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Interspecific comparison of the flight performance between sparrowhawks and common buzzards migrating at the Falsterbo peninsula: A radar study

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Abstract In order to compare the two species' flight performance over the exposed and windy Falsterbo Peninsula, where thermal conditions seldomly are very favorable, we used tracking radar to study flight parameters of sparrowhawks *Accipiter nisus* and common buzzards *Buteo buteo* during autumn migration. The results showed a clear difference between sparrowhawks and common buzzards in their flight altitudes and speeds, and in the wind conditions they encountered. Common buzzards had higher flight altitudes and were more selective of wind. Flight altitude was negatively related to the wind speed, which was most pronounced for common buzzards. Sparrowhawks had higher mean air- and cross-country speeds than common buzzards. Airspeed was negatively related, whereas ground and cross-country speeds were positively related to the tailwind component for both raptors. The differences between sparrowhawks and buzzards could to a large degree be explained by a larger dependence on thermal soaring among the common buzzards; a strategy associated with selectivity for favourable thermal and wind conditions during migratory flight. An additional important explanation for the interspecific differences was the habit of the sparrowhawks to combine migratory flight with hunting for prey, which makes it prone to fly at lower altitudes and use flapping flight to a much larger degree than common buzzards which do not forage during their migratory passage of the Falsterbo Peninsula [*Current Zoology* 60(5): 670–679, 2014].

Keywords Tracking radar, Raptor migration, Sparrowhawk, Common buzzard, Flight performance, Interspecific comparison, Falsterbo peninsula

Two main flight styles are used by migrating raptors: soaring-gliding and flapping-gliding. Smaller species such as falcons, harriers and sparrowhawks mainly use flapping flight while larger species such as buzzards and eagles prefer soaring-gliding flight (Bildstein, 2006; Kerlinger, 1989). Energy required for flapping flight increases steeply with increasing body mass (Panuccio et al., 2013; Pennycuick, 1972, 2008), and the decision of whether to fly by flapping or soaring flight may depend on the trade-off between speed and energy required for the flight (Pennycuick, 1989). The relative body size where soaring is advantageous over flapping flight is smaller for birds using energy minimization, but relatively higher for birds using time minimization as their migration strategy (Hedenström, 1993). Environmental factors such as thermal activity might be important as well. Stronger thermals produce higher climb rates, therefore reducing the relative body size where soaring becomes advantageous to flapping flight, meaning that smaller birds would profit from soaring rather than flapping flight (Hedenström, 1993). If soaring-gliding birds were to minimize energy consumption per distance they should maximize their cross-country speed by adjusting gliding airspeed to the available climb rates in thermals (Pennycuick, 1989).

Wind has a large effect on birds' migration performance. In order to optimize their flight, birds have to evaluate the wind and adjust their speed, altitude and heading direction. Their behavioural strategy might change during the course of migration, birds further away from their migration goal could allow themselves to be drifted to a higher degree whereas birds finishing migration would have to compensate for the wind drift (Alerstam, 1979; Klaassen et al., 2010). It has also been shown that birds tend to fly at the altitudes with more favourable winds (Alerstam, 1979; Richardson, 1976).

The majority of raptors try to avoid crossing larger water barriers because of the absence of thermal updrafts and instead take long detours over land, and in order to shorten their flight distance over water many

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raptors use peninsulas (Bildstein, 2006). Falsterbo Peninsula is situated in south-western Scandinavia and is considered to be one of the best places in Europe to observe raptor migration as many of them concentrate there during autumn migration (Kjellén, 1992; Kjellén and Roos, 2000).

The purpose of this study was to evaluate and compare the migratory flight performance between sparrowhawks *Accipiter nisus* and common buzzards *Buteo buteo* by use of a tracking radar placed on Falsterbo peninsula. Both species are intra-European migrants, yet differ in body size and preference for different flight styles. The following aspects of the migration at the Falsterbo peninsula were analyzed and compared between the two species: (1) flight altitudes, (2) flight speeds, (3) flight directions including the occurrence of forward and reverse migration and (4) flight paths over the peninsula. Rudebeck (1950) made extensive and detailed field observations of the raptor migration at Falsterbo Peninsula and discussed the differences in migratory behaviour between sparrowhawks and common buzzards. This study has the aim to document and investigate some of these interspecific differences by exact measurements of flight performance and trajectories using tracking radar. Owing to differences in body size and flight styles (sparrowhawks prefer flapping-gliding, whereas common buzzards prefer soaring-gliding) differences in flight speed and altitude were expected, with sparrowhawks expected to have higher air and cross-country speeds, but lower flight altitudes. Furthermore, we expected common buzzards to be more selective for favourable wind conditions as they rely more on soaring-gliding flight. However, we expected that the two species would show similar migration directions and routes at the peninsula as both species would try to minimize their flight distance over the Öresund strait towards Denmark.

1 Material and Methods

1.1 Study site and data recording

Raptor migration was studied at Falsterbo Peninsula, Sweden, in 2012. The radar was situated 500 m inland from the shoreline with the radar antenna 5 m above sea level. The sea crossing from Falsterbo to Denmark varies between 20 and 45 km, depending on route.

