The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes

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By altering its flight altitude, a bird can change the atmospheric conditions it experiences during migration. Although many factors may influence a bird's choice of altitude, wind is generally accepted as being the most influential. However, the influence of wind is not clearly understood, particularly outside the trade-wind zone, and other factors may play a role. We used operational weather radar to measure the flight altitudes of nocturnally migrating birds during spring and autumn in the Netherlands. We first assessed whether the nocturnal altitudinal distribution of proportional bird density could be explained by the vertical distribution of wind support using three different methods. We then used generalized additive models to assess which atmospheric variables, in addition to altitude, best explained variability in proportional bird density per altitudinal layer each night. Migrants generally remained at low altitudes, and flight altitude explained 52 and 73% of the observed variability in proportional bird density in spring and autumn, respectively. Overall, there were weak correlations between altitudinal distributions of wind support and proportional bird density. Improving tailwind support with height increased the probability of birds climbing to higher altitude, but when birds did fly higher than normal, they generally concentrated around the lowest altitude with acceptable wind conditions. The generalized additive model analysis also indicated an influence of temperature on flight altitudes, suggesting that birds avoided colder layers. These findings 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 only to optimize wind support. Rather, they preferred to fly at low altitudes unless wind conditions there were unsupportive of migration. Overall, flight altitudes of birds in relation to environmental conditions appear to reflect a balance between different adaptive pressures.

Keywords: flight altitude, generalized additive models, migration, operational weather radar, passerines, variable selection, wind.

Migrant birds, many travelling thousands of kilometres twice each year between their breeding and wintering grounds, encounter a range of atmospheric conditions. By influencing a bird's flight efficiency and ability to navigate, these atmospheric conditions can affect its capacity to maintain its desired course and schedule (Shamoun-Baranes *et al.* 2010). Therefore, one would

expect birds to fly preferentially at altitudes at which atmospheric conditions are most supportive of their migratory flight. For diurnal soaring migrants, flight range is maximized by using 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). At night, however, in the absence of vertical mixing induced by convective thermals, the convective boundary layer col-

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lapses and the atmosphere becomes generally more stratified (Stull 1988). Thus, nocturnal migrants have the option to select (often from within wide ranges) a range of atmospheric conditions (e.g. temperature, humidity and wind condition) by adjusting their altitude.

Most quantitative research has suggested that wind is the greatest influence on flight altitudes of nocturnally migrating birds, whereas other atmospheric variables such as temperature and humidity exert only minor influence (Bruderer *et al.* 1995, Liechti *et al.* 2000, Liechti & Schmaljohann 2007, Schmaljohann *et al.* 2009). Specifically, these studies report a strong correlation between the altitudinal distribution of migrants and altitudinal distribution of either wind profit (the support a bird obtains from a particular set of wind conditions) or some estimate of flight range based largely on wind support. However, these studies have been conducted mainly inside the trade-wind zone of North Africa and the Middle East.

Based on atmospheric general circulation patterns (Rohli & Vega 2007), the northern and southern hemispheres on Earth can be subdivided into three latitudinal zones: the trade-wind zone (0–30°) in which Hadley cells dominate, the mid-latitudes (30–60°) and the polar region (60–90°). In the trade-wind zone and polar regions, wind direction often changes by 180° with altitude. Thus, inside the northern hemisphere trade-wind zone, winds beneficial to migrants 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). Similarly, prohibitive winds are also present every night and at generally predictable altitudes. In the mid-latitudes, however, upper-level winds generally do not reverse direction from the surface, so 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 in the normal altitudes of bird migration are generally above freezing (Bruderer *et al.* 1995, Klaassen & Biebach 2000, Liechti *et al.* 2000, Schmaljohann *et al.* 2009); the same may not be true in other zones. Overall, therefore, it is unclear to what degree the findings of studies of migrants undertaken in the trade-wind zone may apply elsewhere.

Studies outside the trade-wind zone also indicate that wind influences migration altitudes, but not necessarily that birds always select altitudes to optimize wind support. From a visual and radar analysis conducted in the southern USA 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 lowest altitude with acceptable (but not necessarily optimal) winds, when migrants flew at higher altitudes than normal. Gauthreaux suggested that these higher-than-normal altitude flights occurred when winds at lower altitude were prohibitive and winds at higher altitude were supportive. Several studies also suggest that migrants generally fly at higher altitudes with tailwinds than with headwinds (Bruderer 1971, Kerlinger & Moore 1989, Richardson 1990) and one study suggested that migrants remain at lower altitudes when wind speeds are high, irrespective of wind direction (Able 1970).

The influence of wind on migration altitude cannot be understood in isolation from other atmospheric conditions such as precipitation and cloud cover (Eastwood 1967, Bruderer 1971, Kerlinger & Moore 1989), although birds may fly above, below and even within clouds (Bellrose & Graber 1963, Nisbet 1963, Eastwood & Rider 1965, Able 1970, Griffin 1973). 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 a correlation between the altitude below which 90% of migration occurred and the altitude at which freezing temperatures occurred, Bruderer (1971) also suggested that birds may choose altitudes to optimize thermoregulation, although some birds were observed flying in temperatures as low as −15 °C. Elkins (2004) suggested that freezing temperatures may pose problems when air is saturated, as this could lead to ice accumulation on plumage, although Bruderer (1971) reported birds flying in such conditions. Theoretical studies suggest 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, Klaassen 1996, Gerson & Guglielmo 2011). 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 & Dudley 2006) and air density (Pennycuick 2008), along with temperature and humidity, may influence a bird's flight efficiency. In summary, the altitudinal distribution of birds 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 geographical areas and integrating multiple atmospheric variables are desirable to test relationships quantified or suggested in other regions between atmospheric variables and avian migratory altitudes for universal applicability and to improve our understanding of how birds potentially balance these different adaptive pressures when selecting flight altitudes during migration.

