



Contrasting aspects of tailwinds and asymmetrical response to crosswinds in soaring migrants

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Abstract

Billions of migrating birds travel between their breeding and over-wintering areas twice a year, encountering various environmental conditions along their migration routes. Wind is of utmost importance for birds as wind speed and direction may strongly affect the birds’ flight speed and metabolism. Specifically, tailwinds were found to initiate flight and facilitate higher migration intensity and faster migratory movement while lowering the energetic cost of flight. Using radar, field observations and local meteorological measurements, we studied spring migrating raptors in a migration bottleneck in Italy near the Strait of Messina, between Sicily and Calabria. We explored the effects of wind on flight speed and the intensity of migration in soaring migrants. We found that the birds’ ground speed was positively affected by tailwind speed, and thus, tailwind likely allowed the birds to reach their destination faster. In addition, bird airspeed decreased under increasing tailwind speed, presumably lowering the energetic cost of flight. These findings are in line with predictions of optimal migration flight theory, yet, tailwind had an unexpected negative effect on migration intensity. We suggest that tailwind conditions induced a change in route selection by the migrants at a regional scale, causing a local decline in migration intensity. This change involves the undertaking of cross sea flight rather than overland detour. Furthermore, we found a modular response to crosswinds as birds compensated for winds blowing towards the sea and drifted when winds blew towards land. Our findings suggest that migrating raptors respond to en route wind conditions and coastline geography by adjusting several features of their flight in a manner that will increase their travel speed, reduce the energetic cost of flight, and permit a safe journey.

Significance statement

Soaring birds exploit tailwinds to move faster and presumably to reduce the energetic cost of flight during migration. Using radar, we tested how bird flight is affected by tailwind and further predicted that the due to the advantages of using tailwinds, an increased number of birds migrating over the study area. We found that radar-tracked migrating birds flew faster with tailwinds over the study area, but despite this advantage, surprisingly low number of birds migrated when tailwinds prevailed. Furthermore, birds seem to drift with winds blowing from the sea to the land, but not in the opposite direction, suggesting that birds try to avoid drifting over the sea where it is riskier to fly. Hence, our study highlights the complexity of migrant flight behavior in relation to the wind and suggests a flexible response to different wind conditions and coastline geography at multiple spatiotemporal scales.

Keywords Bird migration · Environmental effects · Flight behavior · Honey buzzard · Wind speed · Radar ornithology

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Introduction

Environmental conditions are paramount in shaping migration properties in various organisms and may strongly affect the fitness of migrants (Boano et al. 2010; Fayet et al. 2015; Mellone et al. 2015; Rotics et al. 2016). Fitness-related costs caused by environmental conditions during long-distance migration have consequently modulated the evolution of migration schedules, flight behaviors, and migration route selection (Åkesson and Hedenström 2000; Ma et al. 2011; Bohrer et al. 2012; Flack et al. 2016). A central aspect of flight behavior is how an organism responds to varying atmospheric conditions and geographic features throughout its long-distance journey, and whether volant organisms modulate their response to atmospheric conditions based on their geographic position (Horton et al. 2016).

Among atmospheric conditions, wind is known to strongly influence the speed of migration under different ecological scenarios, and specifically during long-distance migration (Alerstam 1979; Liechti 2006; Mellone et al. 2012; Safi et al. 2013; Rotics et al. 2016; Vidal-Mateo et al. 2016). Because winds are constantly changing in speed and direction, flying animals must continuously adjust their flight behavior to efficiently move and accomplish their migration (Klaassen et al. 2011; Vansteelant et al. 2017b). Moreover, due to the benefits of flying with favorable wind, wind assistance may induce a decision to depart and hence may facilitate a high migration traffic rate (Åkesson and Hedenström 2000; Green et al. 2002; Klaassen et al. 2004) during day and night (Richardson 1978; Gwinner 1990). Several studies have shown that both flapping and soaring migrants travel significantly faster when flying with tailwinds and are hindered by headwind and crosswinds (Spaar and Bruderer 1996, 1997; Malmiga et al. 2014; Vansteelant et al. 2015). Also, bird airspeed decreased under tailwinds (Pennycuik 1978; Alerstam 1979; Liechti 1995). The reduction of airspeed under tailwinds reduces height losses during the gliding phase of flight in soaring migrants and allows birds to cover larger distances in a short time by reducing the time-consuming thermal circling phase of the flight (Spaar and Bruderer 1996). Moreover, reducing airspeed during the gliding phase may increase the overall time spent airborne and may also decrease the risk of reaching the ground or switching to energy-expensive flapping flight (Horvitz et al. 2014; Harel et al. 2016).

Crosswinds can have variable effects on the ground speed of different flying species. For example, in commuting fruit bats, the ground speed remained nearly constant with increasing crosswind speed (Sapir et al. 2014a), while for nine migratory waterfowl species, ground speed decreased with increasing crosswind speed, with the exception of one species that exhibited an opposite trend (Safi et al. 2013). Notably, soaring migrants travel more slowly under crosswinds than under tailwinds (Spaar and Bruderer 1996, 1997;

Vansteelant et al. 2015). In fact, when flying at maximum range airspeed, the airspeed at which energy expenditure per unit distance traveled is minimized (Pennycuik 1978), a bird should reduce its airspeed in tailwinds and increase its airspeed in headwind and crosswinds, depending on the extent to which it compensates for wind drift (Liechti et al. 1994; Sapir et al. 2014b). Crosswinds may induce high energy costs due to the need to compensate for lateral drift and may further cause time losses due to the time it may take birds to return to their intended migratory path. In some circumstances, for example when birds drift away from land towards the sea, crosswinds may even cause mortality due to exhaustion (Thorup et al. 2003).