Observations took place from 15 August to 28 October. However, the observations were possible only with favourable weather conditions, days without strong winds or rain. Depending on the day, observations lasted from around 9–10 AM to 13–17 PM. A tracking radar (200 kW peak power, 0.25 μs pulse duration, 504 Hz pulse repetition frequency, 1.5° pencil beam width, X-band) was used to track birds. Birds were spotted and tracked automatically either by systematically scanning the sky for possible targets with the radar or by observing the sky with a telescope and directing the radar antenna towards the observed birds (Bäckman and Alerstam, 2003).

Data from the radar (distance, elevation and azimuth) were recorded every second and transferred to custom-made software and stored for later analysis. Track durations lasted between 30 seconds and 25 minutes. Birds were tracked at distances of 300 m up to 10 km from the radar. Variations in radar echo amplitude were transformed with a discrete Fourier transform analysis (for more information see: Bäckman and Alerstam, 2003) which allowed wing-beat pattern and frequency for each target to be recorded. Visual observations with a telescope (30x, situated a few meters from the radar) were carried out in parallel to bird tracking with the radar in order to identify the species being tracked, sometimes by two operators, one operating the radar and another observing visually. A custom-made monitor, with a wireless connection to the computer, gave information about the bird's position in the sky (distance, elevation and azimuth) to a field observer. Sparrowhawks had a pronounced flight behaviour pattern of flapping-and-gliding phases, combined with a characteristic wing beat frequency (about 5 Hz) that made it possible to identify this species from the radar echo signature alone without need for visual observation.

In order to measure wind speed and direction, helium-filled balloons were tracked by the radar. The time difference between the tracking of a bird and the preceding or following wind measurement was maximally 2.5 hours. To calculate airspeed and heading direction of a bird the wind vector (at the same altitude) was subtracted from the track vector (Bruderer and Boldt 2001, Mateos-Rodriguez and Liechti 2012, Meyer et al. 2000).

1.2 Analysis of tracks

Tracks recorded for *individual birds* (one bird tracked) or small *flocks* (2 or more common buzzards sometimes travelled close together) were used for data analysis. Before the analysis data were visually checked with custom-made software where elevation, range and azimuth were plotted separately. This allowed tracking errors, inter alia signal jumping between different birds and noise from other sources, to be excluded. Tracks with much noise were excluded from the analysis. Furthermore, to reduce the noise, mean speed/direction were calculated for 10-second intervals for each of the bird tracks and for 30-second intervals for the balloon tracks. From those data points, total means were calculated to get an overall estimate of speed and direction for each bird track.

To calculate cross-country speed relative to the ground the Euclidean distance was calculated between the first point at the start of the track and the final point at the end of the track, which was then divided by the total time the bird had used to fly between the two points. Only tracks longer than 1 km were selected for this analysis. In order to evaluate the flight speeds of the birds travelling in different main directions they were subdivided into two categories: forward migrants, with track directions between 135–359° and reverse migrants with track directions between 0–134°. To analyze wind effects on flight path in relation to topography, wind directions were subdivided into two main categories: winds from the northern semicircle (wind direction between 270.0– 89.9°) and from southern semicircle (wind direction between 90.0–269.9°)

The following statistical tests were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, U.S.A.): Mann-Whitney *U* test, One-Way ANOVA with post-hoc test, *t*-test, regression and correlation analyses.

General linear model (GLM) analyses was also performed with statistical software SPSS 20.0 to test if there was any significant effect (interaction) of wind speed (covariate) between species (fixed factors) for flight altitude (dependent variable).

Circular statistics was performed with software Oriana 4.0 (Kovach Computing Services) to calculate mean direction and mean vector length (r; where r = 1 represents no scatter and r = 0 represents a uniform scatter among individual directions). Watson-Williams test was used to test if there were any differences in heading directions and track directions.

2 Results

In total, 280 tracks were recorded, of which 183 were sparrowhawks and 97 common buzzards. Three sparrowhawk tracks were not included in all of the analyses as no wind data were available for them. For the wind analyses 277 raptor tracks were available. The dominating part of the tracking data refer to flight over land or very close to the coastline and only a few birds were tracked when continuing far offshore (see maps in Fig. 6 below). Flight data over the sea was too limited to allow a distinction between flight over land and sea, and we used data from all available flights over land, coast and sea in our comparative analyses of flight performance of the two study species.

2.1 Flight altitude and wind speed

Most sparrowhawks (90%) were recorded below 328 m above sea level (a.s.l.) and median flight altitude was 150 m (a.s.l.). The highest flying sparrowhawk was recorded at 764 m (a.s.l.). The median flight altitude of the common buzzards was 305 m (a.s.l.) with 90% of them flying below 588 m (a.s.l.). The highest flying common buzzard was recorded at 873 m (a.s.l.) (Fig.1 shows the distribution of mean altitudes for the entire tracks, while the maximum heights given above refer to the top altitude reached by an individual within its tracking time). The median flight altitudes of the two raptor species were significantly different (Mann-Whitney U = 12734.5, n = 280, P < 0.001).

