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RESEARCH PAPER

Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel?

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ABSTRACT

Aims Different aspects of soaring-bird migration are influenced by weather. However, the relationship between weather and the onset of soaring-bird migration, particularly in autumn, is not clear. Although long-term migration counts are often unavailable near the breeding areas of many soaring birds in the western Palaearctic, soaring-bird migration has been systematically monitored in Israel, a region where populations from large geographical areas converge. This study tests several fundamental hypotheses regarding the onset of migration and explores the connection between weather, migration onset and arrival at a distant site.

Location Globally gridded meteorological data from the breeding areas in north-eastern Europe were used as predictive variables in relation to the arrival of soaring migrants in Israel.

Methods Inverse modelling was used to study the temporal and spatial influence of weather on initiation of migration based on autumn soaring-bird migration counts in Israel. Numerous combinations of migration duration and temporal influence of meteorological variables (temperature, sea-level pressure and precipitable water) were tested with different models for meteorological sensitivity.

Results The day of arrival in Israel of white storks, honey buzzards, Levant sparrowhawks and lesser spotted eagles was significantly and strongly related to meteorological conditions in the breeding area days or even weeks before arrival in Israel. The cumulative number of days or cumulative value above or below a meteorological threshold performed significantly better than other models tested. Models provided reliable estimates of migration duration for each species.

Main conclusions The meteorological triggers of migration at the breeding grounds differed between species and were related to deteriorating living conditions and deteriorating migratory flight conditions. Soaring birds are sensitive to meteorological triggers at the same period every year and their temporal response to weather appears to be constrained by their annual routine.

Keywords

***Accipiter brevipes*, *Aquila pomarina*, *Ciconia ciconia*, inverse modelling, migration onset, *Pernis apivorus*, phenology, sea-level pressure, temperature, threshold effect.**

INTRODUCTION

Seasonal variations in food supply are probably the main motivation for bird migration in autumn. Circumstantial evidence comes, for example, from observations that among raptors the first to leave their breeding grounds in autumn are insectivorous species, the first prey group to disappear with declining temperatures, followed by those feeding on poikliothermic vertebrates (fish, amphibians and reptiles) and finally those feeding on birds and mammals (Newton, 1979). Thus, migration and its general timing are strongly influenced by the availability of food, which in turn is affected by declining ambient temperatures during autumn.

For many avian species, the precise onset of migration is influenced by a combination of endogenous and external factors

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(Berthold, 2001). In a number of species, captive and free-living birds start their migratory activity at the same time, indicating that endogenous factors such as a circannual rhythm synchronized with photoperiod, determine the onset of migration (Gwinner, 2003). However, additional factors, particularly those related to weather, also influence the onset of migration (e.g. Alerstam, 1990; Richardson, 1990). For example, for several species of migrants using flapping flight, the onset of migration is related to (or triggered by) the presence of favourable winds (Weber *et al*., 1998; Åkesson *et al*., 2002; Fox *et al*., 2003).

Soaring birds that rely on various forms of atmospheric lift (e.g. convective or obstructive) for flight are strongly dependent on the appropriate meteorological conditions for long-distance flights. The effects of local weather on soaring-bird migration have been studied by several authors (e.g. Maransky *et al*., 1997; Yates *et al*., 2001; Shamoun-Baranes *et al*., 2003a,b; Thorup *et al*., 2003) and reviewed by Kerlinger (1989) and Richardson (1990). Various aspects of soaring-bird migration are affected by wind strength and direction, barometric pressure, relative humidity, temperature and thermal convection. However, the influence of weather on the onset of soaring-bird migration at their breeding grounds is unknown. The meteorological trigger for migration at the breeding grounds may be related to deteriorating living conditions, including food availability and habitat suitability, the migratory flight conditions or a combination of these.

About 1 million soaring birds pass through northern Israel every year during autumn migration (Leshem & Yom-Tov, 1996; Alon *et al*., 2004). Several flocking species show a very consistent migration phenology across years with a variation of only several days in the peak day of passage and an extremely condensed migration season with the mid 90% of the migrating population passing in less than 15 days (Alon *et al*., 2004). The mechanism behind this strong temporal convergence of migrants is still unclear. The small variations in annual timing of migration suggest a combination of endogenous and environmental factors that influence the onset of soaring-bird migration in the breeding areas. Unfortunately the large-scale, long-term and systematic data on migration initiation of soaring birds at breeding areas needed to test this hypothesis are lacking. Israel is an important geographical bottleneck for soaring migrants in the western Palaearctic and the systematic autumn migration counts conducted in Israel provide a unique opportunity to collect data on populations that converge from large geographical areas where data are otherwise unavailable.

In this study inverse modelling is used to investigate the temporal influence of meteorological conditions within the breeding areas on migration initiation based on arrival times of several soaring-bird species in Israel, located thousands of kilometres from the breeding area. By using inverse modelling we have the opportunity to explore several fundamental hypotheses regarding the onset of migration in relation to weather. We therefore focus our analysis on four flocking species with a fairly precise and condensed migratory phenology. We first test if the onset of migration is triggered by meteorological conditions at the area of departure as opposed to the day of the year alone. We then model the influence of different meteorological variables in order to determine whether the migration trigger is related to the living conditions at the breeding grounds or migratory flight conditions. We propose that the coarse temporal scale of soaring-bird migration is determined by an internal rhythm but the fine temporal scale is influenced by meteorological conditions. Therefore, we test whether birds are sensitive to meteorological triggers during the same period every year. Finally, the methodology applied also provides estimates of migration duration, and their validity is compared with measurements from other sources.

METHODS

Survey data

The Israel northern valleys autumn soaring-bird survey, conducted by the Israel Ornithological Center, is a multistation visual observation network where systematic continuous counts are conducted during daylight hours by experienced bird watchers daily from approximately 10 August to 15 October with stations situated across the migration front. During the period of analysis the first day of the survey varied between 3 August and 21 August. Survey stations are located between the Jezreel and Beit Shean valleys in northern Israel, that cover approximately the western and the eastern migratory axes, respectively, of soaring birds over Israel (Leshem & Yom-Tov, 1998). For more details on the survey methodology see Alon *et al.* (2004). Following quality control and removal of double counts between stations, daily sums were calculated for each species for the years 1990–2000 and used in the following analysis.

