Figg. 1 in [28] and [14] for a map of the area). Fog and low clouds are generated in this area because humid air is trapped between the coast and the highland [14]. We collected data using a 12 kW, X-band (9.1 GHz) marine radar rotating at 38 RPM with a 2.1-m antenna that was set horizontally with a 22°vertical beam. The radar covered a sector of 240°(it was blanked towards the observers for the remaining angle) and its detection radius was about 2 km, orienting towards the prevalent direction of the incoming migrants (a compass direction of 215°). Its horizontally rotating antenna enabled computing the direction and speed of the migrating birds based on the detection of their echoes and the reconstruction of their trajectories. Notably, the altitude of the echoes could not be computed. The radar was positioned in an area that is well known for its importance as migratory bottleneck for many species of birds and in particular for soaring raptors [39]. Experienced birdwatchers carried out daily observations near the radar to characterize species composition and migration traffic rate [40]. Radar measurements and direct observations of migrating birds took place daily during the study period and continuously between sunrise and sunset (UTC + 1), interrupted only occasionally by heavy precipitation. Radar tracks were processed using Hypatia-trackRadar, a dedicated software that allows a supervised approach that minimizes errors in estimating bird tracks from the radar echoes [41]. The program translates the echoes to a metric coordinate system and based on time and spatial position of the echoes, it automatically calculates multiple flight parameters, such as groundspeed, track length and duration. In addition, the software allowed to associate the echoes with the species observed by the birdwatchers. We filtered out tracks less than 100 m long and with a groundspeed of less than 5 ($m \cdot s^{-1}$).

Weather data

The presence of fog and low clouds was visually assessed by the radar operators and the birdwatchers. It was recorded assigning a presence/absence value for each hour when visibility was lower than 0.3 km for at least 15 consecutive min, while disregarding isolated passing clouds (for details on the method see [14]). Hourly U (eastward) and V (northward) components of the wind (10 m above ground) were downloaded from the ERA5 dataset of the European Centre for Medium-Range Weather Forecast (ECMWF) repository. ERA5 provides hourly estimates of a large number of atmospheric variables on a 30 km grid. We used the wind components to calculate tailwind and crosswind speeds (hereafter TW and CW, respectively) relative to the mean seasonal (springtime) migration direction of the birds (), which is considered as their overall heading [28, 42].

Movement parameters

In order to test if bird movement changed under different wind and fog conditions, we calculated several variables derived from