Despite better thermal conditions being expected to occur around local noon (Kerlinger, 1995), no significant relationship was observed between time of the day and the average flight altitude, neither in sparrowhawks (r^2 = 0.017, n = 183, P = 0.21; quadratic regression model), nor in common buzzards (r^2 = 0.001, n = 97, P = 0.95; quadratic regression model).

Wind speed had a significant negative effect on flight altitudes for both sparrowhawks (r^2 = 0.106, n = 180, P < 0.001; y = -12.12x + 292.58; linear regression) and common buzzards (r^2 = 0.554, n = 97, P < 0.001; y = -33.14x + 503.5; linear regression) (Fig. 2). Yet, sparrowhawks' flight altitudes were less affected by the wind than common buzzards' (GLM: F_{276} = 29.39, P < 0.001).

An interesting result was revealed when comparing wind speeds at which the two raptor species were flying (Fig. 3). There was a significant difference between the sparrowhawks and common buzzards (t_{274} = 8.7, P < 0.001), with common buzzards flying with on average lower wind speeds than sparrowhawks.

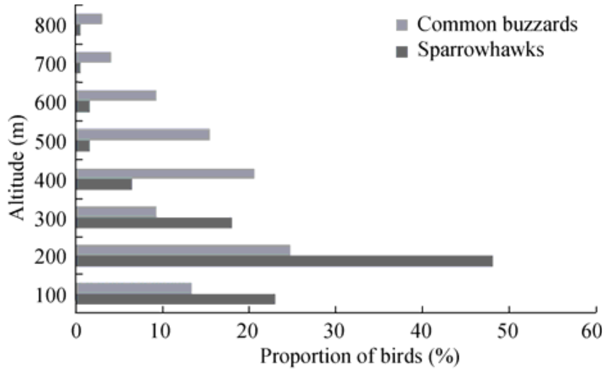

Fig. 1 Percentage of sparrowhawks and common buzzards flying at different altitudes (meters above sea level, average per track)

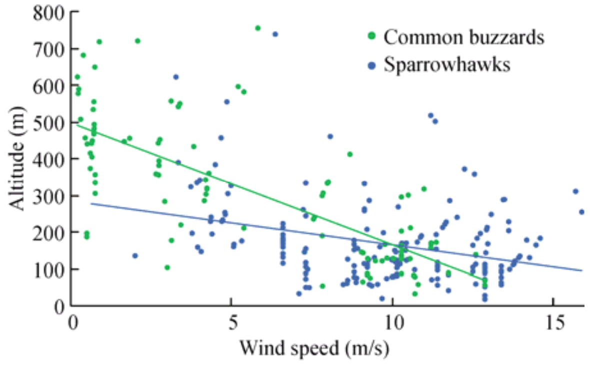

Fig. 2 Flight altitudes of sparrowhawks and common buzzards (meters above sea level, average per track) in relation to wind speed (meters per second)

Sparrowhawks' altitudes (r^2 = 0.106, n = 180, P < 0.001; y = -12.12x + 292.58) were less affected by the wind than common buzzards' (r^2 = 0.554, n = 97, P < 0.001; y = -33.14x + 503.5). The interaction effect altitude*species was significant according to GLM analysis (F_{276}= 29.39, P< 0.001).

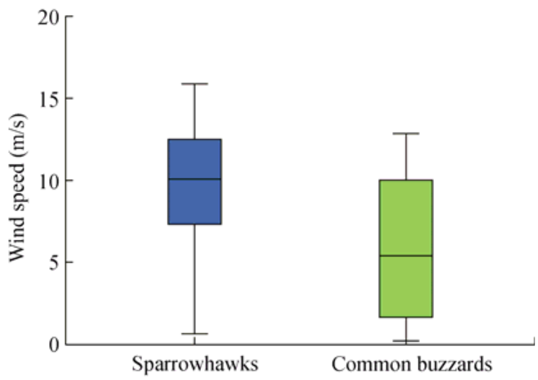

Fig. 3 Wind speed (meters per second) at which sparrowhawks and common buzzards were flying

Common buzzards were flying with on average on lower wind speeds than sparrowhawks (t_{274} = 8.7, P < 0.001). The dark line in the middle of the boxes represents the median. The bottom of the box indicates 25th percentiles, the top – 75th percentile. T- bars (whiskers) extend 1.5 times the height of the box, or show minimum and maximum values.

2.2 Flight speeds

There was a tendency for groundspeeds to differ between species, although the difference was not statistically significant (t_{275} = 1.95, P = 0.053). Sparrowhawks had significantly higher airspeeds than common buzzards (t_{275} = 3.96, P < 0.001) (Table 1).

A significant difference was found in cross-country speed (t_{122} = 3.4, P = 0.001), with sparrowhawks having higher cross-country speed than common buzzards (Table 1).

