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# Factors affecting the flight altitude of migrating waterbirds in Western Estonia

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We studied the effects of weather conditions, temporal factors and distance to coast on the flight altitude of migrating waterbirds in Western Estonia. We used a laser range finder and marine surveillance radar to measure flight altitudes, and identified significant effects on avian flight altitude by several weather components, particularly wind conditions, visibility and cloud cover. Wind components played a particularly significant role. Tailwinds were generally associated with elevated flight altitude, and reductions in flight altitude were usually associated with high wind speed, possibly because of enhanced energetic costs or risk of being blown off course. Behavioural and physical adaptations to the environment also contributed to specific flight-altitude selection. The results provide new insights into factors determining flight altitude and useful information to support environmental impact assessments.

## 1. Introduction

During migration, avian flight altitudes show remarkable diversity, largely associated with energetic costs. For example, the costs of climbing and cruising at a certain altitude are traded-off with the possible advantages of flying at this altitude, in terms of wind assistance (e.g., Alerstam & Lindström 1990, Erni *et al*. 2005). Given that wind speed tends to increase with distance from the ground (e.g., Arya 1988), gaining as much height as possible may be favourable from the outset, at least during tailwind conditions. In particular, it is energetically less costly to fly at a high altitude in thinner air than in denser air encountered at lower altitudes. However, the costs of gaining altitude and the physiological constraints imposed by reduced oxygen availability may reduce the benefit of migrating at high altitudes, especially for large birds (Liechti *et al*. 2000, Klaassen *et al*. 2004, Liechti & Schmaljohann 2007). Hence, the majority of migrating birds are likely to occur at altitudes below 3,000 m a.s.l. (Alerstam 1990, Dinevich *et al*. 2005).

There is a diverse literature on flight altitude mainly focused on daytime migration of large soaring birds and nocturnal migration of passerines (e.g., Spaar & Bruderer 1996, Zehnder *et al*.

2001, Mabee *et al*. 2006, Dokter *et al*. 2010). By contrast, fewer publications deal with species-specific flight altitudes of waterbirds, such as divers, geese, ducks, gulls and waders, and the identification of the factors determining their flight altitude.

The prevailing view is that migratory birds probably do not react to the general weather situation as such, but to key components, particularly wind and rain (Newton 2010). Daytime waterbird migration may occur at relatively low altitudes (<300 m), while the nocturnal migration seems to occur above one kilometre (Cooper & Ritchie 1995). However, flight altitude is highly dependent on the species and the nature of the migration, i.e., seasonal or local migration. Often the flight altitude shows substantial day-to-day variation, which in many cases is likely to derive from wind components. For example, tailwinds of considerable strength provide favourable wind assistance that is often associated with elevated flight altitudes (Jacoby & Jõgi 1972, Alerstam & Gudmundsson 1999, Krüger & Garthe 2001, Dierschke 2002).

Flight altitudes of birds are not just of purely academic interest. In recent decades an increased awareness of the importance of flight altitude has been acknowledged in association with different human activities. Aviation authorities are concerned about the risks of bird collisions with aircraft and the statutory environmental agencies also need to be aware of collision risks associated with major man-made obstacles in the flight paths of migrating birds such as towers, bridges and wind parks, as these are considered potential threats to bird populations (Richardson 1990, Dirksen *et al*. 1998, Hicklin & Bunker-Popma 2001, Garthe & Hüppop 2004, Veltri & Klem 2005, Shamoun-Baranes *et al*. 2006, Krijgsveld *et al*. 2009).

The present study site at Virtsu, Estonia, is situated on the main waterbird spring migration route in the eastern part of the Baltic Sea. Virtsu offers a unique opportunity to obtain measurements of flight altitude on a diverse range of migrating waterbirds that under many circumstances are difficult to obtain. First, we test the hypothesis that (1) flight altitude of waterbirds is higher during tailwinds compared to other wind directions, given that more favourable wind assistance is likely to be obtained by gaining altitude when tailwinds prevail (Gauthreaux 1991). By contrast, strong headwinds are likely to be unfavourable to migrating birds from an energetic perspective, although it might temporarily assist in obtaining a higher cruising altitude.

Strong winds may also affect aerodynamics of flight and blow birds off the optimal course (e.g., Alerstam 1979), making it less profitable to gain altitude especially if strong winds prevail at sea level. We therefore test the hypothesis that (2) low wind speed will enhance flight altitude. We also test whether (3) birds fly higher in good visibility and absence of cloud cover. These conditions do not limit visual cues that may be important for navigation, and do not put altitudinal limitations on waterbirds, such as those caused by multiple layers of clouds.

Precipitation is often associated with limited visibility and cloud cover (Erni *et al.* 2002). We therefore test the prediction that (4) precipitation will also lower flight altitude. Furthermore (5), higher flight altitudes will presumably be observed at the coastline than further offshore, given that migrating waterbirds typically gain altitude as they cross stretches of land (Alerstam *et al*. 1974). Below we evaluate these five predictions and discuss differences between daytime and nocturnal migration. We also compare our results to a previous radar study of spring migration done in the same study area (Jacoby 1983), and put the findings into the perspective of potential hazards to migrating waterbirds posed by man-made superstructures, such as offshore wind farms and bridges.