The aim of this study was to determine how atmospheric conditions influence the nocturnal altitude distributions of migrating birds, using C-band Doppler weather radar in the Netherlands – a location where prevailing atmospheric conditions are quite different from, and less predictable than, those of the trade-wind zone (Rohli & Vega 2007). Because most quantitative research has focused on the influence of wind, and for comparative purposes, we first explore relationships between wind conditions and migratory altitude by applying three approaches from previous research. First, following Gauthreaux (1991), we consider a subset of nights in which birds fly higher than normal and assess whether the altitude of peak migration is correlated with the lowest altitude with acceptable wind support. Secondly,

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 calculated in some studies undertaken in the trade-wind zone (e.g. Liechti *et al.* 2000, Schmaljohann *et al.* 2009). Thirdly, we apply a simulation model, following Bruderer *et al.* (1995), in which the probability of a bird changing altitude is a function of the change in tailwind strength with altitude. Finally, we use generalized additive models (GAMs) to test the relative influence of multiple atmospheric variables that, through observation, theory or statistical inference, have been suggested to influence the altitude of avian migration.

METHODS

Radar measurements of bird density

We used methods described by Dokter *et al.* (2011) to derive altitudinal profiles of bird density (Bd; birds/km³) and average groundspeed (m/s) every 5 min from a C-band Doppler weather-radar located in De Bilt, the Netherlands (52.11°N, 5.18°E; Fig. 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 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 centre of the radar (Fig. 1).
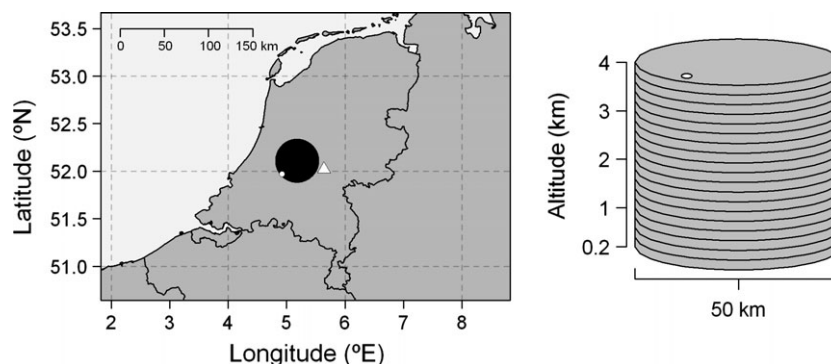
Figure 1. (Left) Map with a black circle indicating the range of the C-band Doppler weather radar in De Bilt, the Netherlands. A white triangle indicates the closest grid point in the HIRLAM dataset, from which weather data were obtained. (Right) Vertical profile of the radar's measurement volume, indicating the 19 altitude bins within which measurements of bird density were calculated. In both images, the small white circle indicates the location of the cloud-measuring LIDAR ceilometer at the Cabauw experimental site for atmospheric research.

As a means of additional quality control, we used HIRLAM wind data (see 'Meteorological data' below) to calculate airspeeds from these groundspeeds by vector subtraction. We set Bd measurements to zero if the associated airspeed was not between 7 and 25 m/s, as this range captures the airspeeds of the majority of nocturnal migrants (Bloch & Bruderer 1982, Bruderer & Boldt 2001) and largely excludes insects (Chapman *et al.* 2008, Alerstam *et al.* 2011, Aralimarad *et al.* 2011).

Bruderer *et al.* (1995) observed that nocturnal migrants can spend the first 2 h after sunset sampling different altitudes 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 2 and 3 h after sunset. We only considered nights in which total migration (i.e. the sum of all median Bd values in the nightly Bd profile) was > 20 birds/km^3, because measurements were less reliable when Bd values were very small. Given this threshold, we retained data from 29% of 238 available spring nights and 18% of 236 available autumn nights.

We then translated 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. The weighted average 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) are shown for each season in Figure 2.

For analytical purposes, we applied the additive log-ratio (ALR) transformation (Aitchison 1982) to 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 centred on 0.3 km, as:

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

This transformation produced an unreal solution for any observation in which pBd was equal to zero, so these observations were excluded from our analysis. tBd served as the response variable in our GAM regression analysis, but tBd values calculated in a reference altitude bin (i.e. where *a* = 1) were not used to fit the GAMs. What remained were 378 and 340 tBd measurements in spring and autumn, respectively. We back-transformed tBd$_a^i$ in all but the reference altitude bin as:

$$pBd_a^i = \frac{\exp(tBd_a^i)}{1 + \sum\limits_{a=2}^{19} \exp(tBd_a^i)}$$

and in the reference altitude bin as:

$$pBd_1^i = 1 - \sum\limits_{a=2}^{19} pBd_a^i$$

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

Meteorological data

We derived altitude profiles, to a height of 4 km, of wind condition (m/s), temperature (*T*; K), atmospheric pressure (A$_P$; mb) and relative humidity (RH; %) using data from the gridded HIRLAM atmospheric model (Cats & Wolters 1996, Undén *et al.* 2002). These data had a spatial resolution of 0.1 × 0.1° on a rotated grid, a temporal resolution of 1 h, and were provided at fixed pressure levels separated by not more than 20 mbar. Using data from the grid point nearest to the centre of the De Bilt radar (~33 km east at 5.64°E, 52.02°N; Fig. 1), we linearly interpolated all variables vertically to the centre 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 h after sunset each night (determined using the R package MAPTOOLS; Lewin-Koh *et al.* 2011). For each observation, we calculated specific humidity (SH; g/kg) following Buck (1981); see Supporting Information for details.