The sea-land interface and coastlines geography are therefore particularly relevant to long-distance migrants that pass over or near large water bodies. Alerstam and Pettersson (1977) reviewed studies documenting sea crossing, concentration of migrants near seashores, and flight directions of avian migrants along coastlines. These authors suggested that the birds decided whether to stop, follow the coast, or cross the sea based on considerations that take into account their tendency to drift over the sea, but not over land. Bird decisions were found to relate to the geographic settings (e.g., the width of the crossing and coastline direction in relation to goal direction), as well as the specific wind conditions at the crossing point. Specifically, soaring migrants prefer flying while exploiting strong thermals in order to attain low metabolism during their travel (Sapir et al. 2010), and since thermals are weak or absent over large water bodies, many soaring migrants try to avoid the crossing of oceans and seas. They consequently tend to take long detours over land (Meyer et al. 2000; Alerstam 2001; Panuccio et al. 2012; Nourani et al. 2016), concentrating in peninsulas, isthmuses, and narrow land corridors (Kjellén and Roos 2000; Bensusan et al. 2007; Bildstein et al. 2009; Nilsson et al. 2014; La Sorte et al. 2016).

One of the most important places where raptors migrate over land corridors is southern Italy at the center of the Mediterranean Sea where tens of thousands of raptors travel each spring after crossing the sea from North Africa. When the birds travel further north to central Italy, many of them pass via the Strait of Messina (e.g., Table S1 in Supplementary Materials) which is located between Sicily and Calabria (Fig. 1) (Panuccio 2011; Panuccio et al. 2016b). During their travel, the birds may encounter various wind conditions, some of which may cause them to drift over the sea. To avoid over-sea flight, the birds may compensate for wind drift when the direction of the wind drifts them beyond the coastline, while no such compensation may take place where the direction of the expected drift is over the mainland. Yet, no such response has been so far documented in soaring migrants. Thus, the study area is particularly suitable to examine the response of soaring migrants to the combination of specific

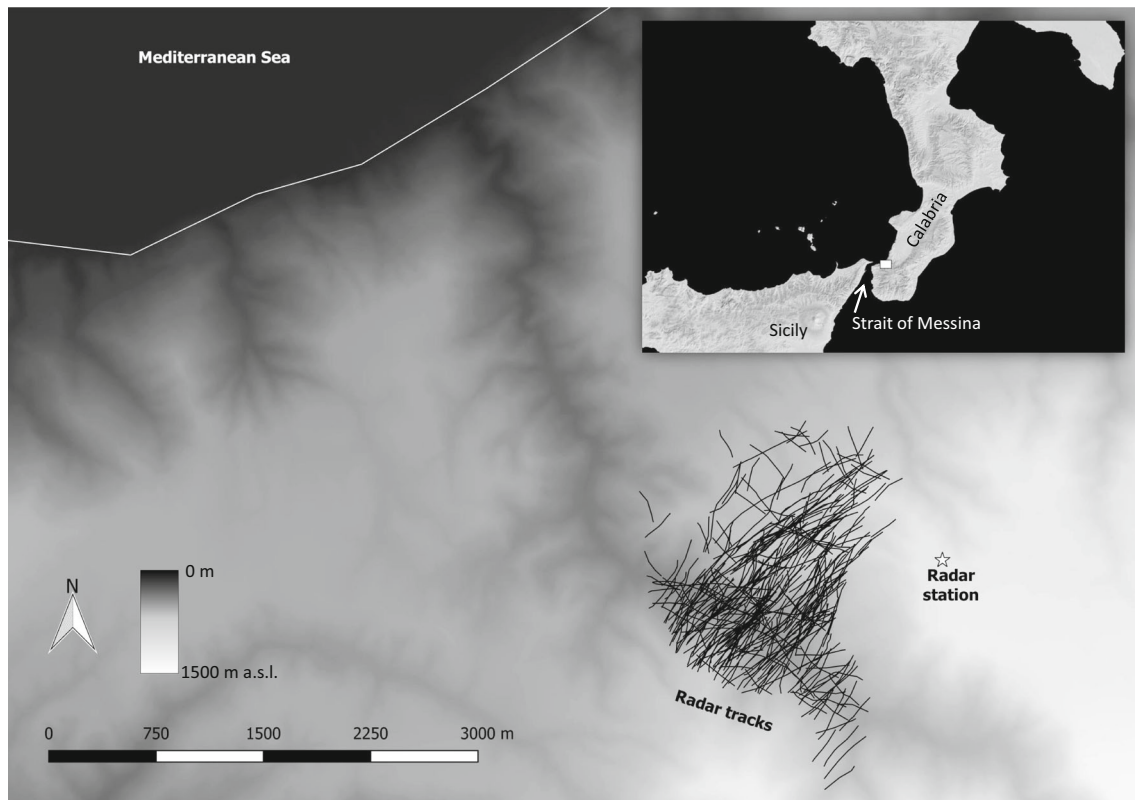


Fig. 1 A map of the study area in Calabria, Italy, with radar tracks of migrating soaring birds on the 14th of May 2014, overlaid on a digital elevation model (DEM) with a resolution of 10 m as provided by “Istituto

Nazionale di Geofisica e Vulcanologia” (Tarquini et al. 2007, 2012). The inset is the location of the study area near the Strait of Messina

meteorological conditions with the geographic features of the study area, potentially uncovering how soaring migrants may modulate their response to the wind according to the expected outcome of their drift. To quantify bird movement in a systematic manner, we used a radar that recorded key migration parameters that are otherwise difficult to obtain using visual observations, including bird speed and direction, as well as migration intensity (Panuccio et al. 2016b). We investigated the relations between different wind conditions and flight speed, drift compensation, and migration intensity of soaring migrants at the Calabrian side of the Strait of Messina. We hypothesize that in accordance with optimal migration flight theory (Pennycuik 1978; Alerstam 1991), soaring birds will respond to tailwind and crosswinds by changing their air and ground speed and will take advantage of tailwinds to migrate where tailwinds prevail. Furthermore, the birds will try minimizing their drift to reduce deviation from their track. To this end, we tested the following predictions:

- (1) Birds ground speed will increase with increasing tailwind speed (Safi et al. 2013).
- (2) Bird airspeed will decrease with increasing tailwind speed (Pennycuik 1978; Alerstam 1979; Liechti 1995).
- (3) Bird airspeed will increase with increasing crosswind speed (Liechti et al. 1994; Hedenström and Alerstam

- 2002; Sapir et al. 2014a) in order to minimize their sideways drift (Sapir et al. 2014b).
- (4) Tailwind conditions will induce increased migration intensity (Richardson 1978; Gwinner 1990; Fox et al. 2003) such that migration traffic rate over the study area will be higher under tailwind conditions.

