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Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds

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Summary

1. Meteorological conditions are critical determinants of bird migration. However, response to weather should vary among species as well as between males and females, as phenotypic traits relevant to migration are also shaped by natural selection acting differentially on species and either sex in other life cycle phases.

2. We studied the covariation between capture frequencies and meteorological conditions at departure and at a stopover site during northward spring migration in 21 species of migratory birds. The stopover site is a small island located at the northern end of a wide ecological barrier (the Mediterranen Sea), that is crossed with non-stop flights by migrants departing from North Africa.

3. Head and crosswinds at departure, and tail and crosswinds at stopover reduced the number of birds captured, although the strength of these effects varied among species. In the subset of 10 sexually dimorphic species, males and females were not differentially susceptible to weather conditions.

4. Because sexual and natural selection pressures on traits relevant to migration vary among species, we investigated whether body mass and wing morphology predicted species susceptibility to weather in analyses controlling for phylogenetic effects, using wing loading, wing aspect ratio, the 'brachial index', and wingtip roundedness and convexity as indicators of the morphology of the flight apparatus.

5. Captures of species whose wing morphology is more typical of long-distance migrants were less affected by tail and crosswinds, suggesting that long-distance migrants are less susceptible to weather.

6. Meteorological conditions at departure independently concurred with those at stopover in determining capture frequencies. The effect of weather on migration covaried with wing morphological traits that co-evolved with migratory strategies. Changes in meteorological conditions driven by current climate change thus have the potential to differentially affect migration phenology in relation to migratory strategy and morphology of individual species.

Key-words: climate change, migration, sex, stopover, weather, wing morphology

Introduction

Migration has evolved in diverse organisms as an adaptation to periodically changing environments, enabling animals to escape adverse ecological conditions and to exploit favourable habitats at the time of crucial life-history events such as reproduction (Berthold 1996; Dingle 1996; Alerstam, Hedenström & Åkesson 2003). In birds, migration schedules may be under strong genetic control, being triggered by firmly periodical changes in external clues (e.g. photoperiod; Berthold 1996; Gwinner 1996; Coppack & Pulido 2004). Several bird species migrate over intercontinental distances, often crossing inhospitable oceans or deserts (Berthold 2000). The severe fitness cost of long-

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range migration is believed to have selected migrants to adaptively manage energy, time as well as exposure to adverse meteorological conditions (Alerstam 1990; Alerstam & Lindström 1990; Richardson 1990; Houston 1998), and to have promoted the evolution of behavioural plasticity allowing for adaptive decisions on when to depart or stopover based on local weather conditions (Alerstam 1981; Biebach 1990; Bairlein & Hüppop 2004).

Selection pressures associated with migration are expected to have different evolutionary effects on morphology and physiology depending on migration behaviour (e.g. migration distance; Pennycuick 1975; Rayner 1988; Hedenström 2008). However, traits relevant to migration (e.g. morphology of the flight apparatus) are also shaped by natural and sexual selection outside the migration period (Rayner 1988, 1996; Norberg 1990, 2002; Hedenström & Møller 1992; Marchetti, Price & Richman 1995). Because natural and sexual selection throughout the annual life cycle are likely to vary among species (or conspecific populations), the level of morphological adaptation to sustain prolonged migratory flights should show interspecific variation. Consequently, response to weather during migration should covary with species phenotype. However, to the best of our knowledge, no study has analysed the differential impact of weather on migration in relation to morphology across species while controlling for common ancestry effects.

Here, we first investigate the relationships between capture frequency at a stopover site of 21 migratory passerines crossing the Mediterranean Sea during northward spring migration and weather conditions both at departure in North Africa (N Africa) and at stopover in Central Italy. Because selection on migration schedules can differ between the sexes (Morbey & Ydenberg 2001), and morphology differs between the sexes (e.g. Hedenström & Pettersson 1986), we also analysed susceptibility to weather of males compared to females. In the second, comparative part of the study, we test the hypothesis that wing morphology predicts species-specific effects of weather on capture frequencies, possibly reflecting departure and stopover decisions (see also below).

Capture frequencies have been used in a number of studies of the effect of weather on bird migration, although it is widely acknowledged that they may not strictly reflect 'true' migration fluxes. Importantly, throughout this study, we will therefore *not assume* that the frequency of captures is proportional to the number of migrating birds. Rather, we assume that the number of birds that decide to depart or stopover at a given site depends on meteorological conditions (see Newton 2008 and below). We then test whether the observed patterns of daily change in capture frequencies at an island potential stopover site covary with meteorological conditions both at departure and at the stopover site. The observation of a covariation between capture frequencies and meteorological conditions consistent with the predictions based on theoretical (e.g. energetic) arguments and current knowledge on the effects of weather on migration would lend support to the idea that capture frequencies to some extent reflect the intensity of migration. Conversely, the observation of patterns of covariation that are not consistent with the expectations would lead to dismiss the assumption that weather affects migration decisions or would invalidate the idea that capture frequency to some extent provides information on migration flux. This approach, albeit indirect, is the only practical way to investigate the effect of weather on migration in the absence of unbiased methods to estimate 'true' species-specific migration fluxes. In fact, at present, methods that allow to estimate species-specific intensity of migration of large numbers of small birds from several species, based e.g. on radar or other techniques (e.g. Stutchbury *et al.* 2009), are still in their infancy, and trapping data at bird ringing stations are likely to be the sole extensive source of information on migratory fluxes for several coming years.

WEATHER CONDITIONS AND MIGRATION DECISIONS

For migratory birds, wind conditions can markedly affect the cost of transport and the risk of being blown off to less-favourable routes; temperature can influence opportunities to refuel by affecting food availability at stopover sites and impacts on physiology; finally, cloud cover can affect the ability to navigate and spot suitable stopover sites (Richardson 1990; Berthold 1996; Newton 2008). Prevailing patterns are for migration speed to be higher with clear sky, high temperatures and tail- or no winds (Richardson 1990; Newton 2008). High or raising temperatures, clear sky and no rainfall are associated with more frequent departures from staging areas (Nisbet & Drury 1968; Richardson 1990; Liechti 2006). Wind speed and direction, however, qualify as the most important factors determining departure and stopover (Alerstam 1978, 1990; Richardson 1990; Liechti, Hedenström & Alerstam 1994; Liechti & Bruderer 1998; Åkesson & Hedenström 2000; Åkesson *et al.* 2002; Erni, Liechti & Bruderer 2005; Liechti 2006). Crosswinds tend to inhibit departure and reduce the distance travelled before stopover (Cochran & Wikelski 2005). Landing decisions in relation to weather have been less frequently investigated, likely because of technical limitations (Thorup *et al.* 2006).

The number of birds stopping over at any given site and time depends on local weather as well as on conditions at previous staging sites affecting departure decisions (i.e. the decision of leaving *or* bypassing a stopover site; e.g. Ahola *et al.* 2004; Hüppop & Winkel 2006). To investigate the effect of meteorological conditions, an insightful approach would thus be to analyse the effects of weather at departure in combination with that at stopover sites – an approach that has hardly ever been taken (Alerstam 1978; Yaukey & Powell 2008). We therefore investigated the effects of change in weather conditions (wind velocity, cloud cover and temperature) at departure sites in N Africa (Jonzén *et al.* 2007; Saino *et al.* 2007), and at a stopover site (Ventotene island; Central Italy) on change in capture frequencies at Ventotene during spring migration.

We predicted that an increase in the tail wind and a decrease in the crosswind components (relative to the estimated SW–NE flight direction) in N Africa lead to an increase in the number of captures (see Table 1 for a summary of predictions). An increase in tail winds at Ventotene was predicted to reduce capture frequencies, after statistically controlling for wind conditions in N Africa, because migrants are more likely to remain aloft under favourable winds, whereas we predicted an opposite effect for crosswind at Ventotene, because crosswinds should increase energy expenditure. An increase in temperature in N Africa was predicted to result in larger numbers of migrants leaving N Africa, and thus in more birds being captured at Ventotene. We had no *a priori* expectations concerning the effect of temperature in Central Italy on stopover, nor about the effect of cloud cover both at departure and at stopover site, partly because we had no information on clouds height and rainfall. Finally, because males benefit more than females from early arrival to the breeding grounds (Morbey & Ydenberg 2001), we predicted that males were less sensitive to unfavourable weather than females.