Wind data were described by two components, U and V (m/s), indicating the speed and direction in 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
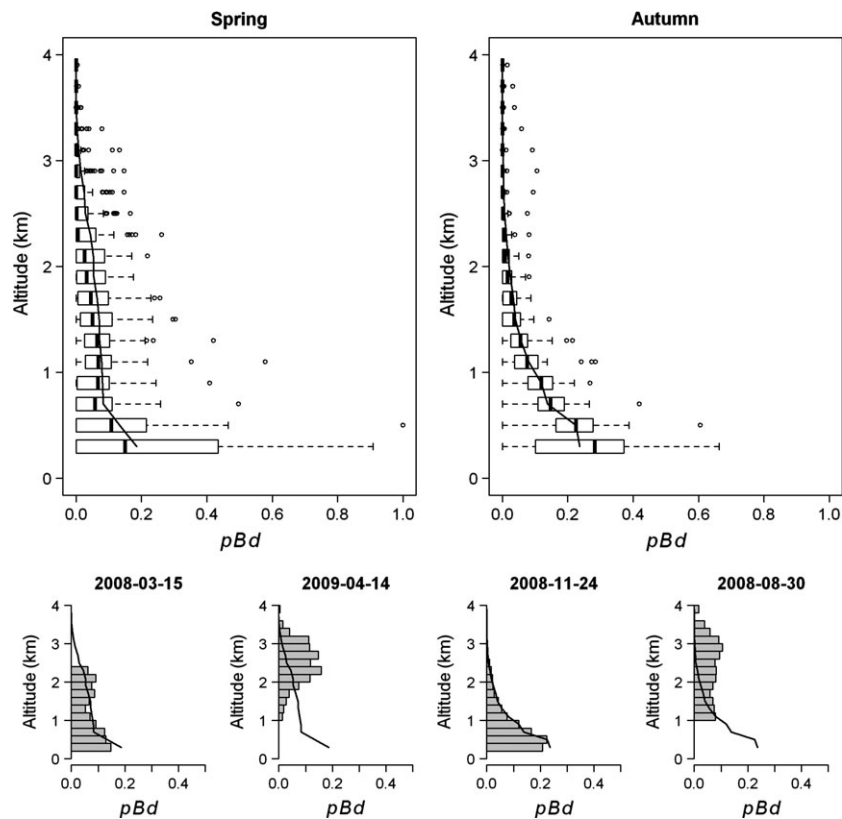
Figure 2. In all plots, a black line indicates the weighted average altitude distribution of proportional bird density (pBd) for the particular season (three plots of spring on left; three plots of autumn on right). In the top two plots, box-plots indicate the range of deviations from the weighted average 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.

expected flight behaviour. We calculated the tailwind (Tw; m/s) component (Shamoun-Baranes *et al.* 2007) and a measure of wind profit (WP; m/s). For both, a preferred migratory direction was required. We assumed an autumn migratory direction of 225°, consistent with the autumn migratory directions used in previous studies in the Netherlands (van Belle *et al.* 2007, Kemp *et al.* 2010) and similar to those observed by radar elsewhere in western Europe (Bruderer *et al.* 1989, Bruderer & Liechti 1998, Zehnder *et al.* 2001). We then reversed this preferred direction to 45° in spring, similar to the mean spring migratory direction of 41° 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 heading (Kemp *et al.* 2012) by:

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

where WP was a function of wind speed (Wspd) and the angular difference between the wind direction and the bird's preferred migratory direction (θ). Because passerines dominate nocturnal migration over Europe (Hahn *et al.* 2009), we set airspeed (z) to 12 m/s, which is representative of many migrating passerine species (Bloch & Bruderer 1982, Bruderer & Boldt 2001). Because birds were assumed to have a fixed airspeed, 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, 38 and 54 observations at individual altitude bins

were removed from all analyses because WP had no real solution. 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 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 $rWP_{sfc} = bWP_{sfc}$ ($WP - WP_{sfc}$). We similarly calculated relative tailwind (rTw) and tailwind relative to the surface (rTw_{sfc}). 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°N, 4.926°E (*c.* 25 km to the southwest of the centre of the De Bilt radar; Fig. 1). We accessed these data via the online Cesar database (The Cesar Consortium 2011). Cloud-base height (m) was calculated every 30 s with 15 m vertical resolution. In spring, 18 observations were removed from the analysis because cloud data were missing. For the regression analyses, we defined nightly cloud persistence (Cp) per altitude bin as the cumulative fraction of cloud-base observations between sunset and 3 h after sunset from 200 m up to the respective altitude bin.

Wind and migratory altitudes: comparisons with previous research

Following Gauthreaux (1991), we identified a 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 (*r*). We defined the lowest altitude bin with acceptable wind support as the lowest altitude bin in which the wind blew towards the N-NE in spring or the S-SW in autumn (Gauthreaux 1991). If no altitude bins satisfied this requirement,

we used instead the altitude bin with the lowest wind speed.

Following studies 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 (Spearman's ρ). We only calculated Spearman's ρ correlations for nights with data available in at least half the altitude bins.

