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Flexible tuning of departure decisions in response to weather in black redstarts *Phoenicurus ochruros* migrating across the Mediterranean Sea

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Departure and stopover decisions are crucial for a successful migration. Such decisions are modulated by a complex interplay between endogenous (physiological state) and external factors, such as weather (e.g. wind) and geography (ecological barriers). In this study of the black redstart *Phoenicurus ochruros*, a short-distance migrant passerine, we investigate the effect of weather, as gauged by tailwind and crosswind conditions, rainfall, temperature, and barometric pressure, on departures from a stopover site in the central Mediterranean Sea, off the western coast of Italy (Ventotene island), during both spring and autumn migration. We found that stopover duration was longer in birds arriving with lower fat stores, and that birds departed with generally favourable weather conditions (favourable tailwinds, weak or no crosswinds, low rainfall, high temperatures, and high pressure). However, the effects of weather on departure decisions were stronger in autumn: this could be related to 1) a seasonal difference in selection pressures for early arrival at the goal areas, that are expected to be stronger in spring than in autumn or 2) a difference in the residual extent of sea crossing since, in autumn, birds are confronted with a much longer non-stop sea crossing (at least 300 km) than in spring (~50 km). In spring we also found males to leave the study site under less favourable tailwinds than females, and adults to leave with more favourable tailwinds than young. Our findings indicate that departure decisions are flexible and differently affected by weather in different seasons, either because of seasonal effects or because of different distances to be covered before reaching the next stopover site. Moreover, our study suggests that sex-specific weather selectivity should be regarded among the proximate factors affecting differential spring migration of either sex.

During migratory flights, birds may be forced to stopover in unfamiliar habitats with unpredictable food availability and predation risk, and may face inclement weather conditions (Alerstam and Lindström 1990, Weber et al. 1999, 2004). Natural selection on migratory performance is likely to be intense (Newton 2008): it has been estimated that >85% of apparent annual mortality of adult birds takes place during migration (Sillett and Holmes 2002). A significant fraction of the migration-related mortality may result from harsh weather encountered during ecological barrier crossing or during stopover (Erni et al. 2005, Liechti 2006, Newton 2008, Strandberg et al. 2009). Most of the time and energy involved in migration are spent during stopover (Hedenström and Alerstam 1997, Wikelski et al. 2003), and stopover and refuelling decisions are crucial determinants of a successful migration (Berthold 2001, Newton 2008). On the whole, migration may induce a cascade of effects on physiology and general state eventually affecting subsequent reproductive events (Bauchinger et al. 2008, Strandberg et al. 2009), and possibly population dynamics via carry-over processes (Newton 2008).

Weather conditions are well known to affect stopover decisions of migrants (Able 1973, Richardson 1990, Liechti and Bruederer 1998, Åkesson and Hedenström 2000, Weber and Hedenström 2000, Dänhardt and Lindström 2001, Erni et al. 2002, 2005, Schaub et al. 2004, Dierschke 2006, Tsvey et al. 2007, Saino et al. 2010a). Theoretical studies suggest that migrants should scale selectivity of weather conditions to the distance to be covered in order to reach the next stopover site (Liechti and Bruderer 1998, Erni et al. 2005, Liechti 2006), i.e. the longer the distance, the greater the effect of weather on departures should be. However, empirical tests of this prediction are scanty (Dierschke and Delingat 2001, Navedo et al. 2010, see also Meyer et al. 2000). It has been demonstrated that rain, temperature, cloud cover and atmospheric pressure can affect departure decisions, though generally wind velocity and direction are the weather parameters exerting the strongest influence on migrants (Alerstam 1978, 1979, Liechti and Bruderer 1998, Åkesson and Hedenström 2000, Dierschke and Delingat 2001, Dierschke 2006, Liechti 2006, Mellone et al. 2011). Indeed, wind velocity is commonly of the same order of magnitude of flight velocity in migratory birds (Liechti and Bruderer 1998), and can either severely increase or strongly decrease the energetic costs of transportation, depending on direction (Liechti 2006). In addition, in order to correctly reach destination, migrants must often face the effects of lateral wind drift, which can displace flight paths away from the correct route. This task can be achieved through drift compensation, which can also significantly increase the cost of transportation. It is therefore expected that birds will be selected to perceive wind conditions and appropriately react to them, by adjusting stopover and departure decisions accordingly, in order to profit from favourable winds (usually moderate tailwinds) and/or to avoid head and crosswinds (Cochran and Wikelski 2005, Liechti 2006). Indeed, studies of migratory intensity, as quantified by radar observations or bird ringing activities, documented that birds do react to wind conditions in the predicted way, as head and crosswinds tend to promote stopover, whereas tailwinds tend to promote departures (Alerstam 1978, Richardson 1990, Liechti 2006, Saino et al. 2010a; review in Newton 2008). Similarly, studies of individually marked birds, carried out either through radio tracking or colour ringing to monitor stopover behaviour and departure decisions have shown that, among nocturnal migrants, wind conditions on the evening of departure were generally more favourable than those of the preceding evening(s) (Åkesson and Hedenström 2000, Dänhardt and Lindström 2001, Klaassen et al. 2004). Most of these studies considered only the effects of tail- or headwinds (Fransson 1998, Åkesson and Hedenström 2000, Dänhardt and Lindström 2001, Dierschke and Delingat 2001, Schaub et al. 2004, Tsvey et al. 2007), whereas the effects of crosswinds were much less investigated (Cochran and Wikelski 2005, Liechti 2006, Klaassen et al. 2011).