Processing of survey data

The response variable analysed in relation to meteorological explanatory variables is the day of arrival in Israel of four species of flocking soaring migrants: *Ciconia ciconia* L. (white stork), *Pernis apivorus* L. (honey buzzard), *Accipiter brevipes* Severtzov (Levant sparrowhawk) and *Aquila pomarina* Brehm CL (lesser spotted eagle). The day of arrival of the first 5% of the migrating population in Israel was calculated each year for each species. The mean day of arrival of the first 5% of the population for all years ($n = 11$) was then calculated for each species (Table 1).

In order to link day of arrival in Israel with meteorological conditions within the breeding area of each species (according to Hagemeijer & Blair, 1997) at the time of departure, estimations had to be made regarding the amount of time it took birds to reach Israel. Measurements of average daily migration distances (Table 2) were used to estimate the minimum number of days prior to arrival in Israel that birds would leave the breeding area. Using these values and calculating the great circle distance between the location in the breeding area selected for extracting meteorological data (Table 1 and Fig. 1, see below for explanation) and northern Israel, it would take at least 8–11 days for a white stork to reach Israel, 6–16 days for a honey buzzard, 5–11 days for a Levant sparrowhawk and 8–18 days for a lesser

Table 1 Mean day of arrival ($\overline{DOA}$), earliest and latest annual day of arrival (*DOA* range), grid cell centre of the meteorological variable used in the final models and range of the parameters, trigger duration (*TD*) and migration duration (*MD*), tested for each species. The final column provides the full range of the period of meteorological sensitivity tested (from *TB*, the beginning of a trigger period to *TE*, the end of a trigger period). See Fig. 1 for a map of meteorological predictor locations and Fig. 2 for migration phenology of each species

Species	$\overline{DOA}$	*DOA* range	Geographical location of predictor	Range *MD* (days)	Range *TD* (days)	First *TB*–last *TE*
White stork	20 Aug	5–28 Aug	55° N, 20° E	6–30	2–30	21 Jun–12 Aug
Honey buzzard	29 Aug	27 Aug–1 Sept	55° N, 25° E	6–30	2–30	30 Jun–21 Aug
Levant sparrowhawk	15 Sept	13–17 Sept	47.5° N, 32.5° E	4–30	2–30	15 Jul–9 Sept
Lesser spotted eagle	22 Sept	18–25 Sept	55° N, 15° E	5–30	2–30	23 Jul–15 Sept

Table 2 Mean daily migration speeds for each species available from the literature used for comparison with estimates of migration duration. Speeds were calculated using data collected from satellite telemetry, motorized glider or tracking radar. The mean daily migration speed for the Levant sparrowhawk is derived using the measured ground speed for autumn (10.9 m s^{-1}) and an estimated 8 h migration duration per day. Relevant references are mentioned in the source column

Species	Mean daily migration speed (km day^{-1})	Measurement	Source	Region
White stork	250	Satellite telemetry	Berthold *et al.* (2000)	Eastern flyway from Poland or Germany to first African staging area
White stork	348	Motorized glider	Leshem & Yom-Tov (1996)	Israel
Honey buzzard	170	Satellite telemetry	Hake *et al.* (2003)	Western flyway from Sweden to African staging area
Honey buzzard	446	Motorized glider	Leshem & Yom-Tov (1996)	Israel
Levant sparrowhawk	314	Tracking radar	Spaar *et al.* (1998)	Israel
Lesser spotted eagle	166	Satellite telemetry	Meyburg *et al.* (2000)	Eastern flyway from Germany to African staging area
Lesser spotted eagle	381	Motorized glider	Leshem & Yom-Tov (1996)	Israel

spotted eagle. In general, the lower values can be considered underestimates because they do not include possible stopovers during migration and they do not follow the true routes of the birds that circumvent large water bodies (i.e. the Black Sea and the Mediterranean Sea).

Meteorological data

Meteorological data in the breeding areas used in the analyses were extracted from the National Centers for Environmental Prediction (NCEP) reanalysis data archives. Data were provided by NOAA-CIRES Climate Diagnostics Center at Boulder, CO, USA (http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.html). The gridded data set has a horizontal resolution of 2.5° latitude × 2.5° longitude global grid and each grid point represents the average grid value over its area. The approximate area of each grid cell in the regions studied here is 40,000 km^2. The daily mean of surface temperature, sea-level pressure and precipitable water were tested separately as triggers of migration onset. Precipitable water is the total atmospheric water vapour contained in a vertical column of unit cross-sectional area and used as an indicator of the amount of moisture potentially available to supply rainfall (http://amsglossary.allenpress.com/glossary/search?id=precipitable-water1).

NCEP meteorological data were extracted from several grid cells within the northern parts of the breeding range of each species (Fig. 1) from areas where birds that pass through Israel during migration are known or estimated to breed. These grid cells were selected in order to focus on the relationship between weather and migration onset. Disentangling the effect of weather on birds initiating migration as opposed to birds already on route would be more difficult when selecting more southern locations within the breeding ranges. Breeding sites of white storks (Berthold *et al.*, 2000) and lesser spotted eagles (Meyburg *et al.*, 2000) tracked with satellite transmitters are located within the respective meteorological data grid cells selected for analysis.

The three meteorological variables tested are spatially autocorrelated beyond one 2.5° × 2.5° grid cell. We focus the analysis on individual grid cells; however, due to the aforementioned autocorrelation the results will apply to a larger region.

Model design

We formulate three mechanisms that explain how the birds' migration is triggered by weather. All three are based on the concept that during a specific period in the year a bird becomes sensitive to particular meteorological conditions. The first mechanism is sensitivity to a meteorological variable, averaged