The airspeed, groundspeed and cross-country speeds were related to the tailwind component (relative to the heading direction of the bird) in both raptors. Airspeed (linear regression; $y = -0.23x + 9.53$, R^2 = 0.11, n = 180, P < 0.001 for sparrowhawks; $y = -0.26x + 8.2$, r^2 = 0.13, n = 97, P < 0.001 for common buzzards) was reduced with following winds and increased with opposing winds, groundspeed (linear regression; $y = 0.54x + 12.29$, r^2 = 0.53, n = 180, P < 0.001 for sparrowhawks; $y = 0.37x + 9.25$, r^2 = 0.27, n = 97, P < 0.001 for common buzzards) and cross-country speed (linear regression; $y = 0.5x + 11.83$, r^2 = 0.42, n = 69, P < 0.001 for sparrowhawks; $y = 0.27x + 7.74$, R^2 = 0.07, n = 54, P = 0.033 for common buzzards) increased with increasing tailwind-component (Fig. 4A and B).

Table 1 Table showing air, ground, and cross-country speeds in meters per second for the sparrowhawks and common buzzards (mean per track)

	Airspeed		Groundspeed			Cross-country speed		
	Mean	*SD*	Mean	*SD*	*n*	Mean	*SD*	*n*
Sparrowhawks	11.0	3.9	8.8	4.1	180	9.6	4.5	70
Common buzzards	9.2	3.5	7.9	3.5	97	7.2	3.2	54

Mean and standard deviation (SD), n = number of tracks (same for air- and groundspeed).

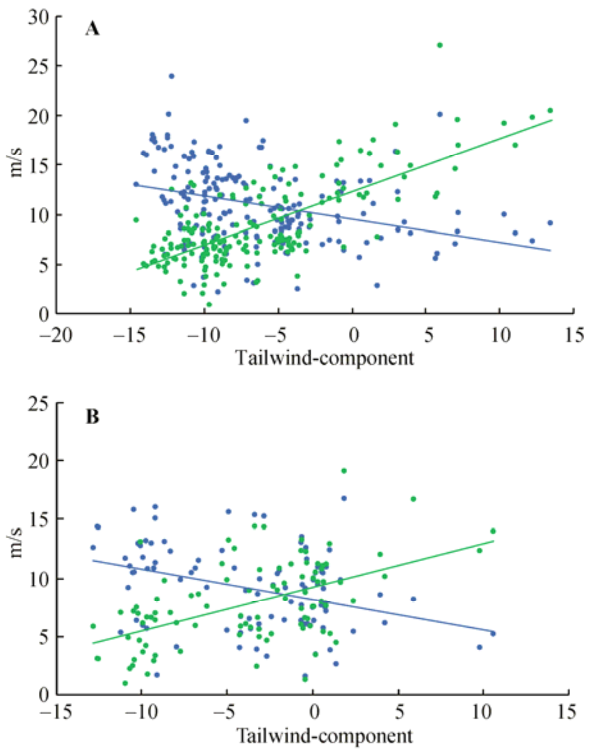

Fig. 4 A) Airspeed (blue) (r^2 = 0.11, n = 180, P < 0.001, y = -0.26x + 8.2) and groundspeed (green) (r^2 = 0.53, n = 180, P < 0.001, y = 0.54x + 12.29) of sparrowhawks in relation to tailwind-component. B) Airspeed (blue) (r^2 = 0.13, n = 97, P < 0.001, y = -0.26x + 8.2) and groundspeed (green) (y = 0.37x + 9.25, r^2 = 0.27, n = 97, P < 0.001, y = 0.37x + 9.25) of common buzzards in relation to tailwind-component

2.3 Migratory directions

Westerly winds dominated during this study, yet there was a difference in the wind directions (Watson-Williams test; F_{275} = 11.77, P < 0.001) in which sparrowhawks and common buzzards were flying. Sparrowhawks were mainly flying with westerly winds, whereas common buzzards were flying with more variable winds (Fig. 5). Mean heading directions of sparrowhawks (272 ± 60°, r = 0.58) and common buzzards (269 ± 70°, r = 0.48) were towards the west, which is the expected migration direction. No significant difference was found between sparrowhawk and common buzzard's heading directions (Watson-Williams test; F_{275} = 0.1, P = 0.75).

Mean track direction of sparrowhawks was towards the northwest, though the mean vector length (r) was very low, meaning that their tracks were very scattered (298 ± 125°, r = 0.09). Common buzzards had less scattered track directions with mean vector value more towards west (278 ± 79°, r = 0.39). When comparing heading and track directions of sparrowhawks one can see that even though some birds were heading towards

