

**ORIGIN OF PASSERINE MIGRATORY WAVES: EVIDENCE FROM THE BLACKCAP
AT A STOPOVER SITE**

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ABSTRACT

Hundreds of millions of birds migrate through Israel every spring, usually in several waves during which a large number of birds are seen flying over Israel for several days, followed by periods in which only a small number are spotted. The aims of this study were to (1) determine whether the spring migration of the blackcap demonstrates a wave pattern, (2) determine the effect of weather conditions en route on the number of blackcaps arriving and forming each wave, and (3) use morphological characteristics and stable isotope composition of the feathers to examine the hypothesis that early arriving blackcaps represent populations breeding in low latitudes while later ones represent northern populations.

We found that (1) our first hypothesis was fully supported, and blackcaps arrive to Israel in “waves”; (2) weather conditions, and in particular wind speed and direction, were significantly related to the number of blackcaps captured; and (3) our morphological and δ C-13 data suggest that birds from the early season originated from more southern latitudes and/or more western longitudes within the breeding range of blackcaps.

Keywords: *Sylvia atricapilla*, Israel, spring migration, migratory waves, stable isotopes, weather conditions

INTRODUCTION

Many of the migrant species that fly over Israel have wide breeding ranges and appear in Israel in three or more migratory “waves” characterized by a large number of birds crossing Israel for several days, followed by a period in which only a small number of birds can be observed (Hall, 1981). Such waves may be created by different timing of migration by males and females or by adult birds departing their breeding grounds at different times than young ones. Another possible cause for a wave pattern is that the individuals of different waves originate from different populations and geographically separated areas (Shirihai, 1996; Howlett et al., 2000). Indeed, it is reasonable to assume that birds breeding in high latitudes will arrive from their winter quarters to their

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Received May 2, 2010; accepted November 14, 2010.

breeding ground (and to their stopover sites en route) later than those breeding in lower latitudes, where spring starts earlier. However, it is well known that weather, and wind in particular (Gauthreaux and Belser, 1998) is a key factor in determining flight schedules of birds (Newton, 2007). For example, Shamoun-Baranes et al. (2006) have shown that arrival dates of white storks, honey buzzards, Levant sparrowhawks, and lesser spotted eagles to Israel were significantly and strongly related to weather conditions en route, and blackcap spring migration strongly depend on weather conditions (Izhaki and Maitav, 1998). Hence, even if different populations start their migration at different times, weather conditions can strongly affect their speed. Consequently, birds from different populations may mix en route and find themselves at the same place en route during the same time window.

Understanding how migratory waves are created, as well as the origins and destinations of individuals present in the same wave, may provide insights into the migration patterns of birds. The traditional method of bird ringing is limited in answering the above questions, since levels of ring returns for migrant songbirds are often very low (e.g., Clark et al., 2000; Stolt et al., 2000). In addition, although radio and satellite tracking are valuable in determining movements of large-bodied migrants capable of carrying heavy transmitters, they cannot currently be applied to small passerines. The deficiencies of these methods have resulted in a lack of data concerning the origin of passerine waves. Isotopic markers have recently made it possible to determine the population and geographical origin of individual birds (reviewed by Webster et al., 2002). Although, to the best of our knowledge, there is no base map of δ C-13 and δ N-15 isotope distribution in Europe, carbon isotopes primarily vary by the type of plant community and can differ among habitats, thus enabling one to differentiate the origin of birds to different habitat types across the Western Palearctic. Recently, Diefendorf et al. (2010) have shown that δ C-13 varies in relation to precipitation, thus enabling a better interpretation of isotope results.

Israel is one of the best areas in which to observe Palearctic bird migration. Over 500 million birds pass through Israel every autumn and spring. Its geographic location, between the Mediterranean in the west and vast desert areas in the east, forces many migratory birds to funnel over Israel (Yom-Tov, 1988; Shirihi, 1996; Shirihi et al., 2001). In spring, many of these birds rest in Israel, after crossing the Sahara desert, to replenish their energy reserves before continuing on their migration to their breeding quarters.

We studied the migration pattern of the blackcap (*Sylvia atricapilla*) across Israel. This species is widely distributed in the Palearctic region and most populations migrate to Africa for the winter. Northern breeding populations are long-distance migrants, those from northern Mediterranean and North-West Africa are partial migrants, and those from the Atlantic Islands are usually residents. The species migrates in a "leap-frog migration pattern", meaning that the northernmost breeding populations migrate further south to their wintering grounds than those from the southern breeding populations (Shirihi et al., 2001). Hahn et al. (2009) estimated that about 60 million blackcaps migrate from Europe alone to Africa, and their migratory behavior has been extensively studied (Helbig, 1992; Howlett et al., 2000; Perez-Tris and Telleria, 2002; Perez-Tris et al., 2004; Frans-