## 2. Material and methods

### 2.1. Study area and data collection

The study area is located at the eastern coast of the Baltic Sea, and includes the Suur Väin strait, the coastal zone of the Virtsu peninsula, and the eastern coast of Muhu island (Fig. 1). Observations were made at the Virtsu lighthouse on the Virtsu Peninsula (58°34’1.64” N, 23°30’8.62” E) from 6 to 24 May 2009. Previous studies suggest that the main departure of seaducks from the spring-season staging areas in Western Estonia primarily occurs between mid and late May (e.g., Jõgi 1970, Leivo *et al*. 1994). Data collection followed a pre-

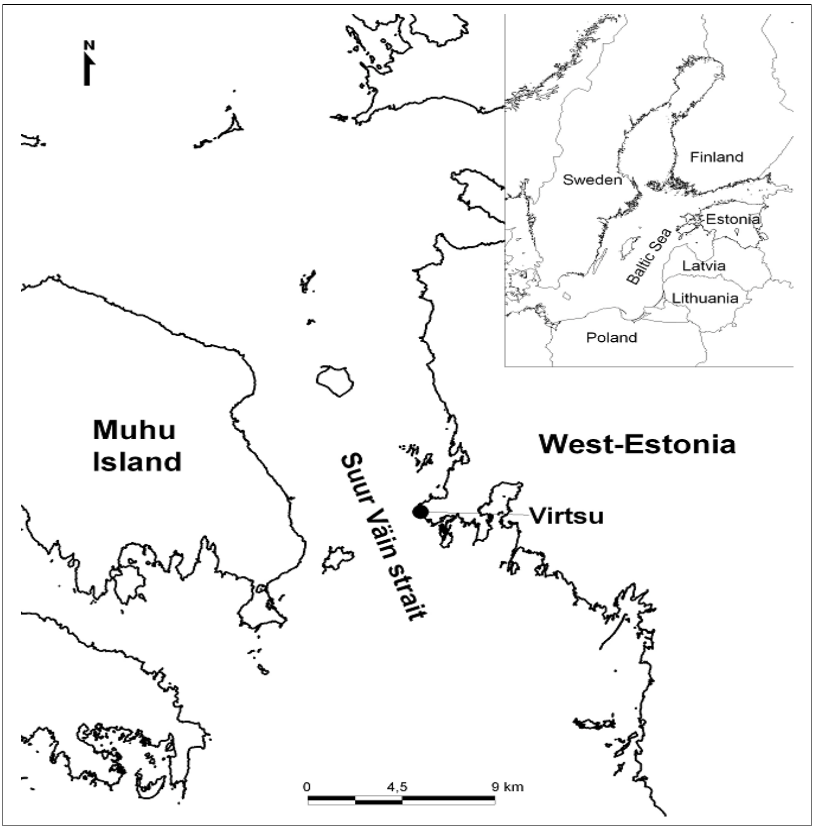

Fig. 1. Location of the study site at Virtsu (black dot), situated in the eastern part of the Baltic Sea (small inserted map).

defined schedule to ensure complete coverage of selected periods of the day. Night-time observations were prioritised because little such information on bird migration exists during this particular period in the region. The period between 10:30 and 16:30 was not covered, as daytime migration is generally well described, and migration during this part of the 24-hour period is generally poor.

Data on flight altitude were compiled using two methods: (1) a laser range finder used during the daylight hours (05:30 to 21:30); and (2) a vertical radar used during the night (22:30 to 04:30), with the hours 04:30 to 05:30 and 21:30 to 22:30 defined as transition periods between day and night. A hand-held laser range finder (Vectronics Vector 21; accuracy ±1 m) was used to obtain direct measurements of flight altitude of specific birds or flocks visible to the observer. A mobile ship radar (Furuno FAR2127BB; 25 kW, X-band) was used for radar observations, with the antenna tilted into vertical position to measure flight altitude of birds over a range of 1.8 km (one nautical mile). Marine surveillance radar gives no information on the species involved during nocturnal migration.

The mass migration of seaducks in May overlaps with the migration many passerines. Hence, in order to obtain information on the species involved in migration, the sessions with vertical radar (59 hours) were alternated with periods of horizontal radar operation (61 hours) during which the heading and ground speed of birds were measured. Ground speeds were converted to equivalent air speeds, using vector subtraction of wind speed (Alerstam 1990) and correcting for atmospheric pressure and temperature at the flight altitudes of birds (Pennycuick 1989). As passerines and waterbirds have quite distinct speeds of migration, equivalent air speed provides a good indicator of the species group involved in nocturnal migration. Typical nocturnal-migrating waterbirds, such as seaducks and divers, share an equivalent air speed of >16 m/s, in contrast to nocturnal passerines such as thrushes and the Dunnock (*Pru-*

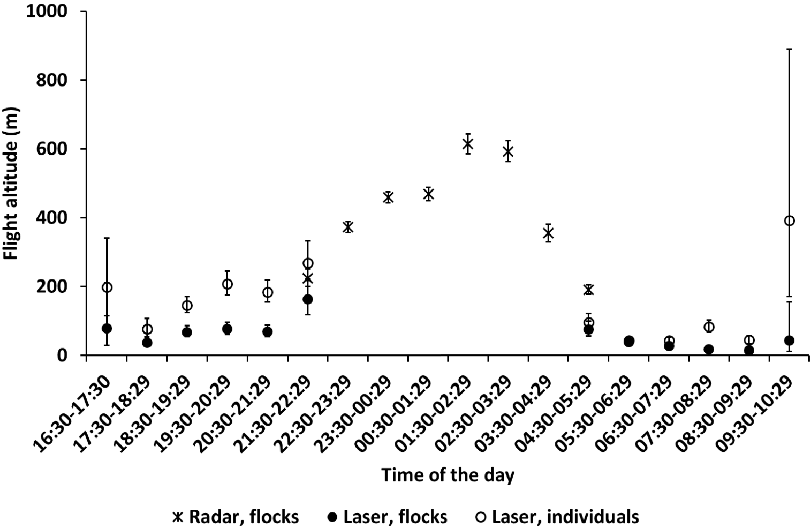

Fig. 2. Mean flight altitude of bird flocks (± 95% confidence limits) obtained by measurements with radar and laser range finder. Data from the range finder were weighted by the number of individuals in the flocks. The night covered the period 22:30 to 04:30.

