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**How birds weather the weather: avian migration in the mid-latitudes**

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## The influence of weather on altitude selection by nocturnal migrants in mid-latitudes

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### 5.1 Abstract

By altering its flight altitude, a bird can change the atmospheric conditions it experiences during migration. Although many factors potentially influence a bird's decision to choose a particular altitude for migration, wind is generally accepted as being the most influential. Nonetheless, studies indicate that the influence of wind is not so clearly defined, particularly outside of the trade-wind zone, and that other factors may play a role. The aim of this study was to determine which factors influenced the altitude distribution of birds during nocturnal migration. We used operational weather radar to measure the flight altitudes of nocturnally migrating birds during spring and autumn in the Netherlands. We first determined if nightly altitude distributions of proportional bird density could be explained by vertical distributions of wind support using three different techniques from previous research. We then applied a stepwise regression analysis using Generalized Additive Models (GAMs) to determine which atmospheric variables, in addition to altitude, best explained variability in proportional bird density per altitude layer per night. We found that migrants generally remained at low altitudes in this area and that altitude alone explained 52 and 73% of the observed variability in proportional bird density in spring and autumn, respectively. Overall, we found weak correlations between altitudinal distributions of wind support and

proportional bird density; however, we found that improving tailwind support with height increased the probability of birds climbing to higher altitude, and, when birds did fly higher than normal, they generally concentrated around the lowest altitude with acceptable (but not necessarily optimal) wind conditions. The GAM analysis also indicated an influence of temperature on flight altitudes, suggesting that birds avoided colder temperatures. Our findings also suggested that birds increased flight altitudes to seek out more supportive winds when wind conditions near the surface were prohibitive. Thus, birds did not select flight altitudes to exclusively optimize wind support and seemed to prefer flying at relatively low altitudes unless wind conditions at the surface were unsupportive of migration but improved at higher altitude. Overall, flight altitudes of birds in relation to environmental conditions reflect a balance between different adaptive pressures.

## 5.2 Introduction

Avian migrants, many traveling thousands of kilometers twice each year between their breeding and wintering grounds, must interact with a range of atmospheric conditions. By influencing a bird's flight efficiency and ability to navigate, these atmospheric conditions can affect the bird's capacity to successfully maintain its desired course and schedule (Shamoun-Baranes et al., 2010). Therefore, one would expect birds to preferentially fly at altitudes where atmospheric conditions are most supportive of their migratory flight. For diurnal soaring migrants, flight range is maximized by utilizing thermal convection to gain altitude between bouts of gliding, and maximum flight altitudes increase with increasing thermal strength and convective boundary layer depth (Shannon et al., 2002; Shamoun-Baranes et al., 2003*b*). At night, however, in the absence of vertical mixing induced by convective thermals, the convective boundary layer collapses and the atmosphere becomes generally more stratified (Stull, 1988). Thus, nocturnal migrants have the option to select (often from within wide ranges) rather distinct atmospheric conditions (e.g. temperature, humidity, and wind condition) by adjusting their altitude.

The majority of quantitative empirical research has suggested that wind is the most influential atmospheric variable on the flight altitudes of nocturnally migrating birds and other atmospheric variables such as temperature and humidity exert only minor influence (Bruderer et al., 1995*b*; Liechti et al., 2000; Liechti and Schmaljohann, 2007; Schmaljohann et al., 2009). Specifically, these studies report a strong correlation between altitudinal distributions of avian migrants and altitudinal distributions of either wind profit (i.e. the support a bird obtains from a particular set of wind conditions) or some estimate of

flight range based largely on wind profit. However, these studies have been primarily conducted inside the trade-wind zone of North Africa and the Middle East.

Based on atmospheric general circulation patterns (Rohli and Vega, 2007), the northern and southern hemispheres on Earth can be subdivided into three latitudinal zones: the trade-wind zone ( $0^{\circ}$ -  $30^{\circ}$ ) in which Hadley cells dominate, the mid-latitudes ( $30^{\circ}$ -  $60^{\circ}$ ), and the polar region ( $60^{\circ}$ -  $90^{\circ}$ ). The wind scenario prevalent in the trade-wind zone, and in the polar region, is such that wind direction often changes by  $180^{\circ}$  with altitude. Thus, inside the (northern hemisphere) trade-wind zone beneficial winds are available on most nights either at high altitude (in spring as migrants move away from the equator) or at low altitude (in autumn as migrants move toward the equator). Accordingly, prohibitive winds are also present every night and at generally predictable altitudes. In the mid-latitudes, conversely, upper-level winds generally do not reverse direction from the surface. Therefore, beneficial winds are not always available and the altitudinal distribution of wind support is less predictable. Furthermore, inside the trade-wind zone cloud cover is infrequent (other than in the Intertropical Convergence Zone) and temperatures within the normal altitudes of bird migration are generally above freezing (cf. Bruderer et al., 1995*b*; Klaassen and Biebach, 2000; Liechti et al., 2000; Schmaljohann et al., 2009). Thus, it is unclear to what degree the relationships derived in these studies apply outside of areas exhibiting these specific atmospheric conditions.

Studies from outside the trade-wind zone also indicate an influence of wind on migratory altitudes; however, these reports do not necessarily suggest that birds always select altitudes to optimize wind support. From a visual and radar analysis conducted in the southern United States at the border between the trade-wind and mid-latitude zones, Gauthreaux (1991) found a strong correlation between the altitude of peak migration and the altitude of most supportive winds when migrants flew at higher altitudes than normal and suggested that these higher-than-normal flight altitudes occurred when winds at lower altitude were prohibitive and winds at higher altitude were supportive. Several studies suggest that migrants generally fly at higher altitudes with tailwinds than with headwinds (see Bruderer, 1971; Kerlinger and Moore, 1989; Richardson, 1990*a*, and references therein), and another study suggests that migrants remain at lower altitudes when wind speeds are high irrespective of wind direction (Able, 1970).

In any case, the influence of wind cannot be understood in isolation from other atmospheric components (Bruderer, 1971). For instance, Bruderer (1971) observed rain and clouds depressing migratory altitudes even when more supportive winds were available at higher altitude. Other observational reports

from outside of the trade-wind zone support this assessment, suggesting that atmospheric variables other than wind may influence the altitude of avian migration (see Eastwood, 1967; Kerlinger and Moore, 1989, and references therein). In particular, there are reports of cloud cover affecting migratory altitudes; though the specific influence is contentious with conflicting reports suggesting that birds tend to fly above (Bellrose and Graber, 1963), below (Nisbet, 1963; Able, 1970), and even within clouds (Bellrose and Graber, 1963; Eastwood and Rider, 1965; Griffin, 1973). Perhaps lending some clarification, Bruderer (1971) observed that birds flew above lower-altitude clouds (even into comparatively less supportive winds at higher altitude) but below higher-altitude clouds (particularly frontal clouds, unbroken clouds, and clouds producing precipitation). Deduced from an observed correlation between the 90% level of migration and the altitude at which freezing temperatures occurred, Bruderer (1971) also theorized that birds may choose altitudes to optimize thermoregulation; though some birds were observed flying in temperatures as low as  $-15^{\circ}\text{C}$ . Elkins (2004) suggested that freezing temperatures may only be troublesome when the air is very saturated with moisture, as this could lead to ice accumulation on plumage; however, Bruderer (1971) reported birds flying in below-freezing temperatures even when the atmosphere was very humid and the formation of ice-crystals was to be expected. Theoretical work suggests that a migrant's flight range may be strongly limited by dehydration, particularly in dry areas, and that migrants should select altitudes that minimize water loss (Carmi et al., 1992; Gerson and Guglielmo, 2011; Klaassen, 1996). Finally, although avian physiology exhibits adaptations resulting in a more efficient exchange of oxygen from the pulmonary to the circulatory system, theory suggests that atmospheric properties highly correlated with altitude such as oxygen partial pressure (Altshuler and Dudley, 2006) and air density (Pennycuik, 2008), along with temperature and humidity, may influence a bird's flight efficiency.

Thus, the altitude distributions of birds observed during migration may reflect a trade-off between multiple objectives, such as optimizing energy expenditure, flight time, safety, and water balance. Therefore, further quantitative analyses, in different geographic areas and integrating multiple atmospheric variables, are desirable to 1) test relationships quantified or suggested in other regions between atmospheric variables and avian migratory altitudes for universal applicability, and 2) to improve our understanding of how birds potentially balance these different adaptive pressures when selecting flight altitudes during migration.