SUSCEPTIBILITY TO WEATHER CONDITIONS AND MORPHOLOGY

Body size and morphology of the flight apparatus can affect the response to weather via diverse pathways (Newton 2008). Body size constrains not only the amount of energy reserves and thus non-stop flight range, but also flight speed. One consequence of the allometric relationship between power needed to fly at 'maximum range speed' (see Newton 2008) and body mass is that the amount of extra-fuel that a bird can carry scales negatively with its size (Hedenström 1993; Alerstam & Hedenström 1998; see Newton 2008). Thus, despite large birds can fly faster, their maximum flight range may be smaller than that of small birds (Newton 2008). Wind direction and velocity relative to flight direction is thus expected to have different effects on migration decisions in relation to size.

Several, potentially opposing selection pressures for flight speed, manoeuvrability and load carrying operate on wing morphology, which therefore reflects the balance of selection by extrinsic biotic (e.g. predation, prey mobility) and abiotic (e.g. wind) factors (Norberg 1979, 2002; Rayner 1988; Hedenström & Møller 1992; Møller, de Lope & Saino 1995; Leisler & Winkler 2003). Studies comparing different species/populations have given a hint to which wing features covary with migratory habits (Winkler & Leisler 1992; Senar, Lleonart & Metcalfe 1994; Lockwood, Swaddle & Rayner 1998) and have focussed on wing aspect ratio and span, wing loading, and shape of the trailing handwing edge (Lockwood, Swaddle & Rayner 1998; Calmaestra & Moreno 2001; Leisler & Winkler 2003). Species/populations where migration is (more) expressed have larger wing aspect ratio and pointedness (Rayner 1988, 1996; Norberg 1990; Marchetti, Price & Richman 1995; Mönkkönen 1995; Lockwood, Swaddle & Rayner 1998; Egbert & Belthoff 2003). Migration is positively associated with wingtip convexity and possibly with smaller wing loading (Calmaestra & Moreno 2001; but see Lockwood, Swaddle & Rayner 1998; Norberg 2002). While it has been suggested that migrants have longer distal compared to proximal wing segments (Winkler & Leisler 1992), as possibly reflected by humerus relative to ulna length ('brachial index'; Nudds, Dyke & Rayner 2007), no study has analysed variation in this trait in relation to migration, although brachial index is smaller among strong flapping fliers (Nudds, Dyke & Rayner 2004). To the best of our knowledge, no study has investigated differential susceptibility to weather in relation to wing morphology while controlling for phylogenetic effects. Here, we speculated that migratory species where wing morphological traits typical of migratory habits (hereafter called more migratory, MM, and, respectively, less migratory, LM, species) are more expressed should be better able to cope with adverse head- and crosswinds. That is, LM species should be more susceptible to wind, being more favoured in departure decision by assisting tail winds and weak crosswinds. Similarly, LM species should be more favoured by tail winds and weak crosswinds and thus stopover less under these conditions. The predictions on the overall effects

Table 1. Predicted and observed effect of meteorological variables on change in capture frequencies in relation to wing features.

		Meteorological variable				
	Typical migrants vs. residents have	Tail wind N Africa(+)+	Crosswind N Africa (–)–	Tail wind Central Italy (–)–	Crosswind Central Italy (+?)–	Temperature Central Italy (+?) +
Wing loading	<	(+) +*/+	(–) –/–	(–) +*/+*	(+) +*/+*	(+) +/+
Aspect ratio	>	(–) –/+	(+) +*/+*	(+) +/+	(–) +/+	(–) –*/–*
Brachial index	<	(+) +*/+*	(–) –/–	(–) +*/+*	(+) +/+	(+) +/+
Roundedness	<	(+) +/+	(–) –/–*	(–) +/–	(+) +/–	(+) –/–
Convexity	>	(–) –/–*	(+) +/+	(+) +/–	(–) +/+	(–) –*/–*

Symbols (+ or –) following meteorological variable name indicate the sign of the predicted (in parentheses) and observed relationship with CACF. < or > symbols in the second column indicate variation in wing features in relation to migratory habits among species/populations reported in literature. Main body of the table: predicted (in parentheses) and observed relationships between wing features and the effect of change in weather on departure and stopover decisions as reflected by species-specific CACF values. For brevity, the predictions for temperature in N Africa are not reported as this variable did not significantly predicted CACF in 20 of the 21 species. In each cell, symbols outside parentheses indicate the sign of the correlation recorded on the entire set of species (to the left of /) or excluding the two short-distance migratory species (to the right of /).

*Significant ($P < 0{\cdot}05$) relationships after controlling for phylogeny.

of wind conditions at the beginning and at the end of an ecological barrier on migration and stop over (see above and Table 1), in combination with the expectation of a larger susceptibility to wind conditions of species whose wings are less adapted to migration, led us to formulate the following specific predictions (see Table 1).

Because LM species have large wing loading, brachial index and wingtip roundedness, although having small aspect ratio and wingtip convexity, we predicted that the (expected) positive effects of tail wind in N Africa on departure and that of crosswind in Central Italy on stopovers were larger among species with large wing loading, brachial index and wingtip roundedness and smaller in species with high aspect ratio wings and less convex wingtips. Conversely, the negative effect of crosswinds in N Africa on departures and that of tail wind on stopovers in Central Italy should be more intense in (LM) species with large wing loading, brachial index and wingtip roundedness, and less intense in (MM) species with high aspect ratio wings and wingtip convexity.

Materials and methods

We analysed daily capture frequencies recorded on the island of Ventotene (40°48′N, 13°25′E), located about 50 km off the western coast of Central Italy, during 12 years in the period 1988–2001 (data for 1989 and 2000 were not available). Trapping periods had variable duration (29–60 days; mean capture date: 29 April) in different years and on average lasted 34·3 days. However, interannual difference in trapping periods is unlikely to have introduced any bias in the data because all species were trapped throughout all periods, and the main analyses were based on differences in capture frequencies between consecutive days (see below). Analyses were based on data for nearly 118 000 individual captures of 21 abundant species (listed in Table 2). The mean number of captures per year ranged from 87 to 1569 across species (mean = 468 individuals). Eighteen of these species are exclusively trans-Saharan migrants breeding throughout Europe and Asia. *Sylvia atricapilla* has trans-Saharan as well as short-distance migratory and resident populations in Europe but we considered that individuals captured while crossing the Mediterranean had high chances of being trans-Saharan migrants (Cramp 1998). Finally, *Erithacus rubecula* and *Phylloscopus collybita* are short-distance (non trans-Saharan) migrants and were therefore excluded from some analyses. Most of these species are nocturnal migrants, with the exceptions of *Delichon urbicum* and *Hirundo rustica* that have mixed migratory behaviour in this respect (Newton 2008).

Birds were trapped daily by means of mist-nets that were operated in the same standard way over the years (Spina *et al.* 1993). In the rare instances of severely adverse weather conditions (heavy rainfall and/or stormy winds), no trapping occurred. Days with no trapping activity and local recaptures were excluded from the present study. Fat scores, reflecting the amount of subcutaneous fat (Pilastro & Spina 1997), were recorded according to Busse (1974) on a scale ranging from 0 (no fat) to 5 (furcula and abdomen bulging with fat).

METEOROLOGICAL DATA

Temperature, cloud cover and wind velocity data were obtained from the ERA-40 Re-Analysis data set (http://www.ecmwf.int/research/era/do/get/era-40) for six grid points (each representing an area of 1·125° lat. × 1·125° long.) in N Africa (Tunisia region) and for an area south-west of Ventotene (hereafter 'Central Italy') (see Fig. 1). The six grid points in N Africa were chosen as the northernmost ones inland or very close (< 20 km) to the coast. Meteorological data in Northern Tunisia reflect weather conditions that migrants subsequently captured at Ventotene experienced at departure (Jonzén *et al.* 2007; Saino *et al.* 2007). The grid point in Central Italy was chosen as the grid point in the quadrant SW of Ventotene and closest to it. We used zonal and meridional wind velocity components (U and V respectively; in m s^{-1}) estimated at altitudinal pressure levels of 925 and 850 hPa, corresponding to about 700 and 1300 m a.s.l. respectively (see Appendix S1). These heights are representative of winds at normal flight altitudes of most of the migrants we considered (Newton 2008). From U and V wind components, we calculated the component along the putative SW–NE route followed by most migrants (Casement 1966) and the (unsigned) component orthogonal to this direction. We refer to 'tail wind' as the SW–NE component of wind velocity (positive values indicate winds blowing from SW). 'Crosswind' indicates the NW–SE component, taken as the absolute value (i.e. speed). Temperature data (in K) refer to a height of two meters above ground level. Cloud cover is the fraction of sky area with clouds, with no information on cloud height. Most of the existing evidence on spring migration through the central Mediterranean suggest broad-front SW–NE movements with enduring flights continuing during daytime also for nocturnal migrants, and migration 'waves' that simultaneously affect different islands (Spina *et al.* 1993). Indirect evidence, based on spatial and hourly capture patterns on several Tyrrhenian islands, suggests that most migrants arrive there after non-stop flights directly from the coast of N Africa (Pilastro *et al.* 1995; Grattarola, Spina & Pilastro 1999; Jenni *et al.* 2000). However, some of the migrants captured at Ventotene might still be birds departing from Sicily, whose main landmass is located S–SE of Ventotene. We therefore also analysed capture frequencies in relation to meteorological conditions in the central and western parts of northern Sicily.