*nella modularis*), which have an equivalent airspeed of <14 m/s (Alerstam *et al.* 2007).

We cannot completely exclude the possibility that we overestimate the proportion of waterbirds in our sample. This is because flight-speed estimates were obtained from echoes using horizontal radar orientation, which covered a larger proportion of scanned lower altitudes compared to the vertically-orientated radar. However, this assumes that passerines fly at higher altitudes than waterbirds, which may be the case, although the difference in this study is probably of minor importance, because long-distance nocturnal waterbird migration over Western Estonia reaches to considerable heights (up to 1,500–2,500 m; Jacoby 1983).

## 2.2. Data analysis

Three data sets were analysed: (1) the entire data obtained by radar at night; (2) a sub-set of the nocturnal radar data, when flight-speed measurements suggested that > 85% of the bird flocks comprised waterbirds; and (3) the data set of waterbirds only, obtained using the laser range finder. Mean flight altitudes of flocks were estimated by log-transformed data (to obtain a normal data distribution). Laser range-finder data were also weighted by the number of individuals in the flocks so as to present mean flight altitudes corrected for the number of individuals migrating at different altitudes. Thus, larger waterbird flocks tended to fly at higher altitude than did smaller flocks ($t = 28.66$, df = 1, $P < 0.0001$, $R^2 = 0.32$, $n = 1{,}786$).

The waterbird sub-set of nocturnal radar data was analysed in relation to the following factors: day number (days from 1 May), time of the day (hour), cloud cover (from 0/8 to 8/8), visibility (km), wind direction (NW, NE, SE and SW), wind speed (m/s) and precipitation (presence/absence). For laser range-finder data, the same factors were analysed with distance to coast (km) and focal bird species as additional model factors, as species-specific measurements of distance were taken perpendicular to the coast, simultaneously with measurements of flight altitude. Weather conditions at the Virtsu observation point were collected every hour. These data were supplemented by data logged automatically every hour at the weather station in Virtsu (data provided by the Estonian Meteorological-Hydrological Institute, EMHI).

Analysis of covariance was applied on log-transformed flight altitude data in order to provide a better fit to the normal distribution of residuals, while incorporating the independent variables. Because vertical radar covers a semi-circular field, the uneven coverage at different altitudes was corrected for by weighting each observation with the reciprocal of the proportional area covered at each altitude. It was not possible to correct for flock size in the radar data, i.e., we predicted the altitude of flocks, not altitudes of individuals, in the analysis.

Table 1. Explanatory variables of the best models predicting the flight altitude of waterbird-dominated bird flocks observed from 22:30 to 00:30 at the Virtsu lighthouse, May 2009, the associated explanatory power (adj. $R^2$) and the ranking of models (ΔAIC) together with the likelihood that a model is the best amongst candidate models (Akaike Weight). Data were derived from vertically-operated radar. Explanatory variables: Speed = wind speed (m/s), Direct = wind direction (SW, SE, NW and NE) and Visib = visibility (km). Only models with substantial evidence are presented (ΔAIC < 2; Burnham & Anderson 2002).

| Factors | Adj. $R^2$ | ΔAIC | Akaike weight |
|---|---|---|---|
| Speed, Direct, Visib | 0.095 | 0.0 | 0.48 |
| Direct, Visib | 0.093 | 0.4 | 0.39 |

Independent variables were *a priori* checked for inter-correlations (Pearson product-moment) and multicollinearity (Condition index CI = sqrt[λmax/λmin], where λ is the eigenvalues of the correlation matrix of the independent variables). As a rule of thumb, correlations were considered weak when $|r| < 0.40$ and collinearity judged to be of concern at CI > 15. The selection of models was based on an information-theoretic approach, using Akaike Information Criterion (AIC), to derive the most parsimonious models, considering all combinations of independent variables. Only main effects were considered. For candidate models, Akaike weights were calculated to derive the best models accounting for 90% of the Akaike weights (Burnham & Anderson 2002). Model averaging of the trend estimates of the best models was undertaken based on the corrected Akaike weights of candidate models only. The precision of the estimates was derived by calculating the weighted unconditional 95% confidence limits. Estimates that had confidence limits that did not overlap with the point of zero were considered to reflect robust trends.

## 3. Results

### 3.1. General flight altitudes

With the reservation that data were collected by two different methods, flight altitudes of bird flocks were significantly higher during night (410 m [402; 418], mean [95% confidence limits on log-transformed data]) than during day (42 m [39; 46]) ($t = 52.57$, df = 1977.7, $P < 0.0001$, *t*-test with Satterthwaite's correction for unequal variances; Fig. 2). Mean night flight altitude was triple that observed during the day (125 m [117; 133], when correcting for the bias that larger flocks were migrating at higher altitudes than smaller flocks (see Material and methods). This effect was most evident during evenings (Fig. 2), the main migration period of seaducks.