Materials and methods

Field data collection

Data collection took place during the spring of 2014 near the edge of a flat highland 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 (Fig. 1). We collected data using a 12-kW, X-band (9.1 GHz) marine radar rotating at 38 RPM with a 2.2-m antenna that was set horizontally with a 22° vertical beam spread and a 1.05° horizontal beam spread. The radar had a detection angle of 240° and a radius of 2 km that was oriented towards the prevalent direction of the incoming migrants (a compass direction of 215°). Experienced birdwatchers

carried out daily observations near the radar from sunrise to sunset between April 9th and May 20th, 2014 to characterize species composition and migration traffic rate (Schmidt et al. 2017). The radar operated for 31 days with in this period (it was switched off when there was rain or snow) for about 9.5 daylight hours every day (approximately during 8:30–18:00). Radar echoes were annotated with regard to bird species and flock size as identified by the nearby observers (Kerlinger and Gauthreaux 1985a, b). Radar echoes were recorded as 1-Hz video frames and were processed using radR 2.5.1, an open-source program written in the “R” statistical programming language and in “C” code (Taylor et al. 2010). Using radR, we assigned coordinates and time stamps to the radar echoes and created a dataset that we then analyzed using QGIS Desktop 2.8.0 (QGIS Development Team 2015). Subsequent radar echoes (points) of the same target were connected to create a track with a unique ID. Missing points were inserted by interpolation. Afterwards, we calculated the length, mean angular direction from North, and mean ground speed of the tracks. Each track represented one or more birds that were identified as a single target on the radar screen. When the track was produced by more than a single bird, the number of individuals in the flock was registered by the observers. In order to partially mitigate the influence of the movement of local birds, tracks that were directed opposite to the migratory direction were excluded (see “Supplementary Online Materials”). Furthermore, data were inspected and targets consisting of small sized, non-soaring birds, local breeding birds, and insects (detected as small echoes within 300 m from the radar) were excluded from the dataset. We also considered only tracks with a minimum length of 200 m and a ground speed between 5 m s^{-1} ($= 18 \text{ km h}^{-1}$) and 19.5 m s^{-1} ($= 70 \text{ km h}^{-1}$), to include only large soaring birds (Spaar and Bruderer 1996).

Speed and direction of winds and birds

Wind direction and speed were obtained at 10-min intervals using a weather station with an anemometer positioned 10 m above the ground near the radar station. Wind data were transformed into two biologically meaningful variables, tailwind assistance (TWA) and crosswind (CRW). TWA is the tailwind component (m s^{-1}) of wind velocity or the wind assistance vector in the presumably preferred direction of the bird (“goal”, see below), with positive and negative values indicating tailwind and headwinds, respectively (Piersma and Jukema 1990; Åkesson and Hedenström 2000; Sapir et al. 2011). CRW is the sideways component (m s^{-1}) of wind velocity perpendicular to the preferred direction of the bird, with positive and negative values indicating crosswinds coming

from the left and the right side of the bird, respectively. TWA and CRW were calculated by the following formulas:

$$\text{TWA} = v_w \cdot \cos((\theta_w + 180^\circ) - \theta_b), \quad (1)$$

$$\text{CRW} = v_w \cdot \cos((\theta_w + 90^\circ) - \theta_b), \quad (2)$$

where v_w is the measured wind velocity (m s^{-1}), θ_w is wind direction (i.e., the direction from where the wind was blowing) in degrees, and θ_b is the presumed preferred direction of the birds. For a graphic representation of the vectors used in the analyses, see Fig. 2 and Table 1.

We calculated the airspeed (v_a , m s^{-1}) for each track using the following formula (Safi et al. 2013):

$$v_a = \sqrt{(v_g - \text{TWA})^2 + (\text{CRW})^2}, \quad (3)$$

where v_g is the ground speed calculated from the radar track.

For the calculations of TWA (eq. 1) and CRW (eq. 2), one must assess the direction of the presumed destination of the migrants (θ_b). There are several approaches to establish this direction, and we used two of these approaches: one is based on long-distance tracking of birds during their migration after flying through the study area (Sapir et al. 2011), and the other approach is based on the mean direction of bird tracks over the study area (Green 2001; see also [Supplementary Materials](#)). We believe that the first approach is preferable because it is

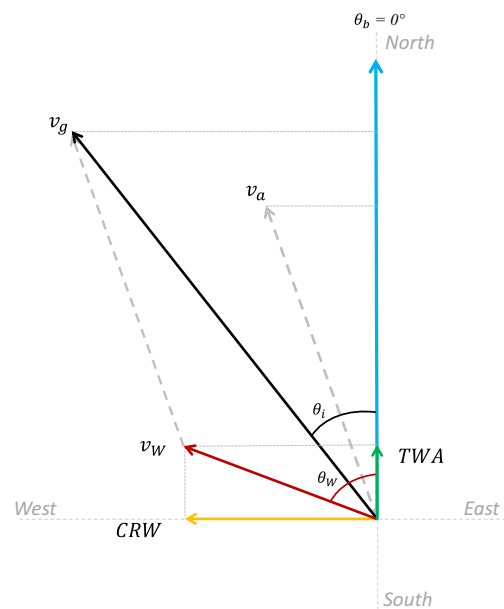


Fig. 2 Graphic representation of the vectors used in the analyses relative to the intended migratory goal (θ_b , light blue arrow). The bird displacement vector is v_g (ground speed, black arrow). The wind vector is v_w (wind speed, red arrow), and it can be decomposed into a forward component (TWA; green arrow) and a side component (CRW; yellow arrow). The airspeed vector is v_a (dashed gray arrow). Units on both axes are in meters per second. For a complete list of symbols and abbreviation, see Table 1