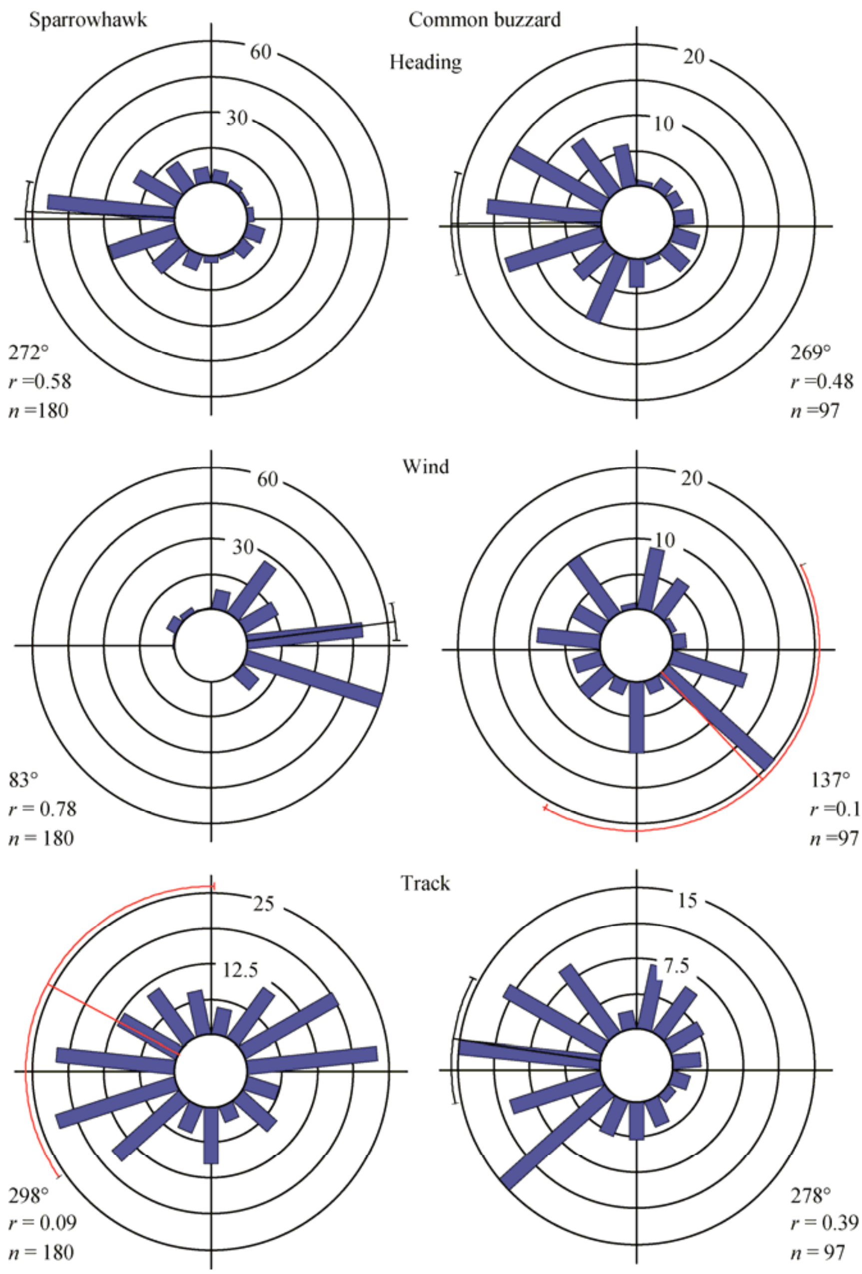

Fig. 5 Wind, track and heading directions of the sparrowhawks and common buzzards

r shows mean vector value. Wind direction is the direction towards which the wind was blowing. The length of the bars represent the number of observations that fall in the same category. Circles represent the scale as indicated by the numbers. Mean directions with confidence intervals are shown in black and, when concentration is low, in red.

the west they ended up flying east. A similar pattern was observed to a lesser extent for common buzzards (Fig. 5).

Reverse migration (track directions towards 0–134°) occurred to a relatively high degree among both raptor species, but the proportion of reverse migrants was higher for the sparrowhawks (71/180 = 39%) than for the common buzzards (22/97 = 23%). This difference in proportions was statistically significant (χ^2 = 7.99, df = 1, P < 0.005). Dominating westerly winds seem to have had an effect on track directions of both species, but to a lesser degree for the common buzzards. Sparrowhawks track directions were more scattered and the difference between mean track and heading directions was greater for the sparrowhawks than for the common buzzards (Fig. 5). This could have been a result of sparrowhawks travelling in opposing and strong winds much more often than the common buzzards (Fig. 3, 5).

2.4 Flight trajectories in relation to wind and topography

When comparing sparrowhawks flying with winds from northern and southern semicircles (see methods) there was a significant difference in heading (Watson-Williams test; F_{107} = 23.8, P < 0.001) and track (Watson-Williams test; F_{107} = 6.5, P = 0.012) directions. Similar patterns were observed for common buzzards, with a significant difference in heading directions (Watson-Williams test; F_{73} = 13.5, P < 0.001), but not in track directions (Watson-Williams test; F_{73} = 3.2, P = 0.08). While the heading directions tended to shift into the wind, track directions tended to shift with the winds. This means that the birds changed their headings into the wind to compensate partly for the wind drift, but also that they sometimes subjected themselves to partial wind drift, departing over the sea across the coastline with minimum wind resistance. The detailed flight trajectories of the two raptor species in northerly and southerly winds are shown in Fig. 6 along with the circular distributions for heading, wind and track directions. As seen from this figure, flights were more concentrated at the southern coastline of the peninsula under northerly winds, with some birds departing over the sea from this coastline, while the flight pattern was more scattered over the peninsula under southerly winds with some migrants departing westwards across the western coastline of the peninsula.

With winds from the southern semicircle, both species of raptors moved westwards over the peninsula, with mean track directions close to west and some were departing westwards over the sea from the western coastline of the peninsula (Fig. 6). When comparing heading directions within the species, in different winds, it seems that both raptor species have reacted similarly by changing their heading directions into the wind direction, thus compensating at least partly for the wind drift when migrating across Falsterbo Peninsula.