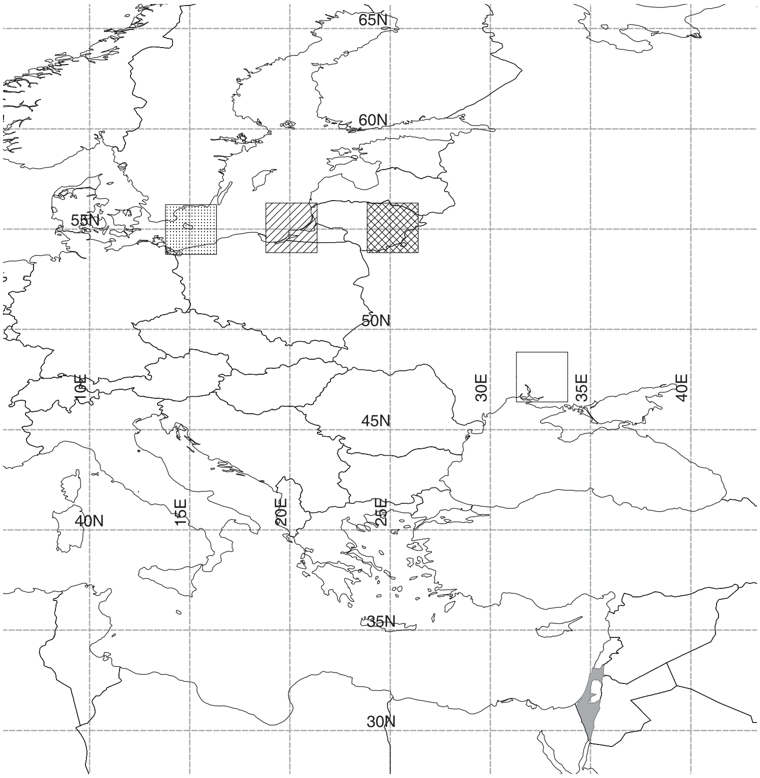

Figure 1 NCEP reanalysis data grid cells representing the area of analysis for the influence of meteorological conditions on migration onset from northern locations within the breeding area of each species. The region of analysis for each species is marked as follows: white stork (hatched), honey buzzard (cross hatched), Levant sparrowhawk (empty box) and lesser spotted eagle (stippled). The horizontal resolution of the meteorological data is 2.5° latitude × 2.5° longitude; each grid point represents the average grid value over its area. Israel, the area of arrival, is marked in grey.

over a specific period. The second mechanism is sensitivity to the accumulated value of a meteorological variable, where accumulation only takes place if the variable exceeds or is below a certain threshold. The third mechanism is sensitivity to the number of days where a meteorological variable exceeds or is below a threshold.

The three mechanisms are translated into three model structures, each with two (mechanism 1) or three (mechanisms 2 and 3) loosely constrained parameters. The parameters used in these models are: migration duration (*MD*, all models), trigger duration (*TD*, all models) and threshold value (*ThV*, mechanisms 2 and 3). The constraints that are imposed on these parameters are listed in Table 1. Finding the appropriate meteorological variables, for the right time frame and spatial domain, is a computationally large undertaking. Inverse modelling is used to back predict the annual day of arrival (*DOA*), a number between 1 and 365, by testing all possible parameter combinations within our selected parameter space. Our choice for parsimonious linear models makes it possible to evaluate an extremely large number of alternatives. The fact that the models implicitly include the relevant time frame for the meteorological conditions in the parameters adds to the computational efficiency.

The models for the three mechanisms are defined as follows. First, the mean day of arrival in Israel ($\overline{DOA}$, expressed as day of the year) is calculated for the period 1990–2000 ($n = 11$). Next, the migration duration (*MD*, in days) is defined as the average period it takes a bird to migrate from its breeding site to its passage over Israel. Finally, the trigger duration (*TD*, in days) is defined as the average period within which a bird is sensitive to meteorological conditions. These three variables form the backbone of each of the three models. In all three models, the parameters define the time frame for which a meteorological variable is considered, namely the period between the beginning of the trigger period ($TB = \overline{DOA} - MD - TD$) and the end of the trigger period ($TE = \overline{DOA} - MD$).

The first mechanism, sensitivity to a meteorological variable averaged over a specific period, is modelled by considering the linear relationship between the average value for a single meteorological variable during the trigger period and the day of arrival in Israel in a given year (*DOA*). The average value is calculated by $\frac{c}{TD}\sum_{t=TB}^{TE} V_t$, where V_t is the daily mean value for the meteorological variable of interest at day *t*. The parameter *c* is for sign and unit conversion only and it has a value of 1 or −1 (depending on the influence of the meteorological variable) and units such that the model part $\frac{c}{TD}\sum_{t=TB}^{TE} V_t$ has days as its unit. It should be noted that the unit of V_t depends on the meteorological variable of interest. The parameter *c* is for instance given in days^2 °C^{-1} when mean daily temperature (in °C) is selected as meteorological variable V_t; and *c* is given in days^2 hPa^{-1} when sea-level pressure is selected as V_t (and expressed in hPa). The mathematical formulation for the first mechanism reads as follows:

$$DOA = TB + \frac{c}{TD}\sum_{t=TB}^{TE} V_t. \tag{1}$$

The second mechanism is termed the threshold exceedance accumulation (TEA) model and considers the sensitivity to the accumulated value of a meteorological variable, where accumulation only takes place if the variable is above or below a certain threshold to predict *DOA*. The model uses a third parameter in addition to *MD* and *TD*, a threshold value, *ThV*, above or below which accumulation occurs. *ThV* has the same units as the daily meteorological variable (V_t). For convenience, the model is split into two different forms (eqns 2a & 2b) to make a distinction between accumulation below or above a threshold:

$$DOA = TB + c\sum_{t=TB}^{TE} AA_t,$$

$$\begin{aligned} AA_t &= (V_t - ThV) & \text{if} \quad & V_t > ThV \\ AA_t &= 0 & \text{if} \quad & V_t \le ThV. \end{aligned} \qquad (2a)$$

and

$$DOA = TB + c\sum_{t=TB}^{TE} AB_t,$$

$$\begin{aligned} AB_t &= (ThV - V_t) & \text{if} \quad & ThV > V_t \\ AB_t &= 0 & \text{if} \quad & ThV \le V_t. \end{aligned} \qquad (2b)$$

The meaning of *TB* and *TE* is as in eqn (1). Two intermediate variables are used for clarity in eqns (2a) and (2b), 'accumulation above a threshold' (AA_t) and 'accumulation below a threshold' (AB_t). For example, for $ThV = 10$ °C, $MD = 10$ days, $TD = 3$ days, with daily mean temperatures 8, 12 and 14 °C during the trigger duration, the sum of $AA_t = 6$ °C, whereas the sum of $AB_t = 2$ °C. The factor $1/TD$ is omitted from the equations since the parameters *TD* and *ThV* are collinear (and therefore only one of the two parameters should be used here).

The third mechanism, termed the threshold exceedance duration (TED) model, models the sensitivity to the number of days where a meteorological variable is above or below a designated threshold, instead of the cumulative value above or below a threshold (as in the TEA model, eqns 2a & 2b). In all other respects the TED model is similar to the TEA model and specified in eqns (3a) and (3b):

$$DOA = TB + c\sum_{t=TB}^{TE} CA_t,$$

$$\begin{aligned} CA_t &= 1 & \text{if} \quad & V_t > ThV \\ CA_t &= 0 & \text{if} \quad & V_t \le ThV \end{aligned} \qquad (3a)$$

and

$$DOA = TB + c\sum_{t=TB}^{TE} CB_t,$$

$$\begin{aligned} CB_t &= 1 & \text{if} \quad & ThV > V_t \\ CB_t &= 0 & \text{if} \quad & ThV \le V_t. \end{aligned} \qquad (3b)$$

In eqns (3a) and (3b) CA_t and CB_t mean, respectively, 'count above a threshold' and 'count below a threshold'; both variables are given in days.