Table 1 Complete list of symbols and abbreviations

| List of symbols and abbreviations | |
|-----------------------------------|---|
| TWA | Tailwind assistance (m s^{-1}) |
| CRW | Crosswind (m s^{-1}) |
| v_w | Wind intensity (m s^{-1}) |
| θ_w | Wind direction ($^\circ$) |
| θ_b | Direction of migration goal ($= 0^\circ$) |
| θ_i | Individual direction ($^\circ$) |
| v_g | Ground speed (m s^{-1}) |
| v_a | Airspeed (m s^{-1}) |

based on actual data regarding goal locations or at least part of the routes of specific individuals, which presumably represent the destination of the population of a certain species that passes over a specific area. During spring migration, many Honey buzzards (*Pernis apivorus*) (about 95% of the birds tracked in this study) arrive to central and northern Europe after passing through Italy (Hake et al. 2003; Meyburg et al. 2011), and consequently, we propose that the intended direction of the passing birds was due north ($\theta_b = 0^\circ$). This information was used in our analyses that are reported in “Results.” We nevertheless considered the second approach, which yielded a different estimated goal direction (mean angular direction of the birds recorded by the radar). The analyses that use this estimated goal direction are reported in the Supplementary Materials (Tables S2–S5) and overall agree very well with the findings of the first approach that are reported in “Results.”

Following the first approach and using $\theta_b = 0^\circ$ in eqs. (1) and (2), these equations can be simplified to:

$$\text{TWA} = v_w \cdot \cos(\theta_w + 180^\circ), \quad (4)$$

and

$$\text{CRW} = v_w \cdot \cos(\theta_w + 90^\circ). \quad (5)$$

To annotate bird radar data with the wind data, the time of each track was matched to the nearest 10-min interval at which wind speed and direction were recorded. The distributions of the annotated wind conditions are presented in Fig. S1 together with bird airspeeds and numbers of tracks.

Statistical analysis

We used linear mixed models (LMMs) to analyze the following dependent variables: bird ground speed v_g , airspeed v_a (3), and bird density (the number of bird tracks per hour and per day that were recorded by the radar), in relation to TWA and CRW (independent variables) at daily and hourly timescales (random factors). We followed a top-down strategy for model

selection: first, we found the optimal structure of the random part of the model and then of the fixed one (Zuur et al. 2009). Random effects were examined considering models with a random intercept and models with a random intercept and a random slope. Models with a random intercept and those with a random intercept and slope did not differ significantly, so setting the time scale (hour or day) as the random intercept was the most parsimonious model. Afterwards, we found the optimal structure of the fixed component following backward stepwise model selection (starting with all factors and reducing them in the following steps), using the Akaike Information Criterion (AIC; Akaike 1973). Following inspection of model residuals and considering the dispersion of the data, we chose linear mixed models as the most appropriate test (Zuur et al. 2009). We also performed the same analyses for all tracks without any averaging over a certain timescale (hour/day) using simple linear models that were selected by their AIC values.

We used linear models to describe the effects of easterly and westerly crosswinds on ground speed and airspeed. To avoid the use of negative and positive values of CRW to represent the direction of the wind, we additionally used the absolute value of CRW and undertook separate analyses for westerly and easterly winds. Westerly and easterly winds were not equally represented in our sample: 368 tracks were recorded under easterly winds and 8050 tracks under westerly winds, during 22 and 178 h, respectively.

Bird density data were natural log-transformed to achieve normality and homoscedasticity. Statistical analyses were performed with R software version 3.2.2 (R Core Team 2015). LMMs were performed with the “nlme” package (Pinheiro et al. 2016). The mean direction of the tracks, circular standard deviations, and Rayleigh’s tests were performed with the “circular” package in R (Agostinelli and Lund 2013).

Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Results

We analyzed a total of 8418 radar tracks that were recorded through the course of the study (31 days). According to the count data of the nearby observers, 17 species were observed. The Honey buzzard (*Pernis apivorus*) was the most abundant species, accounting for 95.39% of all birds counted, with the second most common species being the Marsh harrier (*Circus aeruginosus*), accounting for 1.52% of the counts (see bird count data in Table S1). The mean (\pm circular SD) direction of the tracks was $\mu = 32.77^\circ \pm 26.65^\circ$ with r (length of mean vector) = 0.897 (Rayleigh’s test, $z = 6779.24$, $P < 0.0001$). We tested if the daily bird counts recorded by the observers were

correlated with the daily number of tracks recorded by the radar when the radar and the observers worked simultaneously (27 days), and found that bird counts of these two datasets were positively and significantly correlated (Spearman's correlation $S = 1828.6$, $\rho = 0.44$, $P < 0.05$).

Bird speed

At the daily scale (averaging over whole days), ground speed increased with CRW, which means that westerly winds increased the birds' ground speed, while easterly winds decreased it (Table 2; Fig. 3a). TWA was not included in the selected model, and therefore, no significant effect of TWA on the birds' ground speed was found at the daily scale. At the hourly scale (averaging over whole hours), ground speed was positively related to both TWA and CRW (Table 2), and therefore, southern and western winds increased bird ground speed while northern and eastern winds decreased it (Fig. 3c, d). The same was found when all the tracks were considered in the analysis without any averaging over time (Table 2). TWA had a negative effect on bird airspeed, such that airspeed decreased with increasing southern winds (tailwinds) and increased with northern winds (headwinds). Furthermore, CRW had a positive effect on bird airspeed such that airspeed increased with westerly winds and decreased with easterly winds at all timescales (Table 3; Fig. 3). Hence, the response of the migrants to easterly and westerly winds was asymmetrical. Under easterly winds, which were overall rare in this area during the course of the study (4.38% of all tracks), the migrants decreased their ground speed (Fig. 4a) and increased their airspeed (Table 4; Fig. 4b). Under westerly winds, the birds slightly increased their ground speed (Fig. 4a) as well as their airspeed (Table 4; Fig. 4b). We note that the response of the birds was much stronger under easterly winds than under westerly winds, as the regression coefficient describing the relationship between

wind speed and bird airspeed was four times higher when birds were flying under easterly winds than under westerly winds (Table 4).