3 Discussion

3.1 Flight altitudes and wind effect

The average flight altitudes, both for sparrowhawks and common buzzards were low in comparison with altitudes of similar-sized migrating raptors recorded in other studies: Levant sparrowhawks (280 and 470 m median flight altitudes, Spaar et al., 1998), Honey buzzards (average flight altitude around 600 m, Bruderer et al., 1994; Meyer et al., 2000) (Fig.1). However, those studies were done at lower latitudes where, presumably, thermal conditions were better than at Falsterbo. During autumn migration, both sparrowhawks and common buzzards had a mean altitude of only 300 m above the ground in Switzerland north of the Alps (Schmid et al., 1986). It has been shown that flight altitude correlates positively with climb rate in thermal soaring (Spaar, 1995; Spaar and Bruderer, 1996), meaning that the birds soar to higher altitudes in stronger thermals than in weaker ones. Such observations are also consistent with flight altitudes in migrating American raptors (Kerlinger et al., 1985). Moreover, it has been shown that the strength of thermal updrafts rather than the raptor's body size determines climbing rate in thermal circling (Spaar, 1997).

Another possible reason why sparrowhawk and common buzzard's average flight altitudes were low at Falsterbo might be relatively high wind speeds. The average annual wind speed at Falsterbo peninsula is quite high, about 8.5–9 m/s at 100 m altitude according to meteorological models (Bergström, 2007). Wind is considered to be a very important selective agent (Alerstam, 1979; Butler et al., 1997). As we can see from Fig. 2, both sparrowhawks and common buzzards were flying at lower altitudes with increasing wind speed. This could be due to avoidance of even higher wind speeds at higher altitudes (Alerstam, 1979; Richardson, 1976). Furthermore, a significant interaction effect between species and wind speed on flight altitude showed that the wind speed had a greater influence on flight altitude of common buzzards than of sparrowhawks (Fig. 2). In addition, wind direction could have an effect on bird's flight altitude. As Rudebeck (1950) pointed out, birds flying with tailwinds tend to gain higher flight altitudes. Tailwinds in this case would be winds from north-