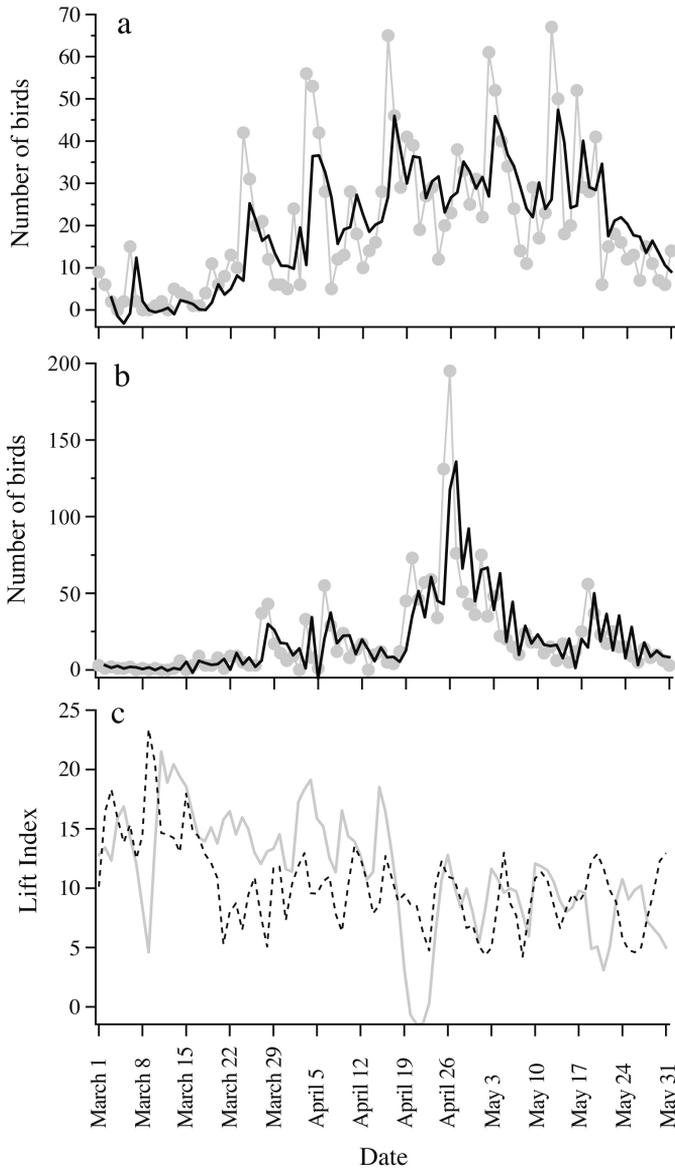


Fig. 1. The distribution of captured blackcaps along the season at the JBO during (a) spring 2005 (n = 1850) and (b) spring 2006 (n = 1900), indicated by the gray line, and the time series analysis (ARIMA) fit indicated by the solid line. Figure 1c shows the lift index (LI) during the sampling period in 2005 (gray solid line) and 2006 (dashed line).

son et al., 2005; Piersma et al., 2005; Fiedler, 2005; Catry et al., 2006; Yom-Tov et al., 2006). The species passes through Israel in waves (Fig. 1).

The blackcap is a polytypic species. Five subspecies of the blackcap are known: *S. a. atricapilla*, which breeds in Europe, Asia Minor, western Asia, and western Siberia; *S. a. dammholzi*, which breeds in the Caucasus, Transcaucasia, and northern Iran; *S. a. paulucci*, which breeds in Corsica, Sardinia, the Balearic Islands, Tunisia, and central Italy; *S. a. Heineken*, which breeds in western and southwest Spain, Portugal, Madeira, the Canary Islands, Morocco, and Algeria; and *S. a. gularis*, which breeds in the Cape Verde Islands and the Azores (Dement'ev and Gladkov, 1968; Cramp, 1992, Shirihai, 1996; Shirihai et al., 2001). Only two of these subspecies and their intermediate forms have been recorded in Israel: *S. a. atricapilla* and *S. a. dammholzi*. The former is the main subspecies on passage, an uncommon winter visitor, and a rare breeder in northern Israel; while the latter arrives in Israel in fewer numbers and is a limited passage migrant, mainly through the eastern and southern parts of Israel (Shirihai, 1996). However, due to the relative scarcity of this subspecies among blackcaps caught in our study site (Jerusalem Bird Observatory; JBO), it is not expected to affect the wave pattern observed in the JBO.

Most Palearctic blackcap populations that breed east of 12–13°E migrate from eastern Africa through Israel toward their breeding quarters in Europe (Cramp, 1992). The most western populations migrate through the Straits of Gibraltar. Similar to other passerines, blackcaps vary in morphological characters (mainly wing length) according to their origin (Perez-Tris et al., 1999; Howlett et al., 2000, Perez-Tris and Telleria, 2001; Perez-Tris and Telleria, 2002; Fiedler, 2005). The longer the distance the population covers upon migration, the longer the wings. Thus, populations from higher latitudes have longer wings compared to the short-distance migrants or resident populations, which have shorter wings (Leisler and Winkler, 2003; Winkler and Leisler, 2005; Fiedler, 2005). Hence, the wing length of blackcaps that migrate through Israel is expected to reflect the latitudinal range in which they breed.