Bird density

Bird density was negatively related to TWA (Table 5) at the daily scale (i.e., the daily number of tracks recorded by the radar) (Fig. 5a) and the same was found at the hourly scale (i.e., number of tracks recorded per hour) (Fig. 5b). In the latter timescale, bird density additionally increased with positive CRW, suggesting that westerly winds induced a more intense migration (Table 5).

Discussion

We found that soaring migrants increased their ground speed and decreased their airspeed when tailwinds prevailed, but unexpectedly, these benefits did not result in more intense migration over the study area, but rather in lower migration traffic rate. Thus, bird response to tailwind seemingly had contrasting aspects, warranting further explanation (see below). We moreover found an asymmetric response of the birds to crosswind, compensating when winds blew towards the sea and drifting when winds blew towards land. We propose that the response of the birds to wind conditions is modulated by the geography of their migration route at two spatial scales. The spatial scales we refer to are the local scale of the study area and its surroundings, and the regional scale that includes the south-Italian peninsula and the sea around it. We propose that the atmospheric and geographical conditions experienced at the local scale can affect the migration route at the regional scale and that regional scale dynamics of migrants may also affect local scale patterns. Our results suggest that migrating

Table 2 Final models of the relationships between bird ground speed (dependent variable) and tailwind and crosswind speed and their interaction at hourly and daily timescales

| Time scale | Model type | Explanatory variable | Estimate | SE | <i>t</i> | <i>P</i> |
|---|--------------------|----------------------|----------|------|----------|----------|
| Daily | Linear mixed model | (Intercept) | 13.95 | 0.19 | 73.6 | < 0.0001 |
| | | CRW | 0.13 | 0.02 | 6.2 | < 0.0001 |
| Hourly | Linear mixed model | (Intercept) | 13.72 | 0.13 | 106.2 | < 0.0001 |
| | | TWA | 0.20 | 0.03 | 6.9 | < 0.0001 |
| | | CRW | 0.17 | 0.03 | 6.5 | < 0.0001 |
| | | TWA × CRW | -0.05 | 0.01 | -5.9 | < 0.0001 |
| No averaging (all tracks) ($R^2 = 0.04$) | Linear model | (Intercept) | 13.68 | 0.08 | 164.8 | < 0.0001 |
| | | TWA | 0.18 | 0.03 | 6.2 | < 0.0001 |
| | | CRW | 0.18 | 0.03 | 6.9 | < 0.0001 |
| | | TWA × CRW | -0.06 | 0.01 | -6.1 | < 0.0001 |

TWA tailwind speed in m s^{-1} , CRW crosswind speed in m s^{-1} (see "Materials and Methods" for additional details)

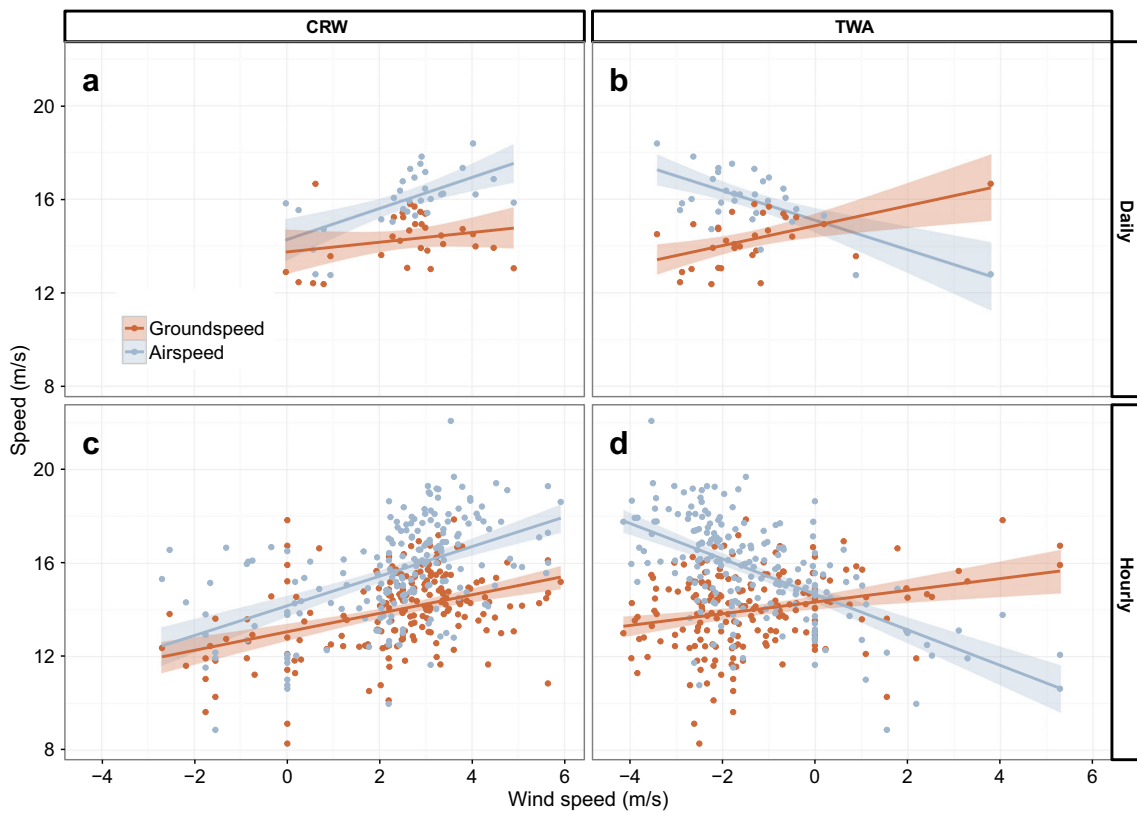


Fig. 3 Average bird speeds fitted with linear regression lines (colored areas 95% CI) in relation to crosswind speed (CRW **a, c**) and tailwind speed (TWA **b, d**) at daily and hourly timescales

raptors modulate different aspects of their migration properties with regard to both wind and geography (see also Mandel et al. 2008; Mellone et al. 2011; Nilsson et al. 2014; Åkesson et al. 2016). Specifically, we show that soaring migrants are able to cover more distance (higher ground speed) under tailwind conditions while lowering their airspeed, and compensate for potential dangerous oversea drift when pushed

by easterly winds but not when drifting by westerlies over land.