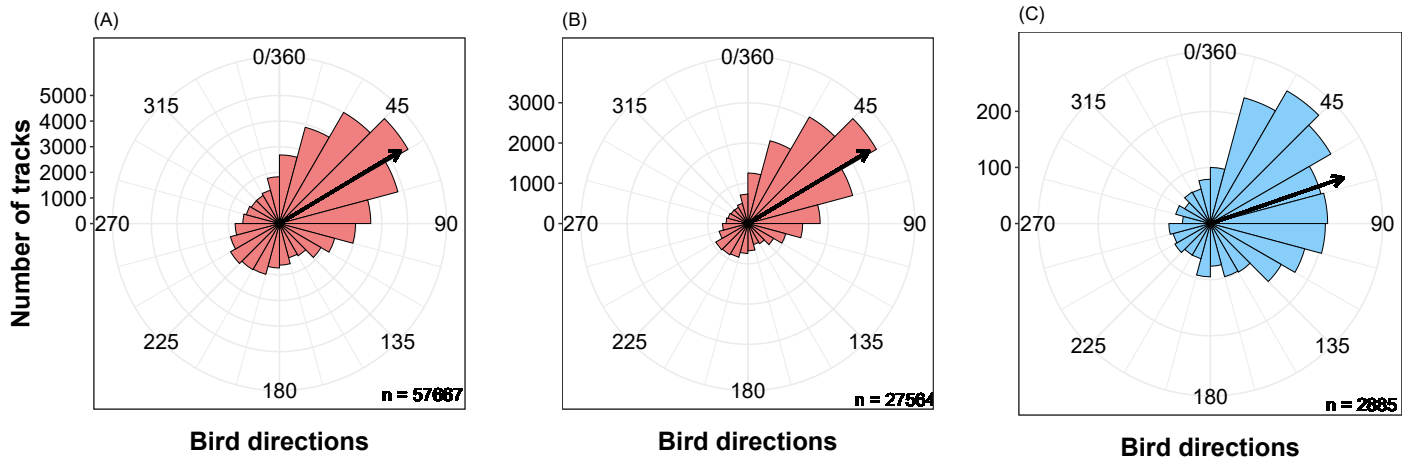

Figure 1: Circular distribution of (A) all tracks recorded under clear skies, (B) tracks recorded under clear skies in selected wind conditions that match those recorded during fog events, and (C) tracks recorded under fog conditions. Black lines are mean circular directions.

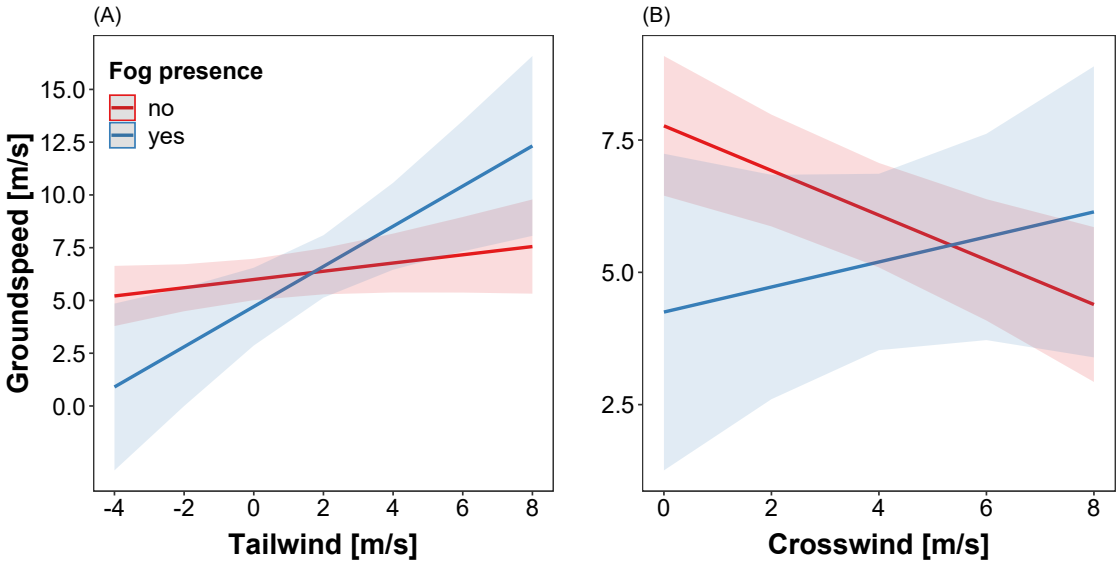

Figure 2: The effects of crosswind and tailwind speed on groundspeed of birds migrating through fog or under clear skies. (A) Regression slopes and 95% C.I. of the groundspeed in relation to tailwind. (B) Regression slopes and 95% C.I. of the groundspeed in relation to crosswind. Crosswinds have only positive values since they represent only wind blowing from the left to the right side of the average migration direction.

the radar tracks, including:

1. Groundspeed: calculated as the simple ratio between distance covered and time passed between two consecutive points. We calculated the groundspeed component relative to the mean direction of migration θ, as a projected segment towards that specific direction.

2. Airspeed: calculated as in [43], using the wind components crosswind (CW) and tailwind (TW) which were calculated in relation to the mean direction of migration θ.

3. Sideways speed: bird lateral speed relative to was calculated by multiplying the bird's groundspeed with the *sin* function of the difference between θ and the individual bird track.

