

Original Article

How do diurnal long-distance migrants select flight altitude in relation to wind?

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To save energy and time, migratory birds are expected to select time periods and flight altitudes with favorable wind conditions. In spring 2006, we studied diurnal migration using tracking radar at the Strait of Messina. A total of 1530 radar tracks were analyzed with respect to flight altitude and wind conditions. The tracks included Honey Buzzards, Marsh, Montagu's, and Pallid Harriers, Black Kites, falcons, swallows, swifts, and herons. Maximum flight altitude recorded was 2495 m above ground level (agl), but 90% of birds were flying below 1135 m. All species investigated showed clear evidence that tailwind assistance at the bird's flight altitude was better than below and similar or better than just above. However, the birds did not select the best flight altitude with respect to tailwind assistance within a given height range of 1000 or 2500 m agl. More likely, they were selective for the first optimum they encountered when climbing, even when better winds occurred at higher altitudes. Understanding the selection of flight altitudes by diurnal migrants is essential for modeling and predicting the temporal and spatial concentration of migratory birds. This kind of information is urgently needed for the evaluation of collision risks in relation to the impact of wind turbines on birds but also for assessing aircraft safety. *Key words:* bird behavior, migration, powered flight, predictive models, selection of flight altitude, tailwind assistance, tailwind component, tracking radar. [*Behav Ecol* 23:403–409 (2012)]

INTRODUCTION

A successful migratory strategy is the result of an optimization process of the 3 most important factors during migration: time, energy, and safety (Alerstam and Lindström 1990; Alerstam 1991). Once the decision for take off is made, a migrant should try to minimize energy and time by choosing optimal flight levels with respect to the meteorological conditions aloft. It has been showed that wind speed and direction is by far the most important factor governing the altitudinal distribution of nocturnal migrants (more than air density, temperature, humidity, or topography; Bruderer and Liechti 1995; Bruderer, Underhill, et al. 1995; Liechti et al. 2000; Schmaljohann et al. 2009). Therefore, migratory animals are expected to be selective for time periods and flight altitudes with the most favorable wind conditions (both wind direction and speed; Alerstam 1979; Liechti 2006; Chapman et al. 2008) to minimize energy costs or time, and if possible, both (Alerstam and Lindström 1990; Alerstam 1991).

Detailed measurements of the vertical distribution of different species of birds are sparse in scientific literature. This is mainly due to the technical difficulty in collecting such data. Measurements of flight altitudes of birds require special equipment, for example, radar or tracking devices such as GPS placed on individual birds. Studies that have collected data on the flight altitudes of identified species are typically focused on one species or group of birds or on birds flying in the lowest air layers where flight altitudes can be estimated visually (e.g., Osborn et al. 1998; Garthe and Hüppop 2004).

Studies investigating the selection of flight altitude due to wind were almost exclusively related to nocturnal migration (e.g., Bruderer and Liechti 1995; Liechti et al. 2000; Schmaljohann et al. 2009; Karlsson et al. 2011). While nocturnal migrants rely on powered (flapping) flight, diurnal migrants are more or less able to choose between powered flight and thermal soaring and gliding. Flight altitude of soaring migrants is strongly influenced by the vertical range of thermal convection (Spaar et al. 2000; Shamoun-Baranes, Leshem, et al. 2003; Shamoun-Baranes, Liechti, et al. 2003). Little is known about altitude selection with respect to favorable wind conditions in diurnal migrants using powered flight.

Previous studies with nocturnal migrants have shown how birds are selective for flight altitudes with favorable winds (Richardson 1978; Gauthreaux 1991; Richardson 1991 and references therein, Bruderer and Liechti 1995; Bruderer, Underhill et al. 1995; Liechti et al. 2000; Schmaljohann et al. 2009). For example, Bruderer, Underhill, et al. (1995) successfully predicted distributions of nocturnal flight altitudes based on the assumptions that birds explore winds at different heights and choose flight levels according to differences in tailwind assistance between neighboring levels.

Recent concern about the adverse effects of collision mortality of birds at man-made structures, such as wind farms or power lines, has highlighted the need to understand the interaction of birds and these structures. In addition to the negative impact on avian populations, the potential for life-threatening and costly collisions between aircrafts and birds has increased dramatically during the last few decades (Richardson and West 2000; Allan 2002). To reduce the risk of bird collisions with man-made structures, models predicting spatial and temporal bird densities under changing environmental conditions are being developed (e.g., bird-aircraft collisions: Bird Avoidance Model, Bouten et al. 2003; bird-wind farms collisions: Desholm and Kahlert 2006; Mateos et al. 2009). In order to

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Received 19 July 2011; revised 25 October 2011; accepted 26 October 2011.

develop a realistic 3-dimensional temporally dynamic model of bird densities, quantitative data are needed on flight altitudes together with a clear understanding of how they respond to a constantly changing environment. Species-specific information about wind dependence of flight altitudes in diurnal migrants is essential input for this kind of model.