The response of the birds affects their speed, which may eventually influence their time of arrival to breeding grounds (Gordo 2007), breeding timing, and reproductive output (Saino et al., 2004a, b; Szép et al. 2006; Gordo and Sanz 2008). Consequently, the ability of migrating birds to

Table 3 Final models of the relationships between airspeed (dependent variable) and tailwind and crosswind speed and their interaction at daily and hourly timescales

| Time scale | Model type | Explanatory variable | Estimate | SE | <i>t</i> | <i>P</i> |
|--|--------------------|----------------------|----------|------|----------|----------|
| Daily | Linear mixed model | (Intercept) | 13.90 | 0.19 | 72.9 | < 0.0001 |
| | | TWA | - 1.02 | 0.03 | - 34.1 | < 0.0001 |
| | | CRW | 0.26 | 0.03 | 9.8 | < 0.0001 |
| | | TWA × CRW | - 0.88 | 0.02 | 0.7 | 0.5059 |
| Hourly | Linear mixed model | (Intercept) | 13.70 | 0.13 | 105.3 | < 0.0001 |
| | | TWA | - 0.81 | 0.03 | - 28.1 | < 0.0001 |
| | | CRW | 0.30 | 0.03 | 12.0 | < 0.0001 |
| | | TWA × CRW | - 0.04 | 0.01 | - 4.5 | < 0.0001 |
| No averaging (all tracks) (<i>R</i> ² = 0.36) | Linear model | (Intercept) | 13.65 | 0.08 | 167.9 | < 0.0001 |
| | | TWA | - 0.84 | 0.03 | - 28.9 | < 0.0001 |
| | | CRW | 0.31 | 0.03 | 12.5 | < 0.0001 |
| | | TWA × CRW | - 0.04 | 0.01 | - 4.8 | < 0.0001 |

TWA tailwind speed in m s⁻¹, CRW crosswind speed in m s⁻¹ (see “Materials and Methods” for additional details)

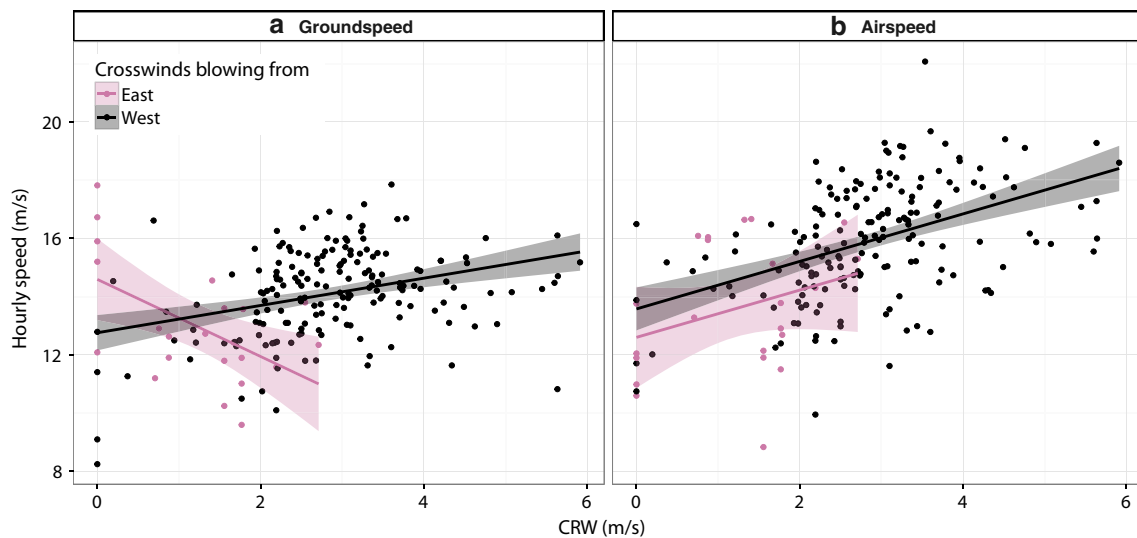


Fig. 4 Hourly averaged ground speed (a) and airspeed (b) fitted with linear regression lines (colored areas 95% CI) in relation to easterly and westerly crosswinds. CRW absolute crosswind speed

successfully modulate their flight properties with regard to different environmental conditions can have far-reaching consequences beyond individual fitness, for example for their population dynamics (Alves et al. 2013; Flack et al. 2016). For soaring migrants, and specifically for Honey buzzards that constitute the vast majority of the soaring migrants in this area, successful negotiation of their movements under variable meteorological conditions is critical for accomplishing their migration in timely manner that will allow them to successfully breed in their highly seasonal breeding habitats (Thorup et al. 2003; Vansteelant et al. 2017a, b). Our findings suggest that migrating Honey buzzards (*Pernis apivorus*) integrate information regarding the highly dynamic meteorological conditions they encounter during their travel with the geographical features of the flyway to take advantage of profitable conditions and avoid risks associated with drifting over the sea during unfavorable weather conditions (Mote 1969; Kerlinger 1984, 1985; Thorup et al. 2003; Agostini et al. 2016).