Ring recoveries from Israel have revealed birds originating from Bulgaria, Czechoslovakia, Denmark, Finland, Latvia, Norway, Sweden, and Ukraine. Of 25 blackcaps that were ringed in Israel and caught in the Palearctic region, the furthest bird was found in Norway, a distance of at least 3875 km away. The average distance that these 25 birds covered was 2281 km (Bar and Nitzan, 1999). However, these data provide a somewhat biased image of the origin and routes of blackcaps that pass through Israel, since the ringing effort is not uniform in the Palearctic region, being much more extensive in Western and Northern Europe than in Eastern Europe or anywhere else in Asia.

The aims of this study were to determine whether the spring migration of the blackcap demonstrates a wave pattern, and to examine whether the morphological characteristics and the isotope composition of the feathers differ significantly among passerines from different waves. In general, we expected that blackcaps breeding at low latitudes (and probably also more western longitudes and low altitudes) to arrive to Israel earlier than those breeding further north. However, since weather has a strong influence on migration speed and length of stopovers, it is possible that different populations may mix

en route. Hence, we have not expected a clear-cut pattern, but a general trend of change, with southern-breeding populations arriving earlier than northern-breeding ones.

METHODS

DATA COMPILATION

Fieldwork was conducted at the Jerusalem Bird Observatory (JBO) located in Jerusalem, Israel, a station that operates throughout the year and where many species are caught. Data for this study were collected daily during the following periods: spring 2005 (1.iii.05–31.v.05) and spring 2006 (1.iii.06–31.v.06). Birds were captured with mist nets (12 m wide and 2.5 m high). The nets were erected from half an hour before first light until noon. The number of nets opened each day (13 nets) and their locations at the JBO were generally fixed in order to maintain consistency.

All blackcaps caught were ringed, sexed, and categorized into one of three age groups: 'unknown', 'second year' (SY—bird known to have hatched in the calendar year proceeding the year of banding and in its second calendar year of life), and 'after second year' (ASY—bird known to have hatched earlier than the calendar year preceding the year of banding). Sex was determined according to the feathers on the top of the bird's head (the cap). Males have black feathers and females have brown feathers. Age was estimated according to plumage characters (Svensson, 1970; Jenni and Winkler, 1994). Each bird was weighed with an electronic balance to an accuracy of 0.1 g. Wing length was measured with a ruler from the carpal joint to the tip of the longest primary, on the closed wing, while the wing was flattened and straightened, to an accuracy of 1 mm (Svensson, 1970). Fat score was measured from 0—no fat, to 4—fat bulging in the bird's throat, stomach, and under its wings (Kaiser, 1993). On most days during the migration seasons, two rectrices (tail feathers) were taken from most of the blackcaps caught, placed in an envelope, and kept at -80°C .

At the end of each migration season a table was constructed showing the number of blackcaps caught each day at the JBO. To test for significant daily fluctuations in bird numbers, we applied an Autoregressive Integrated Moving Average (ARIMA) model (Box and Jenkins, 1976). The optimal model was selected using the Akaike Information Criterion (AIC), which evaluates all possible parameter combinations. The selection was performed among 25 models presenting all the possible combinations of autoregressive, differencing, and moving average parameters with orders between 0–2. This range of orders was chosen since it has been found to explain most time series. Time series calculations were performed using the JMP 7 software (SAS Institute, Inc.).

A small proportion of the birds caught were recaptured a few days later, and these recaptures were excluded from the analyses. For the morphological analysis we used 1,850 and 1,900 birds recorded in spring 2005 and 2006, respectively. Because male blackcaps have been shown to migrate toward their breeding ground significantly earlier than females (Izhaki and Maitav, 1998) and ASY tend to migrate before SY birds (GP, personal observation), all measurements were divided into four sex/age categories:

males or females and ASY or SY. Body weight and wing length were both normally distributed. Body weight was correlated to the amount of fat reserves ($r^2 = 0.687$, $F_{1,1832} = 4012.2$, $p < 0.0001$ and $r^2 = 0.638$, $F_{1,1853} = 3269.4$, $p < 0.0001$ for 2005 and 2006 samples, respectively). To control for the effect of fat, we used the residuals for body weight from the above regressions. Body weight, controlled for fat, significantly accounted for only 1.3% and 0.5% of the variance in wing length ($F_{1,1826p} = 25.1$, $p < 0.0001$ and $F_{1,1814} = 9.6$, $p = 0.002$ for 2005 and 2006 samples, respectively), thus biologically body weight and wing length are completely independent variables.