It should be noted that one intentional simplification in our model concept is that *TD* and *MD* denote average values for trigger duration and migration duration, respectively. Hence our models only calculate the average day of departure (*TE*), not a day of departure that varies per year.

Model calibration

The model parameters were estimated by evaluating all parameter combinations in a hypercube, the limits of which were selected prior to the estimation procedure. The values of the parameter limits are given in Table 1. Biologically meaningful parameter estimates, particularly *MD* and *TD*, and the model root mean square error (RMSE) were used as criteria for selecting the optimal parameter combinations, the meteorological variable and the model framework that best defines the relationship between weather and the onset of migration. The RMSE is a relatively simple measure of model goodness of fit, with lower values for better-fitting models. Many more complicated indices can be used to summarize model fitness (e.g. the Akaike information criterion (AIC) and the Bayesian information criterion (BIC)). These indices penalize the use of additional model parameters. In our study this aspect is not relevant since the models are all over-determined and differ by no more than one parameter. The entire data record for 11 years (1990–2000) was used for parameter estimation. Although different models may provide a similar level of fit between model and measurement, ultimately it was a combination of a biologically meaningful model, the stability of the model and its goodness of fit which was used to select the models most suited for hypothesis testing. The presence of one global optimum in the parameter space as opposed to multiple local optima provided qualitative evidence of model stability (see Appendix S1 in Supplementary Material for the Matlab code). The geographical region for which the meteorological variables are considered are limited to one NCEP reanalysis grid cell per bird. During the exploratory analysis phase, several neighbouring cells were also tested and resulted in models with similar parameter estimates due to the spatial autocorrelation of the tested variables. Temperature, sea-level pressure and precipitable water were tested separately for each species in each model framework. The mean day of arrival, upper and lower limits for *MD* and *TD* and grid locations used in the models are summarized in Table 1. All final models selected and described in the results section were significant to the $P < 0.05$ level after a Bonferroni correction. A Bonferroni correction was applied to account for the fact that three meteorological variables were considered. Having corrected for this, some care should still be taken in using the resulting *P*-values. By considering weather variables over different integration periods, each integration period can be considered a different variable. However, since the variables at different integration periods are strongly autocorrelated (and each in a different way), it was not possible to correct for this as well. Parameter estimates and RMSEs are given for several models with the lowest RMSE and reasonable parameter estimates for each species for model frameworks 1, 2 and 3 in Appendices S2, S3 and S4, respectively, in Supplementary Material.

Model validation

The leave one out cross-validation (LOOCV) procedure (Hastie *et al.*, 2001) was used to test the generalizability and stability of each model. The validation method is performed by systematically leaving one of the 11 data points out from the calibration cycle, then predicting the excluded data point with the calibrated model, and finally comparing the model prediction with the observation. This procedure was run for the best model framework selected during the model calibration phase and repeated for each year in the sample set ($n = 11$) by excluding one annual *DOA* per validation cycle. After finishing the entire LOOCV procedure, the error statistics for the 11 predictions were studied and summarized. The parameter estimates and model performance from each cycle were compared with the results from the calibration phase. Optimally, a stable and general model would result in similar parameter estimates and model performance for each cycle.

RESULTS

The phenology of migration of each species studied differs (Fig. 2). White storks arrive first followed by honey buzzards, Levant sparrowhawks and lesser spotted eagles. White storks also have the largest inter-annual variation in day of arrival (*DOA*) (SD = 6.3 days) followed by lesser spotted eagles (2.1 days), honey buzzards (1.9 days) and Levant sparrowhawks (1.1 days) (see Table 1 for the range of *DOA*).

The migration timing of each species shows a direct response to a single meteorological variable. The parameter estimates included in the best models for each model framework are shown in Tables 3–5. All models presented in Tables 3–5 are significant to the $P < 0.05$ level after a Bonferroni correction (note that this means that meteorological variables give better predictions of annual *DOA* in Israel than $\overline{DOA}$). Furthermore, the RMSEs of the models presented in this study are all significantly lower than for models based on $\overline{DOA}$ alone (Table 3).

White storks

Annual *DOA* is significantly related to sea-level pressure (SLP). The threshold exceedance accumulation (TEA) below the threshold value (*ThV*) for SLP explains migration timing best. This is not only indicated by the lowest RMSE values for this model but also by parameter estimates that are biologically most realistic for this species (see Table 4 and eqn 2b). As the accumulation of SLP below 1010 hPa increases during the period of meteorological sensitivity ($TD = 19$ days), white storks arrive in Israel earlier. There is one clear global optimum in the parameter space (see Appendix S3 in Supplementary Material). Storks are sensitive to SLP from approximately 10–30 July. RMSE values are only slightly higher for TED above (eqn 3a) and TED below (eqn 3b; Table 5, Figs 3a and 4a) the threshold value for SLP (see also Appendix S4 in Supplementary Material). Most LOOCV cycles (9 out of 11) result in similar TEA models. The cycle omitting data for the year 2000 results in a very different top-ranking model ($MD = 17$ days, $TD = 2$ days, $ThV = 1016$ hPa) with a much lower RMSE (1.8).

Annual *DOA* is also significantly related to temperature at the breeding area. The higher the mean temperature the later birds arrive in Israel (eqn 1, Table 3). However, the summed value for *MD* and *TD* is very low and therefore the entire period of meteorological sensitivity and migration duration is unrealistically short. The TED model (see Appendix S4 in Supplementary Material) results in both biologically reasonable parameter estimates and a relatively good fit between model and measurement, although not as good as the SLP models. As the number of days above a threshold value of 17 °C increases during 3 days of meteorological sensitivity, birds arrive later in Israel. Similarly, as the count below the *ThV* increases, birds arrive earlier in Israel.