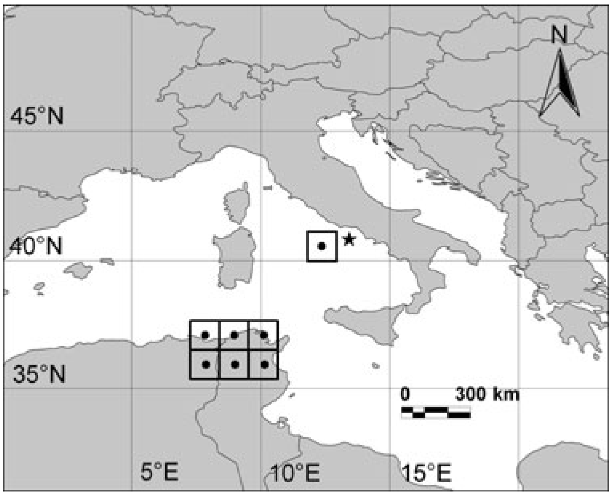

Fig. 1. Departure region in N Africa (see Jonzén *et al.* 2007; Saino *et al.* 2007) for which the effect of meteorological data on capture frequencies at Ventotene, indicated by a star, was analysed. The positions of the grid points to which meteorlogical data refer are indicated by dots.

For the slowest migrants we considered, ground speed in still air is around 30–35 km/h, whereas it is about 40–50 km h^{-1} or even higher for the fastest ones (see Newton 2008), implying that it took between 10 and 16 h to cover the 500 km distance between N Tunisia and Ventotene. Given that (i) most of the species we considered have nocturnal migration; (ii) peak departure of nocturnal passerine migrants typically occurs not only 1–4 h after sunset (Åkesson, Alerstam & Hedenström 1996; Zehnder *et al.* 2001) but also in the middle of the night (Åkesson, Alerstam & Hedenström 1996); and (ii) trapping occurred during daytime, we assumed that meteorological conditions in N Africa relevant to predict capture frequencies at Ventotene were those at 6 and 12 PM of the day preceding that of capture, whereas those relevant at Ventotene were those of the day of capture at 6 and 12 AM.

STATISTICAL ANALYSES

To investigate the effect of weather conditions at departure and stopover on capture frequency at Ventotene, we relied on the analysis of *changes* in the frequency of captures at Ventotene between day_{i+1} and day_i, in relation to *changes* in meteorological variables recorded in N Africa on day_i and day_{i-1}, and in meteorological variables recorded on day_{i+1} and day_i in Central Italy. Meteorological data were averaged among grid boxes in N Africa (data for only one region were used for Central Italy), altitudinal pressure levels and time of the day (both regions) (see Appendix S1 for a justification of this procedure). Changes in absolute capture frequencies (hereafter 'CACF') were expressed as log(capture frequency in day_{i+1} + 1) − log(capture frequency in day_i + 1). CACF values were analysed in repeated-measures linear mixed models with changes in tail wind, crosswind, cloud cover and temperature recorded in N Africa and Central Italy as predictors. Besides the advantage of allowing for efficient detrending of data with respect to the bell-shaped seasonal variation in capture frequencies, using CACF rather than absolute capture frequencies (ACF) also mitigated any potentially confounding effects of multicollinearity (see Appendix S1). However, we tested for multicollinearity among meteorological variables in multiple regression models for each study year separately and found that the variance inflation factor was always well below the commonly accepted threshold of 10. To account for any possible residual bell-shaped seasonal trends in CACF values, the effects of date and date squared were entered as covariates. However, exclusion of the polynomial terms of date did not alter the quality of the results. Year was included as a random grouping (subject) factor in the repeated-measures design. In the models we also controlled for temporal autocorrelation in the data (Knudsen *et al.* 2007) by assuming a first order autoregressive covariance structure. In these analyses, we initially tested for among-years variation in the relationship between CACF and meteorological variables by allowing for random variation in the slopes. We then tested whether exclusion of these random effects led to a significant reduction in the goodness of fit of the model according to the variation in the log-likelihood ratio (based on REML estimation). Analyses were run using PROC MIXED in SAS 9·1 (SAS Institute Inc., Cary, NC, USA). In addition, we analysed ACF, rather than CACF (see Appendix S2).

Confidence intervals of the mean of the coefficients relating CACF to meteorological data were computed based on the sampling variance of each of the estimated coefficients. Variance of the mean equals $\left(\frac{1}{21}\right)^2\sum_{i=1}^{21} V_i$, where V_i is the sampling variance of the coefficient estimate for each species (Jonzén *et al.* 2007; Saino *et al.* 2007). Means and parameter estimates are provided together with their standard error.

COMPARATIVE ANALYSES OF WEATHER EFFECTS IN RELATION TO SPECIES MORPHOLOGY AND RESIDUAL FAT STORES

We estimated species-specific susceptibility to meteorological variables as the slope of the relationships between CACF and meteorological variables obtained from the repeated-measures mixed models described above. Comparative analyses were based on generalized least squares models as implemented by the program Continuous (Pagel 1999). This approach has been adopted in several phylogenetic analyses where the method has been thoroughly described (e.g. Garamszegi *et al.* 2007; see Appendix S3 for details on phylogenetic information and phylogenetic analyses).

Here, we were mainly interested in testing the hypothesis that body size (as indexed by body mass), wing loading and aspect ratio, brachial index and wingtip pointedness and convexity predict the susceptibility of the species to meteorological conditions at departure and at a potential stopover site. In addition, we related species-specific measures of susceptibility to weather conditions to average residual fat stores at landing at Ventotene. Body size and wing and tail length data were obtained from Lislevand, Figuerola & Székely (2007) and were log-transformed. Wing loading was calculated as body mass × wing length^{-2} and log-transformed. Brachial index and aspect ratio data were derived from Nudds, Dyke & Rayner (2007). Wing pointedness and convexity were computed according to Appendix S2 in Lockwood, Swaddle & Rayner (1998) based on data on primary feathers length obtained from ISPRA (F. Spina, unpublished data). For ease of interpretation, as increasing values of the pointedness index indicate more rounded wings, we termed this variable roundedness. For each species, we calculated the daily mean fat score based on all available data of individual captures (Pilastro & Spina 1997).

Results

COVARIATION OF CAPTURE FREQUENCIES WITH METEOROLOGICAL CONDITIONS

We first analysed variation of CACF of individual species between consecutive days by repeated-measures linear mixed models. We initially included change in meteorological variables also as random effects to test for interannual variation in the relationships between CACF and meteorological variables. Tests on covariance parameters provided marginal evidence for an interannual variation in the effects of crosswinds both at departure and in Central Italy and of tail wind on CACF of *H. rustica*, and in the effects of cloud cover in both areas and tail wind in N Africa on CACF of *E. rubecula* (z-values associated to $P < 0{\cdot}05$). Hence, the effects of meteorological variables were consistent among years, with very few exceptions.