WEATHER DATA

During migration, most passerines fly at air speeds of 30–50 km/h. Average flight speed during spring migration may be faster, due to shorter stopovers and longer flights, especially when flying over desert areas (Podulka et al., 2004). In order to test how weather conditions affect the number of blackcaps caught daily in JBO we used the on-line database provided by the Earth System Research Laboratory at the National Oceanic and Atmospheric Administration (NOAA; www.cdc.noaa.gov) for the period 1 March to 31 May in both 2005 and 2006. This database provides various weather parameters at 2.5 degree intervals. We used least square regression to test whether the observed daily fluctuations in blackcap numbers (expressed as proportions) are related to the weather conditions on the autumn return route of blackcaps. We used data for four 2.5*2.5 squares along the JBO longitude (32.5°E) at latitudes 32.5°N, 30.0°N, 27.5°N, and 25.0°N (JBO is located at 32.08°N and 34.8°E). We tested weather data for the date of capture and a day earlier. Proportions of bird number per day were normalized using the Box–Cox transformation. We selected four independent key weather and wind variables: Uwind, Vwind, wind vertical velocity, and the lifted index. Uwind is the surface (10 m) west-to-east zonal wind velocity, Vwind is the surface (10 m) south-to-north meridional wind velocity, and wind vertical velocity is the zonal measure of the upward motion of air in the atmosphere. The lifted index (LI) is the temperature difference between rising air and the temperature of the environment at a given pressure height (500 mb) in the troposphere. When the value is positive, the atmosphere (at the respective height) is stable and when the value is negative, the atmosphere is unstable. Thunderstorms are fueled by strong rising air, thus LI is a good measurement of the atmosphere's potential to produce severe thunderstorms. These four weather variables were independent for both years (tolerance ≥ 0.1 in all cases).

STABLE ISOTOPES ANALYSIS

Stable isotopes vary spatially according to well-defined natural processes, and the isotopic ratios in a geographic area or habitat are reflected in the local food chains (Chamberlain et al., 1997; Rubenstein et al., 2002). Unlike soft tissues, such as liver, blood, and muscle, or even hard tissues such as bones, which have a limited turnover rate of days to months, feathers are unique. They grow in a very short time and become metabolically inert. Thus, the isotopic content of a feather reflects the bird's diet and therefore the geographic area in which it was developed (Mizutani et al., 1990, 1992;

Hobson and Clark, 1992). Isotopic analyses have been successfully used to differentiate between the breeding and non-breeding habitats of various bird species, and to define migration patterns (e.g., Clegg et al., 2003; Kelly et al., 2005; Yohannes et al., 2005; Bensch et al., 2006). Blackcaps molt their flight feathers only once a year, before the autumn migration (late June–late September; Shirihai et al., 1996). We can thus expect the isotopic constitution of the feathers to distinguish between individuals arriving from different regions and habitats.

There is a difference in isotopic ratios of δ Carbon-13 between C3 and C4 plants due to their unique biochemical photosynthetic pathways. The mean δ C-13 ratio of C3 plants is -25‰ whereas C4 plants have a ratio of -12‰ . Since C3 plants predominate in high latitudes and C4 plants are more common in the low latitudes, the δ C-13 ratio decreases gradually with increasing latitude (e.g., Chamberlain et al., 2000). Recently, Diefendorf et al. (2010) have shown that δ C-13 varies in relation with precipitation, thus enabling a better interpretation of isotope results. We used the data in their Appendix to calculate the relationship between δ C-13 and latitude in the breeding range of blackcaps in Europe (40–65°N; Cramp, 1992). In addition, we used global precipitation data (kindly provided by Dr. Mark Lomas, University of Sheffield) to calculate the relationship between annual precipitation and the above range of latitude along the 34.5°E longitude that runs through most of Israel. Similarly, we calculated the relationship between annual precipitation and the longitude along the 50°N parallel between 15 and 65°E, the range of breeding of blackcaps between Germany and Kazakhstan.

Similar to carbon isotopes, nitrogen isotopes also vary geographically and between habitats (Rubenstein et al., 2002). The values of δ N-15 varies with the trophic position in food webs as well as with aridity, and tends to increase with dryness (spanning a range from $<10\text{‰}$ in regions with >800 mm of rainfall a year to $>15\text{‰}$ in areas with <200 mm a year). We anticipate nitrogen ratio to increase with longitude, since central Europe is more humid than western Asia and the Caucasus mountains. Together, these isotopes often provide a better discriminatory power to the isotopic analysis (e.g., Yohannes et al., 2005; Crawford et al., 2008).

We collected 128 and 104 feather samples throughout spring 2005 and 2006, respectively. Prior to the isotopic measurements, the upper parts of the feathers were cleaned using a 2:1 chloroform:methanol solution and rinsed thoroughly to remove oil, dirt, and residual detergent. The feathers were then oven-dried at 60 °C. Next, we clipped the feathers lengthwise into fine sections, using autoclaved scissors, and placed these into clean Eppendorf tubes. The clipped feathers contained sections of up to 2 mm in length. This was done to ensure an integrated isotopic signal representing the blackcaps' diet during the entire period of feather growth, rather than during the growth period of one section of the feather. The analysis itself was done in the laboratory of Prof. Dan Yakir at the Weizmann Institute, Rehovot. A small amount of the cut feathers (0.5 mg) was wrapped in a silver capsule. The capsule was then combusted in an elemental analyzer (Carlo Erba EA1108, Fison, Milan, Italy). The generated products were passed with helium carrier gas directly into the inlet of an isotope ratio mass spectrometer (Opti, Micromass, Manchester, UK). Stable isotope ratios were reported as deviations from a

standard in per mill (‰) using the δ notation:

$$\delta_{\text{sample}} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] * 1000$$

where δ_{sample} is the isotope ratio of the sample relative to a standard, and R_{sample} and R_{standard} are the fractions of heavy to light isotopes in the sample to standard, respectively. It should be noted that the N and C isotope ratios of feather keratin remain fixed after growth.