Following Bruderer *et al.* (1995), we predicted 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 ΔTw). We first calibrated a linear regression to quantify the probability of a bird changing altitude as a function of ΔTw. To do so, we assumed that the difference in pBd between adjacent altitude bins indicated birds' preferences between 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. Therefore, values of *P* > 0.5 indicated that more birds preferred conditions in the next highest altitude bin, whereas values of *P* < 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 ΔTw as Tw in the altitude bin immediately above minus Tw in the current altitude bin, such that positive values for ΔTw 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 iteratively adjusted this distribution according to *P* predicted in each bin by ΔTw until the distribution achieved convergence (root-mean-square error (RMSE) between the previous and current iterations < 0.0001). Like Bruderer *et al.* (1995), we quantified the percentage of variability not explained by this simulation model as the sum of the absolute differences

between simulated and measured pBd divided by the sum of all simulated and measured pBd.

Multivariate analysis

We used GAMs 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. Computations used 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 flight altitude (Alt) as a predictor variable to account for effects attributable to altitude itself, such as birds preferring lower flight 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 predictor variable (Table 1), 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 ρ and percentage of variability explained (Bruderer *et al.* 1995) between 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 ($\alpha \leq 0.05$) in the model and did not cause previously selected variables to become non-significant. Furthermore, we applied a Chi-squared test to confirm that inclusion of each variable resulted in a significant ($\alpha \leq 0.01$) improvement in overall model fit.

Due to the effects of repeated random sampling and the flexibility allowed by GAMs, different final models might 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. In addition, 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.

RESULTS

Weather conditions

Our study area has a Cfb climate-type (temperate with no dry season and warm summers) according to the Köppen–Geiger climate classification system (Peel *et al.* 2007). Figures 3 and 4 provide an overview of the atmospheric conditions in 1-km altitude bands in spring and autumn, respectively. In these figures, both wind speed and direction are provided (wind roses) as well as wind profit (WP; m/s) and tailwind (Tw; m/s), which are non-linearly related to wind speed and direction. In

Table 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.

| Abbreviation	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	m/s	Tailwind strength at a given altitude minus the strongest tailwind in the altitude profile (e.g. Bruderer *et al.* 1995, Liechti *et al.* 2000)
rTw$_{sfc}$	m/s	Tailwind strength at a given altitude minus tailwind strength at the surface, if headwinds are present at the surface, otherwise zero (Gauthreaux 1991)
rWP	m/s	Wind profit at a given altitude minus the best wind profit in the altitude profile (e.g. Schmaljohann *et al.* 2009)
rWP$_{sfc}$	m/s	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	Specific humidity or the mass of water vapour per kilogram of atmosphere (e.g. Gerson & Guglielmo 2011)
Cp	%	Cloud persistence or the percentage of time that clouds were present (cf. Eastwood 1967, Bruderer 1971)
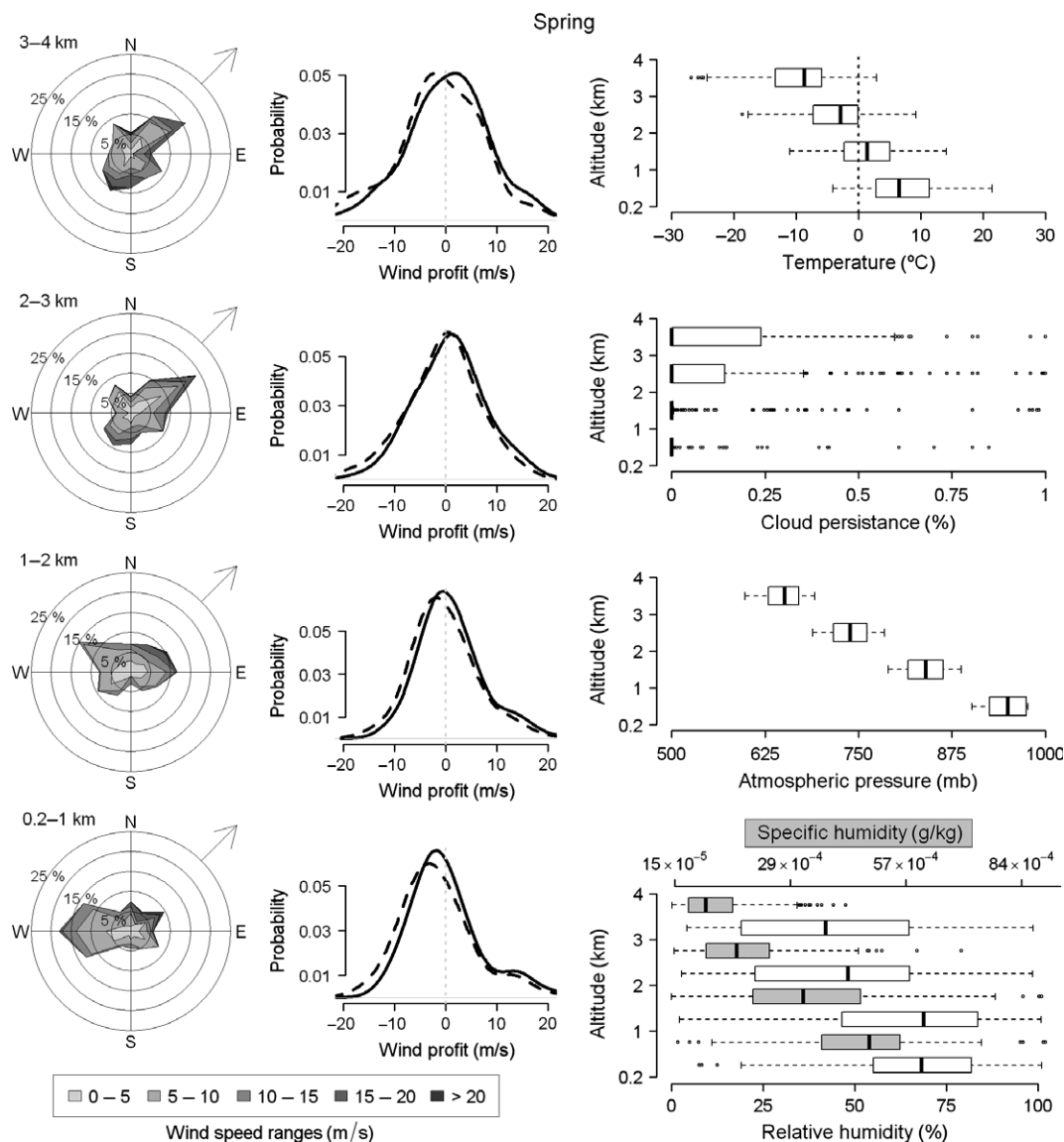
Figure 3. Graphical summaries of the weather conditions for spring from the nightly weather profiles used in our study. Wind condition, described in 1-km altitude intervals, is shown on the left by wind rose plots (wind speed and direction) and probability distributions of tailwind (Tw; solid line) and wind profit (WP; dashed line). Distance from the centre of a wind rose indicates the relative frequency of the wind blowing in a particular direction, and shades of grey 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. 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.