To obtain an indication of the species groups involved in migration at night, flight speeds of radar tracks of birds were compiled using a horizontally operated radar antenna. This analysis showed that 69% of the bird tracks had an equivalent airspeed above 16 m/s, which suggests that two-thirds of the tracks were migrating waterbirds. This proportion varied from 89% during the early night (22:30 to 00:30) to 69% at mid-night (00:30 to 02:30) and 41% during the later part of the night (02:30 to 04:30).

Table 2. Model averages for independent variables derived from the best models predicting the flight altitude of waterbird dominated bird flocks observed from 22:30 to 00:30 at Virtsu Lighthouse, May 2009. Bold signature shows estimates with directional trends (no overlap of the 95% lower [LCLM] or upper [UCLM] confidence limit with the point of zero). Data were derived from vertically operated radar. Explanatory variables: Speed = wind speed (m/s); NE, NW and SE = wind directions compared to SW-winds; and Visib = visibility (km).

| | Intercept | Speed | NE | NW | SE | Visib. |
|---|---|---|---|---|---|---|
| Estimate | 5.4574 | **0.0500** | **–0.5728** | –0.0042 | **0.4179** | **0.0162** |
| LCLM | 5.1176 | 0.0084 | –0.8350 | –0.4016 | 0.1790 | 0.0125 |
| UCLM | 5.7971 | 0.0916 | –0.3107 | 0.3932 | 0.6568 | 0.0199 |

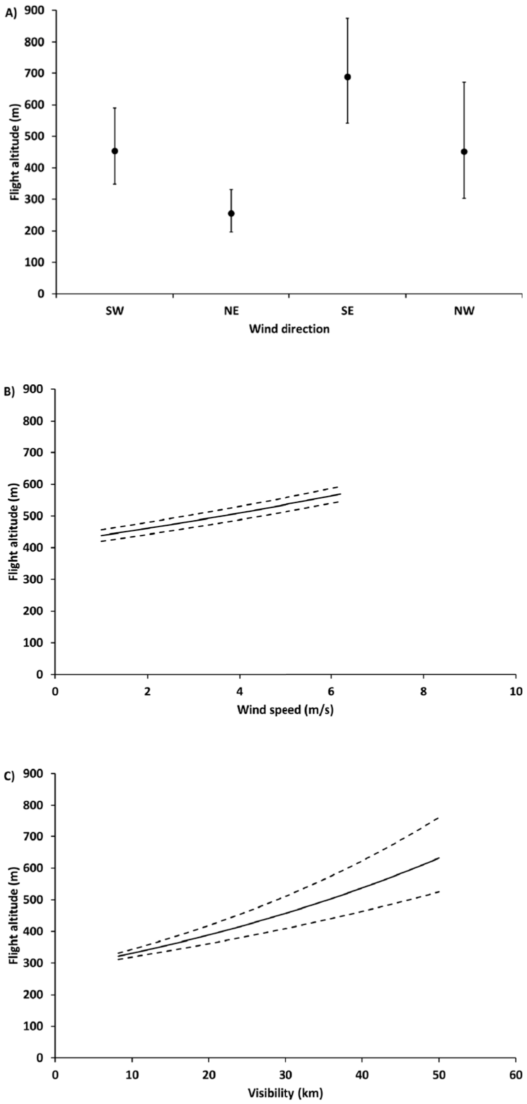

Fig. 3. Predicted flight altitudes obtained from the average model of waterbird data collected by vertically-operated radar at the Virtsu lighthouse between 22:30 and 00:30 in May 2009 as a function of wind direction (A), wind speed (B) and visibility (C). The bars in (A) and the dash lines in (B) and (C) indicate 95% confidence limits of the mean values.

## 3.2. Factors affecting flight altitude at night

The sub-set of nocturnal radar data (22:30–00:30), when the highest percentage of waterbirds were detected, was selected for further analysis. During this period, mean flight altitude was 425 m [414; 437, 95% confidence limits on log-transformed data]. Wind direction and visibility were included in the most competitive models, while wind speed could be eliminated from the model without substantial loss of information (Table 1). All three factors nevertheless showed directional trends (Table 2). The average model predicted that SW winds were associated with higher flight altitude than NE winds, and the same pattern was observed for SE winds against NW winds (Fig. 3A). Most data were collected during periods of southerly winds (59%), i.e., tailwinds, which must be considered in the interpretation of the effect on flight altitude from wind speed, which together with visibility were correlated with flight altitude (Fig. 3B–C). Correlations and collinearity between factors were weak ($|r| = 0.25$–$0.38$ and CI = 7.69).

## 3.3. Factors affecting daytime flight altitude

Flight altitudes collected in daylight during morning and evening hours, using the laser range finder, showed that an inclusion of 6–7 factors was associated with a moderately high explanatory power (Table 3). Amongst the independent factors, wind speed was slightly correlated with distance to coast (–0.42) while other correlations were weak ($|r| < 0.4$). The intercorrelations of factors did not suggest collinearity was of concern (CI = 12.56).

Adding precipitation to a model with time, wind direction and speed, distance to coast, cloud cover and species did not enhance the explanatory power. In fact, the inclusion of precipitation almost halved the likelihood of the model being the best explanation of flight altitudes (Table 3; Akaike weights 0.30 *vs* 0.64). Further analysis using an average model of the two most competitive models showed no directional trend along the factor precipitation, and day number and visibility were excluded from the most competitive models.