Here, we investigate the influence of wind on the flight altitude of diurnal long-distance migrants. The flight altitudes of different species of birds were measured during spring migration across the Strait of Messina, southern Italy. All species investigated are capable of constant powered flight. Otherwise, they would not have been able to cross the Mediterranean Sea from Tunisia to Sicily (min. sea crossing 140 km). In this study, the influence of wind conditions on the vertical distribution of birds during diurnal migration is analyzed for the first time simultaneously for different species. We test the assumption that diurnal migrants with a powered flight mode select flight altitudes with the best tailwind assistance, as previously found in nocturnal migrants. To the best of our knowledge, this is the first study that quantitatively investigates flight behavior of diurnal raptors and other diurnal long-distance migrants such as swifts, swallows, and herons with respect to tailwind assistance.

MATERIALS AND METHODS

In spring 2006, diurnal migration was studied at the Strait of Messina in southern Italy by tracking radar. The station was set up on the Calabrian side of the Strait; the radar was located 600 m away from the coastline (coordinates 38°13'45.2"N/15°38'48.8"E) at an altitude of 100 m above sea level (asl). Data were collected every day from 04 April to 14 May 2006. Observations of diurnal migration covered the whole day, that is, from sunrise to sunset (6.00–20.00 h), regardless of favorable or unfavorable environmental conditions or abundance of diurnal migrants.

A tracking radar of the type “Superfledermaus” was used to record the flight paths of migrating birds. This radar allows automatic tracking of a single medium-sized raptor up to distances of about 8 km; the range for single small passerines (e.g., Barn Swallow) is about 5 km (for details, see Bruderer, Steuri, et al. 1995). As the size of birds may limit the range (and thus height) for identification, we checked detection distances for the different species. The results showed that for all species, including the small swallows and swifts, mean distances of detection were higher than mean flight altitude and also higher than the upper limit of the flight altitudes.

For each track x , y , and z coordinates were recorded every second and visualized on the computer screen. Tracking accuracy was 0.06° in azimuth and elevation and ± 10 m in distance. The data of 20 s were approximated by regression lines; averaging these regression lines provided mean values for flight direction, ground speed, and flight altitude per track. Simultaneously, the tracked target was identified by an experienced observer through a 12.5× telescope mounted parallel to the radar beam. As diurnal migrants often fly in flocks, the observer also determined the flock size. All the targets were chosen by the radar operator, without view to the sky, and, therefore, the results represent a good sample of the ongoing migration during daytime and a random selection of the birds.

In order to record wind directions and speeds at all flight levels, a pilot balloon with an aluminum reflector was released every 6 h and tracked with the radar. The balloon was usually tracked up to 4000 m asl or at least up to the altitude of the highest tracked bird. The heading of the birds was calculated by subtracting the temporally and spatially closest wind vector (measured by the pilot balloons) from the vector of a bird's track.

For the analysis of flight altitudes, birds noted as locals (mainly gulls) were excluded. For the analysis of tracks, only

straight-lined tracks (or part of the tracks, without any soaring phase) were selected, and climb or descent rates exceeding 3 m/s were excluded. Thus, our study covers only birds performing directed migratory flights (gliding or flapping), potentially flying at within selected flight altitudes.

For the data analysis, the tracked birds were assigned to 8 different groups according to the visual species identification: 1) Honey Buzzards *Pernis apivorus*; 2) Marsh Harriers *Circus aeruginosus*; 3) Montagu's and Pallid Harriers *C. pygargus*, *C. macrourus*; 4) Black Kites *Milvus migrans*; 5) Falcons, including Eleonora's Falcon *Falco eleonora*, Hobby *F. subbuteo*, Kestrel *F. tinnunculus*, Peregrine Falcon *F. peregrinus*, Red-Footed Falcon *F. vespertinus*, and unidentified falcons; 6) Swallows, including House Martin *Delichon urbica*, Sand Martin *Riparia riparia*, Barn Swallow *Hirundo rustica*, and unidentified swallows; 7) Swifts, including Alpine Swift *Apus melba*, Common Swift *Apus apus*, Pallid Swift *Apus pallidus*, and unidentified swifts; and 8) Herons, including Great White Egret *Egretta alba*, Gray Heron *Ardea cinerea*, Little Egret *E. garzetta*, and unidentified herons.