Analyses of covariance (ANCOVA) were performed to assess whether time (covariate), sex, age, and their interaction could account for changes in morphology (wing length, body mass, and body mass controlled for fat were considered separately as response variables) or stable isotope levels. To accommodate for the difference in daily sample size, daily average by sex and age of the morphological and isotope levels were used in the ANCOVA.

RESULTS

The results for each of the two years of study are presented separately for migration pattern, morphological variation, weather conditions, and isotopic variation.

MIGRATION PATTERN

During spring 2005 (March–May) 2,390 blackcaps were caught at the JBO. Of this total, 336 were same year recaptures and we only used information from their initial capture in the analysis. The age and sex distribution of the blackcaps was as follows: 50.0% males and 50.0% females, 57.9% second year (SY) birds and 42.1% after second year (ASY) birds. There were more SY than ASY blackcaps for both sexes (58.2% SY to 41.8% ASY females; $\chi^2_1 = 12.3$, $p < 0.001$ and 57.6% SY to 42.4% ASY males; χ^2_1

Table 1

Total number and proportion (%) of blackcaps handled in spring 2005 and 2006 by sex and age. SY—second year; ASY—after second year

Sex	Age	2005		2006	
		n	%	n	%
Females	SY	538	29.1	471	24.8
	ASY	387	20.9	508	26.7
Total females		925	50.0	979	51.5
Males	SY	533	28.8	415	21.8
	ASY	392	21.2	506	26.6
Total males		925	50.0	921	48.5
Total		1850	100.0	1900	100.0

= 10.7, $p < 0.001$; Table 1). Blackcaps of unidentified sex or age were excluded from the analysis.

Analyzing the variation of bird numbers with time revealed distinct wave patterns, each characterized by a period with a high number of blackcaps caught followed by a period of low numbers of trapped birds. This wave pattern was significantly different than uniform or random patterns (Kolmogorov Smirnov test: $Z = 3.2$, $p < 0.0001$), and from normal distribution (Shapiro-Wilk test, $W = 0.91$, $p < 0.0001$). The best time series model was ARIMA(1,2,2), which accounted for 39.8% of the variance (AIC = 727.0, Δ AIC to the next best model = 1.7; AR1 = 0.458, $t = 4.7$, $p < 0.0001$; MA1 = 1.989, $t = 38.3$, $p < 0.0001$; MA2 = -0.999, $t = 19.2$, $p < 0.0001$; Fig. 1a). The next best model was ARIMA(2,2,2; AIC = 728.7, Δ AIC to the next best model = 0.2), which accounted for 40.0% of the variance. It is remarkable that random walk models (i.e., ARIMA models (0,0,0), (0,1,0), and (0,2,0)) appeared among the least-fit models to explain variation in blackcap numbers (Δ AIC to the best model > 19).

During the spring of 2006 (March–May) 2359 blackcaps were caught at the JBO. Of this number, 287 had been captured earlier at the JBO and were excluded from our analysis. The age and sex distribution of the blackcaps were as follows: 48.5% males and 51.5% females; 46.6% second year (SY) birds and 53.4% after second year (ASY) birds. Female SY and ASY blackcaps were equal in numbers (48.1% SY to 51.9% ASY; $\chi^2 = 0.7$, $P = 0.403$) but SY males were significantly more numerous in the 2006 sample (45.1% SY to 54.9% ASY; $\chi^2 = 4.5$, $P = 0.034$; Table 1). Blackcaps of unidentified sex or age were excluded from the analysis.

Similar to spring 2005, blackcaps also passed through Israel in waves in spring 2006. In spring 2005, the number of birds present in each wave was relatively even among waves. However, in spring 2006, the majority of the blackcaps (56%) arrived in one big wave in the middle of the season (18 April–7 May), with small amplitude waves at the beginning and end of the season. This wave pattern was significantly different than uniform or random patterns (Kolmogorov Smirnov test: $Z = 6.0$, $p < 0.0001$; Runs test: $Z = 5.9$, $P < 0.0001$), and from normal distribution (Shapiro–Wilk test, $W = 0.66$, $p < 0.0001$). The best model identified was ARIMA(1,1,2), which accounted for 51.8% of the variance (AIC = 812.3, Δ AIC to the next best model = 0.8; AR1 = -0.393, $t = 1.9$, $p = 0.055$; MA1 = -0.208, $t = 1.1$, $p = 0.257$; MA2 = 0.570, $t = 5.9$, $p < 0.0001$; Fig. 1b). The next best model was IMA(1, 2; AIC = 813.1, Δ AIC to the next best model = 0.7), which accounted for 50.1% of the variance. In agreement with 2005 data, random walk models appeared among the least-fit model to explain variation in blackcap effective (Δ AIC to the best model > 17).