By contrast, the average model predicted directional trends in all other factors, including differences between species (Table 4; the large numbers of estimates are not presented, but $F_{45,1434} = 15.38$ and 15.30, $P < 0.0001$ for the two most competitive models). Flight altitude was higher during evening than in morning hours (60 m [52; 68] *vs* 37 m [32; 42], (predicted mean flight altitude from average model [95% confidence limits on log-transformed data] held constant at no precipitation

Table 3. Explanatory variables of the best models predicting the flight altitude of waterbird flocks observed at the Virtsu lighthouse, daytime May 2009, the associated explanatory power (Adj. $R^2$) and the ranking of models (ΔAIC) together with the likelihood that a model is the best amongst candidate models (Akaike Weight). Altitude data were derived from a laser range finder. Explanatory variables: Day = day number from 1 May, Time = morning or evening, Prec = the presence/absence of precipitation, Speed = wind speed (m/s), Direct = wind direction (SW, SE, NW or NE), Dist = Distance from coast (km), Cloud = cloud cover (0…8/8) and Spec = species. Only models with substantial evidence are presented (ΔAIC < 2; Burnham & Anderson 2002).

| Covariate | Adj. $R^2$ | ΔAIC | Akaike Weight |
|---|---|---|---|
| *All data* | | | |
| Time, Speed, Direct, Dist, Cloud, Spec | 0.651 | 0.0 | 0.64 |
| Time, Prec, Speed, Direct, Dist, Cloud, Spec | 0.651 | 1.5 | 0.30 |
| *Barnacle Goose* | | | |
| Prec, speed, Direct, Dist, Cloud | 0.302 | 0.0 | 0.59 |
| Time, Prec, Speed, Direct, Dist, Cloud | 0.299 | 1.9 | 0.23 |
| *Long-tailed Duck* | | | |
| Time, Speed, Direct, Dist, Cloud | 0.675 | 0.0 | 0.38 |
| Time, Prec, Speed, Direct, Dist, Cloud | 0.675 | 0.2 | 0.34 |
| *Common Scoter* | | | |
| Time, Prec, Speed, Direct, Dist, Cloud | 0.403 | 0.0 | 0.61 |
| Day, Time, Precip, Speed, Direct, Dist, Cloud | 0.411 | 1.9 | 0.24 |
| *Velvet Scoter* | | | |
| Time, Prec, Speed, Direct | 0.224 | 0.0 | 0.20 |
| Time, Speed, Direct | 0.232 | 0.2 | 0.18 |
| Time, Prec, Speed, Direct, Cloud | 0.205 | 1.0 | 0.12 |
| Time, Speed, Direct, Cloud | 0.214 | 1.4 | 0.10 |
| *Red- or Black-throated Diver* | | | |
| Time, Prec, Direct, Dist, Cloud | 0.119 | 0.0 | 0.27 |
| Time, Prec, Speed, Direct, Dist, Cloud | 0.131 | 0.2 | 0.24 |
| Prec, Direct, Dist, Cloud | 0.109 | 1.8 | 0.11 |
| Time, Speed, Direct, Dist, Cloud | 0.135 | 1.9 | 0.10 |

and average conditions of other factors). As with the night-time data, flight altitudes showed the same pattern with respect to wind direction. Thus, flight altitude of waterbirds was higher at SW winds than the opposite NE winds, and the flight altitudes at SE winds were predicted to be higher than in the opposing NW winds (Fig. 4A). Given the prevailing N to NE direction of migration (Leito 2009), the results suggest that headwinds considerably reduced flight altitude. In addition, strong winds (>8 m/s) reduced flight altitude by ca. 80% compared to calm conditions with wind speed <1 m/s with all other factors held constant (Fig. 4B). Full cloud cover was associated with lower flight altitudes amongst waterbirds compared with a cloudless sky, although the reduction in flight altitude was only ca. 10% (Fig. 4C). Finally, waterbirds flying near to the coast did so at lower altitudes than birds migrating further offshore (Table 4, Fig. 4D).

Species-specific differences in the daytime migration patterns were detected, and hence further analyses were undertaken on the five most abundant waterbirds species amongst the genuine migrants. Flocks of Barnacle Goose *Branta leucopsis* had the lowest mean flight altitude (45 m [39; 52], 95% confidence limits) compared to the other four waterbird species, whereas the daytime migration of the Long-tailed Duck *Clangula hyemalis* (133 m [107; 166]), Common Scoter *Melanitta nigra* (138 m [115; 165] and Velvet Scoter *Melanitta fusca* (128 m [101; 162] occurred at altitudes that were approximately three times higher. Red- or Black-throated Divers *Gavia stellata* and *G. arctica* had a mean flight altitude between the geese and the seaducks (73 m [66; 81]).

Wind speed was generally the factor that most consistently affected flight altitudes of individual species at the Suur Väin strait. In four of the five selected species, flight altitude was reduced by

Table 4. Model averages for independent variables derived from the best models predicting the flight altitude of waterbird flocks observed at Virtsu Lighthouse, daytime May 2009. Bold signature shows estimates with directional trends (no overlap of the 95% lower [LCLM] or upper [UCLM] confidence limit with the point of zero). Altitude data were derived from a laser range finder. Explanatory variables: Day = day number from 1 May, Time = morning or evening, the latter being the reference in the model, Prec = the presence or absence of precipitation (the latter being the reference in model), Speed = wind speed (m/s), Direct = wind direction (SW, SE, NW and NE, SW being the reference in the model), Dist = distance to the coast (m) and Cloud = cloud cover (0…8/8). NA: Factor not incorporated in average model. Estimate for the factor "species" is not presented to save space; see text for details.