To determine whether or not birds selected flight altitudes with favorable winds, we investigated 2 aspects. First, whether birds selected flight altitude with optimal tailwind assistance within a given range of altitude. In order to assess this, we computed the difference between the bird's flight altitude and the altitude with the best tailwind assistance within 2 different given height ranges (one from the ground up to 1000 m and a second one up to 2500 m); Second, whether birds selected altitude according to a local maximum of tailwind assistance. For this, we investigated whether tailwind assistance at the bird's flight altitude was on average higher than below and whether it was better than in the height layer just above.

To investigate these questions, we used the following measures. Tailwind and sidewind components (TWC, SWC) were calculated with respect to track direction. Based on the mean flight direction of the corresponding species group and the temporally closest wind profile with respect to the individual bird's track, we defined: 1) TWC_{max} as the maximum value of TWC available within the given height ranges (see above), denoted as $TWC_{max1000}$ and $TWC_{max2500}$, respectively; 2) Z_{max} as the altitude at which the TWC within the selected height range is maximal (denoted as $Z_{max1000}$ and $Z_{max2500}$, respectively); 3) TWC_b and SWC_b as the average of the TWC and SWC from ground level up to the bird's track altitude; 4) TWC_a and SWC_a as the average of the TWC and SWC available in the upper neighbor height level (~ 100 m); 5) TWC_{bird} and SWC_{bird} as the TWC and SWC at the bird's flight level. For the calculations of (3), (4), and (5), we used the flight direction of the individual bird and the temporally and spatially closest wind data. Finally, we computed the differences in TWC and SWC at the birds flight altitude with the conditions below (ΔTWC_b , ΔSWC_b) and above (ΔTWC_a , ΔSWC_a) and the differences to the maximum tailwind assistance ($\Delta TWC_{max1000}$, $\Delta TWC_{max2500}$). In addition, we calculated the difference in height between the birds' flight altitude and the altitude of maximum tailwind assistance ($\Delta Z_{max1000}$, $\Delta Z_{max2500}$). For detailed information, see Supplementary Figure 1.

We used circular statistics according to Batschelet (1981) to calculate mean flight and wind directions, using Oriana v. 2.02e software (Kovach Computing Services 2007). Noncircular analyses were performed with R 2.11.2 (R Development Core Team 2010). Mean \pm standard errors (SEs) are presented, with sample size (n).

RESULTS

A total of 1530 radar tracks of diurnal migrant birds were analyzed, including 347 Honey Buzzards, 197 Marsh Harriers,

121 Montagu's and Pallid Harriers, 19 Black Kites, 232 falcons, 304 swallows, 275 swifts, and 35 herons. Overall, 70% of sightings were single birds and the rest were flocks.

Birds were flying between 10 and 2495 m above ground level (agl), with a median at 490 m agl and the 90th percentile at 1135 m agl (Supplementary Figure 2). Mean flight altitudes were significantly different between the groups of species (analysis of variance [ANOVA] $F = 45.9$, $P < 0.0001$). The highest flight altitudes were achieved by herons (625 m, 1850 m; median and 90th percentile, respectively), swifts (760 m, 1400 m), falcons (630 m, 1450 m), and Montagu's and Pallid Harriers (640 m, 1290 m). Swallows (450 m, 960 m), Marsh Harriers (450 m, 850 m), Honey Buzzards (350 m, 600 m), and Black Kites (280 m, 500 m) showed significantly lower flight altitudes (Scheffé test within the 2 group clusters all $P > 0.1$, between the 2 group clusters $P < 0.001$; Figure 1, Table 1, see also Supplementary Figure 2).

All groups were flying at lower altitudes than the altitude with the best tailwind assistance (within the given height ranges; Table 1, Supplementary Figures 3 and 4). Only swifts flew slightly higher than the best flight altitude when the column of air up to 1000 m was considered ($\Delta Z_{\max 1000} = 39.4 \pm 26.7$ m; Table 1, Supplementary Figure 3). Black Kites and Honey Buzzards were flying much below the optimal flight altitude with respect to tailwind assistance compared with the other groups (large negative ΔZ_{\max} ; Table 1, Supplementary Figure 3), but the difference was significant only when the column of air up to 2500 m was considered ($\Delta Z_{\max 2500}$: ANOVA $F = 14.6$, $P < 0.0001$; Scheffé test, between Black Kites and Honey Buzzards $P > 0.5$, and between these 2 and all the groups $P < 0.05$; Table 1, Supplementary Figure 3).