The main aim of this study is to determine how atmospheric conditions influence the nocturnal altitude distributions of migrating birds in our study

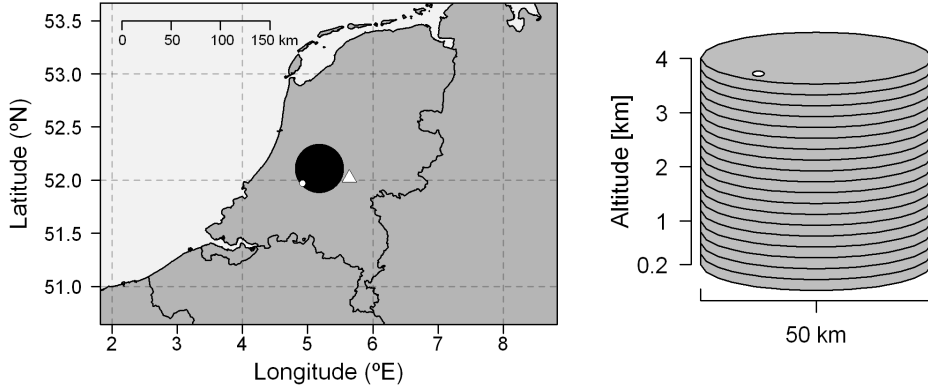
area. We examine altitude distributions of nocturnally migrating birds obtained using C-band Doppler weather radar in the Netherlands – a location where prevailing atmospheric conditions are quite different from those of the trade-wind zone (Rohli and Vega, 2007). Since most quantitative research has focused on the influence of wind, and for comparative purposes, we first explore possible relationships between wind conditions and migratory altitude by applying three approaches from previous research: 1) following Gauthreaux (1991), we consider a subset of nights in which birds fly higher than normal and test if the altitude of peak migration is correlated with the lowest altitude with acceptable wind support; 2) we quantify the nightly correlation between wind profit (i.e. the support a bird obtains from a particular set of wind conditions) and the proportion of birds at each altitude level, as done in some studies inside the trade-wind zone (e.g. Liechti et al., 2000; Schmaljohann et al., 2009), and 3) we apply a simulation model, following Bruderer et al. (1995*b*), in which the probability of a bird changing altitude is a function of the change in tailwind strength with altitude. Finally, rather than studying wind in isolation of other atmospheric conditions and in order to study flight altitude distributions in the context of multiple adaptive pressures, we perform a stepwise regression analysis to explore the potential influence of multiple atmospheric variables that, through observation, theory, or statistical inference, have been suggested to influence the altitude of avian migration. Because the specific influence of many of these atmospheric variables on avian altitude distributions is not known, particularly for this location, we employ Generalized Additive Models (GAMs) in which the relationship between predictor and response variable is not restricted to a predefined parametric form.

## 5.3 Materials and methods

### 5.3.1 Radar measurements of bird density

We used methods described by Dokter et al. (2011) to derive altitude profiles of bird density ( $Bd$ ; birds/km<sup>3</sup>) and average groundspeed (ms<sup>-1</sup>) every five minutes from a C-band Doppler weather-radar located in De Bilt, the Netherlands (52.11°N 5.18°E; Figure 5.1) during spring (1 February - 31 May) and autumn (1 August - 30 November) of 2008 and 2009. Each altitude profile described  $Bd$  and average groundspeed from 0.2 to 4 km above the ground in altitude bins of 200 m. Thus each profile consisted of 19 measurements, each calculated from within a circular measurement window extending 25 km laterally from the center of the radar (Figure 5.1).

As a means of additional quality control, we used HIRLAM wind data (see section 5.3.2) to calculate airspeeds from these groundspeeds by vector



**Figure 5.1:** On the left, a map with a black circle indicating the range of the C-band Doppler weather radar in De Bilt, the Netherlands. A white triangle indicates the closest grid point in the HIRLAM dataset, from which weather data were obtained. On the right, a vertical profile of the radar’s measurement volume indicating the 19 altitude bins within which measurements of bird density ( $Bd$ ) were calculated. In both images, a small white circle indicates the location of the cloud-measuring LIDAR ceilometer at the Cabauw experimental site for atmospheric research.

subtraction. We set  $Bd$  measurements to zero if the associated airspeed was not between  $7$  and  $25 \text{ ms}^{-1}$ , as this range captures the airspeeds of the majority of nocturnal migrants (Bloch and Bruderer, 1982; Bruderer and Boldt, 2001).

Bruderer et al. (1995b), and references therein, observed that nocturnal migrants can spend the first two hours after sunset probing the atmosphere and concentrate in preferred altitudinal strata thereafter. We therefore calculated a representative altitude profile of  $Bd$  for each night (hereafter “nightly  $Bd$  profile”) using the median  $Bd$  value per altitude bin occurring between two and three hours after sunset (i.e. after birds had presumably selected their altitudes in relation to the night’s atmospheric conditions). We only considered nights in which total migration (i.e. the sum of all  $Bd$  in the nightly  $Bd$  profile) was greater than  $20 \text{ birds/km}^3$ , because measurements were less reliable when  $Bd$  values were very small. Given this threshold, we retained 29% of the 238 available spring nights and 18% of the 236 available autumn nights.

We then translated these nightly  $Bd$  profiles into “proportional bird-density ( $pBd$ ) profiles” by dividing  $Bd$  in each altitude bin by the sum of all  $Bd$  in the nightly profile. For our comparisons with previous research, we used these nightly  $pBd$  profiles. In Figure 5.2, we show for each season the weighted aver-

age altitude distribution of  $pBd$  (in which  $pBd$  is weighted by the total  $Bd$  in the associated profile), the range of deviations from that weighted average per altitude bin, and two example distributions (one similar to and one different from the weighted average).

The  $pBd$  values for any given altitude profile were constrained due to the fact that they necessarily summed to a value of one. To deal with this constraint, we applied the additive log-ratio (ALR) transformation (Aitchison, 1982) to these  $pBd$  values. For each of the 19 altitude bins ( $a$ ) of a nightly profile ( $i$ ), we calculated ALR-transformed  $pBd_a^i$  (hereafter  $tBd_a^i$  with respect to  $pBd^i$  in the first or lowest altitude bin, which was centered on 0.3 km, as

$$tBd_a^i = \log \left( \frac{pBd_a^i}{pBd_1^i} \right) \quad (5.1)$$

We did not use any  $tBd$  values calculated in a reference bin (i.e. where  $a = 1$ ) to calibrate our models. This transformation produced an unreal solution for any observation in which  $pBd$  was equal to zero, so these observations were also excluded from our analysis. What remained were 322 and 286  $tBd$  measurements in spring and autumn, respectively.  $tBd$  served as the response variable in our GAM regression analysis. We back-transformed  $tBd_a^i$  in all but the reference altitude bin as

$$pBd_a^i = \frac{\exp(tBd_a^i)}{1 + \sum_{a=2}^{19} \exp(tBd_a^i)} \quad (5.2)$$

and in the reference altitude bin as

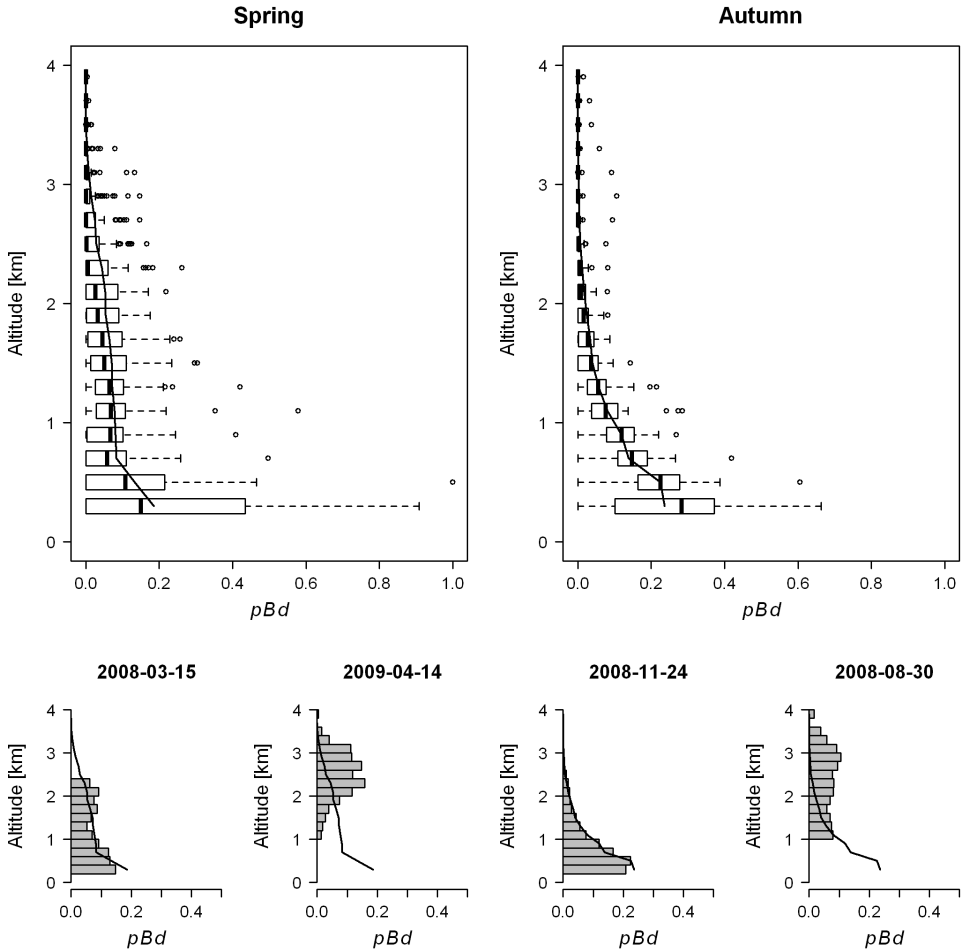
$$pBd_1^i = 1 - \sum_{a=2}^{19} pBd_a^i \quad (5.3)$$