The mean migration direction $\theta$was calculated as the circular mean of all tracks collected from birds that passed through the radar's detection area in fair weather; hence we excluded tracks recorded under foggy conditions in this calculation. Furthermore, we used hourly means of bird movement parameters to match the temporal resolution of the wind components. In addition, we filtered our tracks that deviated more than 100°from the θ (either to the left or to the right of this angle) to exclude the movement of local and non-migrating birds.

Statistical analysis

We used the Watson's U^2 test (Watson's Two-Sample Test of Homogeneity) to compare between the two sets of track directions,

	Groundspeed			Airspeed			Sideways speed		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	6.08	5.10 – 7.06	**<0.001**	6.10	5.10 – 7.10	**<0.001**	-0.78	-1.68 – 0.12	0.091
CW_z	-0.72	-1.13 – -0.30	**0.001**	-0.60	-1.03 – -0.18	**0.005**	-0.74	-1.15 – -0.33	**<0.001**
TW_z	0.32	-0.09 – 0.73	0.130	-0.52	-0.94 – -0.10	**0.016**			
Fog[yes]	-0.90	-2.84 – 1.04	0.363	-0.67	-2.64 – 1.30	0.506	1.66	0.05 – 3.26	**0.043**
CW_z * Fog[yes]	1.12	0.04 – 2.19	**0.041**	1.29	0.20 – 2.39	**0.021**			
TW_z * Fog[yes]	1.24	0.12 – 2.36	**0.030**	1.11	-0.01 – 2.23	0.051			
Random Effects									
σ^2	9.01			9.37			9.13		
τ_{00}	7.18 $_{n.days}$			7.45 $_{n.days}$			5.99 $_{n.days}$		
N	56 $_{n.days}$			56 $_{n.days}$			56 $_{n.days}$		
Observations	296			296			296		

Table 1: The selected linear mixed models reporting the effects of wind and fog on bird average hourly speeds. Continuous predictors are scaled (z-transformed). Significant p-values are in bold.

under fog and without fog [44]. We analysed several movement parameters in relation to wind (tailwind and crosswind components) and fog condition. Specifically, we used hourly means of groundspeed, airspeed, and sideways speed and matched them with wind data at the same temporal resolution (hourly values) to avoid eventual pseudo-replication (having many tracks recorded in a certain hour that are matched with a single wind parameter value). We used Linear Mixed Effect Models (LMMs), with ordinal date as an intercept random effect. We found the optimal structure of the fixed components of the model and ran the models with different combinations of the fixed effect terms in the global model. We used the log-transformed count of tracks per hour as weights in the model. To evaluate model fit, we used the Akaike Information Criterion (AIC; [45]), by applying the function *dredge* from the `MuMIn` package in R [46, 47]. Following inspection of model residuals and considering the dispersion of the data using the `DHARMa` package [48], we chose linear mixed models as the most appropriate test [49]. Statistical analyses were performed in R 4.1.0 [47] using packages `glmmTMB` [50] and `circular` [51]. Plots and table of the models were produced using the package `sjPlot` [52] and `ggplot2` [53].

Results

We recorded a total of 60,552 radar tracks, of these 2,885 (4.8%) were recorded during foggy conditions (Figure 1, see also Figure S1 for the number of tracks per day in fog and fair-weather conditions). We noted that fog occurred only when the wind was blowing towards east, southeast and south, and precisely between 90.92°and 179.22°. We filtered out tracks that were recorded when the wind blew towards directions outside this angular sector and retained 30,449 tracks in our database. Within these selected wind directions, the mean flight direction of birds differed significantly between birds that flew under clear skies (90.8% of the tracks) and fog (9.2% of the tracks) conditions (Watson's U^2 test: $test - statistic = 3.11$, $p < 0.001$), with a mean direction of 57.3°under clear skies and 71.0°under foggy conditions (Figure 1). This result holds true also if we include the excluded tracks recorded in clear skies conditions under all wind directions and compare them to the tracks recorded during fog (Watson's U^2 test: $test - statistic = 1.99$, $p < 0.001$), with a mean direction of all tracks under clear skies conditions of 59.0°. Mean hourly values for groundspeed, airspeed and sideways speed were computed for a total of 296 hours of radar operation. Models with groundspeed and airspeed relative to the mean migration direction retained all the predictors, while the model selected for explaining bird sideways speed retained fog presence and the crosswind component predictors. Soaring migrants flying in foggy and non-foggy