For all groups, the differences between the TWC at the bird's flight altitude and the average TWC below the bird (ΔTWC_b) were positive and significantly different from 0 (Wilcoxon matched pairs test, all $P < 0.05$), and they were not different

between the species (ANOVA $F = 72.5$, $P = 0.1$; Figure 2, Table 2). For all groups, the differences between the TWC at the bird's flight altitude and the average TWC in the upper neighbor height level (ΔTWC_a) were not significant different from 0 (Wilcoxon matched pairs test, all $P > 0.05$), and they were not different between the species (ANOVA $F = 12.7$, $P = 0.4$; Figure 2, Table 2). Thus, the bird's preferred flight altitude was the one with significantly better tailwind assistance than in the air column below, and with similar wind conditions as in the upper neighboring height level. The realized tailwind assistance in relation to the wind conditions below (ΔTWC_b) increased significantly in the second half of the day (ANOVA $F = 5.63$, $P < 0.001$; Figure 3, all species pooled). In relation to the wind conditions above, the effect was much less pronounced and not significant (ΔTWC_a , ANOVA $F = 0.98$, $P = 0.41$; Figure 3).

For all groups, the variables calculated with respect to the sidewind component (ΔSWC_b , ΔSWC_a) were not different from 0 (Wilcoxon matched pairs test, all $P < 0.05$; Table 2, Supplementary Figure 5).

DISCUSSION

Our results show that birds failed to select the flight altitude with maximum tailwind assistance within a given range of altitudes (0–1000 and 0–2500 m), suggesting they do not explore the entire air column of potential flight altitudes to check for the best tailwind assistance. Instead, there is good evidence that migrating birds do evaluate tailwind assistance while climbing up through the air column but following the simple rule of thumb “climb up as long as tailwind assistance is increasing.” This corresponds with previous results successfully predicting distributions of nocturnal passerine migrants' flight altitudes based on the assumptions that birds explore winds at different heights and choose flight levels according to differences in tailwind assistance between neighboring levels

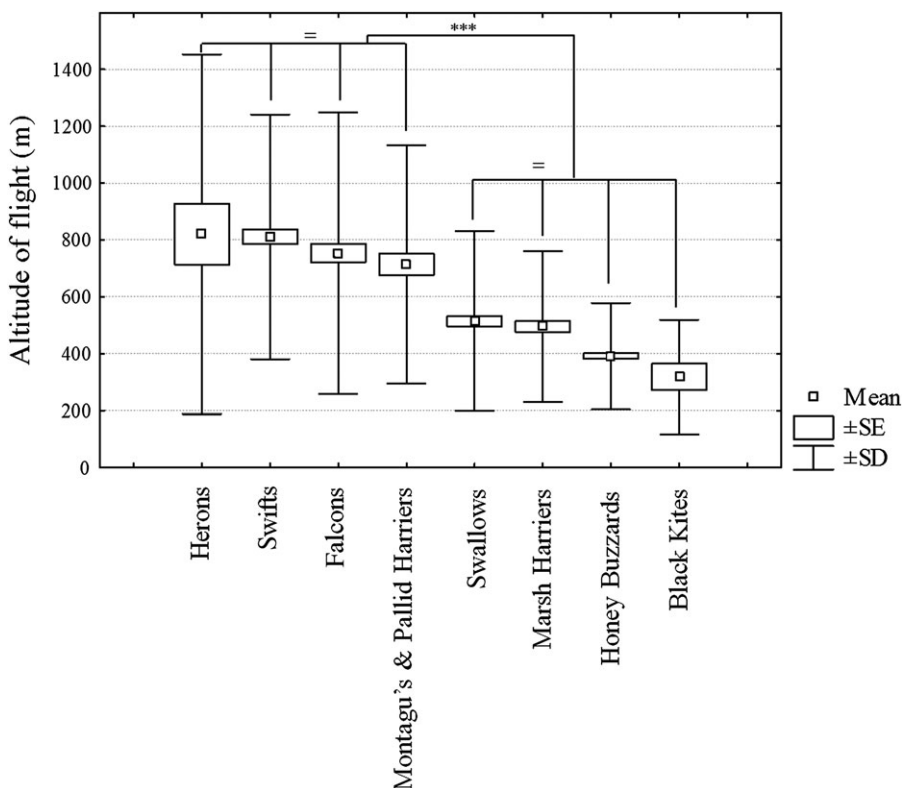


Figure 1
Mean flight altitudes of migrating birds in the Strait of Messina. Mean, SEs, and standard deviation (SD) are given. Significant differences between groups of species are indicated by *** $P < 0.001$; no significant differences by = $P > 0.05$.