In these models, change of temperature in N Africa had a positive effect only on CACF of *Lanius senator* [coefficient = 5·56 (1·22), t = 4·56, $P < 0{\cdot}001$]. To reduce the risk of model overparametrization, in subsequent analyses we therefore removed the effect of temperature in N Africa for all other species. Removal of random effects of the covariates led to a significant reduction in the fit of the models (see Materials and methods) for *Muscicapa striata* (LR = 15·9), *Oriolus oriolus* (LR = 16·9) and *Sylvia borin* (LR = 22·4;

Table 2. Coefficients (SE) from repeated-measures mixed models of change in capture frequencies in relation to change in meteorological conditions

Species	Tail wind N Africa	Crosswind N Africa	Cloud cover N Africa	Tail wind Central Italy	Crosswind Central Italy	Cloud cover Central Italy	Temperature Central Italy
Acrocephalus schoenobenus	**1·54(0·75)**^{a}	−1·09(0·57)	−1·26(6·49)	−0·78(0·55)	**−1·48(0·64)**^{a}	**13·61(6·34)**^{a}	**5·02(1·76)**^{c}
Anthus trivialis	−0·56(0·65)	**−1·02(0·49)**^{a}	**20·20(5·62)**^{d}	−0·44(0·48)	0·22(0·55)	−1·88(5·48)	2·31(1·53)
Delichon urbicum	−1·27(0·69)	0·24(0·52)	−3·72(5·95)	**−1·65(0·50)**^{c}	−0·99(0·59)	**−18·28(5·82)c**	−1·37(1·60)
*Erithacus rubecula**	**1·24(0·55)**^{a}	−0·61(0·42)	−6·05(4·77)	**−1·20(0·40)**^{c}	**−1·08(0·47)**^{a}	0·47(4·65)	2·13(1·29)
Ficedula hypoleuca	**−2·04(0·80)**^{a}	**−1·93(0·60)**^{c}	**15·96(6·87)**^{a}	**−2·4(0·58)**^{d}	**−2·91(0·67)**^{d}	**17·03(6·70)**^{a}	**4·34(1·88)**^{a}
Hippolais icterina	0·27(0·73)	**−1·26(0·55)**^{a}	**26·49(6·33)**^{d}	**−2·08(0·54)**^{d}	**−1·83(0·62)**^{c}	**17·65(6·18)**^{c}	**6·18(1·72)**^{d}
Hirundo rustica	−0·85(0·90)	**1·37(0·68)**^{a}	**−23·69(7·80)**^{c}	**−2·24(0·66)**^{d}	**−2·41(0·77)**^{c}	**−36·37(7·64)**^{d}	−2·50(2·07)
Lanius senator†	0·53(0·79)	**−1·64(0·53)**^{c}	**14·11(5·98)**^{a}	−0·94(0·49)	−0·92(0·57)	6·11(5·67)	−1·50(1·81)
Luscinia megarhynchos	**2·01(0·74)**^{b}	**−2·02(0·56)**^{c}	6·28(6·41)	**−2·44(0·54)**^{d}	**−1·47(0·63)**^{a}	3·48(6·25)	1·85(1·76)
Muscicapa striata‡	−0·91(0·69)	−0·76(0·67)	12·35(10·83)	**−1·77(0·50)**^{b}	−0·92(0·58)	4·46(5·91)	2·75(1·62)
Oenanthe oenanthe	**2·19(0·66)**^{d}	**−3·50(0·50)**^{d}	−4·78(5·72)	−0·86(0·49)	−0·49(0·56)	−3·88(5·58)	−0·11(1·57)
Oriolus oriolus‡	−0·27(0·58)	−0·01(0·63)	3·49(4·77)	**−1·07(0·41)**^{a}	−1·07(0·68)	2·63(6·68)	−0·28(1·4)
Phoenicurus phoenicurus	**1·63(0·77)**^{a}	**−2·85(0·58)**^{d}	−9·10(6·62)	**−2·67(0·56)**^{d}	**−2·00(0·65)**^{c}	9·11(6·46)	2·72(1·81)
Phylloscopus collybita	0·76(0·67)	**−1·54(0·51)**^{c}	6·96(5·82)	−0·93(0·49)	**−1·48(0·57)**^{a}	2·44(5·69)	**4·84(1·57)**^{c}
Phylloscopus sibiliatrix	**−1·70(0·84)**^{a}	**−1·34(0·64)**^{a}	**23·12(7·21)**^{c}	**−2·89(0·61)**^{d}	**−3·88(0·70)**^{d}	**20·64(7·01)**^{c}	**6·06(2·02)**^{c}
Phylloscopus trochilus	0·93(0·85)	**−2·94(0·64)**^{d}	−13·95(7·33)	**−1·59(0·62)**^{a}	**−4·15(0·72)**^{d}	3·24(7·16)	**4·28(1·98)**^{a}
Saxicola rubetra	−0·10(0·83)	**−1·87(0·63)**^{c}	**35·52(7·14)**^{d}	**−1·79(0·61)**^{c}	**−1·47(0·70)**^{a}	**20·68(6·97)**^{c}	**9·2(1·96)**^{d}
Sylvia atricapilla	0·41(0·58)	−0·69(0·43)	−5·59(5·00)	−0·80(0·42)	−0·40(0·49)	−4·96(4·89)	−0·88(1·34)
Sylvia borin‡	**1·73(0·80)**^{a}	−1·2(0·88)	8·72(10·14)	**−2·04(0·71)**^{a}	**−3·66(1·01)**^{b}	6·04(9·82)	3·16(1·86)
Sylvia cantillans	**2·28(0·72)**^{c}	**−3·33(0·54)**^{d}	1·85(6·19)	**−1·76(0·53)**^{d}	**−1·52(0·61)**^{a}	−8·36(6·04)	**4·82(1·69)**^{c}
Sylvia communis	−0·45(0·82)	−1·16(0·62)	**16·48(7·14)**^{a}	**−2·35(0·60)**^{d}	**−2·21(0·70)**^{c}	4·38(6·98)	**6·31(1·93)**^{c}
Mean	**0·350**	**−1·386**	**5·875**	**−1·650**	**−1·719**	**2·773**	**2·826**
LCL (95%)	0·033	−1·638	2·952	−1·883	−1·998	0·008	2·083
UCL (95%)	0·666	−1·134	8·799	−1·418	−1·440	5·537	3·568

Coefficients for date and date-squared are not reported for brevity. Coefficients were multiplied by 10^2. Coefficients in bold are significant ($P < 0·05$). Superscript letters indicate: $^{a}P < 0·05$; $^{b}P < 0·01$; $^{c}P < 0·005$; $^{d}P < 0·001$. Underlined coefficients were significant also in analyses of ACF (see Appendix S2).

*The model based on ACF did not converge.

†The model included the effect of temperature in N Africa.

‡Random effects of covariates retained in the model.

d.f. = 8 and $P < 0·05$ in all cases). These random effects were therefore retained in the final models, presented in Table 2, only for these species.

The results of the analyses of CACF in relation to weather are summarized in Table 2. CACF was positively and significantly predicted by change in tail winds in N Africa for seven species, whereas this relationship was negative and significant for two species. Across species, the mean coefficient of this relationship was significantly larger than 0. However, the effect of change in tail wind in Central Italy was negative for all species and significantly so for 15 species, with the mean coefficient being significantly smaller than 0. Thus, an increase in tail wind in Central Italy led to a generalized reduction in the frequency of captures (Table 2).

The effect of change in crosswind in N Africa on CACF was significantly negative for 12 species, significantly positive for only 1, and was on average significantly negative across species. In Central Italy, a significant negative effect of change in crosswind on CACF was also observed for 14 species, with a mean coefficient significantly smaller than 0.

Change in cloud cover both in N Africa and Central Italy had on average a significant positive effect on CACF, being significantly positive for seven species in N Africa and for five species in Central Italy. One significantly negative effect, however, was found for N Africa and two for Central Italy. These negative effects were recorded for the two hirundine species (*D. urbicum* and *H. rustica*). Finally, there was an overall significantly positive effect of temperature in Central Italy on CACF, with significant positive effects for nine species and no significant negative effects. The mean effect of tail wind on CACF was larger in N Africa than in Central Italy (paired *t*-test, $t = 6·93$, d.f. = 20, $P < 0·001$). The effects of crosswind or cloud cover, however, did not differ significantly between areas (crosswind: $t = 1·00$, d.f. = 20, $P = 0·331$; cloud cover: $t = 1·34$, d.f. = 20, $P = 0·197$).

Across species, we found a negative correlation between the effects of cross- and tail wind in N Africa on CACF ($r = -0·552$, $n = 21$, $P = 0·009$) and this result held when we controlled for phylogeny ($r_{\mathrm{phyl}} = -0·512$, $P = 0·012$). This suggests that when departures of a species were negatively affected by crosswinds they were also negatively affected by head winds. If CACF of a species was strongly negatively affected by tail wind in Central Italy, it was also strongly negatively affected by crosswind in Central Italy ($r = 0·671, n = 21, P = 0·001; r_{\mathrm{phyl}} = 0·739, P < 0·001$).

When two-way interaction terms among wind components in both regions were included in the models, no significant effect was detected for any species (details not shown).

The results based on daily ACF were generally consistent with those based on CACF, although they proved to be less powerful in disclosing significant associations with meteorological variables possibly owing to the presence of seasonal trends (see Table 2 and Appendix S2).

In the models presented in Table 2, a highly significant negative autocorrelation was found between CACF observed in consecutive pairs of days (estimated covariance parameter ranging between $-0{\cdot}494$ and $-0{\cdot}264$, $Z > 5{\cdot}19$ and $P < 0{\cdot}001$ in all cases). This result implies that when an increase in capture frequency was observed between day_{i-1} and day_i, a decrease occurred between day_i and day_{i+1}.