spring, winds blowing predominantly to the northeast at high altitudes (2–4 km; Fig. 3; wind roses at left) translated into an approximately symmetrical distribution of Tw (solid lines in distributions left of centre in Fig. 3) with a positive mean and mode for altitudes higher than 2 km, and a nega-

tive mean and mode for altitudes below 2 km. Regarding WP in spring (dashed lines in distributions left of centre in Fig. 3), the mode and mean were only positive for altitudes in the 2–3 km range. The large difference in WP between the 2–3 and 3–4 km altitude ranges was due to the
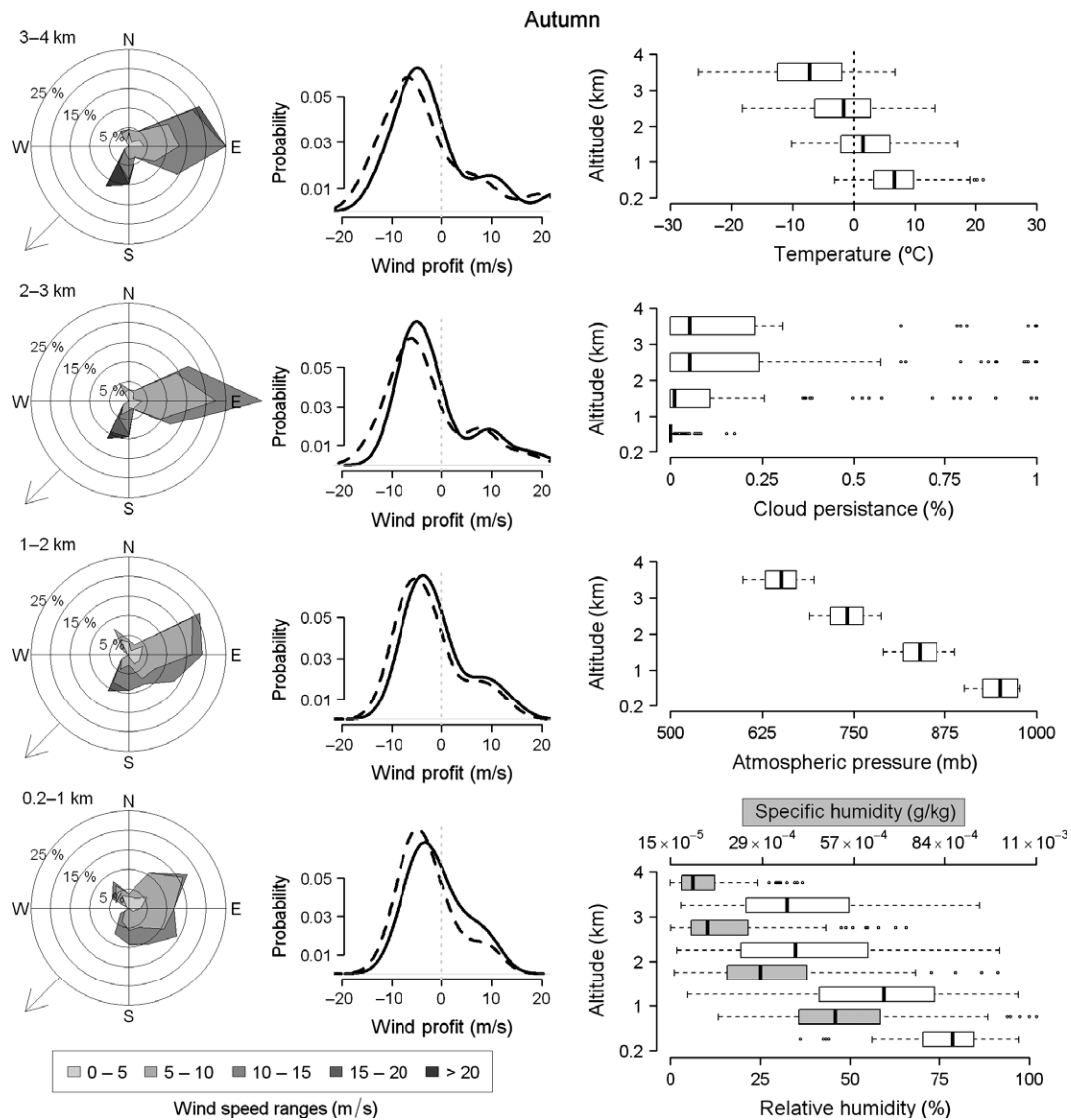
Figure 4. Graphical summaries of the weather conditions for autumn from the nightly weather profiles used in our study; plots follow those described in the caption to Figure 3.