| Model | Intercept | Day | Time | Prec | Speed | NE | NW | SE | Dist | Cloud |
|---|---|---|---|---|---|---|---|---|---|---|
| *All data* | | | | | | | | | | |
| Estimate | 3.2924 | NA | **–0.4796** | –0.1056 | **–0.2188** | **–0.3545** | **–0.7931** | **–0.5153** | **0.1912** | **–0.0315** |
| LCLM | 1.8454 | NA | –0.6158 | –0.847 | –0.2509 | –0.5258 | –0.9368 | –0.7020 | 0.1056 | –0.0507 |
| UCLM | 4.7395 | NA | –0.3435 | 0.1744 | –0.1867 | –0.1831 | –0.6493 | –0.3287 | 0.2768 | –0.0122 |
| *Barnacle Goose* | | | | | | | | | | |
| Estimate | 4.7268 | NA | 0.0393 | 1.6759 | **0.1789** | **–0.9293** | **–1.8190** | 0.1945 | **0.1491** | 0.0379 |
| LCLM | 2.8488 | NA | –0.2465 | –0.0929 | 0.0681 | –1.6500 | –2.2842 | –0.2184 | 0.0076 | –0.0061 |
| UCLM | 6.6048 | NA | 0.3250 | 3.4447 | 0.2897 | –0.2087 | –1.3538 | 0.6074 | 0.2905 | 0.0818 |
| *Long–tailed Duck* | | | | | | | | | | |
| Estimate | 7.1014 | NA | **–1.6678** | –0.2118 | **–0.4590** | **–0.8112** | **–1.3782** | **–1.0574** | **0.2220** | –0.0181 |
| LCLM | 6.5334 | NA | –2.0334 | –0.7116 | –0.5421 | –1.2030 | –1.7513 | –1.4554 | 0.0305 | –0.0683 |
| CLM | 7.6694 | NA | –1.302 | 0.2881 | –0.3759 | –0.4194 | –1.0052 | –0.6595 | 0.3997 | 0.0322 |
| *Common Scoter* | | | | | | | | | | |
| Estimate | 6.2643 | 0.0514 | **–0.6456** | **–0.6508** | **–0.5248** | –0.4970 | 0.0297 | –0.0188 | 0.1650 | **–0.1909** |
| LCLM | 5.1329 | –0.0023 | –1.0064 | –1.2685 | –0.6595 | –0.9996 | –0.1638 | –0.6713 | –0.0467 | –0.2574 |
| UCLM | 7.3957 | 0.1050 | –0.2849 | –0.0332 | –0.3901 | 0.0056 | 0.8100 | 0.2046 | 0.3766 | –0.1243 |
| *Velvet Scoter* | | | | | | | | | | |
| Estimate | 6.2359 | –0.0419 | –0.7060 | 0.0234 | **–0.2712** | –0.4196 | –0.5174 | **–1.0464** | **–0.4085** | –0.0009 |
| LCLM | 4.7594 | –0.1277 | –1.4744 | –0.8816 | –0.4255 | –1.0858 | –1.2402 | –1.8342 | –0.7648 | –0.1280 |
| UCLM | 7.7124 | 0.0439 | 0.0623 | 0.9283 | –0.1169 | 0.2466 | 0.2054 | –0.2586 | –0.0521 | 0.1262 |
| *Red– or Black–throated Diver* | | | | | | | | | | |
| Estimate | 4.2969 | NA | **–0.3297** | –0.6659 | **–0.0701** | –0.0578 | **–0.4688** | 0.0999 | 0.0190 | 0.0210 |
| LCLM | 2.8071 | NA | –0.6553 | –1.9142 | –0.1321 | –0.3647 | –0.6964 | –0.7145 | –0.1571 | –0.0223 |
| UCLM | 5.7867 | NA | –0.0041 | 0.5825 | –0.0081 | 0.2491 | –0.2412 | 0.9142 | 0.1951 | 0.0643 |

strong winds, while for Barnacle Goose flight altitude was enhanced (Table 4). Most data on Barnacle Geese were collected during periods of southerly winds (87%), i.e., tailwinds, which potentially explain the aberrant pattern in this species. In addition, wind speed was moderately correlated with wind direction ($r = 0.46$) and cloud cover (–0.44), and the value of the condition index (CI = 14.96) was close to the threshold for collinearity concern. Excluding cloud cover from the candidate models changed the sign of the correlation between wind speed and flight altitude in three out of four cases, suggesting that the effect of wind speed on flight altitude in Barnacle Goose was not robust.

The prevailing SW winds were associated with higher flight altitude compared to northerly winds in some species (Table 4). Furthermore, flight altitude was higher in the evening compared to morning in three species (Table 4). Cloud cover and precipitation showed less consistent trends, as these factors only influenced the flight altitude of one species (Table 4). Distance to coast affected three species, but not in the same direction across species, as flight altitude of the Velvet Scoter was inversely correlated with distance to coast.

## 4. Discussion

### 4.1. Factors affecting flight altitude

Our study provides new insights into the factors that determine flight altitude in waterbirds. Relatively high mean flight altitude of 425 m during night, when flight speeds indicated a dominance of waterbirds, likely resulted from a combination of