Honey buzzards

Honey buzzard *DOA* is positively related to SLP, the higher the mean SLP at the breeding site, the later honey buzzards arrive in Israel (mechanism 1, Table 3). The TED model both below and

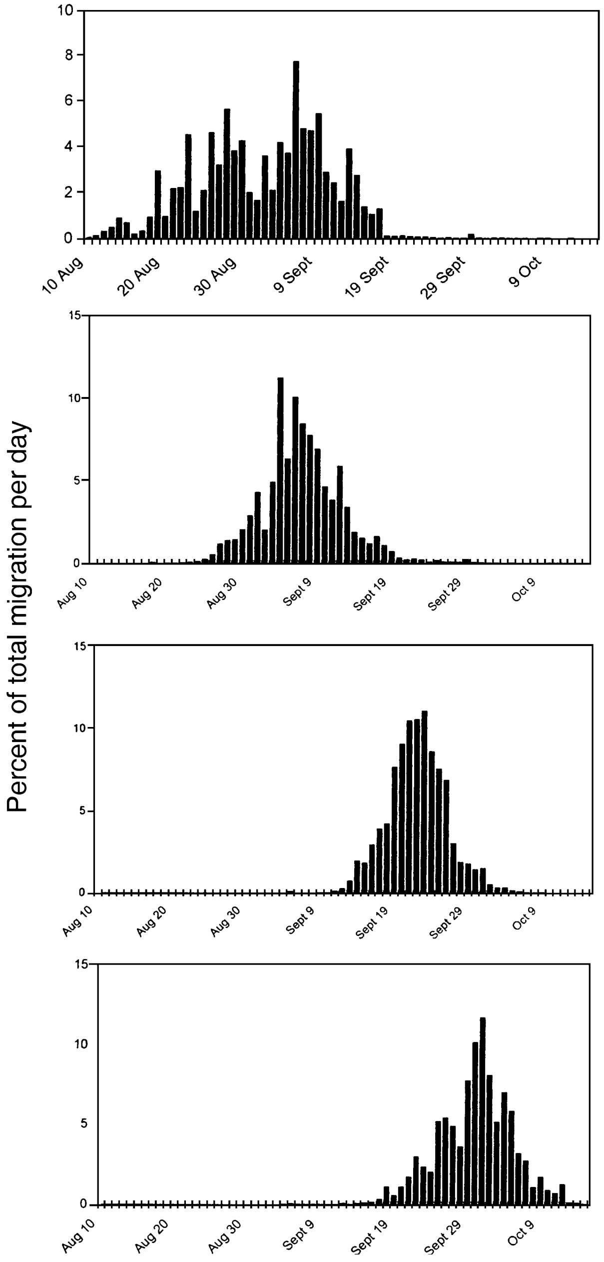

Figure 2 Migration phenology of white storks, honey buzzards, Levant sparrowhawks and lesser spotted eagles (top to bottom) for 1990–2000. Represented on the y-axis is the percentage of total daily migration for the sum of 1990–2000.

Table 3 Parameter estimates included in the final versions of Model 1 as described in the Methods section. The migration duration (*MD*), trigger duration (*TD*), meteorological variable, *c* parameter (eqn 1), root mean squared error (RMSE), R^2 and *P*-values are given for each model. For comparison, the RMSE is shown when mean day of arrival ($\overline{DOA}$) is used as the only predictor (RMSE $\overline{DOA}$) for annual *DOA*. The acronyms SLP and TEMP represent sea-level pressure and temperature, respectively

Species	*MD* (days)	*TD* (days)	Variable	*c*	RMSE	R^2	*P* value	RMSE $\overline{DOA}$
White stork	6	6	TEMP	1	3.99	0.57	0.01	6.12
Honey buzzard	20	11	SLP	1	1.12	0.54	0.02	1.65
Levant sparrowhawk	4	3	SLP	1	0.61	0.76	0.003	1.21
Lesser spotted eagle	11	2	SLP	–1	0.93	0.80	< 0.001	2.13

Table 4 Parameter estimates in the final versions of the threshold exceedance accumulation models (TEA, eqn 2b). The migration duration (*MD*), trigger duration (*TD*), threshold value (*ThV*), accumulation direction, *c* parameter, root mean squared error (RMSE), R^2 and *P*-values and meteorological variable are shown. SLP represents sea-level pressure

Species	*MD* (days)	*TD* (days)	*ThV* (hPa)	Accum.	*c*	RMSE	R^2	Variable	*P*-value
White stork	22	19	1010	Below	–1	3.52	0.67	SLP	0.005
Honey buzzard	20	11	1018	Below	–1	0.94	0.67	SLP	0.004
Levant sparrowhawk	8	25	1015	Below	–1	0.50	0.82	SLP	< 0.001
Lesser spotted eagle	11	2	1013	Below	1	0.84	0.84	SLP	< 0.001

Table 5 Parameter estimates included in the final versions of the threshold exceedance duration models (TED, eqns 3a & 3b). The migration duration (*MD*), trigger duration (*TD*), threshold value (*ThV*), exceedance above or below, *c* parameter, root mean squared error (RMSE), R^2 and *P*-values and meteorological variable are shown. The acronyms SLP and PW represent sea-level pressure and precipitable water, respectively

Species	*MD* (days)	*TD* (days)	*ThV*	Exceedance	*c*	RMSE	R^2	Variable	*P*-value
White stork	22	24	1010 hPa	Above	1	3.66	0.64	SLP	0.007
White stork	22	24	1010 hPa	Below	–1	3.66	0.64	SLP	0.007
Honey buzzard	18	15	1014 hPa	Above	1	0.69	0.82	SLP	< 0.001
Honey buzzard	18	15	1014 hPa	Below	–1	0.69	0.82	SLP	< 0.001
Levant sparrowhawk	8	24	1011 hPa	Above	1	0.43	0.87	SLP	< 0.001
Levant sparrowhawk	8	24	1011 hPa	Below	–1	0.43	0.87	SLP	< 0.001
Lesser spotted eagle	14	4	22 kg m^{-2}	Above	1	0.80	0.85	PW	< 0.001
Lesser spotted eagle	14	4	22 kg m^{-2}	Below	–1	0.80	0.85	PW	< 0.001

above a *ThV* of 1014 hPa (mechanism 3, Table 5) is the best model framework to describe annual *DOA*. As the number of days with SLP below 1014 hPa increases during the 15 days of meteorological sensitivity (*TD*) the earlier honey buzzards arrive in Israel (eqn 3b, Figs 3b and 4b). Similarly, as the number of days with SLP above the *ThV* increases, birds arrive later in Israel. In this model, honey buzzards are sensitive to SLP from approximately the last week in July through to the first week in August There is one global optimum within the searched parameter space (Fig. 5) resulting in very similar RMSE values. Threshold values for the top 10 ranking models with the lowest RMSE are within ±2 hPa of the long-term daily mean for 21 July to 7 August (1016 hPa) with an *MD* + *TD* ranging between 31 and 34 days (see Appendix S4 in Supplementary Material). During the validation phase, models are very stable with similar parameter estimates.