WEATHER CONDITIONS

Preliminary results indicated that for both years, the weather data providing best fit for the day of capture were those of latitude 32.5°N, and 30.0°N for the day before capture. In 2005, weather conditions on the date of capture and latitude 32.5°N explained 18.04% of the variance in daily capture rate ($F_{(4,87)} = 4.8$, $p < 0.0015$). The significant effects were Vwind, Uwind, and vertical velocity. Weather conditions on the day before

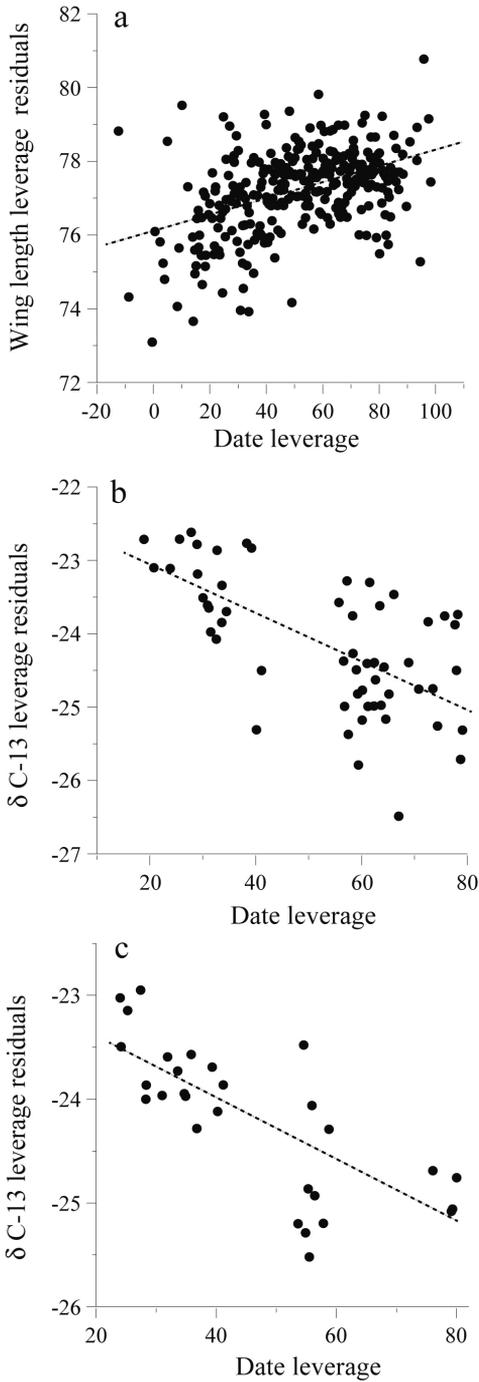


Fig. 2. Partial leverage plots. (a) Daily mean wing length during 2005 (slope = 0.022, $F_{(1,292)} = 50.4$, $p < 0.0001$); (b) daily mean δ C-13 during 2005 (slope = -0.032, $F_{(1,54)} = 31.6$, $p < 0.0001$); (c) daily mean δ C-13 during 2006 (slope = -0.031, $F_{(1,27)} = 29.7$, $p < 0.0001$) as a function of capture date.

capture and latitude 30.0°N (about 230 kms south of JBO) explained 12.73% of the variance in daily capture rate ($F_{(4,87)} = 3.17$, $P = 0.0175$). The only significant effect was Uwind.

In 2006, weather conditions on the date of capture and latitude 32.5°N explained 11.97% of the variance in daily capture rate ($F_{(4,87)} = 2.96$, $p < 0.0242$). The only significant effect was LI. Weather conditions at the day before capture and latitude 30.0°N explained 13.87% of the variance in daily capture rate ($F_{(4,87)} = 3.50$, $p < 0.0106$). The only significant effect was LI.

MORPHOLOGICAL VARIATION

In 2005, significant variation were detected in wing length as a function of the capture date (ANCOVA, $F_{(6,287)} = 14.9$, $p < 0.0001$). Wing length significantly increased in size from March to May (slope = 0.022, $F_{(1,292)} = 50.4$, $p < 0.0001$; Fig. 2a). Significant differences in wing length were also detected between the sexes ($F_{(1,292)} = 3.9$, $p = 0.049$), ages ($F_{(1,292)} = 35.3$, $p < 0.0001$), and their interaction ($F_{(1,292)} = 5.3$, $p = 0.022$). SY animals had the same wing length, but ASY males had longer wings than ASY females. Changes in body weight as a function of capture date were not detected before (ANCOVA; $F_{(6,288)} = 1.1$, $p = 0.364$) or after controlling for fat (ANCOVA; $F_{(6,288)} = 1.1$, $p = 0.353$). All other effects and interactions were insignificant.

In 2006, significant trends were detected in wing length (ANCOVA; $F_{(6,271)} = 7.4$, $p < 0.0001$). Wing length significantly increased in size from March to May (slope = 0.007, $F_{(1,276)} = 4.6$, $p = 0.032$). Significant differences in wing length was also detected between the ages ($F_{(1,276)} = 37.3$, $p < 0.0001$). Changes in body weight as a function of capture date were detected (ANCOVA; $F_{(6,271)} = 2.9$, $p = 0.01$). Body weight significantly increased with time (slope = 0.019, $F_{(1,276)} = 10.8$, $p = 0.0012$). However, this increase was only found to be significant in females ($F_{(1,276)} = 5.7$, $p = 0.018$). After controlling for body fat, these trends in body weight were no longer significant ($F_{(6,271)} = 1.1$, $p = 0.368$). All other effects and interactions were insignificant.