Table 1
Radar data for diurnal migrating birds identified to species assigned to 8 different groups

Species	<i>n</i>	V_g		V_w		Z		TWC_{bird}		SWC_{bird}		$\Delta TWC_{max2500}$		$\Delta Z_{max2500}$		$\Delta TWC_{max1000}$		$\Delta Z_{max1000}$		<i>n</i> ₁₀₀₀
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Honey Buzzards	347	12.5	0.2	4.4	0.2	391.0	19.4	0.9	0.2	2.8	0.2	-6.9	0.3	-1541.3	47.9	-3.8	0.2	-221.3	20.1	346
Marsh Harriers	197	12.0	0.3	6.0	0.2	495.0	26.0	2.5	0.3	3.6	0.2	-7.1	0.4	-1132.5	63.5	-3.9	0.3	-189.2	27.2	188
Montagu's and Pallid Harriers	121	11.9	0.4	5.4	0.3	714.1	32.9	1.0	0.4	3.4	0.3	-7.5	0.5	-970.9	80.0	-4.5	0.4	-97.7	38.3	94
Black Kites	19	9.9	0.9	6.5	0.8	317.9	83.0	0.7	0.9	4.6	0.7	-8.9	1.1	-1638.6	204.1	-5.6	0.9	-379.3	85.0	19
Falcons	232	13.0	0.2	5.9	0.2	754.0	23.4	1.8	0.3	3.7	0.2	-8.1	0.3	-919.3	58.5	-4.4	0.3	-166.9	28.8	168
Swallows	304	14.0	0.2	5.9	0.2	514.0	21.0	2.7	0.2	3.8	0.2	-6.1	0.3	-1248.6	51.1	-3.2	0.2	-195.0	22.3	279
Swifts	275	14.4	0.2	6.5	0.2	810.3	21.4	2.6	0.3	4.2	0.2	-8.8	0.3	-965.6	53.8	-4.3	0.3	39.4	26.7	195
Heron	35	13.6	0.6	5.6	0.5	820.9	61.4	2.1	0.7	3.1	0.4	-6.5	0.8	-779.0	150.0	-2.9	0.8	-0.04	79.3	22

Number of tracks (*n*); Ground speed (V_g , m/s); Wind speed (V_w , m/s); Flight altitude (Z , m); TWC_{bird} and SWC_{bird} (m/s); $\Delta TWC_{max2500}$, $\Delta Z_{max2500}$, $\Delta TWC_{max1000}$, and $\Delta Z_{max1000}$ in m/s. For further description of these variables, see MATERIALS AND METHODS. Sample size when the column of air only up to 1000 m is considered (*n*₁₀₀₀). Mean and scatter (SE) is shown for the different variables.

(Bruderer, Underhill, et al. 1995). It is also in line with several studies and models demonstrating that nocturnal migrants aloft choose altitudes with favorable wind direction and speed (e.g., Gauthreaux 1991; Bruderer, Underhill, et al. 1995; Klaassen and Biebach 2000; Liechti et al. 2000; Erni et al. 2005; Liechti and Schmaljohann 2007; Schmaljohann et al. 2008). In contrast, a recent study detected almost no effect of tailwind assistance on the ground speed of nocturnal passerines, but they did not investigate the corresponding range of tailwind assistance available in time and space (Karlsson et al. 2011). Our results show how diurnal migratory species make a restricted selection out of the actual wind conditions encountered during flight.

We focused our study on powered flight because flight altitude in soaring flight is mainly based on thermal activity (e.g., Spaar and Bruderer 1997), which was not investigated here. Nonetheless, the species included in this study cover a wide range of flight styles, from continuous flapping (powered by muscles, e.g., swallows) to soaring birds (powered often by thermals and updrafts, e.g., Honey Buzzards). However, despite these differences, all of the species analyzed generally seem to follow the same rule of climbing up as long as tailwind assistance is increasing. Nevertheless, we found some species-specific results.

