Migrating birds avoid flying through fog and low clouds

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Abstract
Different weather conditions are known to affect bird migration, yet the influence of fog and low clouds on migrating birds has been rarely examined so far, and hence, their impact on bird movement is not well understood. Fog avoidance could be a consequence of visual limitations within the fog or may be the outcome of deteriorated soaring conditions due to the obstruction of the sun. We carried out a radar study at the Strait of Messina, which is a bottleneck for migrating birds traversing the Central Mediterranean Sea, to determine if the intensity of diurnal soaring bird migration was influenced by fog and other weather variables. We recorded bird movements using an X-band radar, which can detect birds flying within the fog, and recorded weather conditions using local meteorological observations. We examined if bird passage rate (number of tracks/hour) at the radar site was influenced by fog, wind speed and direction, air temperature and the time of day. Our findings suggest that fog was the most important factor affecting bird migration intensity as recorded by the radar, indicating that birds actively avoided flying into fog. In addition, wind direction affected bird migration intensity, with lower numbers recorded with southerly tailwinds and higher numbers recorded with westerly crosswinds. Our findings highlight a consequence of widespread meteorological conditions, and of fog in particular, on migrating birds, with implications for bird migration navigation, path length and flight energetics.

Keywords Avian long-distance migration · Bird flight · Ecological barrier · Fog · Radar · Soaring raptors

Introduction
Weather conditions may influence the movement of birds, and several studies have suggested that migrating birds show a high selectivity of weather conditions during their journeys (Elkins 2004; Newton 2008). Generally, migration is facilitated by clear skies and tailwind assistance and hampered by precipitation and opposing winds (Erni et al. 2002). Fog and low clouds lower the visibility during flight and, thus, may negatively affect the orientation of birds (Alerstam 1990; Richardson 1990; Chiaradia et al. 2007) as well as disrupting various other migratory behaviours (e.g. Alerstam and Ulfstrand 1974). For instance, tracks of Sandhill Cranes (Grus canadensis) recorded on a foggy day were more circuitous than on days with good visibility (Kirsch et al. 2015). If the fog extends over a large area, birds could end up tens or even hundreds of kilometres away from their intended migratory routes and may became exhausted, as has been recorded for a flock of turkey vultures (Cathartes aura) flying over a fog-covered sea where the birds eventually alighted on a boat (Mote 1969). Consequently, fog may cause mass-mortality events of migrating birds (Newton 2007). Fog may also affect migration timing because migrating birds may postpone their departure from stopover sites as they wait for better weather conditions and even undertake reverse migration when poor visibility prevails (Lack 1960; Murton and Ridpath 1962; Alerstam 1990; Richardson 1990; Pastorino et al. 2017). Indeed, fog was found to delay the arrival of birds at an offshore island in California (Pyle et al. 1993).
Studying bird movements into fog

Although fog may negatively affect the number of visually detected migrating birds, it is not clear whether bird numbers are low because the fog has deterred migration or because the observers could not see the passing birds (Hall et al. 1992). Studies quantifying the effect of fog on active bird migration are rare (Richardson 1990) also because of the difficulty in measuring visibility since large-scale meteorological data obtained by remote-sensing usually do not contain the spatial and temporal characteristics of visibility data. Thus, direct, usually local, observations are still the only possibility to get reliable information on the occurrence of fog. The present work aims to address an important knowledge gap regarding the possible effects of fog on the migration of diurnal migrating birds in the Central Mediterranean.

Rader can detect echoes of birds in low visibility conditions, such as darkness and fog (but not rain), allowing rigorous examination of the effects of fog on bird migration. We consequently carried out a study of diurnal migrating birds at an important migratory bottleneck along the Central Mediterranean Flyway using a surveillance radar. The study was done in Calabria, just north of the Strait of Messina (southern Italy), an area that is particularly suitable for this research because fog and low clouds are common in this area where diurnal migrants travel in high numbers. In addition, we examined if migration intensity is correlated on the two sides of the Strait of Messina and, thus, if it is representing the same migration flow. We hypothesise that fog and low clouds will be avoided by diurnal migrating birds. We consequently predict that bird passage rate as detected by radar will decrease under these weather conditions. Due to their location along the presumably same migratory flyway, we also predict that migration intensity on the two sides of the Strait of Messina will be correlated when no fog or low clouds are present, but, due to the decrease in migration intensity under fog, this correlation will be weaker or will not exist under such conditions. Since it is known that other weather factors such as wind speed and direction, air temperature and humidity (Richardson 1990; Liechti and Bruderer 1998; Shamoun-Baranes et al. 2003; Kemp et al. 2010; Panuccio 2011) may additionally affect bird migration intensity, we additionally tested the effects of these factors on bird passage rate.