A significant limit of many previous studies investigating stopover behaviour and departure decisions of migrants is the inability to analyse whether any effect of weather varied according to age and sex. This is mostly because of the limited sample sizes, as well as because many species cannot readily be aged/sexed in the field. Age is likely to be an important determinant of how individuals react to variation in extrinsic conditions, including weather, either because of morphological constraints (juveniles of many species may have a lower flight efficiency because of a less aerodynamic wing shape; Pérez-Tris and Telleria 2001, Mila et al. 2008) or because of juveniles' lower foraging ability or social rank (Woodrey and Moore 1997, Heise and Moore 2003, Moore et al. 2003), which may hamper fuel accumulation. Moreover, the relative fitness benefits and costs of early arrival to the breeding grounds may differ between the sexes during the pre-breeding migration, commonly leading to earlier migration and arrival of males relative to females (i.e. protandry; Kissner et al. 2003, Rubolini et al. 2004, Tøttrup and Thorup 2008, Saino et al. 2010b; review in Morbey and Ydenberg 2001). Among the proximate mechanisms leading to protandry, differential selectivity of the sexes to en route weather conditions has received little attention (Coppack and Pulido 2009; but see Saino et al. 2010a). Although previous studies carried out under controlled conditions have shown no sex differences in stopover behaviour, thus suggesting that differences in timing at arrival are more likely to originate from different onset of migration of males and females from the wintering grounds or from at least partial segregation of the wintering ranges (Coppack and Pulido 2009, Spottiswoode and Saino 2010), the possibility indeed exists that males and females respond differently to en route variation in weather conditions.

We studied the stopover behaviour of the black redstart *Phoenicurus ochruros* on a central Mediterranean island (Ventotene, off the coast of southern Italy) during autumn (post-breeding) and spring (pre-breeding) migration in relation to weather conditions, while accounting for potential counfounding effects of variation in stopover site quality (both within- and between-seasons) by standardizing refuelling opportunities via food provisioning (see Methods). We considered several weather parameters that may affect departure decisions, including wind (both tailwinds and crosswinds). We formulated the general prediction that birds should depart from Ventotene with more favourable weather (i.e. tailwinds, weak crosswinds, no rainfall, high or rising temperature, and high pressure), and investigated whether the selectivity of weather conditions at departure differed between seasons, which may occur owing to e.g. differences in the distance to be covered before safely reaching the next stopover site (see Methods) or seasonal differences in selection pressures towards early arrival to target areas, that are expected to be stronger in spring than autumn (Newton 2008). We also explored whether weather effects differed according to age classes (both seasons) and sexes (spring). During spring, sex differences in selectivity of weather conditions at departure may be expected because selection pressures for early arrival to the breeding grounds are generally stronger in males than females (Morbey and Ydenberg 2001, Newton 2008). Males may thus be less sensitive than females to unfavourable weather conditions at departure. Finally, we analysed variation in stopover duration in relation to season, arrival date, fuel load, age and sex. We formulated the general prediction that lean birds should be more likely to stopover at Ventotene than fat ones, based both on evidence from the same study area (Goymann et al. 2010, Tenan and Spina 2010), as well as from other studies (Jenni and Schaub 2003).

Methods

Study species, site and general protocols

The black redstart is an insectivorous short-distance migrant breeding widely across Europe (Cramp 1998). Northern populations are mostly composed of migrants that winter within the Mediterranean basin, including north Africa (Cramp 1998), and recoveries indicate a central European origin of the migrants that cross Italy (Spina and Volponi 2008). The black redstart is a nocturnal migrant (Berthold 1983) moving across Italy in early spring (mainly March) and late autumn (October–November) (Pedrini et al. 2008, Spina and Volponi 2008). The species appears proterandric during spring migration, with males migrating 10 d before females (unpubl.) (but see Macchio et al. 1999).

The study was conducted on the island of Ventotene (40°48′N, 13°25′E), a small (124 ha) island located ca 50 km off the coast of central Italy in the Tyrrhenian Sea (Fig. 1). In autumn, landbirds rest on Ventotene before embarking on the crossing of the sea stretch separating the island from Sicily and North Africa, with a non-stop flight between 300 and 600 km. On the other hand, during spring birds arrive on the island after the same non-stop crossing of the Mediterranean Sea, and make only a very short stopover before continuing their trip towards the breeding areas (it was estimated that 97% of birds landing on Ventotene are transients stopping over only for a few hours; Tenan and Spina 2010, see also Goymann et al. 2010). Thus, the position of Ventotene with respect to the extent of sea crossed by redstarts during migration differs markedly between spring and autumn (Fig. 1). Although this fact may result in a bias towards leaner birds stopping over at Ventotene in spring vs autumn, this does not appear to be the case in the present sample, as can be judged from the very similar mean fat score of birds trapped during both seasons (Table 2).