Levant sparrowhawks

Levant sparrowhawk *DOA* is significantly and positively related to mean SLP, the higher the barometric pressure the later birds arrive in Israel (mechanism 1, Table 3). The TED model (below and above) for SLP (mechanism 3, Table 5) is the best model. The more days below 1011 hPa (*ThV*) during the period of meteorological sensitivity (*TD* = 24 days) the earlier Levant sparrowhawks arrive in Israel (eqn 3b, Figs 3c and 4c). Similarly the more days above the *ThV*, the later Levant sparrowhawks arrive in Israel. As with the honey buzzards, one global optimum existed within the parameter space. According to this model framework meteorological variables can trigger migration between mid-August and the first week in September. Although there are different combinations of *TD* and *MD* resulting in similar model fit, all combinations of the top 10 ranking TED models result in

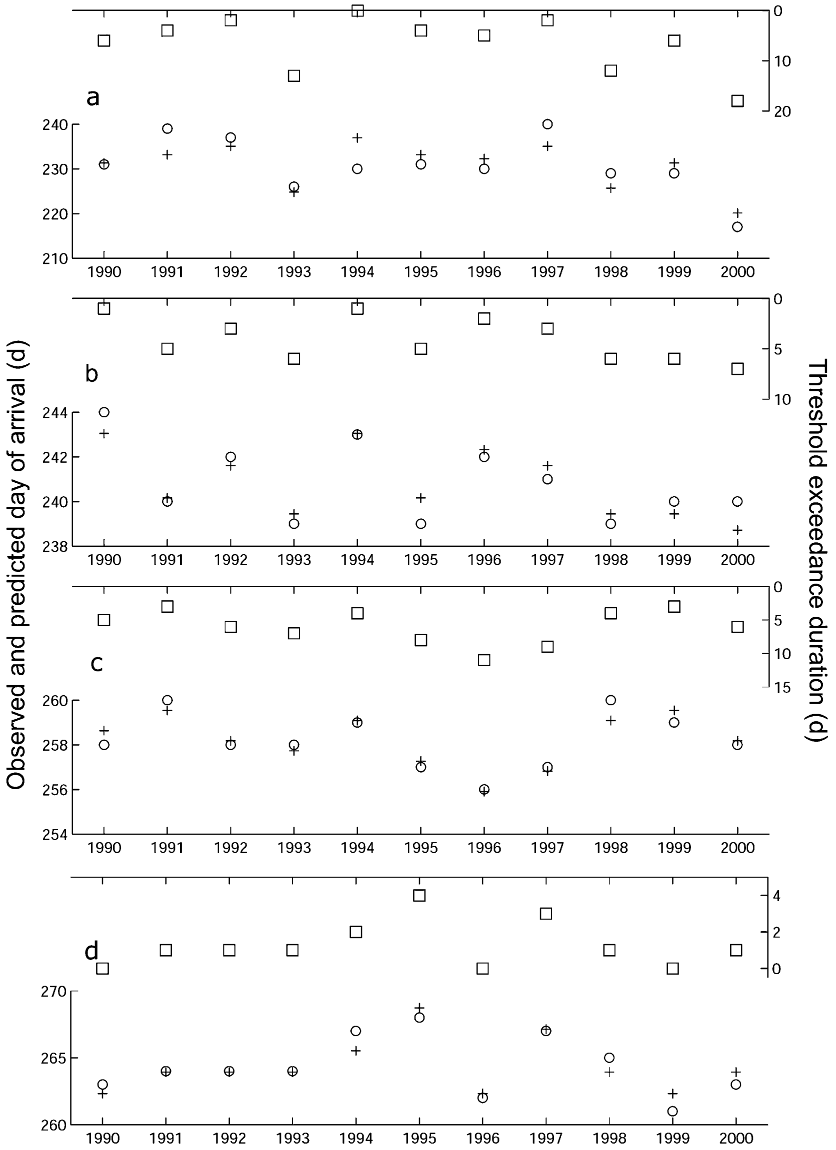

Figure 3 Annual observed (○) and predicted (+) day of arrival (*DOA*, values between 1 and 365) based on the most parsimonious threshold exceedance duration (TED) model for each species. The annual predictive TED (□) is shown in the upper axis of each plot. Species and meteorological variables from top to bottom are: (a) white stork, SLP (eqn 3b, TED below); (b) honey buzzard, SLP (eqn 3b, TED below); (c) Levant sparrowhawk, SLP (eqn 3b, TED below); (d) lesser spotted eagle, PW (eqn 3a, TED above). See Table 5 for parameter estimates. The acronyms SLP and PW represent sea-level pressure and precipitable water, respectively.

the beginning of the sensitivity period 32–33 days before *DOA* in Israel (see Appendix S4 in Supplementary Material). The difference between the earliest and latest *DOA* is only 4 days, therefore over-interpretation of these models should be avoided.

Lesser spotted eagles

Lesser spotted eagle *DOA* is significantly and positively related to mean precipitable water and negatively related to mean SLP (mechanism 1, Table 3). The higher the mean precipitable water or the lower the mean SLP, the later birds arrive in Israel. Predictions applying the TED model above and below the *ThV* for precipitable water resulted in the best explanatory models (mechanism 3, Table 5). Birds arrive later as the number of days with precipitable water above 22 kg m^{-2} increases (eqn 3a, Figs 3d and 4d). Similarly, as the number of days below the *ThV* increases, birds arrive earlier. Lesser spotted eagles are sensitive to precipitable water during approximately the first week of September. There is one clear global optimum in the parameter space (see Appendix S4 in Supplementary Material). A lower sum of *MD* and *TD* is associated with a lower threshold value.

Annual *DOA* is also strongly influenced by SLP (Tables 3 and 4, see also Appendices S2 & S3 in Supplementary Material). The best model including SLP is the TEA model below SLP (eqn 2b) with a *ThV* of 1013 hPa. For example, the higher the accumulation below 1013 hPa, during 2 days, the later birds arrive in Israel. However, both MD (11 days) and *TD* (2 days) were fairly short, therefore the TED model incorporating precipitable water is more biologically meaningful.