We present the results of our analysis after back-transforming GAM predictions to  $pBd$  wherever possible.

### 5.3.2 Meteorological data

We derived altitude profiles, to a height of 4 km, of wind condition ( $\text{ms}^{-1}$ ), temperature ( $T$ ; K), atmospheric pressure ( $A_P$ ; mb), and relative humidity ( $RH$ ; %) using data from the gridded HIRLAM atmospheric model (Cats and Wolters, 1996; Undén et al., 2002). These data had a spatial resolution of  $0.1^\circ \times 0.1^\circ$  on a rotated grid, temporal resolution of one hour, and were discretized vertically at fixed pressure levels separated by not more than 20 mb. Using data from the grid point nearest to the center of the De Bilt radar ( $\sim 33$  km east at  $5.64^\circ\text{E}$   $52.02^\circ\text{N}$ ; see Figure 5.1), we linearly interpolated all variables to





**Figure 5.2:** In all plots, a black line indicates the weighted average altitude distribution of proportional bird density ( $pBd$ ) for the particular season (three plots of spring on left; three plots of autumn on right). In the top two plots, box-plots indicate the range of deviations from the weighted average  $pBd$  per altitude bin. Boxes indicate the upper and lower quartiles and median, “whiskers” indicate values  $< 1.5$  times the inter-quartile range beyond the quartiles, and points indicate outliers. Along the bottom are two example distributions from each season: one that closely approximates the weighted average distribution for that season and one that is quite different from the weighted average distribution for that season. The title of each plot indicates the night (at sunset) during which the distribution occurred.

the center of each altitude bin. We then calculated “nightly weather profiles”, comparable to the nightly *Bd* profiles, by linearly interpolating these weather conditions in time along each altitude bin to 2.5 hours after sunset each night (determined using the R package `mapprools` Lewin-Koh et al., 2011). For each observation, we then calculated specific humidity (*SH*; g/kg), describing the mass of the water vapor present per kilogram of atmosphere, as

$$SH = \frac{w}{1 + w} \quad (5.4)$$

where the mixing ratio (*w*) was defined as

$$w = \frac{0.622e}{A_P - e} \quad (5.5)$$

vapor pressure (*e*) was given by

$$e = e_s \cdot \frac{RH}{100} \quad (5.6)$$

and saturation vapor pressure (*e<sub>s</sub>*), as given by Buck (1981), was

$$e_s = (1.0007 + 3.46 \cdot 10^{-6} \cdot A_p) \cdot 6.1121 \cdot \exp\left(17.502 \cdot \frac{T - 273}{240.97 + (T - 273)}\right) \quad (5.7)$$

for temperatures above freezing and

$$e_s = (1.0003 + 4.18 \cdot 10^{-6} \cdot A_p) \cdot 6.1115 \cdot \exp\left(22.452 \cdot \frac{T - 273}{272.55 + (T - 273)}\right) \quad (5.8)$$

for temperatures below.

Wind data were described by two components, U and V ( $\text{ms}^{-1}$ ), indicating the speed and direction into which the wind was blowing. The U vector described the wind’s east/west component (toward east being positive) and V described the north/south (toward north being positive). Several variables were derived from the U and V wind components to represent wind conditions relative to a bird’s expected flight behavior. We calculated the tailwind (*T<sub>w</sub>*;  $\text{ms}^{-1}$ ) component (Shamoun-Baranes et al., 2007), and a measure of wind profit (*WP*;  $\text{ms}^{-1}$ ). For both variables, a preferred migratory direction was required. We assumed an autumn migratory direction of  $225^\circ$ , consistent with the autumn migratory directions used in previous studies in the Netherlands (e.g. van Belle et al., 2007, and Chapter 4) and similar to migratory directions

observed by radar in several locations throughout Europe – e.g.  $220^\circ$  at a coastal site in southern Spain (Bruderer and Liechti, 1998);  $230^\circ$  for southern Germany and Switzerland (Bruderer et al., 1989); and  $225^\circ$  at Falsterbo in southwestern Sweden (Zehnder et al., 2001). We then reversed this preferred direction to  $45^\circ$  in spring, similar to the mean spring migratory direction of  $41^\circ$  observed by radar in western Europe (Dokter et al., 2011). According to our formulation of  $WP$ , birds were assumed to have a fixed airspeed and fully compensate for side-wind displacement by adjusting their groundspeed and heading (see  $EQ^{\text{Airspeed}}$  in section 3.3.2 of Chapter 3 for details).

$$WP = Wspd \cdot \cos \theta + \sqrt{z^2 - (Wspd \cdot \sin \theta)^2} - z \quad (5.9)$$

where  $WP$  was a function of wind speed ( $Wspd$ ) and the angular difference between the wind direction and the bird’s preferred migratory direction ( $\theta$ ). Because passerines dominate nocturnal migration over Europe (Hahn et al., 2009), we set the birds’ airspeed ( $z$ ) to  $12 \text{ ms}^{-1}$ , which is representative of the airspeeds calculated for many migrating passerine species (Bloch and Bruderer, 1982; Bruderer and Boldt, 2001). Since birds were assumed to have a fixed airspeed in this equation, conditions existed in which full compensation for side-wind displacement was not possible. Under such conditions (i.e. with a negative value occurring under the square root), this formulation did not have a real solution. In spring and autumn, respectively, 119 and 147 observations at individual altitude bins were removed from all analyses because  $WP$  had no real solution. In order to represent wind at a particular flight altitude in relation to the most supportive wind conditions in the vertical profile, we calculated relative wind profit ( $rWP$ ), which we defined as  $WP$  at a given altitude minus the best  $WP$  in the associated nightly weather profile; thus, zero was the highest value possible for  $rWP$ . To reflect the observation by Gauthreaux (1991) that birds flew at higher altitude to avoid low-altitude headwinds, we calculated a measure of  $WP$  relative to the  $WP$  at the surface ( $WP_{sfc}$ ), which we will refer to hereafter as  $rWP_{sfc}$ . To do so, we first defined  $WP_{sfc}$  in binary terms ( $bWP_{sfc}$ ), with  $bWP_{sfc}$  being one if  $WP_{sfc}$  was negative and zero if  $WP_{sfc}$  was non-negative. We then defined  $rWP_{sfc} = bWP_{sfc} \cdot (WP - WP_{sfc})$ . We calculated relative tailwind ( $rTw$ ) and tailwind relative to the surface ( $rTw_{sfc}$ ) in a similar manner. We considered  $rWP$ ,  $rTW$ ,  $rTw_{sfc}$ , and  $rWP_{sfc}$  in our GAM analysis.

Cloud cover was measured by a Vaisala CT75K LIDAR ceilometer at the Cabauw experimental site for atmospheric research (abbreviated Cesar) located at  $51.97^\circ\text{N}$   $4.926^\circ\text{E}$  ( $\sim 25$  km to the southwest of the center of the De Bilt radar; see Figure 5.1). We accessed these data via the online Cesar database (The Cesar Consortium, 2011). Cloud-base height (m) was calculated every

30 seconds with 15 m vertical resolution. Three nights in spring were removed from the analysis because cloud data were missing. For our stepwise GAM regression analyses, we defined nightly cloud persistence ( $Cp$ ) per altitude bin.  $Cp$  was parameterized as the cumulative fraction of cloud-base observations between sunset and three hours after sunset from 200 m up to the respective altitude bin.