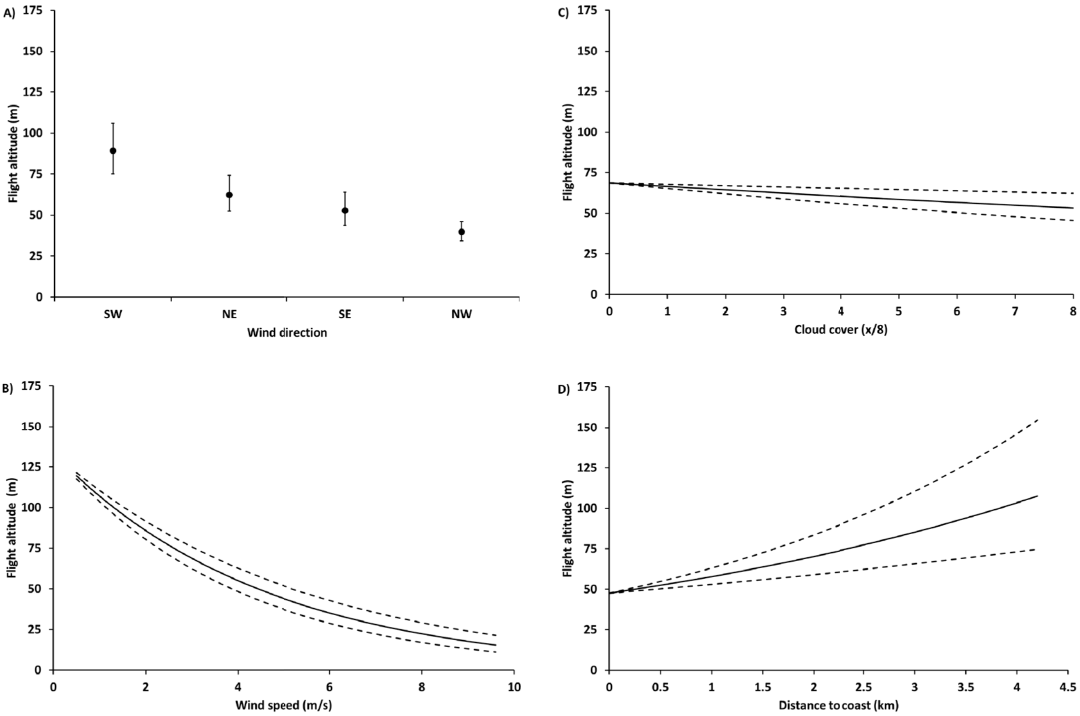

Fig. 4. Predicted flight altitudes obtained from the average model of the waterbird data collected by a laser range finder at the Virtsu lighthouse during daytime hours (16:30–22:30 and 04:30–10:30) in May 2009 as a function of wind direction (A), wind speed (B), cloud cover (C) and distance to coast (D). The bars in (A) and the dash lines in (B), (C) and (D) indicate 95% confidence limits of the mean values.

increased probability of finding favourable weather conditions for migration at high altitudes and the migration pattern itself (Newton 2008). Thus, the most numerous species, namely Common Scoter, Velvet Scoter and Long-tailed Duck, undertake their main migration towards the breeding areas after sunset (Jacoby 1983), and such long-distance migration occurs typically at higher altitude compared to movements of staging birds (Dirksen *et al.* 2000). Fattening prior to long-distance migration is a general trait in waterbirds; however, this is associated with increased flight costs given that metabolism depends on body mass (Witter & Cuthill 1993). Hence, the selection of optimal flight altitude to reduce energy expenditure is essential and likely makes higher altitudes attractive.

Flight altitude was considerably lower during daytime. This confirmed our initial presumption and was supported by a previous study that showed that the flight altitude of migrating scoters and Long-tailed Ducks over Western Estonia increased during evening and peaked a few hours after sunset (Jacoby 1983). However, interpretation of the time-related results of the present study should be made with caution, as nocturnal and daytime data were collected using different methods. For instance, flight altitudes measured at night by a vertically-mounted radar unit may underestimate bird occurrences close to the sea, because bird echoes are mixed with echoes from sea clutter (e.g., Hüppop *et al.* 2004). In addition, radar is more likely to detect larger than smaller flocks, and because large flocks were shown to migrate at higher altitude (at least during evening hours) the lower detection rate of small flocks may underestimate bird occurrence at lower altitudes at night.

By contrast, flight altitudes measured by the laser range finder during the day may overestimate bird occurrences at lower altitudes because it relies upon visual detection of birds, which becomes increasingly unreliable at higher altitudes. We attempted to counteract this bias by using spatial information of migration patterns from a horizontally-operated radar unit, assisting the field observer that measured flight altitudes using the range finder. The remarkable variability in mean flight altitudes of various key species indicated that the number of measurements with the range finder was not just a declining function of altitude, which would be expected were the data collection hampered only by a decreasing detection rate with altitude.

Given the nature of limitations associated with the two methods, we believe that the difference between nocturnal and daytime flight-altitude estimates was in reality smaller than that found in the present study. But the difference is still likely to be real, as the radar data suggested an increase in flight altitude just after sunset as described earlier by Jacoby (1983), although this pattern was based on few data points. Because of these methodological limitations, further analysis of data from day and night was undertaken separately.

We found that wind was of predominant importance amongst the weather components in affecting flight altitudes. In accordance with our initial presumptions, flight altitude was in general higher during tailwind conditions (southerly winds). However, overall patterns were more complex in so far that the most remarkable differences in flight altitudes were recorded during opposing wind directions both during day and night (SW *vs* NE and SE *vs* NW). This supports the view that birds select certain strata of the sky under specific conditions (e.g., Bruderer & Liechti 1995, Bruderer *et al*. 1995, Newton 2008). Observed patterns may possibly derive from the fact that birds adjust flight direction and height to make optimal use of tailwinds (here southerly winds), but that they redirect and reduce flight altitude during adverse wind conditions (northerly winds) along the primary migratory direction to minimize the energy expenditure for flight during migration (Alerstam 1990).