DISCUSSION

Meteorological factors triggering migration

The timing of migration of white storks, honey buzzards, Levant sparrowhawks and lesser spotted eagles in Israel is strongly and

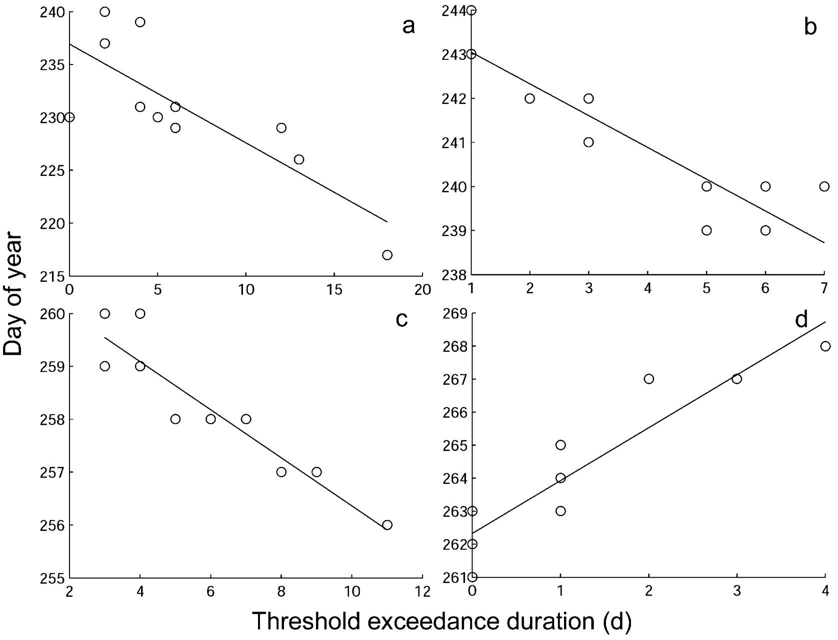

Figure 4 The relationship between observed day of arrival (*DOA*, values between 1 and 365) and the threshold exceedance duration (TED) using parameter estimates of the most parsimonious models as follows: (a) white stork, SLP (eqn 3b, TED below); (b) honey buzzard, SLP (eqn 3b, TED below); (c) Levant sparrowhawk, SLP (eqn 3b, TED below); (d) lesser spotted eagle, PW (eqn 3a, TED above). See Table 5 for relevant parameter values. The acronyms SLP and PW represent sea-level pressure and precipitable water, respectively.

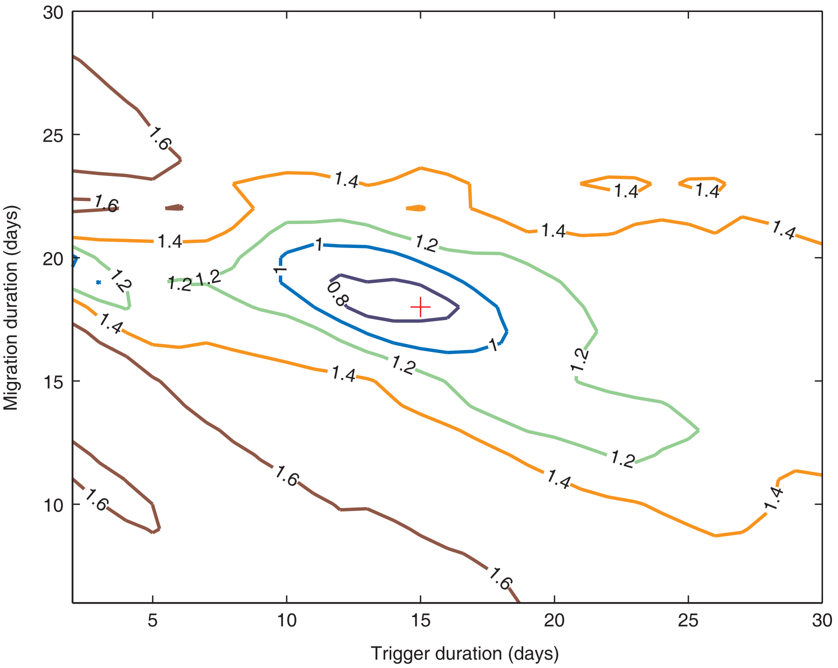

Figure 5 The two-dimensional parameter space for trigger duration (*TD*) and migration duration (*MD*) with a constant threshold value (*ThV*) of 1014 hPa (eqn 3b, Table 5), for the honey buzzard threshold exceedance duration (TED) model. The best model, with the lowest root mean squared error (RMSE), is marked by a plus sign. The shape of the RMSE surface for each parameter combination is shown by the contour lines. The surface shows that there is a global optimum in this parameter space. Due to strong autocorrelation in the weather variables *MD* with *TD* are interchangeable around the global optimum.

significantly influenced by quantifiable meteorological conditions within the respective breeding areas prior to arrival in Israel. This study suggests that weather is one of the main external factors that triggers the onset of soaring-bird migration. To the best of our knowledge this is the first time that such a strong and significant response of migration initiation to a single variable for a species has been shown. Furthermore, a clear link between arrival time, departure and weather several days and hundreds of kilometres apart has never been quantified. By applying inverse modelling the data collected systematically at geographical bottlenecks can provide new insight into processes, such as migration onset, occurring at the breeding grounds where data are scarce or unavailable. The models tested in this study further our understanding of the relationship between weather at the breeding areas, the onset of migration and the arrival of the initial population of soaring flocking migrants in Israel. Although the modelling technique applied in this study is exploratory in nature, due to the large number of variable combinations that had to be compared, it is a useful framework for gaining insight into prior hypotheses.

In general, SLP was consistently one of the best predictors of *DOA* for all species. White storks, honey buzzards and Levant sparrowhawks departed earlier as the number of days with SLP below a certain threshold increased. Low and falling barometric pressure usually signify the development of a low-pressure system accompanied by increasing relative humidity, cloud cover and atmospheric instability, stronger winds and hazardous weather such as rain, hail, thunder and lightning. Both warm fronts and cold fronts are often associated with low-pressure systems due to the counter-clockwise movement of air around the depression. As pressure begins to fall, temperatures first rise with the approach of the warm front. When a cold front arrives, northerly winds transport cooler air and temperatures drop significantly. The approach and particularly the persistence of such weather systems at the breeding area probably signify deteriorating living conditions triggering birds to leave. Experimental evidence has shown that several species of birds can detect small changes in barometric pressure (Kreithen & Keeton, 1974; von Bartheld, 1994). The paratympanic organ, present in most birds, may function as the barometric receptor (von Bartheld, 1994; Neeser & von Bartheld, 2002) enabling birds to sense and therefore respond to changes in barometric pressure.

White storks were also found to depart earlier as the number of days or the accumulation below a temperature threshold increase. Lower temperatures directly influence poikliothermic organisms such as invertebrates, reptiles and amphibians and are likely to indicate a decrease in availability of food for species such as white storks, honey buzzards and Levant sparrowhawks feeding on such prey.