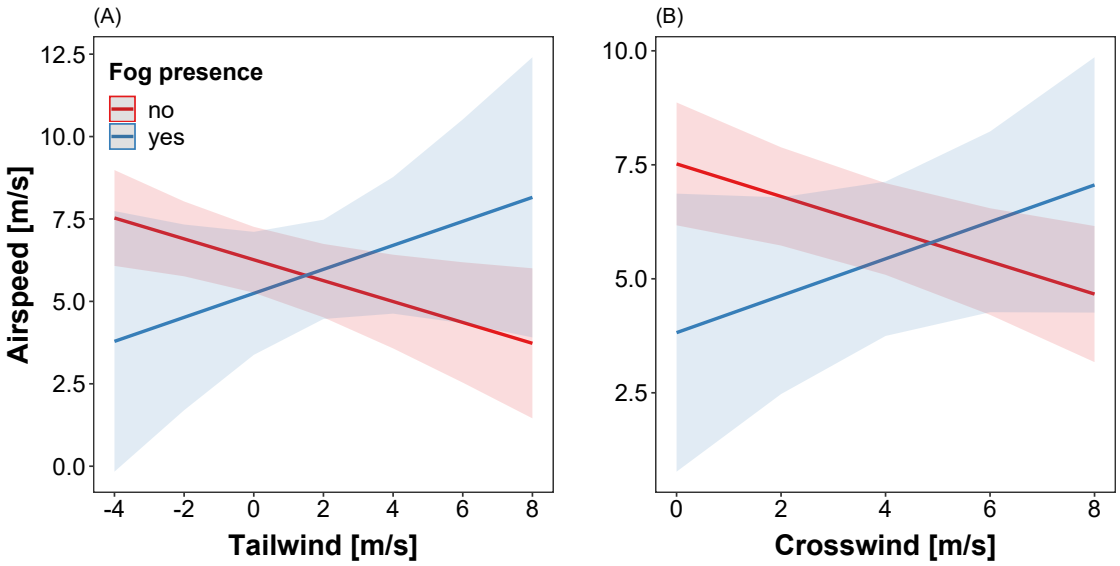

Figure 3: The effects of crosswind and tailwind speed on airspeed of birds migrating through fog or under clear skies. (A) Regression slopes and 95% C.I. of the airspeed in relation to tailwind. (B) Regression slopes and 95% C.I. of the airspeed in relation to crosswind. Crosswinds have only positive values since they represent only wind blowing from the left to the right side of the average migration direction.