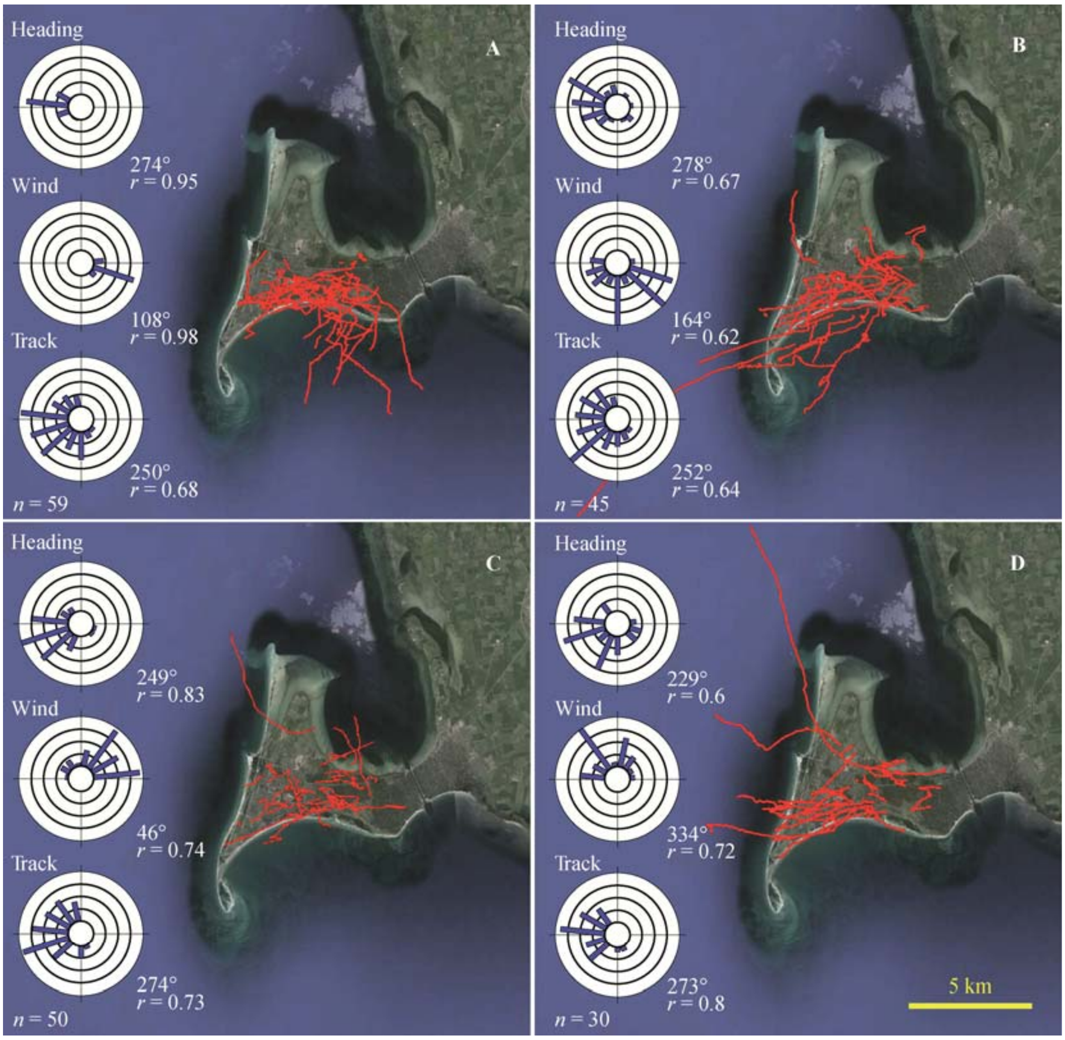

Fig. 6 Maps showing raptors' flight paths over Falsterbo Peninsula in relation to wind
A. Sparrowhawks flying with winds from northern semicircle. **B**. Common buzzards flying with winds from northern semicircle. **C**. Sparrowhawks flying with winds from southern semicircle. **D**. Common buzzards flying with winds from southern semicircle. Circular graphs show distribution of wind, heading and track directions. The length of the bars represent the number of observations that fall in the same category.

eastern direction. However, these winds are not very common at Falsterbo Peninsula during autumn migration (about responses to winds by hawks and buzzards see also Kerlinger, 1989; Kerlinger and Gauthreaux, 1984; Panuccio et al., 2010).

There could be several main reasons for differences in altitude (Fig. 1) and wind selectivity (Fig. 3) between sparrowhawks and common buzzards. First, as energy expenditure for flapping flight increases with increasing body mass it is more energetically efficient for larger birds, such as common buzzard, to use soaring-gliding rather than flapping-gliding flight (Pennycuick, 1972; Hedenström, 1993). As common buzzards gain more from soaring-gliding flight than the sparrowhawks they could be more prone to select better thermal conditions and obtain higher altitudes. It is likely that strong winds were associated with poor thermal conditions, and that the common buzzards therefore avoided windy days in order to be able to exploit better thermal conditions on days with weaker winds.

Secondly, many small songbirds migrate through Falsterbo Peninsula, and sparrowhawks use this opportunity to forage. While flying low, sparrowhawks might look for prey thus using a strategy of fly-and-forage migration (Strandberg and Alerstam, 2007). Rudebeck (1950–51) described a very regular occurrence of hunting by sparrowhawks during autumn migration at Falsterbo. It was estimated that about 10 % of all chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* were removed by raptors, mainly sparrowhawks, during a six-week period of autumn migration at a study area not far from the Falsterbo Peninsula (Lindström, 1989). Therefore, flying at lower altitudes and hunting prey could be an optimal behaviour for the sparrowhawks.

However, one should not forget that these results could be influenced to some degree by a selection bias of the study. While migrating common buzzards were observed and tracked mainly in moderate and weak winds when thermals were available, sparrowhawks migrated in considerable numbers also in stronger winds. This may have caused the numbers of sparrowhawks tracked under weak and following winds (when they may climb to higher altitudes) to become underrepresented in our data set in relation to the number tracked when flying at lower altitudes under stronger winds (when no or little potential tracking time was occupied by the tracking of common buzzards). This means that we cannot conclude from our data that sparrowhawks preferentially select headwinds for their migratory flights, only that they frequently migrate under such winds, in contrast to the common buzzards, which avoid such winds.

Contrary to some studies (Heintzelman, 1975; Kerlinger et al., 1985; Mellone et al., 2012; Spaar and Bruderer, 1996) which found the highest flight altitudes to be reached by raptors around noon, there was no significant relationship between time of the day and average flight altitude for the sparrowhawks and common buzzards. These results might arise because of relatively weak thermal updrafts (no significant correlation between time of the day and climb rates) and/or the windy conditions at the Falsterbo Peninsula.

3.2 Air- and ground speeds

Airspeeds of the sparrowhawks and common buzzards (Table 1) were quite similar to airspeeds reported in the study of Bruderer and Boldt (2001) (9.8 and 9.6 m/s respectively). However, Bruderer and Boldt (2001) subdivided flight into three categories (gliding flight without wing beats, flapping flight with a relatively high proportion of wing flaps and mixed behaviour with gliding supported by occasional wing flaps) but no such subdivision was made in this study. Mean airspeed of sparrowhawks, 11 m/s, was also very similar to diurnal flapping migrants of Levant sparrowhawks migrating in southern Israel (10.4 m/s), but the resulting mean groundspeed of 8.8 m/s was smaller than that of Levant sparrowhawks (15.2 m/s, Spaar et al., 1998). The lower mean groundspeed was the result of relatively strong and opposing winds encountered by the sparrowhawks at Falsterbo Peninsula.