### 5.3.3 Wind and migratory altitudes: comparisons with previous research

Following the analysis of Gauthreaux (1991), we considered a specific subset of nights in which the altitude bin with the largest proportion of birds was above 400 m. Using only these nights (35 in spring and 18 in autumn), we quantified the correlation between the altitude bin with the largest  $pBd$  and the lowest altitude bin with acceptable wind support using Pearson’s product moment correlation coefficient (hereafter “Pearson’s  $r$ ”). We defined the lowest altitude bin with the acceptable wind support, again following Gauthreaux (1991), as the lowest altitude bin in which the wind blew toward the N-NE in spring or the S-SW in autumn. If no altitude bins satisfied this requirement, we used instead the altitude bin with the lowest wind speed.

Following the approach taken in several studies from inside the trade-wind zone (e.g. Liechti et al., 2000; Schmaljohann et al., 2009), we quantified the nightly correlation between vertical distributions of  $pBd$  and wind support ( $Tw$  and  $WP$ ) using Spearman’s rank correlation coefficient (hereafter Spearman’s  $\rho$ ): a non-parametric measure of association in which a value of one indicates a perfect positive correlation, negative one a perfect negative correlation, and zero no correlation. We only ever calculated Spearman’s  $\rho$  correlations for nights with a majority of their observations present.

Following the approach taken by Bruderer et al. (1995b), we applied a simulation model to predict nightly altitude distributions of  $pBd$ . According to this model, the probability of a bird changing altitudes was a function of the difference in  $Tw$  strength between adjacent altitude bins (hereafter  $\Delta Tw$ ). We first calibrated a linear regression to quantify for our dataset the probability of a bird changing altitude as a function of  $\Delta Tw$ . To do so, we assumed that  $pBd$  in one altitude bin compared to  $pBd$  in an adjacent altitude bin indicated the birds’ preference between the bins. Thus for each observation, we defined  $P$  as  $pBd$  in the altitude bin immediately above the current bin divided by the sum of  $pBd$  in both bins. As such, values of  $P$  greater than 0.5 indicated that more birds preferred conditions in the next highest altitude bin, while values of  $P$  less than 0.5 indicated that more birds preferred conditions in the current altitude bin. We then applied a logit transformation to  $P$  (hereafter  $P_L$ ) to

serve as the response variable in the regression. Accordingly, we calculated  $\Delta Tw$  as  $Tw$  in the altitude bin immediately above minus  $Tw$  in the current altitude bin, such that positive values for  $\Delta Tw$  indicated increasing tailwind support in the next highest altitude bin. We then calibrated a linear regression (i.e.  $P_L = a + b\Delta Tw$ ; where  $a$  and  $b$  were coefficients calibrated from the data) based on the normal distribution. Each observation was weighted by the square-root of the sum of  $Bd$  in the two altitude bins from which  $P$  was calculated. According to the regression relationship that resulted, we simulated a distribution of  $pBd$  for each night in our study. We began each night's simulation with a probability distribution in which all birds were expected to be in the lowest altitude bin, and we iteratively adjusted this distribution according to  $P$  predicted in each bin by  $\Delta Tw$ . We continued to iterate until the distribution achieved convergence, which we defined to occur when the root-mean-square error (RMSE) between the previous and current iterations was  $< 0.0001$ . As did Bruderer et al. (1995b), we quantified the percentage of variability explained by this simulation model as

$$1 - \frac{\sum_{i=1}^n |x_i - y_i|}{\sum_{i=1}^n x_i + y_i} \quad (5.10)$$

where  $x_i$  are measured values and  $y_i$  are predicted.

### 5.3.4 GAM analysis

We applied a Generalized Additive Modeling (GAM) approach (Hastie and Tibshirani, 1990) based on a Gaussian distribution to explore potential relationships between atmospheric variables (from the nightly weather profiles) and  $tBd$  (i.e. ALR-transformed  $pBd$  at each altitude from the nightly bird-probability profiles). We applied penalized likelihood fitting to estimate the smoothness of terms in our GAMs. The computations were done in the R language (R Development Core Team, 2010) using the `gam()` function from the `mgcv` package (Wood, 2008).

We began with a base model that contained only altitude (*Alt*) as a predictor variable to account for any persistence in the altitude distributions of migrating birds that may be attributable to altitude itself, for example, arising from birds preferring lower altitudes to facilitate navigation using ground-based points of reference (Liechti et al., 2000). From this base model, we performed forward stepwise regression, using repeated random sampling as a means of cross-validation, to arrive at the best performing combination of predictor variables for each season. For each possible predictor variable, we tested a model containing that variable by repeatedly (50 times) selecting a random 80% of available nights for calibration – leaving 20% for testing. We

recorded the RMSE, Spearman's  $\rho$ , and percentage of variability explained – following the method of Bruderer et al. (1995b) described above – between our back-transformed model predictions and  $pBd$  from the 20% of nights left for testing. We retained the variable that produced the smallest average RMSE value. Using the same repeated random sampling procedure, we tested adding subsequent variables to the model. We added the variable that led to the lowest cross-validation RMSE, was significant ( $\alpha < 0.05$ ) in the model, and did not cause previously selected variables to become non-significant. Further, we applied a chi-squared test to confirm that the inclusion of each variable resulted in a significant ( $\alpha < 0.01$ ) improvement over the previous model. The variables we tested in this analysis are listed in Table 5.1 where we provide a short description of each variable and give a reference for our motivation to include it in our analysis.

Due to the effects of repeated random sampling and the flexibility allowed by GAMs, different final models may result from this stepwise procedure if it were run multiple times. Therefore, we performed the entire forward stepwise analysis 50 times for each season. We retained the set of predictor variables that occurred most often per season and described the performance of the models containing those variables. As well, we reported the number of times each individual variable was selected in a final model to indicate the stability of the selection procedure and the relative importance of each variable in predicting  $tBd$ .

## 5.4 Results

### 5.4.1 Weather conditions

The geographical area in which our study was conducted has a Cfb climate-type (i.e. temperate with no dry season and warm summers) according to the Köppen-Geiger climate classification system (Peel et al., 2007). Consistent with the results in Chapter 4, nightly weather profiles indicated that wind speeds generally increased with altitude, and, particularly in autumn, winds blew more frequently and forcefully from the west. Consequently, wind conditions were generally more supportive of the northeasterly movement of spring migration than the southwesterly movement of autumn migration (Figures 5.3 and 5.4). In both seasons,  $T$ ,  $SH$ , and  $RH$  decreased with altitude. Autumn temperatures were somewhat higher than spring at all altitudes (Figures 5.3 and 5.4).

**Table 5.1: Variables tested as predictors of proportional bird density ( $tBd$ ) in a forward stepwise GAM regression analysis. Descriptions of variables are given in the last column along with a reference justifying the inclusion of the variable.**

Variable	Units	Description and motivation
$Alt$	km	The height of the middle of an altitude bin above ground, which is included by default (Liechti et al., 2000)
$rTw$	$\text{ms}^{-1}$	Tailwind strength at a given altitude minus the strongest tailwind in the altitude profile (e.g. Bruderer et al., 1995 <i>b</i> ; Liechti et al., 2000)
$rTw_{sfc}$	$\text{ms}^{-1}$	Tailwind at a given altitude minus tailwind at the surface, if tailwind at the surface is negative, otherwise zero (Gauthreaux, 1991)
$rWP$	$\text{ms}^{-1}$	Wind profit at a given altitude minus the best wind profit in the altitude profile (e.g. Schmaljohann et al., 2009)
$rWP_{sfc}$	$\text{ms}^{-1}$	Wind profit at a given altitude minus wind profit at the surface, if wind profit at the surface is negative, otherwise zero (Gauthreaux, 1991)
$T$	K	Air temperature (e.g. Bruderer, 1971; Carmi et al., 1992)
$RH$	%	Relative humidity (e.g. Klaassen, 1996)
$SH$	g/kg	Mass of water vapor per kilogram of atmosphere (e.g. Gerson and Guglielmo, 2011)
$Cp$	%	Percentage of time that clouds were present (cf. Eastwood, 1967; Bruderer, 1971)