The other wind component, wind speed, showed a consistent and usually negative correlation with flight altitude, considering both overall and species-specific analyses. Very strong winds significantly reduce the propensity of birds to migrate (Alerstam 1978), but wind strength also seems to place severe constraints on the proportion of the sky that can be used by migrating birds. This emphasizes the importance of the costs that migratory birds may incur: flying in strong winds is energetically costly and elevates the risk of being blown off course. Perhaps we also underestimate the influence of unpredictable gusts of wind and the turbulence provided at strong winds.

Wind speed showed a positive correlation with flight altitude in two cases (waterbird sub-set at night, and Barnacle Goose). However, these data sets were skewed, as the majority of data was collected in tailwind situations, especially for the Barnacle Goose. Hence, under these circumstances we expect a positive correlation between wind speed and flight altitude, assuming that wind speed increases with altitude, and that the birds would seek the most favourable wind conditions to reduce energy expenditure during migration.

Finally, different atmospheric conditions (visibility, cloud coverage and precipitation) partially explained flight altitude, although these effects were not as consistent as the wind conditions. As expected, poor visibility was associated with lower flight altitudes, but only at night. Visual cues are important for migrating birds, which at night may include stars and sky-light polarization (e.g., Ottosson *et al.* 1990). These cues may not be available during periods of limited visibility, and therefore information such as wave patterns on the water (Richardson 1990) and other visual cues at sea level could assist navigation during such conditions and explain the correlation between visibility and flight altitude found in the present study. During daytime, waterbirds were already found to migrate close to the sea surface, and adjustments of flight altitude in response to visibility may therefore not be essential.

Cloud cover was inversely correlated with waterbird flight altitude by day, and we therefore suggest that clouds simply provide a ground-visibility barrier for the birds, although we cannot exclude the possibility that some birds were migrating above the clouds (not visible to the observer). At night, cloud cover did not affect the waterbird-dominated migration just after sunset. The flight altitudes of waterbirds were also less sensitive to precipitation than expected, possibly because waterbirds are physically adapted to wet elements.

Lower flight altitudes observed close to coastline in the overall analysis of daytime migration (all species included; Fig. 4D) was most likely a result of a high proportion of local staging birds moving to mainland habitats. As an example, many gulls and Barnacle Geese were staging along the coast within the study area. Many of these birds flew at low altitude in coastal areas, in contrast to those that were observed offshore. Velvet Scoters had a higher flight altitude than Barnacle Geese as they passed through the study area and, in accordance with our initial presumption, this seaduck also showed higher flight altitude at the coastline compared to further offshore, as they may perceive land as a potentially hostile landscape. Finally, we found no evidence that seaducks flew at higher altitudes in late May compared to mid-May, as previously found by Jacoby (1983).

### 4.2. Management implications

Modern day development pressures have increased the number of major physical constructions in the landscape that are likely to impact avian migration routes. Such structures include wind farms, tall buildings, extensive telecommunication-tower networks and higher and longer bridges, all of which have the potential to pose threats to migratory birds. The location of these man-made structures should be based on careful spatial planning and appropriate impact assessment, considering particularly their effects on migration routes of birds. In this respect, the presence of important migration hot-spots should be acknowledged. But it is also essential to combine information about flight paths, flight altitudes and interactions with, for example, weather in order to properly assess collision risks and behavioural responses imposed by these structures.

Our data demonstrates the usefulness of flight-altitude information, considering that man-made super-structures will probably increase in European landscapes and at sea in the near future. For example, recent plans at the present study area include building a bridge across the Suur Väin strait (see Fig. 1). The maximum height of the planned bridge ranges from 10 to 50 m, and includes towers with cables holding the bridge; the height of these towers could be up to 145 m a.s.l. (WSP Finland OY 2010). The Suur Väin strait in Western Estonia has been recognised as one of the most important migration routes for waterbirds in Northern Europe, with an estimated 1–2 million individuals passing the proposed trajectory of the bridge during migration in spring (Kontkanen 1995, Rusanen 1995), involving >30% of the flyway population for the Red- and Black-throated Divers, Long-tailed Duck and Velvet Scoter (Leito 2009). Clearly, the planned bridge could increase waterbird collision risks or to become an ecological barrier that forces migrating birds to take detours. Our data suggest that as much as 60% of the daytime migration was observed at altitudes below 150 m, i.e., the potential collision risk zone in the case of a bridge proposal (Leito 2009). We will soon have several cases where detailed information on flight behaviour (including flight altitude) will be extremely useful in underpinning pre-construction ornithological assessments of the impact of such structures.

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### Vesilintujen lentokorkeuteen vaikuttavat tekijät Länsi-Virossa

Tutkimme sääolojen, ajoittaisten tekijöiden sekä etäisyyden rannikosta vaikutuksia muuttavien vesilintujen lentokorkeuteen Länsi-Virossa. Laseretäisyysmittarin ja meritarkkailututkan avulla havaitsimme, että lentokorkeuksiin vaikuttivat useat säätekijät, etenkin tuuliolot, näkyvyys ja pilvipeitto. Tuulella oli erityisen suuri merkitys: takatuuli nosti lentokorkeutta, kun taas vastatuuli alensi sitä, kenties kasvavan energiankulutuksen tai reitiltä eksymisriskin takia. Myös käyttäytymis- ja fysiologiset sopeumat ympäristöön vaikuttivat lentokorkeuden valintaan. Tulokset tarjosivat uutta, tärkeää tietoa lentokorkeuteen vaikuttavista tekijöistä, ja tietoja voidaan soveltaa ympäristövaikutuksien arvioinnissa.

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