The higher airspeeds of sparrowhawks than of common buzzards corresponds with predictions. This difference could have been the result of several factors. First, sparrowhawks could have been using flapping flight to a large extent as thermal conditions were not very good and by that could have increased their airspeed compared to common buzzards. This was observed by Rudebeck (1950) who noted that sparrowhawks relied on thermals much less than common buzzards, even when good thermals were available. Secondly, sparrowhawks were flying in higher wind speeds compared to common buzzards (Fig. 3), and as the winds were dominantly from the west, most of the sparrowhawks encountered opposing winds (headwinds). Therefore, the stronger opposing winds which sparrowhawk encountered could explain why there was no significant difference between the species in the groundspeed.

3.3 Cross-country performance

Sparrowhawks' cross-country speed relative to the ground was comparable to similar sized Levant sparrowhawks migrating in southern Israel (Spaar et al., 1998). However, in their study, Spaar et al. (1998) split cross-country speed into different flight styles: flapping-gliding (11.9 ± 5.6 m/s), soaring-flapping (7.1 ± 3.3 m/s) and soaring-gliding (9.2 ± 2.8 m /s). The cross-country speed of the sparrowhawks flying at Falsterbo (9.6 ± 4.5 m/s) was most similar to soaring-gliding cross-country speed of Levant sparrowhawks.

The average cross-country speed of common buzzards of 7.2 m/s (25.9 km/h) was somewhat lower than honey buzzards' cross-country speed of 10.4 m/s (37.4 km/h) flying in Israel. However, it was very similar to the cross-country speed of steppe buzzards *Buteo buteo vulpinus* flying with opposing winds (7.7m/s) in southern Israel. Steppe buzzards, however, had significantly higher cross-country speed when flying with side winds (9.7 m/s) and following winds (11.4 m/s) (Spaar and Bruderer, 1997). This difference could have resulted from several factors, for example lower thermal activity in Falsterbo peninsula than in Israel, difference in migration strategy, common buzzards being intra-European migrants and thus not as much constrained in time as honey buzzards which are tropical migrants. North of the Alps in Switzerland the mean cross-country speed of sparrowhawks and common buzzards on autumn migration were 9.3 and 7.5 m/s, respectively, which is very similar to the speeds at Falsterbo (Schmid et al., 1986).

The resulting cross-country speed was higher for the sparrowhawks, and this is in agreement with the expectation that migrants using flapping flight to a higher degree (sparrowhawks) attain higher cross-country speeds than more pure soaring migrants (common buzzards) (Pennycuick, 1989). Moreover, Falsterbo Peninsula is a place where birds start to cross the sea to the other side of the Öresund strait. Raptors have to judge whether they are going to depart across the sea or delay departure, depending on environmental conditions such as wind speed, wind direction and time of day. This became very obvious when a big flock of common buzzards were circling at Falsterbo peninsula at around 4.00 p.m. and while some birds were migrating south, others flew back in reverse migration. It has been shown that raptors are less likely to cross a water barrier in the afternoon rather than in the morning (Panuccio, 2010). In addition common buzzards were more selective of lower wind speeds (see results), probably associated with better thermal activity and they might have spent more time evaluating conditions for migration than sparrowhawks. This decision time might also have contributed to lower average cross-country speed. Nevertheless, both raptor species increased their cross-country speed with increasing tailwind assistance (Mellone et al., 2012).

3.4 Migratory directions

Mean migratory directions of the sparrowhawks and common buzzards coincided with the expected westerly directions. Though no significant difference was found between the species in mean heading direction (as predicted), the distribution of sparrowhawks heading directions tended to be more concentrated than the distribution of heading directions of common buzzards (Fig. 5), which could be the result of more variable wind directions for common buzzards than for sparrowhawks.

A bimodal distribution of track directions appeared which identifies forward and reverse migrants (Fig. 5). Moreover, when comparing heading and track directions of sparrowhawks it seems that while some birds were heading towards the migratory direction they ended up flying backwards in the reverse direction. In comparison, the occurrence of reverse migration, although clearly taking place in some cases, was less pronounced among common buzzards. Some of the cases of reverse migration among the sparrowhawks appeared to be the result of a strategy to hunt by flying in the migratory direction at low altitude into strong winds, after which the bird climbed and allowed itself to be transported backwards by the strong winds, resuming hunting flight into the strong winds but having experienced a net transport in the reverse direction.

3.5 Flight in relation to topography and different winds

The coastlines seem to have an effect on the raptors flight paths, as many of the tracks follow the south coast of the peninsula (Fig. 6). This was not the case for nocturnally migrating passerines tracked at the same site, where the local coastlines did not seem to have any important effect on the flight directions (Nilsson et. al., 2014).

A number of sparrowhawks which encountered winds from the northern semicircle departed over the sea from the southern coastline before reaching the tip of the Falsterbo Peninsula (Fig. 6). Similar observations at Falsterbo Peninsula were made by Rudebeck (1950), who pointed out that there were relatively fewer migrating sparrowhawks (compared to common buzzards) at Falsterbo when winds were blowing from north-west directions. He argued that the sparrowhawks were less confined to the coastline compared to common buzzards, and more prone to depart from the southern coastline of the province of Scania and flying out over the sea. It seems that this difference in topographical preference in relation to wind between the sparrowhawks and common buzzards could be observed on the small scale of Falsterbo Peninsula as well. Nevertheless, both species had very similar track directions, which resulted with mean vector values towards west-south-west.

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