Spring

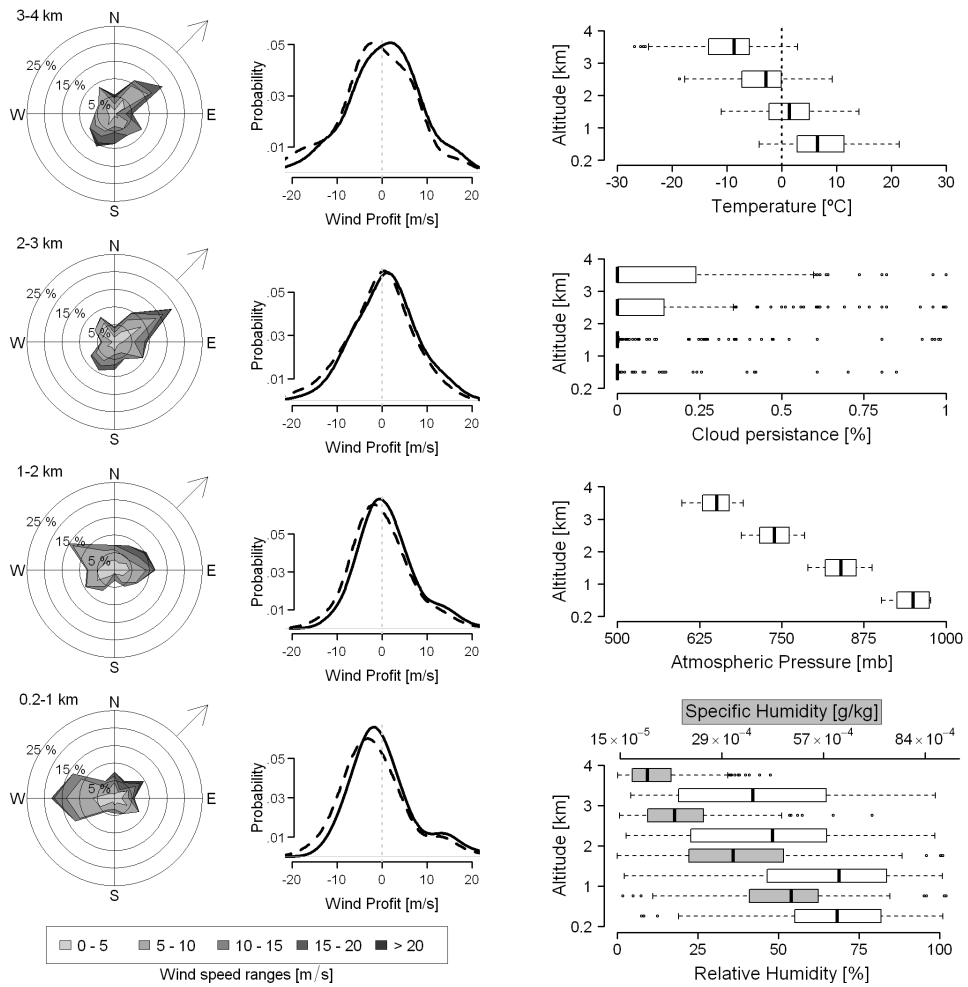


Figure 5.3: Graphical summaries of the weather conditions for spring from the nightly weather profiles used in our study. Wind condition, described in one kilometer altitude intervals, is shown on the left by wind rose plots and probability distributions of tailwind ( $T_w$ ; solid line) and wind profit ( $WP$ ; dashed line). Distance from the center of a wind rose indicates the relative frequency of the wind blowing into a particular direction, and shades of gray indicate the individual relative frequencies of the different wind speed ranges for a particular direction. Concentric circles indicate relative frequencies in increments of 5%, with the outer circle indicating 25% relative frequency. Continued on next page...



**Figure 5.3 (continued):** On the right, box-plots indicate distributions of temperature ( $T$ ), cloud persistence ( $Cp$ ), atmospheric pressure ( $A_P$ ), and relative ( $RH$ ) and specific humidity ( $SH$ ) per 1 km altitude interval. Boxes in these box-plots indicate the upper and lower quartiles and median, “whiskers” indicate values  $< 1.5$  times the inter-quartile range beyond the quartiles, and points indicate outliers. A dashed vertical line in the temperature plot indicates the freezing point.

#### 5.4.2 Wind and migratory altitudes: comparisons with previous research

Pearson’s  $r$  correlations between the lowest altitude with acceptable wind support, as defined by Gauthreaux (1991), and the altitude with the largest proportion of birds on nights when the highest bird density was in an altitude bin above 0.4 km (see Figure 5.5) were significantly positive in spring ( $r = 0.59$ ;  $n = 35$ ;  $P < 0.001$ ). In autumn, this correlation was also significantly positive ( $r = 0.68$ ;  $n = 18$ ;  $P < 0.01$ ); however, this significant correlation would not exist without the leverage of a single point exhibiting a Cook’s distance of 2.3 (see Figure 5.5).

Nightly Spearman’s  $\rho$  correlations between wind support (considering either  $Tw$  or  $WP$ ) and  $pBd$  (see Figure 5.4.2; and compare to Liechti et al., 2000; Schmaljohann et al., 2009) were rather weak in both spring (means of 0.15 and 0.17, respectively) and autumn (means of 0.12 and 0.30, respectively). Correlations were more positive when considering  $WP$  (i.e. when accounting for side winds) than  $Tw$ , though the difference was only significant in autumn (paired two-sided Mann-Whitney test;  $n_{spring} = 62$ ,  $n_{autumn} = 36$ ;  $P \leq 0.001$ ).

In reproducing the analysis by Bruderer et al. (1995b), our linear regression model suggested a statistically significant but very weak relationship between  $\Delta Tw$  (i.e. the change in tailwind strength between altitude bins) and  $P_L$  (i.e. the logit of the proportional difference in  $pBd$  between altitude bins). The resulting equation for autumn ( $P_L = -0.34 + 0.06\Delta Tw$ ,  $n = 361$ ,  $r^2 = 0.01$ ,  $P \leq 0.05$ ) suggested a weaker and less-significant relationship between  $\Delta Tw$  and  $P_L$  than in spring ( $P_L = -0.29 + 0.13\Delta Tw$ ,  $n = 559$ ,  $r^2 = 0.05$ ,  $P \leq 0.001$ ). In both seasons, and contrary to the results of Bruderer et al. (1995b), we found that the intercept in the equations was highly significant.

The simulations resulting from the regression relationships between  $\Delta Tw$  and  $P_L$  explained 56% and 73% of the variability in nightly distributions of  $pBd$  in spring and autumn, respectively. These values were somewhat higher than those reported by (Bruderer et al., 1995b, ; i.e. 56% for spring and 63% for autumn). For comparison with other results in this paper, the average Spearman’s  $\rho$  correlation between the measured and simulated distributions