higher frequency of strong (> 15 m/s) opposing winds in the 3–4 km altitude range. Consistent with Kemp *et al.* (2010), wind speeds generally increased with altitude and, particularly in autumn, winds blew more frequently and forcefully from the west (Fig. 4; wind roses at left). Also in autumn, the distributions of WP and Tw were skewed to the right for all altitude layers and the mode and mean had roughly the same negative values. In summary, wind conditions were generally more supportive of the northeasterly movement of spring migration than the southwesterly movement of autumn migration. In both sea-

sons *T*, SH and RH decreased with altitude. Autumn temperatures were higher than spring at all altitudes.

Wind and migratory altitudes: comparisons with previous research

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 (Fig. 5) were significantly positive in spring
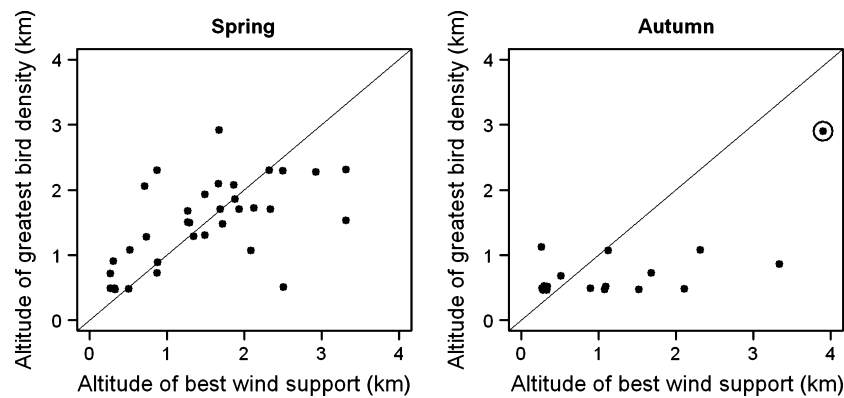
Figure 5. Scatter plots indicating the correlation between the altitude with best wind support (as calculated by Gauthreaux 1991) and the altitude with most intense migration for those nights in spring (left; $n = 35$; $r = 0.59$; $P \leq 0.001$) and autumn (right; $n = 18$; $r = 0.68$; $P \leq 0.01$) 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 theoretically perfect positive correlation.

($r = 0.59$; $n = 35$; $P \leq 0.001$) and autumn ($r = 0.68$; $n = 18$; $P \leq 0.01$), but the latter depended upon the leverage of a single point with a Cook's distance of 2.3 (Fig. 5).

Nightly correlations between wind support (considering either Tw or WP) and pBd 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, although 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 of Bruderer *et al.* (1995), our linear regression models suggested a statistically significant but very weak relationship between ΔTw (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) in both autumn ($P_L = -0.34 + 0.06\Delta$Tw, $n = 361$, $r^2 = 0.01$, $P \leq 0.05$) and 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.* (1995), we found that the intercept in the equations was highly significant. Nonetheless, very little variation in the response was explained by these models, suggesting that ΔTw had little overall influence on P_L.

The simulations resulting from the regression relationships between ΔTw and P_L explained 56 and 73% of the variability in nightly distributions of pBd in spring and autumn, respectively, compared with 56 and 63% reported by Bruderer *et al.*

(1995). The average Spearman's ρ correlation between the measured and simulated distributions was 0.54 in spring and 0.76 in autumn, and the average RMSE value between measured and simulated pBd was 0.067 in autumn and 0.085 in spring. The Supporting Information accompanying this article 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 did not vary greatly from night to night, and most exhibited a rather exponential decrease with altitude.

Multivariate 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. These models were selected and calibrated with tBd serving as the response variable but we back-transformed our predictions and discuss model performance on the scale of pBd wherever possible. Table 2 reports the number of times each potential predictor variable was selected in one of these 50 final models. Flight altitude (Alt) was included in these models by default and alone explained a large proportion of variability in pBd (52 and 73% in spring and autumn, respectively). This was roughly the same amount of variability explained by our simulation approach. Measures of wind assistance relative to surface wind condi-

Table 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. Altitude was included in each model by default.

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

tions (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.

Table 3 shows that the most frequently selected ('best') model was the same in both seasons, with rTw_{sfc} having been selected first and T thereafter. The functional relationship of Alt, rTw_{sfc} and T to tBd in these models is illustrated in Figure 6. Furthermore, the Supporting Information accompanying this article 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 'layering events' or higher-altitude peaks in pBd (Dokter *et al.* 2012).