The analyses of CACF in relation to weather were repeated while accounting for the effect of sex for 10 sexually dimorphic species (*Ficedula hypoleuca*, *H. rustica*, *L. senator*, *Oenanthe oenanthe*, *O. oriolus*, *Phoenicurus phoenicurus*, *Saxicola rubetra*, *Sylvia. atricapilla*, *Sylvia cantillans*, *Sylvia communis*; Rubolini, Spina & Saino 2004). We found a significant interaction between the effects of sex and change in crosswind at departure on CACF in *O. oenanthe* ($F_{1,756} = 4{\cdot}53$, $P = 0{\cdot}034$), with CACF of males being less negatively affected by increasing crosswinds (difference in the slopes = 1·27 (0·60)), whereas no other interaction effects emerged for the remaining species. Hence, weather had generally no differential effects on migration of males and females.

The analyses of CACF were rerun using meteorological variables at Ventotene and in Sicily, rather than in N Africa, as predictors. The fit of the models including meteorological variables in N Africa, as estimated by means of their bias-corrected Akaike information criterion (AICc) values, was better than that of the models based on data from Sicily for 17 out of the 21 species (see Appendix S4 for details and discussion).

INTERSPECIFIC VARIATION IN THE EFFECTS OF METEOROLOGICAL VARIABLES

We calculated the slopes of the relationships between CACF and change in meteorological variables for each year separately by applying autoregression analyses while including all meteorological variables entered in the models in Table 2. The 21 (species) × 12 (years) coefficients thus obtained for each variable were subjected to an analysis of covariance with species as a factor. There was a significant between-species variation in the slopes of the relationships between CACF and tail wind, and crosswind in N Africa, cloud cover in both regions, and temperature in central Italy ($F_{20,231} > 2{\cdot}06$, $P < 0{\cdot}006$ in all cases). Hence, the species differed in susceptibility to these variables. However, there was no significant between-species variation in the effect of tail wind ($F_{20,231} = 0{\cdot}765$, $P = 0{\cdot}754$) and crosswind in Central Italy ($F_{20,231} = 1{\cdot}52$, $P = 0{\cdot}075$).

RELATIONSHIPS BETWEEN THE EFFECTS OF METEOROLOGICAL VARIABLES ON CACF AND RESIDUAL FAT STORES AT STOPOVER

There was a strong positive association between the effect of tail wind in N Africa on CACF and mean fat score at Ventotene, both in correlation analyses based on raw species data and in those where we controlled for phylogeny (simple correlation: $r = 0{\cdot}701$, $n = 21$, $P < 0{\cdot}001$; $r_{\text{phyl}} = 0{\cdot}710$, $P < 0{\cdot}001$; Fig. 2). In addition, the effect of crosswind in N Africa on fat scores was negative (simple correlation: $r = -0{\cdot}520, n = 21, P = 0{\cdot}016; r_{\text{phyl}} = -0{\cdot}505, P = 0{\cdot}013$). The correlations of fat score with wind conditions or temperature in Central Italy were non-significant (details not shown).

EFFECTS OF METEOROLOGICAL VARIABLES ON CACF IN RELATION TO SPECIES MORPHOLOGY

As an index of species-specific susceptibility to weather, we used the coefficients reported in Table 2. The results of correlation analyses corrected for phylogeny are reported in Table 3 and Fig. 3.

The negative effect of crosswind in N Africa and the positive effect of temperature in Central Italy on CACF were weaker in larger than in smaller species, and these relationships held when we removed from the sample the two short-distance migrants. The positive effect of tail wind in N Africa on CACF increased in species with higher wing loading and brachial index, although only the effect of brachial index remained significant when the two short-distance migrants

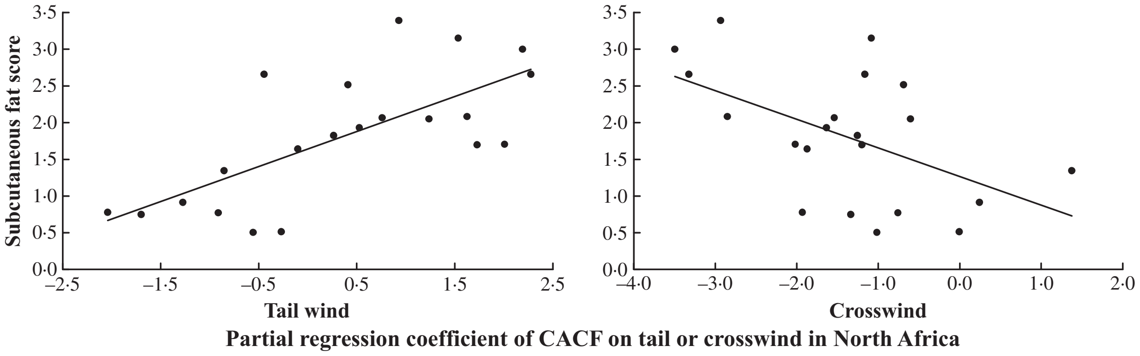

Fig. 2. Relationship between fat score and the effect of wind in N Africa on CACF.

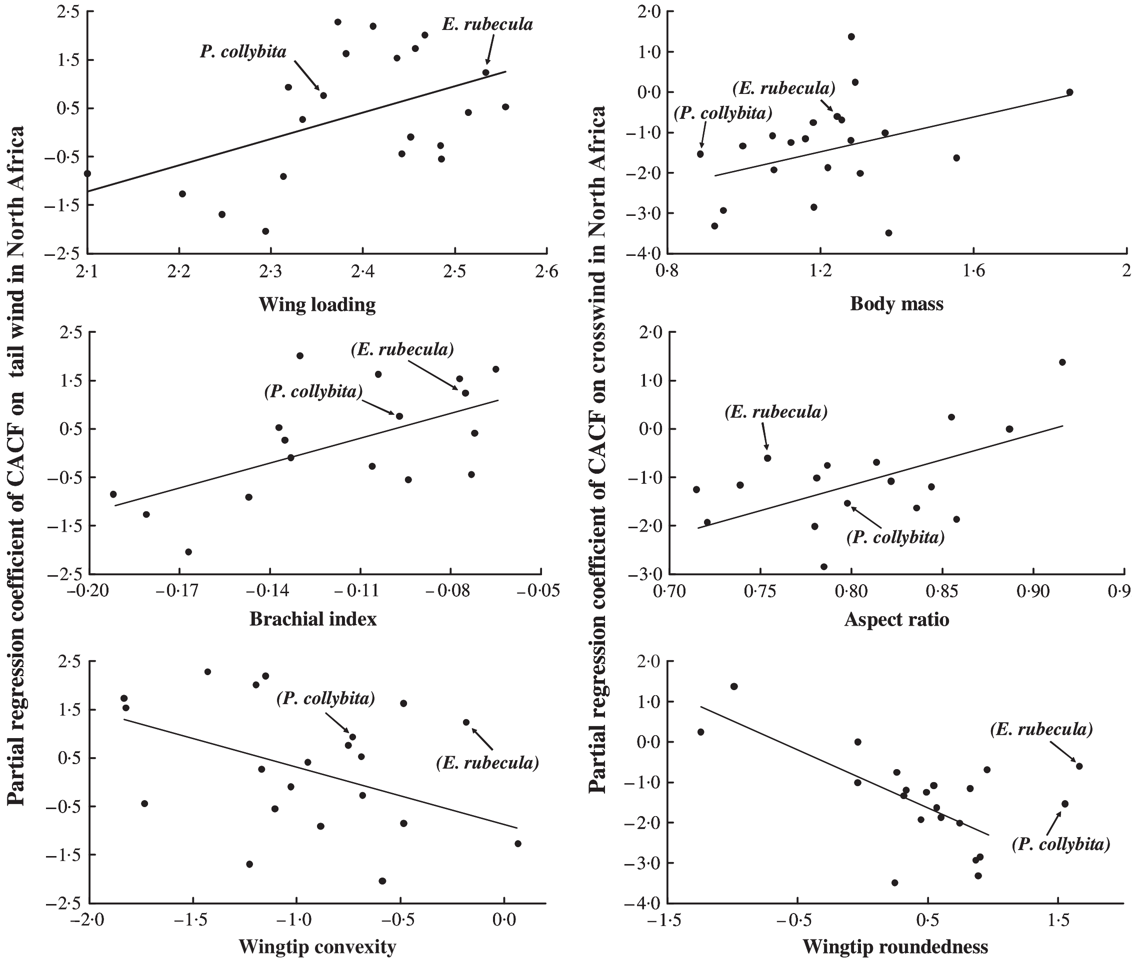

Fig. 3. Among-species relationships between the effects of wind in N Africa on CACF and morphology. Lines are fitted by simple regression analysis to data points of long-distance migratory species (i.e. excluding *Erithacus rubecula* and *Phylloscopus collybita*), as indicated by parentheses, with the exception of the relationship between the effect of tail wind and wing loading that was significant only in the analysis based on all species; this relationship was marginally non-significant ($P = 0{\cdot}052$) among long-distance migrants.

were removed from the analyses. The positive effect of tail wind declined with wing convexity, i.e. in species more adapted to migration. The negative effect of crosswind at departure was mitigated in species with high aspect ratio wings. In addition, when the two short-distance migrants were excluded, this negative effect was found to be mitigated in species with pointed wings. Hence, CACF of species with wing features associated with migration were less negatively affected by crosswinds at departure. The negative effect of tail winds in Central Italy on CACF was weaker in species with higher wing loading and brachial index, both for all species and among long-distance migrants. Crosswinds in Central Italy had an overall negative effect on CACF, but this effect was reduced in species with higher wing loading. The positive effect of temperature in Central Italy on CACF was smaller in species with larger wing convexity and in species with large aspect ratio in the analyses based on all species as well as in those including only long-distance migrants.