Materials and methods

Fieldwork and study area

The fieldwork was carried out between 8 April and 20 May 2014, during the migration period of many long-distance Afrotropical-Palearctic migrants (Cramp and Simmons 1980). The radar was positioned in Calabria at the northern side of the Strait of Messina (Southern Italy), an area that is well known for its importance as migratory bottleneck for many species of birds and in particular for soaring raptors (Zalles and Bildstein 2000; Panuccio 2011). Site location (hereafter named Aspromonte; 38° 13′ 50.7″ N, 15° 47′ 58″ E) was at an edge of a flat highland at about 1050 m above sea level (Fig. 1), an area frequently exposed to fog. Fog and low clouds are generated in this area because humid air is trapped between the coast (about 5 km away) and the highland. We simultaneously made visual observations from a comparison site located along the same migration bottleneck (hereafter called Serro; 38° 13′ 19.4″ N, 15° 28′ 00.5″ E, see detail below), where fog is uncommon and where, similarly to the Aspromonte site, two observers with binoculars and a telescope recorded birds in active migration. Visual observations allowed us to test if migration passage rate at the two watchpoints was correlated during our study period. Moreover, hourly numbers of visually detected birds at Serro were used to verify if the lack of migration recorded by the radar corresponds to a lack of migration at the whole bottleneck area. Lastly, observations at both Serro and Aspromonte allowed recording the composition of diurnal migrant species in this flyway.

Serro is located in Sicily, south of the strait at an altitude of about 270 m above sea level and at a distance of 3.5 km from the coastline. This site is located about 29.5 km west of the Aspromonte site, and the migratory flow at the two watchesites is known to be strongly correlated (Agostini et al. 2007). Radar measurements and direct observations of migrating birds were carried out daily at both sites during the study period and continuously between 8:30 and 17:30 (UTC + 1), interrupted only occasionally by the onset of heavy precipitation.

Weather data

Hourly weather data were recorded by a meteorological station positioned at an altitude of 10 m above the ground, close to the radar station at Aspromonte. The data included wind speed (m/s), wind direction, air humidity (%), air pressure (mbar) and air temperature (°C) and were automatically recorded every hour in the middle of the hour (i.e. 12:00). The presence of fog and low clouds was visually assessed by the radar operators and 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. We verified, by moving in the area by car, that the spatial extent of the fog was much larger than the radar range. Noteworthy, the fog did not reach the shore and usually started from the first reliefs. In order to compare the data collected by our field meteorological station with...
the synoptic weather conditions, we downloaded wind data from the ECMWF (European Centre for Medium-Range Weather Forecasts; Molteni et al. 1996; Bechtold et al. 2008) reanalysis data repository and compared wind direction and speed taken at midday for each day of the fieldwork period. ECMWF wind data (10 m above ground) consist of the U and V components (m/s) of wind speed and these were transformed to wind direction (in degrees) and wind speed (m/s).

Radarsystem

We used a 12-kW, X-band marine surveillance radar (9.1 GHz), with an open array of 2.2-m antenna set horizontally (Bruderer 1997a) that rotated at 38 rpm (GEM, Italy, http://www.gemrad.com/). The radar antenna was positioned on a tripod at about 2 m above ground. The radar can detect bird movement in any weather condition with the exception of precipitation, yet the radar echoes in this system cannot distinguish among flying targets that are within the range of the radar. Moreover, since our study relies on the non-visible migration, many of the birds tracked by the radar could not be identified by the observers. The radar range was approximately 2 km; yet, single birds and small flocks of passerines could have sometimes go undetected, in particular when they were flying at the edge of the radar range. The detection area was limited towards a 230° sector in the direction of the migratory flow (Fig. 1), while the remaining sector was blank due to ground clutter.