conditions over the study area had in general similar groundspeed (Table 1), but differed in their response to tailwind and crosswind speed (Figure 2). Under clear skies, birds slightly increased their groundspeed with increasing tailwind speed, while in foggy conditions, bird groundspeed substantially increased with increasing tailwind speed (Table 1; Figure 2A). With headwinds the groundspeed in clear skies remained rather stable, while birds flying in foggy conditions substantially decreased their groundspeed (Table 1; Figure 2A). Increasing crosswind speed under clear skies induced a substantial decrease of groundspeed, while groundspeed increased with crosswind speed under foggy conditions (Table 1; Figure 2B). It should be noted that due to the filtering of the tracks, the crosswind component contains only positive values, indicating a wind blowing towards the bird's right hand side (Figures 2, 3, 4). Soaring migrants flying over the study area had similar airspeeds when flying in foggy and clear sky conditions (Table 1). Under clear skies birds reduced their airspeed with increasing tailwind speed, as expected, while under foggy conditions they increased their airspeed with increasing tailwind speed (Table 1; Figure 3A). Birds flying under clear skies decreased their airspeed with increasing crosswind speed, while those flying under fog increased their airspeed with increasing crosswind speed (Table 1; Figure 3B). Bird sideways speed differed significantly when the birds were travelling through fog and while flying under clear skies (Table 1; Figure 4A). In foggy conditions, sideways speed increased towards the right side of the migration goal (positive values), hence towards inland. Birds travelling under clear skies had a negative sideways speed, meaning that they moved more towards the coast (Table 1; Figure 4A). While the general response of the birds to crosswind was similar, they tended to direct their flight towards inland areas under weak crosswinds and towards the coast with increasing crosswind speed (Table 1; Figure 3B). Due to this change in direction with increasing crosswind speed, it seems that the birds were ranging between under-compensating for lateral drift to over-compensating as the crosswind component increases and this response is modulated by atmospheric conditions since their response differed under clear skies and foggy conditions. When crosswinds were weak, birds flew towards the general direction of the presumed migration goal (dashed line in Figure 4), but at the same crosswind conditions, bird that flew in the fog over-compensated the wind drift by traveling towards the coast. With increasing crosswind speed, the birds eventually compensated for the lateral drift by flying towards the presumed migration goal (Figure 4).

Discussion

Our findings demonstrate that fog affects bird orientation and the modulation of flight speed in relation to wind during migration. We found that the birds' flight directions are more scattered under foggy conditions and that the mean migration direction changed when fog was present. As described in an earlier study, soaring migrants' densities are drastically reduced in fog [14] (also see Figures S1 and S2), and the present study uncovers the reasons for this avoidance, suggesting that bird orientation can be disrupted and the cost of transport could be elevated such that the migration trip may become more risky and costly. For example, the birds may waste precious time getting out of the fog by displacing themselves to some unpredicted or distant places [12, 16], or worse, they could hit some natural or artificial obstacles. To avoid

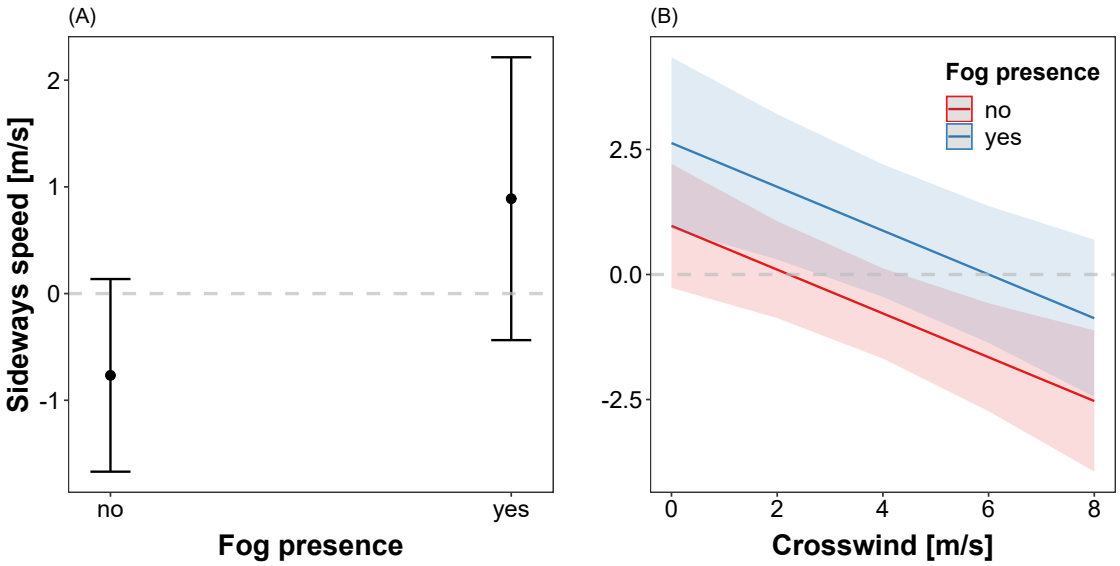

Figure 4: The effects of crosswind on bird sideways speed. (A) Sideways speed mean and 95% C.I. (whiskers) for tracks in foggy and clear weather conditions. (B) Regression slopes and 95% C.I. of the sideways speed in relation to the crosswind component. For visualization purposes two regression lines were generated to identify the two different atmospheric conditions with respect to the presence of fog (yes/no). The dashed line marks the y-intercept at 0 m/s sideways speed, representing the presumable direction of flight towards the migration goal. Crosswinds have only positive values since they represent only the wind blowing from the left to the right side of the average migration direction.