Simple correlation analyses without controlling for phylogeny gave results that were only partly consistent with those based on phylogenetic correction (Table 3), suggesting that a phylogenetic signal existed in the data. Although a general agreement emerged in the sign of the correlation coefficients in the two sets of analyses, some of the significant effects detected in phylogenetic analyses disappeared in simple correlation analyses and *vice versa*.

Susceptibility to weather could vary among species if species that migrate relatively late face on average better weather and/or a relatively short breeding season prompts these species to migrate faster. However, we found no relationship between susceptibility to wind or temperature and median capture date (computed as the mean of the yearly median capture dates) in simple correlation analyses as well as in correlation analyses controlling for phylogeny (unsigned $r < 0{\cdot}291$, $n = 21$, $P > 0{\cdot}200$; unsigned $r_{\text{phyl}} < 0{\cdot}236$, $P > 0{\cdot}27$).

Discussion

We analysed the covariation between meteorological conditions at staging or wintering sites in N Africa and en route, and capture frequencies at a stopover site located at the end of crossing of the Mediterranean for 21 species of passerines during spring migration. We then investigated how the effects of meteorological conditions on migration decisions varied in

Table 3. Phylogenetic correlation coefficients between the effects of wind and temperature on change in capture frequencies of the different species, and their morphological characters

	Tail wind N Africa	Crosswind N Africa	Tail wind Central Italy	Crosswind Central Italy	Temperature Central Italy
All species					
Body mass*	−0·119	**0·453**^{a}	0·285	0·339	**−0·443**^{a}
Wing loading*	**0·461**^{a}	−0·198	**0·566**^{c}	**0·444**^{a}	0·037
Aspect ratio†	−0·016	**0·576**^{b}	0·249	0·092	**−0·561**^{a}
Brachial index†	**0·581**^{b}	−0·157	**0·464**^{a}	0·209	0·106
Wing roundedness*	0·345	−0·345	0·157	0·029	−0·043
Wing convexity*	−0·291	0·323	0·029	0·082	**−0·444**^{a}
Long-distance migrants					
Body mass‡	−0·105	**0·488**^{a}	0·418	0·391	**−0·467**^{a}
Wing loading‡	0·424	−0·304	**0·549**^{b}	**0·448**^{a}	0·052
Aspect ratio§	0·060	**0·672**^{c}	0·301	0·119	**−0·574**^{a}
Brachial index§	**0·519**^{a}	−0·307	**0·401**^{a}	0·207	0·056
Wing roundedness‡	0·299	**−0·680**^{d}	−0·046	−0·087	−0·041
Wing convexity‡	**−0·438**^{a}	0·261	−0·060	0·029	**−0·502**^{a}

Bolded values were statistically significant ($P < 0{\cdot}05$). Underlining indicates that the relationship was statistically significant ($P < 0{\cdot}05$) in simple correlation analyses. Superscript letters indicate: $^{a}P < 0{\cdot}05$; $^{b}P < 0{\cdot}01$; $^{c}P < 0{\cdot}005$; $^{d}P < 0{\cdot}001$. $*n = 21$; $†n = 17$; $‡n = 19$; $§n = 15$ species.

relation to species morphology. In Table 1, we provide a synopsis of the observed and predicted patterns of variation in daily changes in capture frequencies in relation to weather and of variation in the effects of weather in relation to species morphology. The effects of meteorological variables, and particularly those recorded at the putative departure area in N Africa, were mostly consistent with our expectations based on previous knowledge and theoretical arguments on migration behaviour, lending support to the idea that capture frequencies positively correlate with the actual number of migrating birds.

EFFECTS OF WIND

In agreement with our predictions, increasing head and crosswinds in N Africa had average negative effects on capture frequencies at Ventotene, strongly suggesting that the number of individuals leaving Africa decreased under head- and crosswinds. The effect of crosswind was consistent across species, the significant relationships being generally negative. However, consistency of tail compared to crosswind effects in N Africa was smaller, though in most cases (seven of nine) the significant relationships were positive. The sign of the effect of crosswind was positive only for the two hirundine species, whose CACF were reduced by tail winds. This different response to weather by swallows is consistent with previous findings (Elkins 1983).

Extensive interspecific variation in susceptibility of measures of migratory intensity (either at departure or stopover) to tail winds is not a novel finding (e.g. Alerstam 1978) and has proven to be difficult to explain. As we discuss later, we show here for the first time that part of this variation can be explained by species morphology. Species whose departures were more negatively influenced by head winds were also more negatively influenced by crosswinds. However, the effects of tail winds were smaller than those of crosswinds (paired *t*-test on unsigned values; $t = 2{\cdot}27$, d.f. $= 20$, $P = 0{\cdot}034$), suggesting that crosswinds were more powerful than tail winds in determining departure decisions. Diverse arguments can be invoked to explain the effects of wind on departures. First, the speed of wind components along flight direction influences the cost of transport as well as the costs to compensate for lateral drift, which increases with crosswinds (see Newton 2008). Moreover, crosswinds can increase the risk that migrants are blown off to suboptimal routes. The negative effect of tail wind in Central Italy on stopover was also consistent with the expectation, based on the assumption that birds tend to minimize migration duration because of the fitness benefits of early arrival. Birds approaching Central Italian coasts under tail winds may have more reserves to stay aloft and decide to continue their flight to exploit favourable winds ahead.

Several interpretations can also be invoked to explain the negative effect of strong crosswind in Central Italy on stopovers, which was opposite to our prediction. First, migrants deviate to some extent from their SW–NE route when facing strong crosswinds and turn to more favourable flight directions. Second, while in N Africa, migrants react to local meteorological variables that predict conditions they could encounter ahead, if departing, by exploiting clues (e.g. short-term change in barometric pressure) that we did not consider. Third, strong crosswind close to Italian coasts may be associated with progressively deteriorating weather conditions, prompting migrants to proceed along their route to escape locally worsening conditions.

Contrary to our prediction, we found remarkably consistent effects of weather on capture frequencies of either sex. This suggests that protandrous migration and arrival (Møller 2004; Rubolini, Spina & Saino 2004; Rainio *et al.* 2007) is not explained by higher susceptibility of females to meteorological conditions.

Interestingly, across species the amount of fat stores increased with increasing positive effect of tail wind and increasing negative effect of crosswind in N Africa on departures. Hence, species that were more susceptible to wind conditions upon departure managed to arrive with larger fat stores on the other side of the Mediterranean. This result obviously suggests that by exploiting favourable winds migrants can markedly reduce the energy costs of migration by flapping flight.

EFFECTS OF TEMPERATURE AND CLOUD COVER

The effect of temperature in Central Italy on stopover was positive. Previous studies investigating the effects of temperature on the number of migrants stopping over obtained mixed evidence, which may be explained by seasonal, topographical and species-specific differences (Alerstam 1978; see Richardson 1990; Newton 2008). The generalized lack of significant effects of temperature in N Africa (with one exception) contrasts with the expectation from previous evidence of temperature effects on departures (Richardson 1990; Newton 2008) and we have no clear explanation for this. We did not formulate any explicit predictions about the effect of cloud cover. However, we found an overall positive effect of cloud cover on stopover. The positive effect in Central Italy could arise because some species may decide to land at the first suitable staging site when an overcast sky hinders navigation and visibility or is associated with rainfall. The effect of cloud cover in Central Italy was all but consistent in strength among species (though being significantly positive overall), suggesting that they may migrate at different altitudes. The significant positive effects of cloud cover in N Africa, however, is surprising, as most previous studies have suggested that cloudy sky inhibits departures (Cochran & Kjos 1985).