Data processing

We continuously captured the radar screen as 1-Hz video frames. We then processed the videos with radR 2.5.1 package in R software (Taylor et al. 2010; Francis et al. 2014; Kirsch et al. 2015; Panuccio et al. 2016). radR calculated the number and length of the tracks of birds recorded by the radar. To exclude targets that are likely to be insects (which are usually detected by the radar only at close range and for much shorter duration than birds), we excluded tracks shorter than 200 m, tracks with less than four consecutive echoes, tracks within 200 m of the radar, and tracks characterised by an air-speed lower than 6 m/s and higher than 30 m/s as suggested by previous research (Bruderer and Boldt 2001; Schmaljohann et al. 2008; Kemp et al. 2010; McLaren et al. 2012). The hourly number of retained tracks was considered as the migration traffic rate of birds in the radar coverage area. Local birds (mainly hooded crows (Corvus cornix), ravens (Corvus corax) and common buzzards (Buteo buteo)) were generally scarce in the area and only seldom were recorded by the observers within the range of the radar. We assume that their influence on bird passage rate was low and rather constant throughout the study period. However, in order to reduce the noise due to movement of local birds, tracks that were directed opposite the mean direction of migration were excluded from the analysis. Because of our conservative approach regarding radar track selection, many of the tracks could probably be referred to large soaring birds that are tracked by the radar for longer distances than small birds.

Fig. 1 The study area with the radar station (Aspromonte) on the continental side of the Strait and the watchpoint (Serro) located on the Sicilian side (indicated by a binocular symbol). The radar range is indicated in grey.
As a first step, we verified if fog was caused by a particular wind direction to avoid a misinterpretation of the results. In particular, we used the presence/absence of fog as a dependent binary variable in a binary logistic regression analysis (hereafter BLRA) while wind speed and direction and their interaction (see below) were independent variables. Moreover, to compare the two wind data sets (from our meteorological station and from ECMWF reanalysis), we performed the Watson two-sample test for homogeneity on the two samples of wind directions that were considered circular data (Pewsey et al. 2013). Wind speed from the two data sets was compared using Mann-Witney U test. After that, to examine if the watchpoint at Serro may serve as a reliable comparison station to the one in Aspromonte, we used Mann-Witney U test to compare number of birds counted there during days with and without fog events in Aspromonte.

The dependent variable in all the rest of our analyses was bird passage rate in the form of hourly number of radar tracks. To examine which variables affected bird passage rate, we tested the following independent variables:

1. Fog—categorical variable (presence/absence)
2. Air temperature—continuous variable (°C)
3. Air humidity—continuous variable (%)
4. Wind direction—categorical variable of three classes according to previous research in the area (Agostini et al. 2007, 2016; Panuccio 2011; Becciu et al. 2018). (a) Southern, when the wind was blowing from the following sectors: S-SSW-SW-WSW, corresponding to tailwind; (b) northern, when the wind was blowing from the following sectors: N-NNE-NE-ENE, corresponding to headwind; and (c) westerly wind when the wind was blowing from: W-WNW-NW-NNW, corresponding to crosswind). We excluded from the analysis hours with wind coming from the eastern sectors: SSE-SE-ESE-E because it occurred only for 6 h during the whole study period.
5. Wind speed (m/s) and its interaction with wind direction
6. Bird visually detected in Serro—continuous variable (number per hour). We used the hourly number of migrating birds (all species) counted at Serro as an index of the intensity of the migratory flow in the Strait of Messina area because no fog occurred at this site, and thus, visually recorded bird density at this site was not affected by fog.
7. Time of day—continuous variable. Since the migration of soaring birds, that are the commonest recorded bird species, is known to vary throughout the day (Kerlinger...
We added the time of the day to our models to account for the possible influence of this factor on bird migration intensity. To account for possible effect of the time of day, we calculated for each observation the difference between the local noon and its observation time such that these values were negative before noon and positive afterwards (Mellone et al. 2012; Panuccio et al. 2017). We used the variance inflation factor (library HH for R software, Heiberger 2015) with a threshold of 3 to test for collinearity of the predictors entered simultaneously in the statistical model.

We used generalized linear model (McCullagh and Nelder 1989; Dobson 1990) (hereafter GLM) with negative binomial error distribution using MASS package in R software (R software version 3.1.2) to investigate the effects of the independent variables on bird passage rate, as calculated from radar tracks. We selected variables using a step function based on their AIC values (Akaike 1973). We furthermore tested the significance of each variable in the selected, most parsimonious model, using ANCOVA. We used Pearson correlation to examine the relationship between the number of counted European honey buzzards (Pernis apivorus), the most abundant bird species in our counts, at the two watchsites (Table 1); we limited this analysis to days without fog. We used the same test to examine if the number of birds visually detected in Aspromonte correlated with recorded radar tracks during hours with good visibility.