Although soaring flight intervals were excluded (see MATERIALS AND METHODS), average flight altitude of Honey Buzzards followed a typical daily pattern as indicated by the development of the planetary boundary height layer (Kerlinger et al. 1985; Kerlinger 1989; Spaar 1995; Leshem and YomTov 1996; Liechti et al. 1996). Flight altitudes increased during the morning and peaked in the early afternoon (Supplementary Figure 6a). Marsh Harriers and Black Kites showed a diurnal pattern in which the highest flights occurring in the last interval before sunset (Supplementary Figure 6b,c). For the other species, no clear daily pattern was found (Supplementary Figure 6d-h). A few studies have analyzed the direct influence of weather on flight altitudes of soaring birds and have shown a strong relationship between thermal convection and their flight altitudes (Pennycuik 1972; Spaar 1995; Spaar et al. 2000; Shannon et al. 2002; Shamoun-Baranes, Leshem, et al. 2003; Shamoun-Baranes, Liechti, et al. 2003; Shamoun-Baranes et al. 2006). In those studies, soaring birds have been measured flying up to altitudes of several hundreds to thousands of meters and rely on thermal or orographic lift for extended flight. In our study area, Honey Buzzards, the only species studied which seems to regularly use soaring on thermals to gain height has one of the lowest mean flight altitudes. This could be due to the topographic characteristics of the study area that is close to the sea where thermal activity is known to be lower than in other areas.

The possibility of alternating flight styles from flapping-gliding to soaring-gliding opportunistically allows many species to migrate under various environmental conditions. For example, Marsh Harriers and Black Kites show a diurnal pattern in which the highest flights occur in the last interval before sunset. This corresponds with observations in Israel, where Spaar and Bruderer (1997) observed harriers increasing flight altitudes throughout the day, culminating toward sunset. Many individuals were recorded before or soon after sunrise in active powered flight, when thermal activity was still nonexistent (e.g., harriers and falcons, cf. Supplementary Figure 6). Their high flight altitudes combined with good tailwind assistance indicates that they may have migrated through the night. Nocturnal migration of raptors has previously been reported (e.g., Levant Sparrowhawks *Accipiter brevipes*; Stark and Liechti 1993; Spaar et al. 1998). Birds taking off in the morning have to explore the air column first, thus incurring a reduction of mean realized tailwind

assistance. As the day progresses, they reach the height where tailwind assistance is better than below and does not improve just above (Figure 3).

Mean flight altitude of the raptors recorded in this study was similar to those reported for North America (Kerlinger 1989) and Israel (Bruderer et al. 1994; Liechti et al 1996; Spaar and Bruderer 1997). However, Spaar (1995) highlighted that flight characteristics of different species are more similar under the same meteorological conditions than the behavior of the same species under different conditions. Thus, the intraspecific variation under changing environmental conditions suggests some caution when comparing species, not only raptors, in different areas because the differences between species may be the result of differences in the flight performance of the species itself or in the actual environmental conditions, which in turn may induce specific behavioral reactions. In our study, migrants known to soar frequently (Honey Buzzard, Marsh Harrier, Black Kite), flew at relatively low altitudes, perhaps due to the lack of good thermals. Those species known to prefer powered flight during migration (herons,

swifts, falcons), where flying at relatively high altitudes. We assume that flight altitude is also influenced by species-specific climbing costs and the length of the flight stages. Herons are known to fly during day and night and therefore might be able to explore winds also at higher altitudes (Liechti and Schaller 1999). With respect to the different flight altitudes between the species groups, it must be taken into account that there was high variability in wind conditions during the course of the season and therefore, the different species groups with different phenologies where not migrating under the same environmental conditions.

Management implications

This study is not only aimed at improving our understanding of biological processes and the altitude at which birds migrate but is also of practical relevance to predicting the flight altitudes of birds under changing meteorological conditions and improving our knowledge of birds' interactions with man-made structures.