A striking pattern that emerged from models of CACF in relation to meteorological effects is the negative autocorrelation of changes in capture frequencies between pairs of consecutive days. This pattern could arise because the larger the number of birds leaving N Africa on one day is, the fewer migrants are left to depart the following day (see Alerstam 1978). This result may provide an insight into the patterns of arrival of migrants to their staging areas in N Africa. If a regular influx of migrants to N Africa occurs, we should expect no negative autocorrelation between changes in capture frequencies at Ventotene between consecutive pairs of days because newcomers replace individuals that have just left. Thus, negative autocorrelations may reflect pulses of arrivals to N Africa. At present, however, this is just a speculation, as we do not have quantitative information to support this interpretation.

Importantly, the effects of meteorological conditions on the number of migrants captured at Ventotene were generally consistent within species among years. In addition, the slopes of the relationships for most meteorological variables computed for individual years significantly differed among species. Hence, individual species seem to react in similar ways to weather across years and differ in their response to weather conditions. This evidence prompted us to investigate which species' morphological features predict their response to weather.

COMPARATIVE ANALYSIS OF WEATHER EFFECTS IN RELATION TO SPECIES MORPHOLOGY

We used the slopes of the relationships between CACF and meteorological variables (see Table 2) to analyse interspecific variation of response to weather in relation to body size and wing features. Most migrants are believed to at least partly compensate for lateral drift by modifying their heading (Newton 2008). The compensation angle decreases with flight speed which, in turn, scales positively with body size (Newton 2008). Hence, the compensation angle to correct for lateral drift, and thus flight costs, may be smaller for large species. This may explain why crosswinds had weaker negative effects on departure of large species.

Longer wings with high aspect ratio have evolved among migratory species/populations (Lockwood, Swaddle & Rayner 1998). High aspect ratio can reduce the cost of transport and thus increase non-stop flight range (Lockwood, Swaddle & Rayner 1998). The more negative effect of crosswinds in N Africa on departures of LM species is therefore consistent with the prediction, because departure of LM should be more reduced by unfavourable crosswinds. In addition, LM species should be more susceptible to temperature as a factor influencing availability of food for refuelling at stopover, if they are less adapted to sustain prolonged migratory flights. The negative correlation between aspect ratio (which is smaller in LM species) and the effect of temperature in Central Italy therefore also fits the expectation because LM species may be more prone to stopover and refuel at relatively high temperatures, when insect food may be more abundant although this interpretation is merely speculative. Similar arguments can be applied to interpret the correlation between the effects of wingtip convexity (a feature more expressed in MM species) and temperature in Central Italy. The negative correlation between convexity and the (overall positive) effect of tail wind in N Africa, or that between wingtip roundedness (a feature less expressed in MM species) and the (overall negative) effect of crosswind on departures are also consistent with the expectation because they suggest that departures of LM species are more increased by tail winds and more decreased by crosswinds compared to MM species.

Wing loading may be smaller in MM than LM species/populations (Calmaestra & Moreno 2001; Fiedler 2005; but see Lockwood, Swaddle & Rayner 1998; Norberg 2002). The positive correlation between the effect of tail wind in N Africa on departures and wing loading corroborates our expectation that tail winds favour more the LM species. The relative length of the distal wing segments, as reflected by the brachial index, has been suggested to increase with migration distance (Winkler & Leisler 1992). Larger positive effect of tail wind in N Africa on species with large brachial index is thus consistent with the expectation that departure by LM species is favoured under tail winds.

Because the slopes of the annual relationships between CACF and wind conditions in Central Italy did not vary among species, we will not discuss here the correlation between the effect of wind in Central Italy and wing morphology.

Present results confirm the importance of meteorological conditions in determining departure of migrants from staging sites and stopover. Differently from most previous studies, however, the effect of weather conditions on either side of an ecological barrier was investigated while controlling for concomitant effects on the other side. As we expected, susceptibility to weather conditions was smaller in species whose wing morphology is more typical of migratory species. These novel findings have several implications for the study of migration and the consequences of climatic change on bird phenology. First, the interpretation of differential effects of weather on migration among species should take morphology into account. Second, it can be predicted that species best suited for migration should show smaller phenotypic plasticity in migration timing because they are less affected by meteorological conditions en route. The phenology of long-distance migrants has been shown to have responded less to climatic change than that of short-distance migrants (Lehikoinen, Sparks & Zalakevicius 2004; Rubolini *et al.* 2007). Present results may suggest that smaller susceptibility of migration timing to climate change partly depends on decisions of long-distance migrants being less susceptible to weather.

In conclusion, we showed that the number of migratory birds captured at the end of an ecological barrier can be predicted by meteorological conditions both at departure sites in N Africa and at the site of capture. The effects of weather, although being consistent between sexes and among years for any given species, were found to vary among species and part of this variation was found to be accounted for by variation in body size and wing morphology. Species with wing features typical of migratory species were found to be less susceptible to meteorological conditions. This finding may imply that morphology may predict species' ability to respond both evolutionarily and phenotypically to changing climatic conditions by adjusting their migration schedules.

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References

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehikoinen, E. (2004) Variation in climate warming uncouples arrival and breeding dates. *Global Change Biology*, **10**, 1610–1617.

Åkesson, S., Alerstam, T. & Hedenström, A. (1996) Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *Journal of Avian Biology*, **27**, 95–102.

Åkesson, S. & Hedenström, A. (2000) Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology*, **3**, 140–144.

Åkesson, S., Walinder, G., Karlsson, L. & Ehnbom, S. (2002) Nocturnal migratory flight initiation in reed warblers: effect of wind on orientation and timing of migration. *Journal of Avian Biology*, **33**, 349–357.

Alerstam, T. (1978) Analysis and a theory of visible bird migration. *Oikos*, **30**, 273–349.

Alerstam, T. (1981) The course and timing of bird migration. *Animal Migration* (ed. D.J. Aidley), pp. 9–54. Cambridge University Press, Cambridge.

Alerstam, T. (1990) *Bird Migration*. Cambridge University Press, Cambridge.

Alerstam, T. & Hedenström, A. (1998) The development of bird migration theory. *Journal of Avian Biology*, **29**, 343–369.

Alerstam, T., Hedenström, A. & Åkesson, S. (2003) Long distance migration: evolution and determinants. *Oikos*, **103**, 247–260.

Alerstam, T. & Lindström, Å. (1990) Optimal migration: the relative importance of time, energy and safety. *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 331–351. Springer, Berlin.

Bairlein, F. & Hüppop, O. (2004) Migratory fuelling and global climate change. *Advances in Ecological Research*, **35**, 33–47.

Berthold, P. (1996) *Control of Bird Migration*. Chapman and Hall, London.

Berthold, P. (2000) *Vogelzug. Eine aktuelle Gesamtübersicht*. Wissenschaftliche Buchgesellschaft, Darmstadt.

Biebach, H. (1990) Strategies of trans-Saharan migrants. *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 352–367. Springer, Berlin.

Busse, P. (1974) Biometrical methods. *Notatki Ornitologiczne*, **15**, 114–126.

Calmaestra, R.G. & Moreno, E. (2001) A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in Passeriformes. *Ardea*, **89**, 405–414.

Casement, M.B. (1966) Migration across the Mediterranean observed by radar. *Ibis*, **108**, 461–491.

Cochran, W.W. & Kjos, C.J. (1985) Wind drift and migration of thrushes: a telemetry study. *Bullettin of Illinois Natural History Survey*, **33**, 297–330.

Cochran, W.W. & Wikelski, M. (2005) Individual migratory tactics of the New World Catharus thrushes. *Birds of Two Worlds* (eds R. Greenberg & P.P. Marra), pp. 274–289. John Hopkins University Press, Baltimore.

Coppack, T. & Pulido, F. (2004) Photoperiodic responses and the adaptability of avian life cycles to environmental change. *Advances in Ecological Research*, **35**, 131–150.

Cramp, S. (1998) *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press, Oxford.

Dingle, H. (1996) *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford.

Egbert, J.R. & Belthoff, J.R. (2003) Wing shape in house finches differs relative to migratory habit in eastern and western North America. *Condor*, **105**, 825–829.

Elkins, N. (1983) *Weather and Bird Behaviour*. Poyser, Calton.

Erni, B., Liechti, F. & Bruderer, B. (2005) The role of wind in passerine autumn migration between Europe and Africa. *Behavioral Ecology*, **16**, 732–740.