**Results**

We carried out 267 h of simultaneous radar tracking and visual observations at Aspromonte and Serro between 7 April and 20 May 2014.

**Weather**

No fog occurred throughout the course of the study at Serro watchpoint, whereas fog was recorded during 65 h (24.3% of the time) at Aspromonte. The wind directions recorded by the meteorological station next to the radar reflected synoptic wind data from ECMWF models ($W = 0.03, P > 0.1$). Wind speed recorded at the field station was on average $4.3 \pm 3$ m/s while that from ECMWF was $3.4 \pm 1.8$ m/s; this difference was significant ($U = 1, P < 0.001$). The analysis (BLRA) explaining the presence/absence of fog and low clouds shows that neither wind speed and nor wind direction affected fog occurrence, as well as their interaction (Table S1). Therefore, fog occurred regardless of wind conditions (Fig. 2).

**Visual counts**

The number of visually counted birds in Serro was not influenced by the presence of fog in Aspromonte as showed by the result of the Mann-Witney $U$ test ($W = 0.7, P > 0.1$). At the Aspromonte site, the observers counted a total of 21,290 birds, of which 16,717 were raptors and storks (Table 1). A total of 19,256 birds were counted at Serro during the hours of radar operation at Aspromonte, of which 11,583 were raptors and storks (Table 1). Similarly, also at Serro, the commonest visually detected species was the European honey buzzards (58.3%) but significant numbers of non-raptor birds were counted such as common/pallid swifts (Apus sp.) (15.2%), bee-eaters (Merops apiaster) (9.3%), house martins (Delichon urbica; 8.7%) and barn swallows (Hirundo rustica) (6%; Table S2). The correlation between the daily visual counts (excluding foggy days, see the “Materials and methods” section) at Serro and Aspromonte located on the two sides of the strait for the commonest visually detected diurnal migrant in the area, the European honey buzzard (11,235 and 16,003 individuals counted at Serro and Aspromonte, respectively; Table 1) was significant and positive ($r = 0.56, P < 0.01$).
Radar passage rates

We analysed 18,909 radar tracks from Aspromonte. The number of birds counted at Aspromonte when no fog was present at the site corresponded to the daily number of recorded radar tracks at the same time ($r = 0.73$, $P < 0.001$). Based on its low AIC value, we selected a model that consisted of five explanatory variables: fog, air humidity, air pressure, wind speed, wind direction and the interaction between the latter two variables. The AIC value of this model is substantially lower ($\Delta$AIC > 3.9) than those of the other models (Table S3). The ANCOVA results suggest that three of these variables were statistically significant. In particular, the presence/absence of fog and low clouds was the most important variable explaining the variation in the hourly number of diurnal migratory birds that were recorded by the radar (Table 2). Foggy conditions drastically decreased the number of echoes detected by the radar (estimated $\beta$ values for the effect of fog was $-1.3 \pm 0.2$; Fig. 3). Air pressure significantly and positively influenced the hourly number of birds tracked by the radar (estimated $\beta$ value was $0.07 \pm 0.02$). In addition, wind direction significantly influenced bird passage rate with lower numbers recorded when southern winds were blowing (estimated $\beta$ value was $-0.02 \pm 0.01$) and higher numbers recorded when wind was blowing from the west (estimated $\beta$ value was $0.2 \pm 0.1$; Fig. 4).

Discussion

The dramatic drop in the number of tracks detected by the radar in Aspromonte when fog and low clouds occurred provides strong evidence that diurnal migrants avoid flying through fog and low clouds.