We found that soaring migrants adjusted their ground speed and airspeed with respect to wind speed and direction. Our results regarding the relationships between tailwind support and bird airspeed and ground speed confirmed prediction 1,

which states that birds are expected to achieve higher ground speed with tailwinds, and prediction 2, which states that bird airspeed is expected to decrease with tailwind. In fact, as far as prediction 1 is concerned, the ground speed of soaring migrants (primarily Honey buzzards in this case) increased with tailwind at the hourly scale, as found for many other flying species of birds, bats, and insects (Srygley and Dudley 2008; Safi et al. 2013; Sapir et al. 2014a; Shamoun-Baranes et al. 2017), and specifically in soaring raptors (Spaar and Bruderer 1996; Mellone et al. 2015). A recent study found that Montagu’s harriers (*Circus pygargus*), which use both soaring and flapping flight during migration, increased their daily flight duration and distance when under tailwind conditions and interrupted their flight under headwinds (Klaassen et al. 2017). Honey buzzards select tailwinds to travel faster and further as well (Vansteelant et al. 2015; Panuccio et al. 2016a), and while doing so, the birds can move faster through geographical barriers such as water bodies (Panuccio et al. 2016a). At the daily scale, we did not find the same effect, probably because of the variability in wind conditions over this longer time period, and the averaging of the different responses of the migrants to these variable conditions. The significant response at the hourly scale and the non-

Table 4 Linear models with ground speed and airspeed as dependent variables and easterly and westerly wind speeds as explanatory variables

| | Ground speed | | | | | Airspeed | | | | |
|--------------|--------------|------|----------|----------|-----------------------|----------|------|----------|----------|-----------------------|
| | Estimate | SE | <i>t</i> | <i>P</i> | <i>R</i> ² | Estimate | SE | <i>t</i> | <i>P</i> | <i>R</i> ² |
| (Intercept) | 14.74 | 0.27 | 55.5 | <0.0001 | 0.14 | 11.80 | 0.30 | 39.5 | <0.0001 | 0.16 |
| Easterly CRW | -1.03 | 0.13 | -7.9 | <0.0001 | | 1.24 | 0.15 | 8.3 | <0.0001 | |
| (Intercept) | 13.28 | 0.07 | 188.1 | <0.0001 | 0.02 | 15.53 | 0.08 | 183.9 | <0.0001 | 0.01 |
| Westerly CRW | 0.30 | 0.02 | 13.7 | <0.0001 | | 0.28 | 0.03 | 10.6 | <0.0001 | |

CRW crosswind speed in m s⁻¹ (see “Materials and Methods” for additional details)

Table 5 Final models of the relationships between number of tracks (transformed with natural logarithm) as dependent variable and tailwind and crosswind speed and their interaction at daily and hourly timescales

| Time scale | Explanatory variable | Estimate | SE | <i>t</i> | <i>P</i> |
|------------|----------------------|----------|------|----------|----------|
| Daily | (Intercept) | 4.50 | 0.27 | 16.67 | < 0.0001 |
| | TWA | -0.43 | 0.14 | -3.07 | < 0.01 |
| Hourly | (Intercept) | 2.24 | 0.18 | 12.40 | < 0.0001 |
| | TWA | -0.22 | 0.06 | -3.91 | < 0.001 |
| | CRW | 0.15 | 0.05 | 2.77 | < 0.01 |

TWA tailwind speed in m s^{-1} , CRW crosswind speed in m s^{-1} (see “Materials and Methods” for additional details)

significant response at the daily scale may suggest that the temporal scale at which the birds actually sense, and respond to, wind conditions is more detailed than the daily scale (Nathan et al. 2005). As for prediction 2 that was supported by our results, optimal flight theory for flapping migrants portrays that the reason for the decrease of airspeed with increasing tailwind speed is likely due to energy saving during migration (Pennycuick 1978; Liechti et al. 1994; Liechti 1995; Safi et al. 2013). For soaring migrants, reducing airspeed under tailwinds allows the birds to attain low sink rate and by that to cover larger distances while decreasing the risk of reaching the ground or switching to energy-expensive flapping flight (Spaar and Bruderer 1996; Horvitz et al. 2014; Harel et al. 2016).

As for prediction 3, theoretical calculations suggest that birds should increase their airspeed in response to crosswind in order to reduce their lateral drift or to fully compensate for it (Liechti et al. 1994). This response has been so far documented only in fruit bats (Sapir et al. 2014a). Bird response to crosswind over the study area fitted only partially to prediction 3. In fact, ground speed increased in relation to crosswind from the west and decreased under easterly crosswind, and bird response to crosswind was asymmetrical in relation to crosswind direction (from the east or from the west),

depending on the expected outcome of the potential drift. This may suggest that birds employed an adaptive drift when westerly winds that advanced the birds over land in Calabria prevailed, while compensating for drift when easterly winds blew and may consequently carry the birds over the sea. This compensation was found under headwinds, as well as under tailwinds (see below). Avoiding flight over the sea may allow the birds to keep low metabolic rates using soaring flight (Baudinette and Schmidt-Nielsen 1974; Bevan et al. 1995; Sapir et al. 2010) and may further lower mortality risks *en route* (Thorup et al. 2003). We note that a recent study demonstrated an asymmetric response of nocturnally migrating songbirds to crosswind near the North American Atlantic coast in which the birds drifted when flying over inland areas, but compensated for drift to avoid flying over the ocean near the coast (Horton et al. 2016). The reason for this response of nocturnally or early-morning migrating passerines to crosswinds near coasts might be due to increased predation risks when the nocturnal flight extends to daytime hours (Bourne 1980) and possible dehydration (Klaassen 2004). Yet, exhaustion due to enduring flight over water and eventually mortality caused by drowning may constitute a strong selection force for both diurnal soaring birds and nocturnal flapping passerines during migration. Yet, flight over the sea may still be