In contrast, lesser spotted eagles are apparently detained in the breeding area when the conditions for soaring are poor, reflected by an increasing number of days with precipitable water above a threshold. In general, high amounts of precipitable water reflect high humidity below a low-tropospheric inversion or higher amounts of rainfall. Several studies have found that rainfall inhibits soaring-bird flight (e.g. Kerlinger & Gauthreaux, 1985; Kerlinger, 1989; Yates *et al*., 2001; Sergio, 2003). Lesser spotted eagles are also influenced by SLP, arriving later in years with increasing accumulation below a SLP threshold, similarly reflecting delayed arrival with poor soaring conditions. However, the duration of the migratory season is more realistic in models including precipitable water.

It is interesting to note that all species in this study are more sensitive to the accumulation of days or value above or below a meteorological threshold than to mean meteorological conditions. Similar forms of meteorological sensitivity are found in phenological studies of plants (Karlsson *et al*., 2003; Cesaraccio *et al*., 2004; Bourque *et al*., 2005; Orlandi *et al*., 2005) as well as studies on developmental and activity phases in insects (Nahrung & Allen, 2004; Zou *et al*., 2004; Jacobo-Cuellar *et al*., 2005). In all of these studies a clear relationship was found with either the number of degree-days or the accumulation of degree units above or below a particular temperature threshold. This similarity in meteorological sensitivity across diverse taxa may signify a fundamental biological response in organisms responding annually to environmental seasonal variation. This may also indicate a form of synchronization with food sources they exploit, particularly for birds feeding on poikliothermic prey.

Alerstam (1990) and Richardson (1990) describe three main factors that govern a migrant's choice of weather for migration: the living conditions in the area the birds are leaving, flight conditions during migration and living conditions in the area birds are heading. This study clearly shows two different mechanisms that underlie the meteorological conditions that trigger autumn soaring-bird migration, namely deteriorating living conditions and deteriorating flight conditions. These two mechanisms do not necessarily function independently of each other but interact, affecting onset of migration at different scales. For example, the first migrants to depart the breeding grounds rely mainly on poikliothermic prey (Newton, 1979; Leshem & Yom-Tov, 1996). The pressure on these species to respond to deteriorating living conditions (and hence reduced food availability) would be stronger than on species feeding exclusively on homoeothermic prey. White storks, honey buzzards and Levant sparrowhawks feed on poikliothermic prey, depart earlier and are influenced by weather that directly affects their living conditions, particularly food availability. On the other hand, lesser spotted eagles migrate very late in autumn, feed predominantly on homoeothermic prey and experience a stronger pressure to respond to soaring-flight conditions. The relative influence of these mechanisms may also depend on flight energetics. Birds with lower wing loads (such as the honey buzzard and Levant sparrowhawk) may have more flexibility in their flight strategy selection and experience weaker pressure to respond to soaring-flight conditions than species with larger wing loads such as the lesser spotted eagles.

Migration duration and compensation

The migration duration predicted for each species is very close to expectations based on measurements of daily flight distance found in the literature (Leshem & Yom-Tov, 1996; Spaar *et al*., 1998; Berthold *et al*., 2000; Hake *et al*., 2003; Meyburg *et al*., 2004). Due to the structure of the model the annual day of departure cannot be estimated and birds depart some time between the trigger and migration duration. Apparently, due to high temporal autocorrelations for certain variables (as high as 0.6 for a lag of 7 days), the relationship between *DOA* and the weather pattern is quite stable within a period of several days to weeks so that several combinations within this period predict the same amount of variability in annual *DOA*.

Differences between predicted and observed *DOA* were relatively small in the final models selected for each species. The models tested in this study implicitly assume constant migration duration and focus on a single meteorological variable that triggers migration. However, variations in migration duration or migration speeds should be expected, and several meteorological factors (especially wind) influence migration on route. Variability in migration speeds has clearly been shown for white storks migrating along the same route described in this study (Shamoun-Baranes *et al*., 2003a). Spaar *et al*. (1998) found that Levant sparrowhawks used a mixed flight strategy during migration in southern Israel and cross-country speeds were strongly affected by wind. Furthermore, they suggest that Levant sparrowhawks can speed up migration by adapting a mixed flight strategy if feeding *en route* is possible. Satellite telemetry studies of honey buzzards and lesser spotted eagles have both shown large variations in migration speeds (Hake *et al*., 2003; Meyburg *et al*., 2004).

Timing within the annual routine

Results from this study strongly support the hypothesis that initiation of soaring-bird migration is influenced by endogenous as well as exogenous factors. Furthermore, the temporal period within which birds are more sensitive to environmental cues is apparently constrained within the context of their annual routine, at least within the range of weather conditions measured during this study. However, extreme meteorological events may postpone or trigger migration, disrupting the annual routine. This suggests a balance between flexibility in adapting to changing environmental conditions and constraints within their annual routine. Incorporating such mechanisms in conceptual models will be an interesting subject for future research (e.g. McNamara *et al*., 1998).

The relevance of spatial scale

Several authors have raised the question as to whether birds react to local climate and limited parameters or to large-scale weather systems (e.g. Alerstam, 1990; Richardson, 1990). Scheifinger *et al*. (2002) describe a 'chain of causality, which communicates the temporal and spatial variability of atmospheric circulation patterns down to the timing of local phenological events'. Perhaps by focusing analysis on local atmospheric variables that are more quantifiable, but considering the link to large-scale synoptic systems and atmospheric circulation patterns, our understanding of how birds adapt to a complex changing environment can be better understood.

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BIOSKETCHES

Judy Shamoun-Baranes is interested in how various aspects of avian flight are influenced by and adapted to atmospheric dynamics at different scales in space and time. She is also interested in the microstructure of feathers as an avian identification technique.

Emiel van Loon is interested in any statistical question in relation to biological and geophysical problems. His main focus is the development of data assimilation techniques for biological and hydrological systems. He also investigates robust techniques to describe and estimate observation errors in hydrology as well as field biology. His previous work has focused on hydrological modelling.

Both Judy Shamoun-Baranes and Emiel van Loon are currently working in a multidisciplinary team that develops models to predict bird movement at different scales.

Editor: Tim Blackburn

SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Modelling Matlab code and relevant data files.

Appendix S2 Parameter estimates for the top five average meteorological conditions models (model 1, eqn 1).

Appendix S3 Parameter estimates for the top five threshold exceedance accumulation (TEA) models for each species (eqn 2b).

Appendix S4 Parameter estimates for the top 10 threshold exceedance duration (TED) models for each species (eqns 3a & 3b).