In the best model for both seasons, a rather linear decrease in tBd occurred with increasing Alt (Fig. 6), and Alt explained more variability in tBd than any other variable (Table 3). The functional form of rTw_{sfc} in the best model for both seasons indicated that, when Tw was negative at the surface, larger proportions of birds occurred at altitudes at which Tw was stronger than at the surface (Fig. 6); 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 lower 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 6 show a sparseness of data points at these extremes, with confidence intervals (areas shaded grey in Fig. 6) around predictions made in this part of the domain being larger as a result.

DISCUSSION

Often, the paradigm used to understand bird migration is one of optimization (Alerstam 2011). The criteria optimized may include 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 & Biebach 2000, Liechti *et al.* 2000, Schmaljohann *et al.* 2009). However, time and safety, for example the risk of becoming disorientated or not efficiently

Table 3. The most frequently selected models from the 50 stepwise model-selection iterations 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 (eight in spring and 24 in autumn), we report the average of the mean RMSE (on the scale of pBd), Spearman's ρ and variance explained (as defined by Bruderer *et al.* 1995) at each level of complexity.

Season	No. of variables	Final GAM model	RMSE	Spearman's ρ	Variance explained
Spring	1	Alt	0.096	0.32	52.2
	2	Alt + rTw_{sfc}	0.087	0.38	55.0
	3	Alt + rTw_{sfc} + T	0.084	0.44	57.1
Autumn	1	Alt	0.064	0.74	73.1
	2	Alt + rTw_{sfc}	0.059	0.79	73.8
	3	Alt + rTw_{sfc} + T	0.058	0.77	75.4
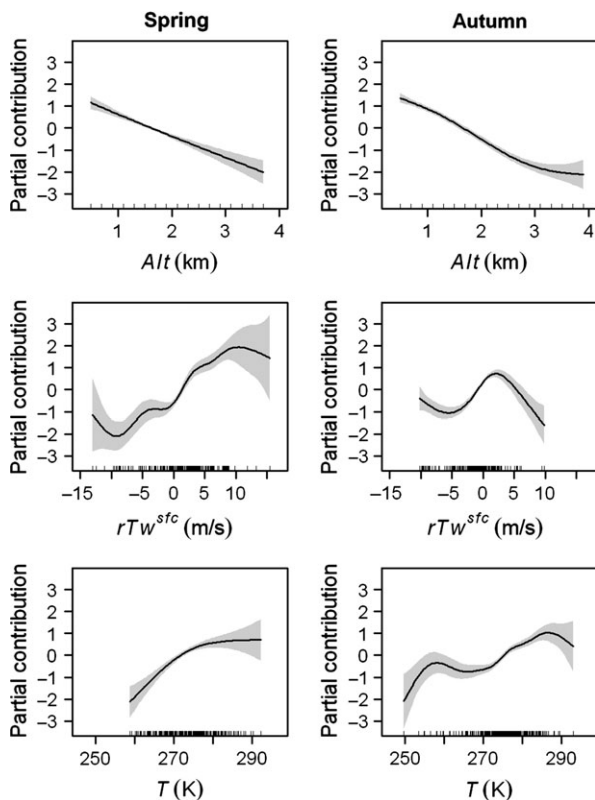
Figure 6. Plots indicating the partial contributions of the variables constituting the most frequently selected models resulting from the 50 forward stepwise model-selection iterations for spring (left column) and autumn (right column). Variables are given from top to bottom in the order they were (most 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 contribution of each predictor variable.

finding a suitable stopover site, may also be important adaptive constraints on altitude selection. In general, nocturnal migrants should select flight altitudes with greater wind support when minimizing travel time or energy expenditure to reach the migration target, and empirical studies of avian flight altitude distributions have often reached this conclusion (e.g. Bruderer *et al.* 1995, Liechti *et al.* 2000, Schmaljohann *et al.* 2009).

Our study also suggests that birds prefer flight altitudes with more supportive winds (see Fig. 5 and the partial contribution of rTw$_{sfc}$ in Fig. 6), 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 Supporting Information for spring). 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, and wind support explains a relatively small amount of the variability we observed in migratory altitudes (Table 3). Recall as well the significant negative intercepts in the regression equations describing the relationships between ΔTw and P$_{L}$. These intercepts mean that in spring and autumn, ΔTw has to be > 2.23 and 5.67 m/s, respectively, before a majority of birds prefer the next highest altitude bin (and even then ΔTw explains very little variability in P$_{L}$). Unsurprisingly, the altitude distributions predicted by the resulting simulations are all very similar (see supporting online material): all simulated birds start at the surface; some (but few) birds move into the next highest bin, because ΔTw has to be quite large for a majority of birds to climb; of those initial few that climbed, few birds again move into the next highest bin, and so on. The result is a general decrease in the proportion of birds with flight altitude. It is reasonable then that Alt itself in our GAM models explains roughly the same amount of variability in pBd as our simulation approach and also suggests a general decrease in the proportion of birds with altitude (Fig. 6). Apparently, birds are not exclusively selecting flight altitudes based on wind conditions that would optimize time or energy expenditure.

From an aerodynamic perspective, migrating at higher altitudes should be beneficial since the decrease in air density associated with higher altitudes reduces frictional resistance, 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, Bruderer (1971), Gauthreaux (1991) and Dokter *et al.* (2012) observed birds flying at lower altitudes even when winds were more supportive at higher altitudes. Our results corroborate this assessment: the average altitude distribution of pBd (Fig. 2), the significant negative intercepts in our comparison with the analysis of Bruderer *et al.* (1995), and the functional relationship between Alt and tBd revealed in our GAM analysis (Fig. 6) all suggest a preference for lower flight altitudes. Furthermore, our comparison with Gauthreaux (1991) shows that even when birds

do fly higher than normal, they concentrate around the lowest altitude with acceptable, though not necessarily optimal, wind conditions (Fig. 5).