Autumn

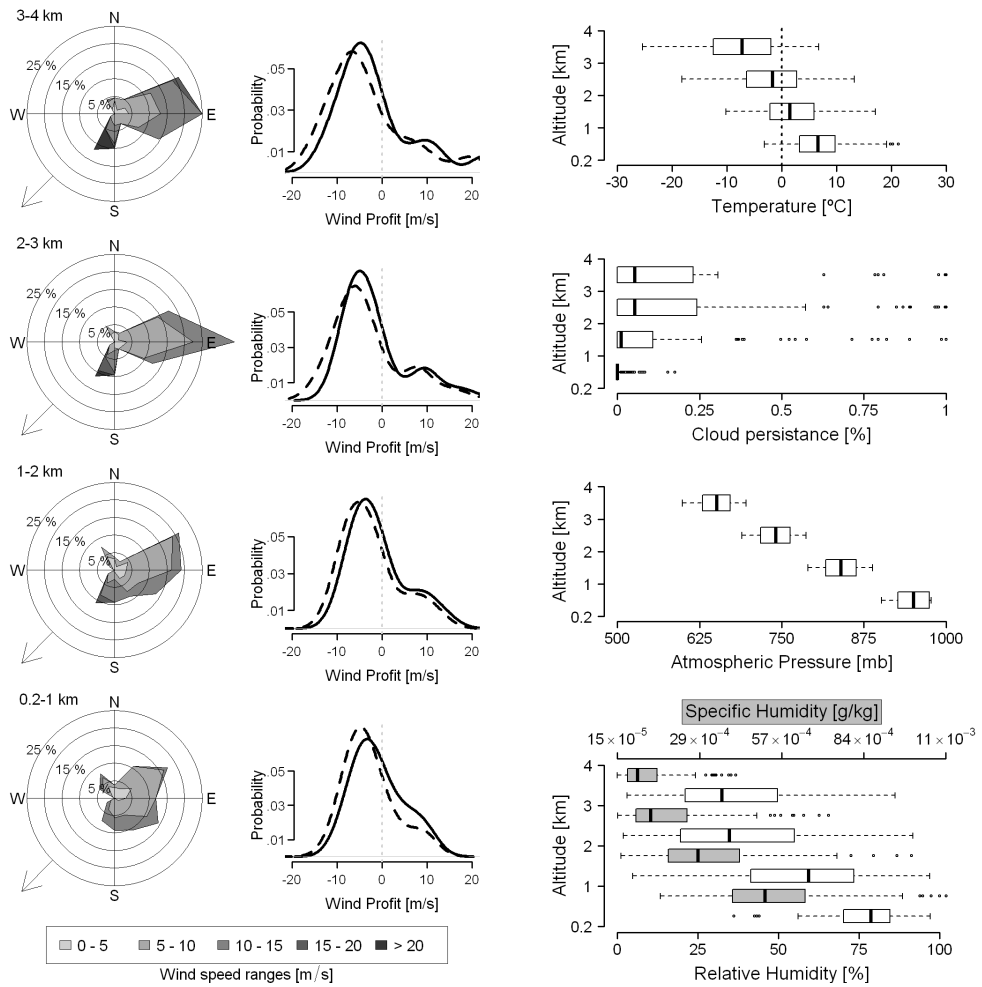


Figure 5.4: Graphical summaries of the weather conditions for autumn from the nightly weather profiles used in our study. Wind condition, described in one kilometer altitude intervals, is shown on the left by wind rose plots and probability distributions of tailwind ( $T_w$ ; solid line) and wind profit ( $WP$ ; dashed line). Distance from the center of a wind rose indicates the relative frequency of the wind blowing into a particular direction, and shades of gray indicate the individual relative frequencies of the different wind speed ranges for a particular direction. Concentric circles indicate relative frequencies in increments of 5%, with the outer circle indicating 25% relative frequency. Continued on next page...

Figure 5.4 (continued): On the right, box-plots indicate distributions of temperature ( $T$ ), cloud persistence ( $C_p$ ), atmospheric pressure ( $A_P$ ), and relative ( $RH$ ) and specific humidity ( $SH$ ) per 1 km altitude interval. Boxes in these box-plots indicate the upper and lower quartiles and median, “whiskers” indicate values  $< 1.5$  times the inter-quartile range beyond the quartiles, and points indicate outliers. A dashed vertical line in the temperature plot indicates the freezing point.

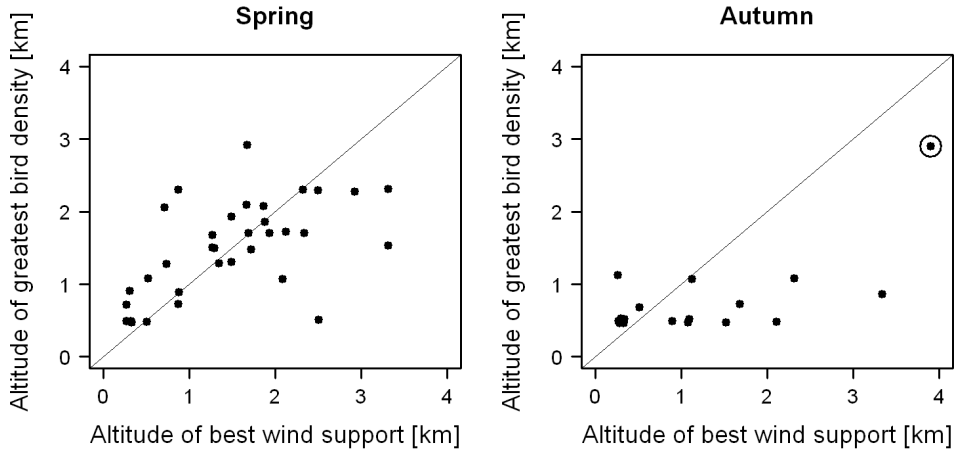
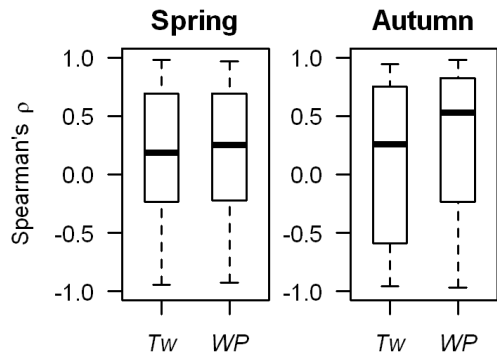


Figure 5.5: Scatter plots indicating the correlation between the altitude with best wind support (as calculated by Gauthreaux (1991)) and the altitude with most intense migration for those nights in spring (left;  $n = 35$ ;  $r = 0.59$ ;  $P \leq 0.001$ ) and autumn (right;  $n = 18$ ;  $r = 0.68$ ;  $P \leq 0.01$ ) when the altitude bin with most intense migration was  $> 0.4$  km. In autumn, the correlation and its significance are critically dependent on the leverage of a single observation (circled). A diagonal line indicates a theoretical perfect positive correlation.

Figure 5.6: Box-plots indicating the distributions of nightly Spearman’s  $\rho$  correlations between  $pBd$  and wind support, considering either the tail-wind component ( $Tw$ ) or wind profit ( $WP$ ), for spring (left) and autumn (right). Boxes indicate the upper and lower quartiles and median, “whiskers” indicate values  $< 1.5$  times the inter-quartile range beyond the quartiles.



was 0.54 in spring and 0.76 in autumn. Appendix D shows, for each night considered in this study, distributions of  $pBd$  resulting from these simulations alongside measured distributions of  $pBd$  and  $Tw$ . The simulated distributions of  $pBd$  do not vary a great deal from night to night, and most exhibit a rather exponential decrease with altitude.

### 5.4.3 GAM analysis

We performed a forward stepwise regression analysis 50 times per season to arrive at a robust combination of predictor variables that best explained the observed variability in the altitude distributions of avian migrants. While these models were selected and calibrated with  $tBd$  (i.e.  $pBd$  after an additive log-ratio transformation) serving as the response variable, we back-transformed our predictions and will therefore discuss model performance on the scale of  $pBd$  wherever possible. In Table 5.2, we report the number of times each potential predictor variable was selected in one of these 50 final models. Altitude ( $Alt$ ) was included in these models by default and explained a large proportion of the variability in  $pBd$  by itself (52% and 73% in spring and autumn, respectively). This was roughly the same amount of variability explained by our simulation approach following Bruderer et al. (1995b). Measures of wind assistance relative to surface wind conditions (i.e.  $rWP_{sfc}$  and  $rTw_{sfc}$ ) were selected more often than measures of wind assistance relative to all wind conditions in the nightly profile (i.e.  $rWP$  and  $rTw$ ), and  $rTw_{sfc}$  was selected more often than  $rWP_{sfc}$ . Temperature ( $T$ ) and measures of humidity ( $RH$  and particularly  $SH$ ) were often selected in a final model.

In Table 5.3, we present the model that resulted most often per season for each level of complexity (i.e. number of predictor variables). The most frequently selected or ‘best’ model was the same in both seasons, with  $rTw_{sfc}$  having been selected first and  $T$  having been selected thereafter. The functional relationship of  $Alt$ ,  $rTw_{sfc}$ , and  $T$  to  $tBd$  in these models is illustrated in Figure 5.7. As well, Appendix E shows, for each night considered in this study, measured distributions of  $pBd$ , with their associated  $T$ ,  $Tw$ ,  $SH$ , and  $Cp$  distributions, alongside the weighted average seasonal distribution of  $pBd$  and the distribution of  $pBd$  predicted by the best GAM model for that season. The predicted distributions from these GAM models vary more than those from the simulation and do a better job of capturing “peaks” in  $pBd$  at higher altitude.

In the best model for both seasons, a rather linear decrease in  $tBd$  occurred with increasing  $Alt$  (Figure 5.7), and  $Alt$  explained more variability in  $tBd$  than any other variable (Table 5.3). The functional form of  $rTw_{sfc}$  in the best model for both seasons indicated that, when  $Tw$  was negative at the

**Table 5.2:** The number of times each potential predictor variable was selected in a final GAM model during the 50 stepwise model selection iterations for spring and autumn is shown. Altitude was included in each model by default.

Abbreviation	Variable	Times selected	
		Spring	Autumn
<i>Alt</i>	Altitude	50	50
<i>rTw</i>	Relative <i>Tw</i>	11	3
<i>rTw<sub>sfc</sub></i>	<i>Tw</i> relative to surface	45	50
<i>rWP</i>	Relative <i>WP</i>	14	1
<i>rWP<sub>sfc</sub></i>	<i>WP</i> relative to surface	16	6
<i>T</i>	Temperature	19	32
<i>RH</i>	Relative humidity	0	13
<i>SH</i>	Specific humidity	7	15
<i>Cp</i>	Cloud persistence	2	0

**Table 5.3:** The most frequently selected models from the 50 stepwise model-selection iterations are shown for spring and autumn. Predictor variables other than altitude were selected according to repeated random sampling cross-validation. For each season, we indicate the most frequently occurring model for each level of complexity (i.e. number of predictor variables). From those model-selection iterations that produced the most frequently occurring models at the highest complexity (8 in spring and 24 in autumn), we report the average of the mean RMSE (on the scale of *pBd*), Spearman’s  $\rho$ , and variance explained – as defined by Bruderer et al. (1995b) – at each level of complexity.