ISOTOPIC VARIATION

In 2005, we detected significant trends in δ C-13 (ANCOVA; $F_{(6,49)} = 6.9$, $p < 0.0001$) but not in δ N-15 (ANCOVA; $F_{(6,49)} = 1.3$, $p = 0.266$). δ C-13 values significantly decrease as a function of capture date (slope = -0.032, $F_{(1,54)} = 31.6$, $p < 0.0001$; Fig. 2b). The interaction between sex and age was also significant ($F_{(1,54)} = 5.6$, $p = 0.022$). ASY animals had the same δ C-13 levels, but SY females had higher δ C-13 levels than ASY males. All other effects and interactions were insignificant.

In 2006, we detected significant trends in δ C-13 (ANCOVA; $F_{(6,22)} = 5.3$, $p = 0.0015$) but not in δ N-15 (ANCOVA; $F_{(6,22)} = 0.15$, $p = 0.987$). δ C-13 values significantly decrease as a function of capture date (slope = -0.032, $F_{(1,27)} = 29.7$, $p < 0.0001$; Fig. 2c). All other effects and interactions were insignificant.

LATITUDE, PRECIPITATION, AND ISOTOPIC VARIATION

Within the breeding range of blackcaps (39.5–65°N), there was a significant negative relationship between δ C-13 and latitude ($R^2 = 0.2263$, $F_{2,129} = 37.7373$, $p < 0.0001$). Due

to lack of data we could not calculate a longitudinal trend for $\delta C-13$. Within latitude range of 39.5–57.5°N, precipitation was positively related to latitude ($R^2 = 0.6702$, $F_{1,14} = 28.4582$, $p = 0.0001$), but dropped significantly farther north between 58.5–64.5°N ($R^2 = 0.8988$, $F_{1,5} = 44.4204$, $p < 0.0001$). Within the longitude range of 15–65°E there was a significant negative relationship between precipitation and longitude ($R^2 = 0.9435$, $F_{1,49} = 818.9160$, $p < 0.0001$).

DISCUSSION

The migration of many migrant birds is not uniform in time and many species rest at stopovers along the way. Such stopovers are not necessarily for refueling, since many of the resting birds are in good condition (Bairlein, 1985). Birds may stay for several days, apparently mainly due to weather conditions (see Newton, 2007, for summary), and once they start migrating again they create “migratory waves”. Our time series analyses support the hypothesis that blackcaps migrating through Israel during spring arrive in “waves”, and the peaks in numbers of birds are real and not just random perturbations. The timing of the peaks is related to weather patterns about 270 km south of Israel, particularly wind speed and direction.

The fact that the number of waves differed between years may be explained as follows. Each wintering blackcap population has been selected to return to its breeding ground at a time when breeding conditions are optimal. North of the equator, spring starts earlier in the south than in the north, and blackcaps breeding in northern latitudes arrive later at their breeding grounds than those breeding further south. Dement’ev and Gladkov (1968) provided arrival dates of blackcaps at various localities in the former Soviet Union, and we used these data to determine the relationship between arrival date and latitude. Using the data in Dement’ev and Gladkov (1968), we found that mean arrival date (calculated from the range given; April = 1) is significantly related to latitude ($r^2 = 0.4068$, $F_{1,10} = 6.8591$, $p = 0.0256$; Arrival date = $2 * \text{Latitude} - 73.26$). These results indicate that for each degree latitude, the arrival date is later by two days. It is thus expected that northern populations will start migrating and passing through Israel later than southern ones. Hypothetically, the above mode of migration would predict a continuous stream of birds over Israel. However, any deviation from a direct route or stopover due to weather conditions or other reasons would break a continuous flow and generate the wave pattern.

It is known that meteorological factors play a major role in blackcap spring migration (Izhaki and Maitav, 1998). When weather conditions at the wintering grounds and/or during migration are unfavorable, migrating blackcaps tend to halt their migration and wait for more favorable conditions. This phenomenon may result in birds from different localities reaching JBO at different times or all arriving at the same time, thus creating a wave pattern. On the other hand, when weather conditions are relatively stable, a continuous stream of birds is expected. Our data show that the daily number of blackcaps caught in JBO was significantly related weather conditions about 270 km south of Jeru-

salem the day before arrival and around Jerusalem at capture day. Not surprisingly, the most important factors were the velocity of south–north and vertical winds. Vertical air currents lift the birds of the ground and south–north wind blows in the direction of their spring migration, and both save the birds energy on their flight north. Spring weather conditions varied more in 2005 than in 2006 (Coefficient of variation (CV): 347.3 and 178.3 for Vwind, 42.8 and 35.2 for Liftindex, respectively). For example, CV of wind vertical velocity in spring 2005 was almost twice as large as that during spring 2006. These conditions are reflected in the larger number of waves observed in 2005, and the much larger variation in the number of blackcaps caught in each wave during that year in comparison to 2006 (81.9 and 139.6, respectively). However, the percent of variation in the number of blackcaps caught explained by weather conditions in both years was relatively small and ranged between 10%–18%. Hence, the unexplained variance may be linked to other climatic factors (e.g., temperature; Wikelski et al., 2003; Schmaljohann et al., 2007), or bird behavior not associated with climate conditions.