Fiedler, W. (2005) Ecomorphology of the external flight apparatus of blackcaps (*Sylvia atricapilla*) with different migration behavior. *Annals of the New York Academy of Sciences*, **1046**, 253–263.

Garamszegi, L.Z., Biard, C., Eens, M., Møller, A.P., Saino, N. & Surai, P.F. (2007) Maternal effects and the evolution of brain size in birds: overlooked developmental constraints. *Neuroscience and Biobehavioral Reviews*, **31**, 498–515.

Grattarola, A., Spina, F. & Pilastro, A. (1999) Spring migration of the Garden Warbler (*Sylvia borin*) across the Mediterranean Sea. *Journal of Ornithology*, **140**, 419–430.

Gwinner, E. (1996) Circadian and circannual programmes in avian migration. *Journal of Experimental Biology*, **199**, 39–48.

Hedenström, A. (1993) Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **342**, 353–361.

Hedenström, A. (2008) Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **363**, 287–299.

Hedenström, A. & Alerstam, T. (1998) How fast can birds migrate? *Journal of Avian Biology*, **29**, 424–432.

Hedenström, A. & Møller, A.P. (1992) Morphological adaptations to song flight in passerine birds: a comparative study. *Proceedings of the Royal Society of London, B: Biological Sciences*, **247**, 183–187.

Hedenström, A. & Pettersson, J. (1986) Differences in fat deposits and wing pointedness between male and female willow warblers caught on spring migration at Ottenby SE Sweden. *Ornis Scandinavica*, **17**, 182–185.

Houston, A.I. (1998) Models of optimal avian migration: state, time and predation. *Journal of Avian Biology*, **29**, 395–404.

Hüppop, O. & Winkel, W. (2006) Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *Journal of Ornithology*, **147**, 344–353.

Jenni, L., Jenni-Eiermann, S., Spina, F. & Schwabl, H. (2000) Regulation of protein breakdown and adrenocortical response to stress in birds during migratory flight. *American Journal of Physiology*, **278**, R1182–R1189.

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, E., Edvardsen, A., Solvang, R. & Stenseth, N.C. (2007) Response to comment on ''Rapid advance of spring arrival dates in long-distance migratory birds''. *Science*, **315**, 598.

Knudsen, E., Lindén, A., Ergon, T., Jonzén, N., Vik, J.O., Knape, J., Røer, J.E. & Stenseth, N.C. (2007) Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Climate Research*, **35**, 59–77.

Lehikoinen, E., Sparks, T.H. & Zalakevicius, M. (2004) Arrival and departure dates. *Advances in Ecological Research*, **35**, 1–31.

Leisler, B. & Winkler, H. (2003) Morphological consequences of migration in passerines. *Bird Migration* (eds P. Berthold, E. Gwinner & E. Sonnenschein), pp. 175–176. Springer Verlag, Berlin.

Liechti, F. (2006) Birds: blowin' by the wind? *Journal of Ornithology*, **147**, 202–211.

Liechti, F. & Bruderer, B. (1998) The relevance of wind for optimal migration theory. *Journal of Avian Biology*, **29**, 561–568.

Liechti, F., Hedenström, A. & Alerstam, T. (1994) Effects of sidewinds on optimal flight speed of birds. *Journal of Theoretical Biology*, **170**, 219–225.

Lislevand, T., Figuerola, J. & Székely, T. (2007) Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*, **88**, 1605.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. (1998) Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology*, **29**, 273–292.

Marchetti, K., Price, T. & Richman, A. (1995) Correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. *Journal of Avian Biology*, **26**, 177–181.

Møller, A.P. (2004) Protandry, sexual selection and climate change. *Global Change Biology*, **10**, 2028–2035.

Møller, A.P., de Lope, F. & Saino, N. (1995) Sexual selection in the barn swallow *Hirundo rustica* .4. Aerodynamic adaptations. *Journal of Evolutionary Biology*, **8**, 671–687.

Mönkkönen, M. (1995) Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology*, **9**, 520–528.

Morbey, Y.E. & Ydenberg, R.C. (2001) Protandrous arrival timing to breeding areas: a review. *Ecology Letters*, **4**, 663–673.

Newton, I. (2008) *The Migration Ecology of Birds*. Academic Press, London.

Nisbet, I.C.T. & Drury Jr, W.H. (1968) Short-term effects of weather on bird migration: a field study using multivariate statistics. *Animal Behaviour*, **16**, 496–530.

Norberg, U.M. (1979) Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest and the treecreeper in relation to locomotor pattern and feeding station selection. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **287**, 131–165.

Norberg, U.M. (1990) *Vertebrate Flight*. Springer Verlag, Heidelberg.

Norberg, U.M. (2002) Structure, form and function of flight in engineering and the living world. *Journal of Morphology*, **252**, 52–81.

Nudds, R.L., Dyke, G.J. & Rayner, J.M.V. (2004) Forelimb proportions and the evolutionary radiation of Neornithes. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**(suppl. 5), 324–327.

Nudds, R.L., Dyke, G.J. & Rayner, J.M.V. (2007) Avian brachial index and wing-kinematics: putting movement back into bones. *Journal of Zoology*, **272**, 218–226.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Pennycuick, C.J. (1975) Mechanics of Flight. *Avian Biology*, Vol. 5 (eds D.S. Farner & J.R. King), pp. 1–75. Academic Press, London.

Pilastro, A. & Spina, F. (1997) Ecological and morphological correlates of residual fat reserves in passerine migrants at their spring arrival in southern Europe. *Journal of Avian Biology*, **28**, 309–318.

Pilastro, A., Baccetti, N., Massi, A., Montemaggiori, A., Roselli, A. & Spina, F. (1995) Direction of migration and fat consumption rate estimates in spring migrating garden warblers (*Sylvia borin*). *Ricerche di Biologia della Selvaggina*, **12**, 435–445.

Rainio, K., Tøttrup, A.P., Lehikoinen, E. & Coppack, T. (2007) Effects of climate change on the degree of protandry in migratory songbirds. *Climate Research*, **35**, 107–114.

Rayner, J.M.V. (1988) Form and function in avian flight. *Current Ornithology*, **5**, 1–66.

Rayner, J.M.V. (1996) Biomechanical constraints on size in flying vertebrates. *Miniature Vertebrates* (ed. P.J. Miller), pp. 83–109. Symposia of the Zoological Society of London 69. Oxford University Press, Oxford.

Richardson, W.J. (1990) Timing of bird migration in relation to weather: updated review. *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 78–101. Springer, Berlin.

Rubolini, D., Spina, F. & Saino, N. (2004) Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology*, **15**, 592–601.

Rubolini, D., Møller, A.P., Rainio, K. & Lehikoinen, E. (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, **35**, 135–146.

Saino, N., Rubolini, D., Jonzén, N., Ergon, T., Montemaggiori, A., Stenseth, N.C. & Spina, F. (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Climate Research*, **35**, 123–134.

Senar, J.C., Lleonart, J. & Metcalfe, N.B. (1994) Wingshape variation between resident and transient wintering Siskins *Carduelis spinus*. *Journal of Avian Biology*, **25**, 50–54.

Spina, F., Massi, A., Montemaggiori, A. & Baccetti, N. (1993) Spring migration across central Mediterranean: general results from the 'Progetto Piccole Isole'. *Vogelwarte*, **37**(Suppl.), 1–94.

Stutchbury, B.J.M., Tarof, S.A., Done, T., Gow, E., Kramer, P.M., Tautin, J., Fox, J.W. & Afanasyev, V. (2009) Tracking long-distance songbird migration by using geolocators. *Science*, **323**, 896.

Thorup, K., Alerstam, T., Hake, M. & Kjellén, N. (2006) Traveling or stopping of migrating birds in relation to wind: an illustration for the osprey. *Behavioral Ecology*, **17**, 497–502.

Winkler, H. & Leisler, B. (1992) On the ecomorphology of migrants. *Ibis*, **134**(Suppl. 1), 21–28.

Yaukey, P.H. & Powell, S.C. (2008) Numbers of migratory birds stopping over in New Orleans, Louisiana, USA in relation to weather. *The Wilson Journal of Ornithology*, **120**, 286–295.

Zehnder, S., Åkesson, S., Liechti, F. & Bruderer, B. (2001) Nocturnal autumn bird migration at Falsterbo, South Sweden. *Journal of Avian Biology*, **32**, 239–248.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Correlation of meteorological variables among areas and regions, altitudinal pressure levels and times of the day.

Appendix S2. Analyses based on absolute capture frequencies.

Appendix S3. Sources of phylogenetic information and phylogenetic analysis methods.

Appendix S4. Analyses of CACF based on meteorological data at Ventotene and in Sicily.