Season	Number of variables	Final GAM model	RMSE	Spearman’s $\rho$	Variance explained
Spring	1	<i>Alt</i>	0.096	0.32	52.2
	2	<i>Alt</i> + <i>rTw<sub>sfc</sub></i>	0.087	0.38	55.0
	3	<i>Alt</i> + <i>rTw<sub>sfc</sub></i> + <i>T</i>	0.084	0.44	57.1
Autumn	1	<i>Alt</i>	0.064	0.74	73.1
	2	<i>Alt</i> + <i>rTw<sub>sfc</sub></i>	0.059	0.79	73.8
	3	<i>Alt</i> + <i>rTw<sub>sfc</sub></i> + <i>T</i>	0.058	0.77	75.4

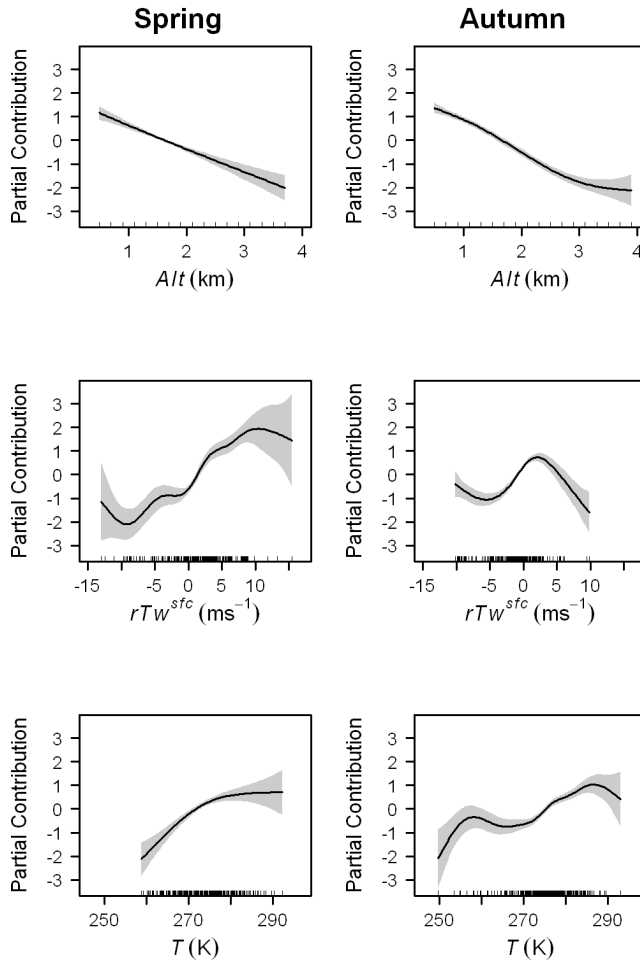


Figure 5.7: Plots indicating the partial contributions of the variables comprising the most frequently selected models resulting from the 50 forward stepwise model-selection iterations for spring (left column) and autumn (right column). Variables are given from top to bottom in the order they were (most often) selected. In each plot, the x-axis indicates the range of the predictor variable, and rug plots along the bottom indicate the occurrence of a particular value of that predictor variable. The y-axis indicates the partial contribution of each predictor variable on the scale of  $tBd$  (i.e.  $pBd$  or proportional bird density after the additive log-ratio transformation). Shaded areas indicate two standard errors from the estimate. Model predictions (on the scale of  $tBd$ ) are obtained by summing the partial contributions of each predictor variable.

surface, larger proportions of birds occurred at altitudes at which  $Tw$  was stronger than at the surface (Figure 5.7); conversely, smaller proportions of birds occurred at altitudes at which  $Tw$  was weaker than at the surface. The functional form of  $T$  in both seasons suggested that birds generally avoided colder temperatures. In both seasons, the functional forms of  $rTw_{sfc}$  and  $T$  nearer their extremes exhibited sinuosity and changes in direction that may be driven by relatively few data points. Rug plots in Figure 5.7 show a sparseness of data points at these extremes, with confidence intervals (areas shaded gray in Figure 5.7) around predictions made in this part of the domain being higher as a result.

## 5.5 Discussion

Often, the paradigm used to understand bird migration is one of optimization (Alerstam, 2011), where behavior is described in the context of optimizing one or more predefined criteria. The criteria often considered in the context of bird migration are time, energy, water balance, and predation risk. When studying flight altitude selection in the context of optimality, energy and water balance have been the primary criteria considered (e.g. Klaassen and Biebach, 2000; Liechti et al., 2000; Schmaljohann et al., 2009); however, time and safety, for example the risk of becoming disoriented or not efficiently finding a suitable stopover site, may also be important adaptive constraints on altitude selection. In general, (and particularly in the absence of complicating factors such as those outlined below), nocturnal migrants should select altitudes with greater wind support when minimizing travel time or energy expenditure to reach the migration target, and empirical studies of avian altitude distributions have often reached this conclusion (e.g. Bruderer et al., 1995*b*; Liechti et al., 2000; Schmaljohann et al., 2009).

Our study also suggests that birds prefer altitudes with more supportive winds (see Figure 5.5 and the partial contributions of  $rTw_{sfc}$  in Figure 5.7), and specific examples in our study suggest that birds are quite capable of identifying and selecting profitable winds (e.g. 4-9 May 2008; see Appendix E). We also find that increasing tailwind strength with altitude ( $\Delta Tw$ ) increases the probability of birds climbing to higher altitude. However, while our results suggest that birds prefer supportive winds, we find little or no correlation between the nightly vertical profiles of either  $WP$  or  $Tw$  and the altitude distributions of  $pBd$  (Figure 5.4.2), and wind support explains a relatively small amount of the variability we observed in migratory altitudes (see Table 5.3). Recall as well the significant negative intercepts in the regression equations describing the relationships between  $\Delta Tw$  and  $P_L$  in the approach following

Bruderer et al. (1995*b*). These intercepts mean that in spring and autumn  $\Delta Tw$  has to be greater than 2.23 and 5.67  $\text{ms}^{-1}$ , respectively, before a majority of birds prefer the next highest altitude bin. Thus, the simulations from these regression relationships are heavily influenced by these intercepts, and the intercepts are likely a reflection of the average distribution of  $pBd$ . It is reasonable then that  $Alt$  itself in our GAM models explains roughly the same amount of variability in  $pBd$  as our simulation approach following Bruderer et al. (1995*b*). Apparently, birds are not exclusively selecting flight altitudes based on wind conditions that would optimize time or energy expenditure. As has been shown in other areas (Bruderer, 1971), the effects of wind on migratory altitude cannot be considered in isolation from other atmospheric factors. This is likely due to birds considering multiple objectives (and trade-offs between these objectives) during migratory flight.

From an aerodynamic perspective, migrating at higher altitudes should be beneficial since the decrease in air density associated with higher altitudes reduces frictional resistance (i.e. parasite drag) thereby increasing the distance a bird is able to fly with a given amount of energy and reducing the time it will take to do so (Pennycuick, 2008). Despite this potential benefit, both Gauthreaux (1991) and Bruderer (1971) observed birds flying at lower altitudes even when winds were somewhat better aloft, suggesting that lower altitudes may be favored over higher ones. Our results corroborate this assessment: the average altitude distribution of  $pBd$  (Figure 5.2), the significant negative intercepts in our comparison with the analysis of Bruderer et al. (1995*b*), and the functional relationship between  $Alt$  and  $tBd$  revealed in our GAM analysis (Figure 5.7) suggest a preference for lower altitudes. As well, our comparison with the analysis by Gauthreaux (1991) shows that, even when birds do fly higher than normal, they concentrate around the lowest altitude with acceptable, though note not necessarily optimal, wind conditions (Figure 5.5). In aggregate, our results suggest that climbing to high altitude in this region may be a risky and/or costly endeavor or that there are additional benefits associated with migrating at lower altitude.