Blackcap wing length decreases from north to south (Dement'ev and Gladkov, 1968), and the proportion of δ C-13 in tissues is expected to decrease with increasing latitude. Such geographical pattern has been observed in North America, but there is no base map of δ C-13 distribution in Europe. Diefendorf et al. (2010) have shown that there is a global trend of decrease in δ C-13 in relation to precipitation. Using their data we found that within the latitudinal breeding range of blackcaps (between 39.5 and 65°N) δ C-13 decreased from south to north (Fig. 2). Due to lack of data we could not test whether there is a similar longitudinal trend. However, precipitation increases from latitude 39.5°N to 57.5°N, but the trend is reversed further north, and precipitation decreases longitudinally along the 50°N parallel from west to east. Hence, the finding that there is a negative trend between arrival date and δ C-13 suggests that late arrivals are birds that molted their feathers (and presumably bred) further north (but not at the extreme breeding range) and/or east than early-arriving birds. The above interpretation should be taken cautiously, as there is no base map of δ C-13 distribution in Europe and Western Asia. Together with our data on wing length, this generally supports the hypothesis that birds breeding at high latitudes arrive in Israel later in spring than birds that breed closer to Israel. In both 2005 and 2006, wing length significantly increased in size from March to May and δ C-13 values significantly decreased as a function of capture date. These results are similar to Paxton et al.'s (2007) findings (based on stable isotopes analysis) that Wilson's warbler (*Wilsonia pusilla*) in North America has a pattern of "leap-frog migration", in which individuals that had bred the previous season in southern latitudes migrated earlier than individuals that had previously bred in more northern latitudes. However, not all bird species follow this pattern. For example, the timing of migration at a Costa Rican stopover site of the Swainson's thrush (*Catharus ustulatus*) is not related to the breeding latitude, as inferred from the isotopic ratio (Wilson et al., 2008). It is well known that wing length is highly correlated with the birds' migration distance (Marchetti et al., 1995; Fiedler, 2005), and short-distance migratory bird species have shorter wings than their long-distance migrating relatives. For the blackcap, which has a "leap-frog" migration pattern, northern breeding populations are long-distance migrants. The fact

that during both 2005 and 2006 wing length of blackcaps tended to increase during spring in all sex/age groups supports the above assumption.

Birds that breed at a high latitude need more energy to fuel their migration, and carry more energy reserves in the form of muscle and fat tissues. For example, female sharp-shinned hawks (*Accipiter striatus*) from higher latitudes had significantly higher estimated fat levels than those from lower latitudes (Smith et al., 2003, but see Wilson et al., 2008, for a different pattern). Hence, one would expect that body mass of blackcaps arriving late in season would be heavier than of those arriving at the start of the season. However, only in 2006 did we detect a significant increase in body weight (without controlling for fat) with time. Controlling for the effect of fat should indicate whether birds from higher latitudes are really heavier (e.g., having more muscle mass). In both years we did not detect significant differences in body weight (controlled for fat) as a function of capture date. One possible explanation is that all blackcaps have similar lean weight and arrived at the JBO in a similar deprived condition after a long journey above the Saharo-Arabian Desert belt, where little food and water is available for refueling. An alternative explanation is based on the fact that migrating birds use not only fat, but also muscle tissue, as a source of energy (Battley et al., 2000). Birds arriving from further away (i.e., higher latitudes) may have used more of their tissue reserves, hence arrive at JBO at similar lean body mass as migrants from lower latitudes.

Our data relating to the δ C-13 also supported the hypothesis that blackcaps arriving early in Israel in spring are on the way to breeding grounds at lower latitudes or more western longitudes, and it appears that as the migration progresses, those blackcaps that pass through Israel later in the season are aiming for more northern latitudes or eastern longitudes. Unlike δ C-13 values, δ N-15 values did not show any significant pattern. Since we did not find background data for the geographic distribution of δ N-15, we are unable to relate our δ N-15 to a geographic region.

To conclude, our data show that blackcaps migrating through Israel during the spring do not pass through continuously, but travel in waves. Our morphological data suggest that birds from the early season are aiming for the lower latitudes while later birds aim for the higher ones. Isotope δ C-13 data support the above conclusion but also suggest that early birds aim to lower latitudes or more western longitudes.

ACKNOWLEDGMENTS

We thank Prof. Dan Yakir and Mrs Manuela Negreanu for letting us use their facilities at the Weizmann Institute; Prof. Ido Izhaki for his useful comments; Dr. Yossi Leshem for his advice; Dr. Mark Lomas, University of Sheffield, for kindly providing to us precipitation data; Ido Izhaki and an anonymous reviewer for their useful comments; Naomi Paz for editorial help; and all of the JBO team for their help. The German-Israel Foundation (G.I.F. Young Scientist Program No. I-2098-1401.13/2004 to DH) and the Israel Cohen Chair for Environmental Zoology (to YYT) supported this study.

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