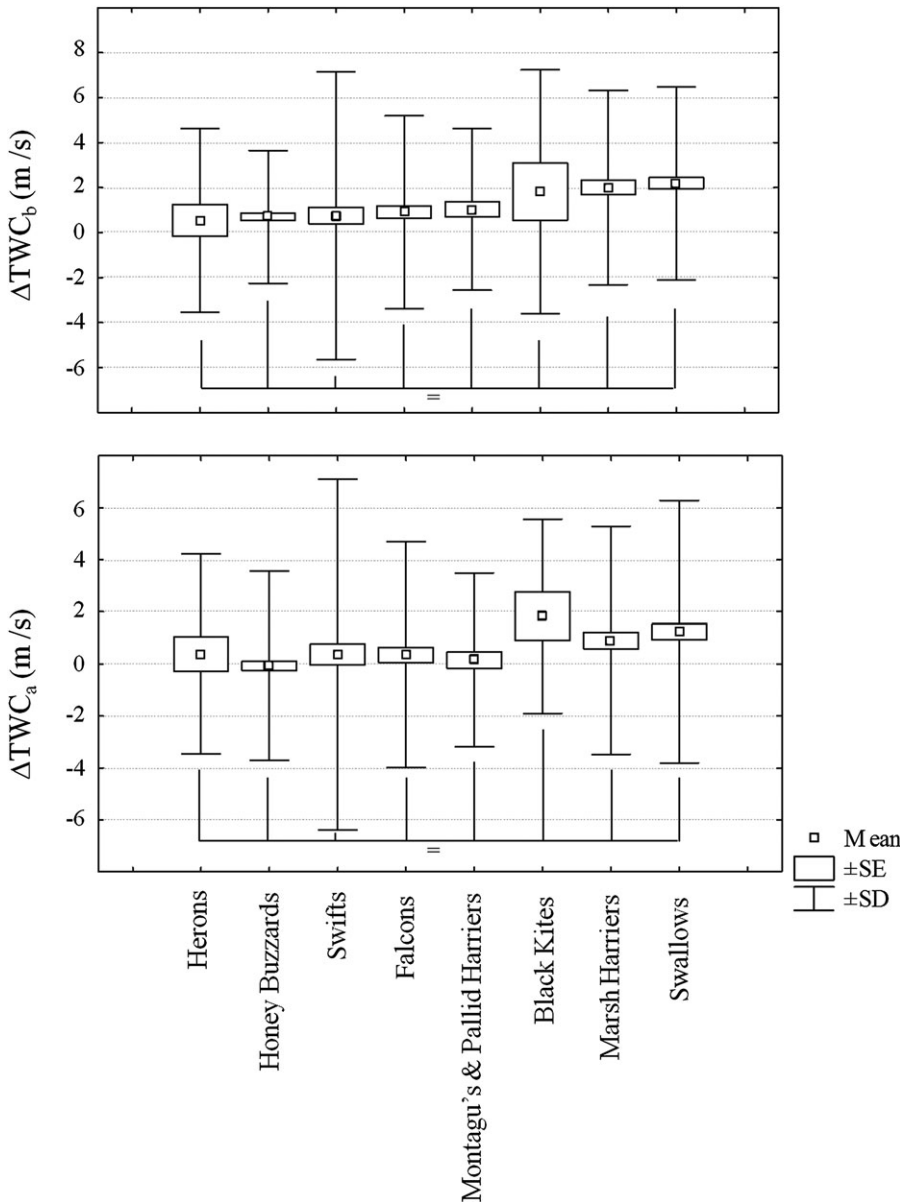


Figure 2
 Mean tailwind assistance realized in relation to wind below (ΔTWC_b) and above (ΔTWC_a). Mean, SEs, and standard deviation (SD) are given. No significant differences between groups of species are indicated by = $P > 0.05$.