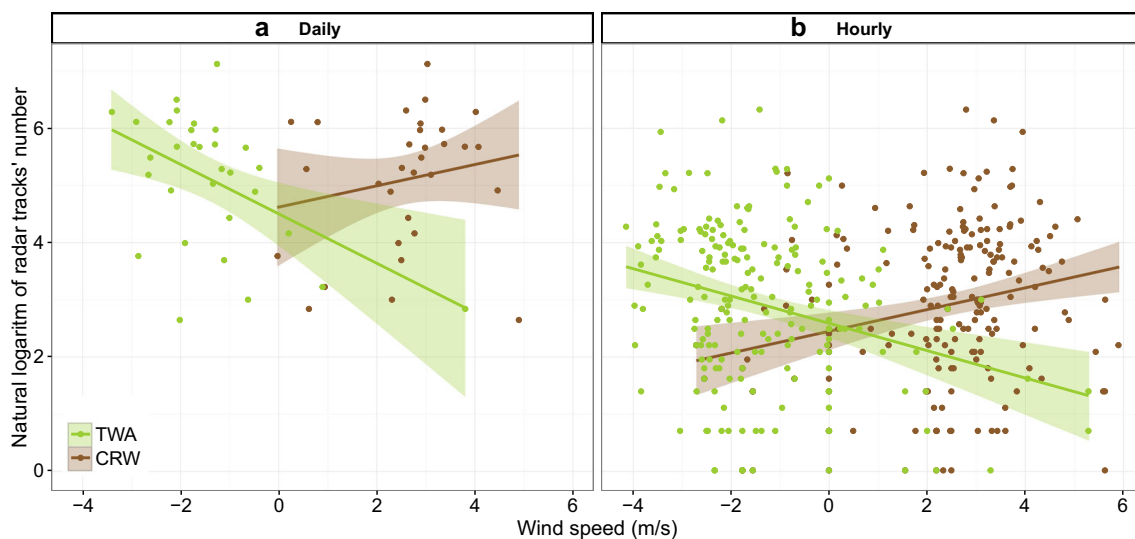


Fig. 5 The number of radar tracks in relation to wind speed at daily (a) and hourly (b) timescales fitted with linear regression lines (colored areas 95% CI). TWA tailwind speed in m s^{-1} , CRW crosswind speed in m s^{-1}

advantageous when considering an alternative long detour over land in some geographic areas, especially when assisting winds may facilitate a rapid cross sea migration (Alerstam 2001; see below). Why birds experiencing tailwind conditions did not drift over the sea could relate to different factors. For example, these individuals were more risk-averse and avoided flying over the sea whenever possible, and migrate through the area when most other birds avoided flying through it (see below). Also, birds may avoid flying over the sea when their physiological state is deteriorated and may not allow them to undertake an enduring cross sea flight.

Surprisingly, soaring birds migrated over the study area in greater numbers under headwind conditions, in contrast with prediction 4 that predicted increased migration intensity with tailwinds, as has been found in numerous studies of migrating animals (Richardson 1978; Perdeck and Speek 1984; Gwinner 1990; Erni et al. 2002; Van Belle et al. 2007; Alerstam et al. 2011; Hu et al. 2016). Migrants are expected to avoid headwinds in order to migrate more quickly and spend less energy during flight (Alerstam and Hedenstrom 1998; Klaassen et al. 2017; Vansteelant et al. 2017b). The apparent advantageous assistance of tailwind to the birds' overall flight speed (as demonstrated by their high ground speed under tailwinds) seemed to be ignored by the birds. We suggest that a likely reason for this counterintuitive pattern is probably sea crossing directly from the Sicilian side of the Strait of Messina or from the Calabrian coast (west of the study area) when tailwinds prevailed in the entire region, including, but not only, in the study area (Agostini and Panuccio 2005; Panuccio 2011; Agostini et al. 2015, 2016). These flights, nevertheless, were not recorded as they took place beyond the range of the radar. We propose that the spatial scale of wind assistance patterns possibly extended over tens or even several hundreds of kilometers, allowing the birds to undertake a long cross sea journey and eventually causing a local decline in migration intensity in the study area under these conditions. Hence, wind assistance affected route selection of Honey buzzards and likely other soaring migrants passing over Sicily and Calabria such that they did not fly over land following the coastline but rather flew over the sea. This is expected when the cost of transport while flying over the sea is overall lower than that of the overland detour (Meyer et al. 2000; Alerstam 2001; Agostini et al. 2015; Nourani et al. 2016). A straight sea crossing from the Strait of Messina towards the north (about 200 km before reaching the mainland) would allow soaring birds to reduce migration distance by about 80 km compared to a detour over the land. Wind and thermal conditions affected migratory directions in autumn soaring migrants that crossed the Strait of Gibraltar: sea crossing occurred in favorable following and easterly winds, but no sea crossings were observed in unfavorable westerly winds and headwinds. Under the latter wind conditions, migration was carried out above land through a long detour until the

birds reached the shortest crossing point in the Strait of Gibraltar (Meyer et al. 2000). Panuccio et al. (2016a) suggested that Honey buzzards crossing the Aegean Sea selected days with strong tailwinds, presumably increasing the bird's ground speed and decreasing the total flight duration while passing through this area. We note that unlike flapping migrants such as songbirds, waterfowl, and waders that primarily consider their cost of transport in relation to the added mass of the fuel they carry during their travel (Alerstam 2001), soaring migrants may additionally consider the costs and risks of flying using flapping flight over the sea as opposed to their regular soaring flight over land. To date, there are no explicit theoretical formulations that predict when overland detours versus cross sea shortcuts by soaring migrants are expected, as has been done for flapping flyers by Alerstam (2001).

Our study highlights the complexity of the dynamic aerial environment and changing geographic features throughout the migrants' travel route, requiring high behavioral plasticity of their flight properties to properly respond to the spatiotemporal dynamics of their aerial environment. Cross taxa comparisons and studies undertaken in different geographic areas may help assessing the generality of our findings. It is furthermore important to address meteorological and geographic effects on the migrants' cost of transport throughout the entire migration routes in order to deduce energy consumption considerations, route choice, and carry-over effects that may substantially affect animal fitness.

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Compliance with ethical standards

Ethical approval This study did not require any ethical approval.

Conflict of interest The authors declare that they have no conflict of interest.

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