this risk, birds flying in fog often land and wait until the fog is over to resume their migration [13, 18]. Fog may prevent spotting key landmarks for maintaining a certain route direction, consequently influencing bird behaviour and movement. We found that soaring birds flying under clear skies modulated their ground and air speed in relation to tail- and headwind as predicted by optimal migration flight theory [29, 30]. Nonetheless, bird response to the wind was substantially altered under foggy conditions. For instance, ground speed was overall similar under different tailwind conditions in clear skies, but significantly increased with increasing tailwind component in fog. Unexpectedly, we recorded an elevated airspeed with increasing tailwinds when the birds flew in fog suggesting that birds did not respond optimally to tailwinds. The increase in airspeed and consequently groundspeed might be due to the need to quickly get out from the area that is covered by fog. Yet, such behaviour may expose birds to higher risk of collision with structures that could become invisible in the fog, such as buildings, communication towers, power lines and wind turbines [18, 54, 55]. An increase in bird airspeed under fog also occurred when crosswind increased. Furthermore, changes in bird sideways speed in foggy conditions could result in more scattered tracks that diverge from the intended migration goal, as can be expected under limited visibility conditions in general [13, 16, 18]. Probably, soaring migrants that face increasing crosswinds (from sea to land, as in Figure 4B) under any conditions, tend to fly towards land. During foggy situations, this behavior could favor temporary landing to wait for the disappearance of the fog. To the best of our knowledge, the present study is the first to show how fog influences the flight properties of soaring migrants, to date. The lack of data on the spatial and temporal properties of fog in meteorological databases limits broad-scale analysis of the effects of fog on migrating animals, and only a handful of small-scale studies have been done so far to study these phenomena (e.g. [14, 15]). Some of these studies investigated orientation behaviour under fog, including a study that found that fog prevented Little penguins (*Eudyptula minor*) to cross land to reach their nests walking, probably affecting their orientation and delaying their nest attendance [11]. Other studies, mostly anecdotal, suggested that fog also affected migrating dragonflies [12], migrating storks [13] and vultures [16]. In nocturnal species, fog could amplify the glow of artificial lights and consequently influence the orientation of birds [18, 56] and insects [3]. As already proposed by Panuccio et al. [14], we believe that the consequences of flying in fog must be considered when estimating bird collision risks in human-made structures in areas where fog is common. The scatter of flight directions under foggy conditions that we documented could be genuine but might also be explained by our inability to properly define the spatial extent and the intensity of the fog around the radar station. It is possible that some birds were outside the fog when tracked (or perhaps above it), and some experienced different visibility of landmarks when flying in the fog due to variations in fog intensity. By occasionally observing birds during fog events near the radar site, we noticed that the birds which travelled in fog steeply decrease their flight elevation and flew very close to the ground, probably to reacquire contact with some landmarks. The possibility to measure altitude along with changes in the birds' horizontal position would be of great help in the future to explain flight behaviour in low visibility conditions.

We note that radar technology provides a valuable mean to collect data and quantify behavioural changes in birds flying in fog, as direct observations of birds in these conditions are impossible [3]. In conclusion, our findings show that birds flying in fog adjust their flight behaviour when visibility is limited, with possible consequences that could lower bird survival. Finally, our findings represent the first empirical evidence of the modulation of flight behaviour under foggy conditions in migratory birds, highlighting how birds may cope with the risks of flying in low visibility.

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