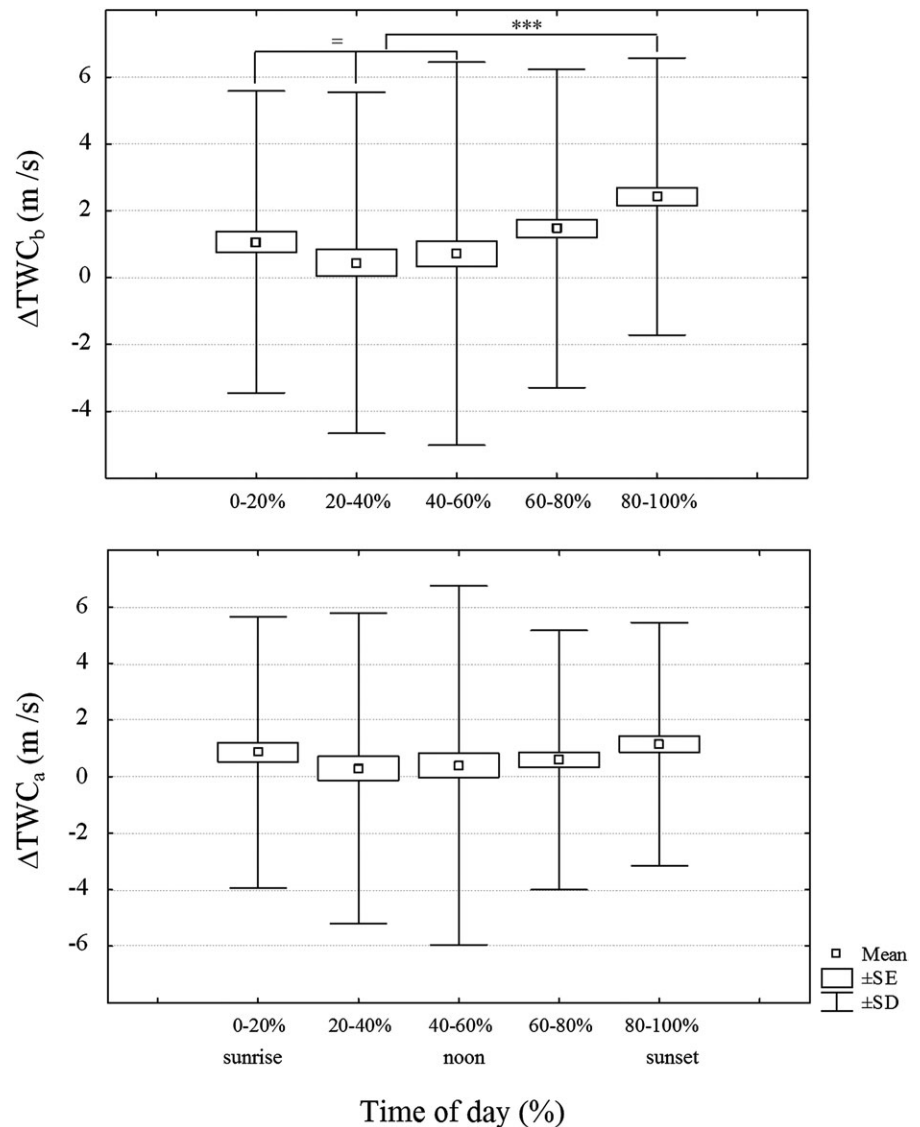


Figure 3
Diurnal variation in mean tail-wind assistance realized in relation to wind below (ΔTWC_b) and above (ΔTWC_a). All groups are pooled. Mean, SEs, and standard deviation (SD) are given.

Models at different temporal resolutions can be used to predict the flight altitudes under different meteorological condi-

Table 2
Radar data for diurnal migrating birds identified to species assigned to eight different groups

Species	<i>n</i>	ΔTWC_b		ΔSWC_b		ΔTWC_a		ΔSWC_a	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Honey Buzzards	347	0.7	0.2	0.3	0.1	-0.1	0.2	0.1	0.1
Marsh Harriers	197	2.0	0.3	0.5	0.2	0.9	0.3	-0.1	0.2
Montagu's and Pallid Harriers	121	1.0	0.4	-0.6	0.3	0.2	0.4	0.0	0.3
Black Kites	19	1.8	1.0	0.3	0.7	1.8	1.2	0.0	0.7
Falcons	232	0.9	0.3	-0.1	0.2	0.4	0.3	0.0	0.2
Swallows	304	2.2	0.3	0.7	0.2	1.2	0.3	0.2	0.2
Swifts	275	0.8	0.3	0.3	0.2	0.4	0.3	0.1	0.2
Herons	35	0.5	0.7	-1.0	0.5	0.4	0.8	-0.4	0.4

Number of tracks (*n*); mean and scatter (SE) of ΔTWC_b , ΔSWC_b , ΔTWC_a , and ΔSWC_a in m/s. For further definition of these variables, see MATERIALS AND METHODS.

tions (e.g., Shamoun-Baranes et al. 2006). These types of models are of practical relevance in conservation because birds can collide with tall man-made constructions and aircraft. Currently, risk analysis and mitigation recommendations with respect to collisions between birds and wind turbines are an urgent necessity (e.g., Osborn et al. 1998; Barrios and Rodriguez 2004; Garthe and Hüppop 2004). Additionally, avoiding collisions between birds and aircrafts has been an ongoing task for many decades with increasing significance. Thus, understanding the behavioral mechanisms behind the selection of flight altitudes by migrating birds is crucial for predictive models. We expect that the implementation of such a rule of thumb in future models will reduce discrepancies between predictions and observations.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

We thank E. Bächler for managing the field station and collecting all the data together with the field observers U. Melone, H. Gander, and N. Agostini. The radar system was set up and maintained by T. Steuri and E. Bächler. The survey was embedded in an environmental impact

assessment financed by “Stretto di Messina S.p.A.” related to the project of building a bridge across the Stretto di Messina. F. Spina organized contacts and the permission for running the radar system. We thank Bruno Bruderer, Lukas Jenni, and 2 anonymous referees for their comments and suggestions on previous versions of this manuscript and Sarah Frey and Adam Hadley for their improvement of the English.

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