In addition to the time and energy required to reach higher altitudes (Hedenström & Alerstam 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 curtail the potential benefits of high-altitude migratory flight, resulting in a general tendency to remain at lower flight 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 previously mentioned decrease in frictional resistance, a decrease in lift (Pennycuick 2008). In addition, 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 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 is often more than compensated for by reduction in friction, but slightly more aerobic power is required, and thus more oxygen, yet available oxygen decreases with altitude. This necessitates an increase in pulmonary ventilation that causes a further increase in rate of water-loss (Carmi *et al.* 1992). So while the rate of water-loss increases at higher temperatures (Schmaljohann 2008) as birds attempt to reduce heat-stress by evaporative cooling, more water may be lost at lower 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 low temperatures (Fig. 6). Avoidance of very high temperatures is not apparent, perhaps simply because temperatures were not high enough for this effect to occur (see distributions of T in Figs 3 & 4 and the rug plots along the bottom of plots illustrating the functional relationship of T to tBd in Fig. 6).

Previous studies, mostly in the trade-wind zone, have shown that birds select flight altitudes based largely on wind conditions (Bruderer *et al.* 1995, Liechti *et al.* 2000), specifically selecting flight altitudes to minimize energy costs rather than water-loss (Schmaljohann *et al.* 2009). In those areas 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. Similarly, and in agreement with the results of Dokter *et al.* (2012), our GAM results suggest that birds will seek out supportive winds at higher altitude if winds near the surface are prohibitive (see the partial contribution of rTw_{sfc} in Fig. 6), 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 SOM for 9 October 2008, 27 October 2009 and 4–25 May 2008). In contrast, we do not generally see migrants climbing to higher altitude when wind conditions at the surface are already supportive (see SOM for 24–25 November 2008, 15 October 2009, 7 April 2008 and 2–3 March 2009).

Another possible difference between the migratory behaviour 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 & Biebach 2000, Liechti & Schmaljohann 2007, Schmaljohann *et al.* 2009) or the Gulf of Mexico (Gauthreaux 1991). Crossing such an ecological barrier may significantly alter behaviour, as it may be beneficial to cross the barrier as quickly as possible. In cases where minimizing time is essential, finding and using the most beneficial winds may be critical. When not crossing such a 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 and increasingly shallow angles between a bird and its ground-based points of reference with altitude will inhibit navigation.

That Cp 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. Moreover, cloud cover can be difficult to quantify, particularly by altitude bin, as it can be discontinuous and heterogeneously distributed in space and time. Bruderer (1971) observed that the type and quality of a cloud determines its influence on migratory altitudes, yet many aspects of cloud cover cannot yet be measured or modelled 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 flight 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 respond to different selection pressures, and hence react differently to atmospheric variables. Nonetheless, our GAM models explain a rather high proportion of the variability in migratory altitudes, and the variables selected in our GAM analysis are probably representative of the general behaviour of migrants in this area. There are some decisions we made during the modelling procedure, however, that could be reconsidered in the future. For instance, during the data selection phase, we filtered out nights with low migration intensity in order to increase data quality. These thresholds may differ by study and, by influencing the training dataset, may influence resulting models. In addition, the formulation of WP used in this study required more behavioural assumptions than Tw (Kemp *et al.* 2012) and, because WP cannot be solved for all wind conditions, data were removed from analyses. In this study, however, Tw was generally a better predictor of flight altitude distribution than WP, perhaps because of the fewer assumptions involved. Thus in future studies with mixed populations, a composite representation of wind support which is less rigid in its assumptions may be more suitable. We also found that, when trying to capture complex relationships with wind in the context of available wind conditions within a night, Tw or WP relative to the best available wind conditions was less intuitive and was also selected in fewer models than Tw or WP relative to wind conditions at the surface. We therefore recommend that the latter formulation be used in future studies.

Our GAM results show that birds remained mainly at low flight altitudes. Because this behaviour is not consistent with time or energy minimization when wind conditions improve with altitude, the behaviour 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 altitudes, and birds can make acceptable forward progress, costs 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 more tolerant of costs associated with high-altitude flight and willing to climb to higher altitude to find supportive winds and maintain an acceptable travel speed. Even so, birds stop climbing once they can maintain an acceptable travel speed.

CONCLUSIONS

In general, we may expect birds to adapt their flight altitudes to account for flight time, energy expenditure, water balance and safety, yet the relative importance of these pressures may vary between species, regions, seasons and phases of migration. In our study area, birds seem to balance considerations of time, energy, water and safety and do not select altitudes for migration based solely on wind conditions. This result supports a recent trend in the 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 behavioural adaptations to atmospheric conditions on a large scale (e.g. avoidance of headwinds), individuals may be flexible in their responses to conditions en route.

This study highlights the 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 covering much of Europe, there is great potential for analyses comparing locations in order to distinguish the influences of atmospheric (and non-atmospheric) variables, quantify the priority or precedence birds give to these variables, and determine how this depends on the condition of other factors, geographical location and time of year. Ultimately, we may determine

that altitude selection in birds is based on just a few general rules (e.g. they prefer lower flight altitudes but avoid headwinds) 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 (Alerstam 1981). 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 behaviour (Bowlin *et al.* 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. GAM results.
Figure S2. Simulation model results.
Data S1. Specific humidity calculation.