In addition to the fact that it takes time and energy simply to reach higher altitudes (Hedenström and Ålerstam, 1992; Liechti et al., 2000), there are several atmospheric variables correlated with altitude that, particularly through their potential influence on a bird's rate of water-loss, could curb the potential benefits of high-altitude migratory flight, resulting in a general tendency to remain at low altitudes (Carmi et al., 1992; Klaassen, 1995, 1996, 2004). Atmospheric pressure necessarily decreases with altitude, which forces a corresponding decrease in oxygen partial-pressure and, along with the aforementioned decrease in frictional resistance, a decrease in lift (i.e. induced drag



Pennycuick, 2008). As well, temperature in the troposphere generally decreases with altitude, unless a low-level temperature inversion is present, and decreasing temperature reduces the amount of moisture the air is able to hold. Therefore when birds inhale the colder (and likely drier) air at higher altitude, they warm that air (increasing the amount of water the air is able to hold), saturate the air with water from their own body, and then lose the water through exhalation (Klaassen, 1996). The decrease in lift with altitude is not such a problem from a aerodynamic perspective, since there is often more benefit from the reduction in friction than detriment from the reduction in lift; however, slightly more aerobic power is required, and thus more oxygen, yet available oxygen decreases with altitude. This necessitates an increase in pulmonary ventilation which forces a further increase in the rate of water-loss (Carmi et al., 1992). So while the rate of water-loss increases in higher temperatures (see Schmaljohann, 2008, and references therein) as birds attempt to reduce heat-stress by evaporative cooling (Klaassen, 1996), potentially more water is lost in colder temperatures due to the difference in temperature between cooler ambient air and warmer exhaled breath (Klaassen, 1996). Our GAM analysis suggests that birds avoid very cold temperatures (see Figure 5.7). Avoidance of very warm temperatures in these models, however, is not apparent. Perhaps temperatures in the Netherlands did not reach the threshold for “very warm” often enough during the migration seasons we examined to be well-represented in our models (see distributions of  $T$  in Figures 5.3 & 5.4 and the rug plots along the bottom of plots illustrating the functional relationship of  $T$  to  $tBd$  in Figure 5.7).

Despite studies suggesting that flight range may be limited by dehydration, previous empirical studies have shown birds selecting altitudes based largely on wind conditions (e.g. Bruderer et al., 1995*b*; Liechti et al., 2000), and specifically selecting altitudes to minimize energy costs rather than water-loss (Schmaljohann et al., 2009). Recall, however, that these studies were primarily conducted in the trade-wind zone where the influence of Hadley cell rotation, and the associated shift of wind direction with altitude, can result in winds near the surface being persistently prohibitive, while wind conditions at higher altitude are less-prohibitive or even supportive. Our GAM results suggest that birds are more likely to seek out supportive winds at higher altitude if winds near the surface are prohibitive (see the partial contribution of  $rTW_{sfc}$  in Figure 5.7), and many of the cases in our study in which birds flew at higher altitude are associated with prohibitive winds near the surface and less-prohibitive or even supportive winds at higher altitude (see e.g. 9 October 2008 and 27 October 2009 & 4-25 May 2008 among many others in Appendix E). In contrast, we do not generally see migrants climbing to

higher altitude when wind conditions at the surface are already supportive (see e.g. 24-25 November 2008 and 15 October 2009 & 7 April 2008 and 2-3 March 2009 in Appendix E). Perhaps high-altitude migration is due primarily to avoidance of prohibitive winds near the surface rather than selection of optimal winds at higher altitude, which would be in accordance with findings in this and previous studies. An interesting avenue for future research would be to study if migrants fly at higher altitudes only when wind conditions are sufficiently prohibitive near the surface and more supportive at higher altitude, and perhaps to identify thresholds for ‘sufficiently prohibitive’ and ‘more supportive’. From an evolutionary perspective, it would be interesting to see if these thresholds were adjusted along the migration route according to the general atmospheric circulation patterns of a region and season.

Another possible difference between the migratory behavior we observed in the Netherlands and what has been observed in some previous studies is that birds in the Netherlands are not in the process of crossing an ecological barrier. Several systematic examinations of avian altitude distributions in relation to weather have been conducted in the proximity of an ecological barrier such as the Sahara desert (e.g. Klaassen and Biebach, 2000; Liechi and Schmaljohann, 2007; Schmaljohann et al., 2009) or the Gulf of Mexico (Gauthreaux, 1991). Crossing such an ecological barrier may significantly alter behavior as it may be beneficial to cross the barrier as quickly as possible. In cases where minimizing time is essential, finding and utilizing the most beneficial winds may be of paramount importance. Alternatively, when not crossing an ecological barrier, a bird may be willing to accept sub-optimal winds at lower altitudes in order to conserve moisture, reduce the risk of being blown off course by high-speed winds at higher altitude, search for suitable stopover habitat, or navigate more easily. If birds navigate using ground-based visual cues (Bruderer, 1982; Fortin et al., 1999), increasing atmospheric turbidity (being unavoidable as light travels greater distances through the atmosphere) and increasingly shallow angles between a bird and its ground-based points of reference with altitude likely inhibit navigation.

That  $C_p$  was not selected often in our models should not lead necessarily to the conclusion that clouds had no influence on altitude selection. It is possible, for instance, that we introduced a bias in our dataset by only considering nights with relatively intense migration. As well, clouds can be difficult to quantify, particularly per altitude bin, as they can be discontinuous and heterogeneously distributed in space and time. Bruderer (1971) observed that the type and quality of cloud cover determined its influence on migratory altitudes, yet many aspects of cloud cover cannot be measured or modeled yet systematically. Thus, relevant features of a particular cloud formation may not have been

captured in our formulation of  $Cp$ .

A shortcoming of the methods we, and others, have applied to model the altitude distributions of avian migrants arises from the tendency to assume uniformity in avian decision making over time and space. For example, we necessarily use a single preferred direction in the calculation of  $WP$  and  $Tw$  when it is quite possible that migrants with different endogenous directions were considered in our analyses. Furthermore, species migrating at different times of the season may prioritize adaptive pressures, and therefore atmospheric variables, differently. Nonetheless, our GAM models explain a rather large percentage of the variability in migratory altitudes, and the variables selected in our GAM analysis are likely representative of the general behavior of migrants in this area. This is particularly likely since the same predictor variables, indicating similar relationships with migratory altitude, were selected in both seasons.

Our GAM results show that birds predominantly remain at low flight altitudes in this region. Since this behavior is not consistent with time or energy minimization when wind conditions improve with altitude, the behavior may indicate birds balancing the optimization of time and/or energy with considerations of their safety, water balance, and perhaps other criteria. When wind conditions are supportive already at low altitude, and birds can make acceptable forward progress, negative impacts on their safety and water balance associated with high-altitude flight may offset potential gains in time and energy from more supportive winds at higher altitude. When wind conditions are unsupportive at low altitude, however, birds may be willing to climb to higher altitude, accepting an increase in their rate of water-loss and a decrease in safety, so that they can find supportive winds and maintain an acceptable travel speed. Even so, birds stop climbing once they reach an altitude with acceptable wind conditions rather than continuing to climb and incurring increasingly negative effects on their safety and water balance.

## 5.6 Conclusion

In general, we may expect that birds can and should adapt their flight altitudes in such a way as to account for flight time, energy expenditure, water balance, and safety, yet the relative importance of these pressures may change between species, regions, seasons, and phases of migration. In some situations, traveling as fast as possible in a desired direction may take precedence, making the influence of wind paramount. In our study area, where freezing temperatures, cloud cover, and frequent frontal systems exist, birds seem to balance considerations of time, energy, water, and safety and do not appear to

select altitudes for migration based solely on wind condition. This result supports a recent trend in literature suggesting that passerine migrants may not be as selective of tailwind support as previously suspected (Alerstam et al., 2011; Karlsson et al., 2011). Thus, while birds exhibit some general behavioral adaptations to atmospheric conditions on a large scale (e.g. avoidance of headwinds), individuals may be flexible in their responses to conditions en route – perhaps even depending on the persistent atmospheric (or geographic) conditions in an area.

This study highlights the potential gains to be made using existing weather radar to study migratory movements with high temporal and altitudinal resolution. With an existing network of similar radars already covering so much of Europe, the potential exists for a great deal of informative analyses allowing specifically the types of comparisons between different locations needed to separate the individual influences of and quantify trade-offs between different atmospheric (and non-atmospheric) variables; quantify the priority or precedence birds give these variables; and determine if this priority or precedence depends on the condition of other variables, geographical location, and time of year. Ultimately, we may determine that altitude selection in birds is based on just a few general rules and is otherwise quite flexible; alternatively, we may realize that there are a great many endogenous and interdependent rules that we were previously unable to disentangle. Likely, the situation is, as described by Alerstam (1981), “a harmonious mixture of rigid and flexible behavior adapted to a bewildering number of factors affecting the safety and economics of the migratory journey”. An integrative combination of analytical tools, measurements across multiple spatial and temporal scales, and experiments that enable researchers to consider multiple objectives and trade-offs simultaneously are likely to bring us much further in our understanding of migratory behavior (Bowlin et al., 2010).

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