Although our radar track data constitute mainly raptors, it also contains data from non-raptor individuals and it is likely that the general reduction in migration intensity under fog conditions could be a general pattern in diurnal migrants. The behaviour of raptors during migration and their response to weather may depend on geography (Klaassen et al. 2011), topography and time of the day (Panuccio et al. 2016). Specifically, Richardson (1990) suggested that soaring birds, which constitute the majority of the individuals recorded in the present study, rarely fly in dense fog because their migration mostly occurs under sunny conditions and with strong updrafts that are necessary for soaring (Horvitz et al. 2014). This form of flight is energetically cheap for large birds (Hedenström 1993) and as such it is commonly used by many large flyers. Migrating raptors may avoid flying when fog occurs because these conditions prevent the formation of convective updrafts necessary for soaring flight (Kerlinger 1989; Bildstein 2006; Mandel et al. 2008). Moreover, the flight behaviour of birds moving across fog suggests that they may be disorientated under these weather conditions (Alerstam 1990; Alerstam and Ulfstrand 1974; Chiaradia et al. 2007; Kirch et al. 2015; Pastorino et al. 2017). Therefore, migrants moving in spring across the Strait of Messina may try to avoid flying through foggy areas because the low visibility experience within fog may challenge their navigation, posing a substantial burden in addition to the lack of thermals that may limit their soaring flight. Because of the difficulty to measure the spatial extension of fog, we cannot exclude that the possibility that migrating birds stop in the area when encountering fog and wait for better visibility conditions. However, we suggest that, in our study case, migrants likely circumvent the area where fog occurs as suggested by the intense passage of birds at Serro during days when fog occurs in Aspromonte.

Air pressure additionally affected bird passage rate such that higher numbers of birds migrated under barometric high. Similar findings, regarding the positive effects of fair weather conditions were described in the past (Lack 1960; Kerlinger 1989; Richardson 1990). In addition, the direction of the wind influenced bird passage rate. In the present study, south and south-westerly winds negatively affected the intensity of migration, probably because migrating birds are crossing the Tyrrenian Sea rather than detouring it over land under these condition (Fig. 1) as suggested by other studies (Agostini et al. 2007; Panuccio 2011; Becciu et al. 2018). Westerly winds likely pushed migrating birds into the radar range by drifting.

| Table 2 | Results of the ANCOVA testing the effects of different independent variables on the hourly number of birds. This model was selected based on its lowest AIC score. Asterisks indicate statistical significant variables |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Explanatory terms | Estimates | Std. error (±) | F    | P    |
| Fog | $-1.3$ | $0.16$ | $37.9$ | $< 0.001^*$ |
| Air pressure | $0.07$ | $0.02$ | $8.2$ | $0.005^*$ |
| Air humidity | $0.007$ | $0.004$ | $1.8$ | $0.2$ |
| Wind direction | Crosswind | $0.2$ | $0.1$ | $4.0$ | $0.02^*$ |
| Wind speed | $-0.01$ | $0.03$ | $0.9$ | $0.3$ |
| Wind speed × wind direction | Crosswind | $0.02$ | $0.03$ | $2.2$ | $0.1$ |
| Tailwind | $-0.02$ | $0.04$ | | | |
them from the coastal area. During northern winds, soaring migrants tend to cross the Strait of Messina at its narrowest point just southwest to our study area, which may increase migration intensity at the Aspromonte radar range (see also Panuccio et al. 2016; Becciu et al. 2018). A different radar study showed that birds were able to cross the Strait of Messina with good tailwind assistance but they did not select the best flight altitude with respect to wind direction (Mateos-Rodriguez and Liechti 2011). However, since the Strait of Messina is only 3 km wide at its narrowest point, it should not be considered a true barrier for migrating land-birds that may move across our study area also during unfavourable weather conditions (i.e. headwinds coming from the north). Further investigation is needed to assess if migratory birds stop their flight and wait for better visibility when facing fog along their migration path or try to continue their migration, by circumventing the fog and moving through fog-free areas. To further assess this option from tracks of migrating birds, it is important to better describe the spatial and temporal characteristics of the fog and, specifically, its spatial extent. This will permit studying the effects of fog at both local and regional scales.

The results of this study highlight the importance of integrating different survey methods of bird migration to obtain information not only on the behaviour of birds but also on bird passage rate (Bruderer 1997b; Buler and Dawson 2014). In particular, since under bad visibility conditions, visual observations are mostly useless (Hall et al. 1992); the use of radars may allow measuring the intensity of bird migration even when visibility is poor. Our findings may also be used to investigate the impact of human-built structures on birds, particularly during migration and other movements, which is of crucial importance for bird conservation (Hüppop et al. 2006; Lambertucci et al. 2015). In particular, collision risks of birds with man-made structures like wind turbines depend on different factors, among which are weather conditions. Specifically, collision prevalence increases when visibility is poor (Drewitt and Langston 2006), and therefore, this must be taken into account when estimating collision risks in areas where fog is common. We suggest directing future research on exploring the behavioural responses of soaring versus flapping migrants under different visibility conditions because these two groups may respond differently to these conditions due to the critical role of updrafts for soaring flight, possibly leading to differences in risks of collision with man-made
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