The study site was located on the island's northernmost tip, characterized by Roman ruins within a rocky environment that makes it a highly attractive habitat for black redstarts. The study site covers ca 0.5 ha and observations were performed all day long from a vantage point, with the aid of binoculars and telescopes, by two observers. The study was carried out during spring (7 March–7 April) and autumn (14 October–15 November) 2007. Mealworms *Tenebrio molitor* were provided continuously from 9 bowls, well scattered over the 0.5 ha ruins, located at the same

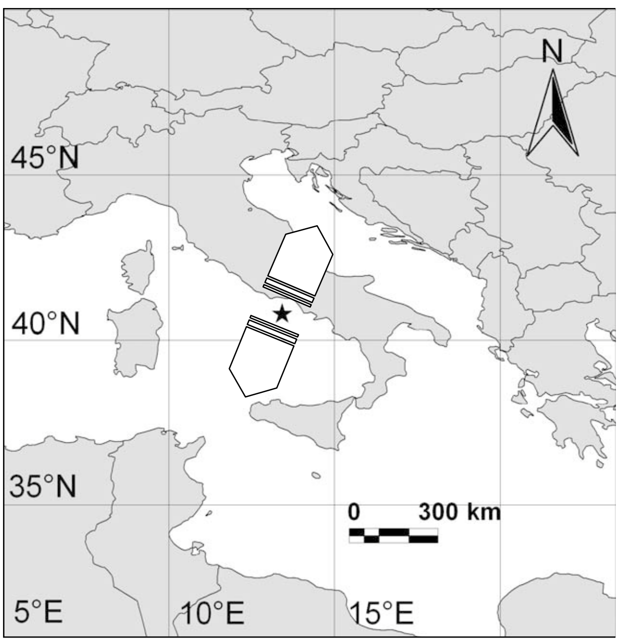

Figure 1. Map showing the location of Ventotene island (star), off the coast of southern Italy, within the context of the hypothesized migratory route of black redstarts during spring (arrow pointing NNE) and autumn (arrow pointing SSW) migration.

place during both seasons, in order to stimulate settlement of redstarts at the study site and maximise the chances of resighting marked birds. Importantly, food provisioning allowed us to standardize quality of the study site in terms of refuelling opportunities both within and between seasons: despite this procedure is expected to affect the natural stopover patterns at Ventotene, continuous food provisioning allowed us to minimize the possibility that birds left the study site because of poor feeding opportunities, while at the same time maximising chances that departures occurred mainly because of motivation to resume migration or variation in weather conditions, which was the focus of our study. Though we did not make standardised behavioural observations, levels of territorial aggression at the bowls were very low, and often up to 4 birds gathered around bowls to feed without any apparent interaction. Moreover, bowls were well scattered through the area, so that birds could easily switch from one bowl to the other in case of disputes. During the entire study period, only two males managed to take possession of a given bowl, but chased away only few of the conspecifics coming to feed there. Stopover of redstarts was not disturbed by interference from other species, since very few ecologically similar migrants (e.g. wheatears *Oenanthe oenanthe*) occurred at the study site during the migration period of black redstarts.

Birds were captured by baited cage traps (11–12 traps operating simultaneously) during the whole day, except for the two hours before sunset, that were dedicated exclusively to observations. All the traps were continuously monitored and birds were immediately taken out of the trap, measured and quickly released. For each individual, we recorded standard biometrics (third primary feather length, tarsus length, body mass) and fat score (on a 0–8 scale, according to Kaiser 1993). Age and sex were determined following Svensson (1992) and Jenni and Winkler (1994): birds were classified as 'young' (in autumn, birds fledged within the calendar year of capture; in spring, birds fledged in the previous calendar year) or 'adults' (in autumn, birds fledged before the current calendar year; in spring, birds fledged before the previous calendar year). Only adult birds can be reliably sexed in this species (Svensson 1992). All measurements were taken by the same observer (MM). Each bird was individually marked with a metal ring and a combination of colour plastic rings.

After release we recorded every observation of a marked individual. To reduce the possibility that capture and handling stress affected stopover behaviour and departure decisions, only individuals that were observed at least two hours after the last capture event (including recaptures, when the bird was immediately released from the trap) were considered in the analyses. We assumed the first and the last day of observation of a bird to be the day of arrival and the day of departure from the study site, respectively. This assumption is tenable, because the island is very small, disturbance was very limited (there were few avian/terrestrial predators and almost no ecologically similar migrants), the study site was located in an open rocky area almost devoid of vegetation (thus very favourable for observations), and, most importantly, there was almost no exchange of marked birds between a ringing station located at exactly the opposite tip of the island (i.e. ca 2 km from the study site), operating at the same time, and our study site. In fact, 24 out of 1022 (2.35%) birds previously marked at the ringing station were later recaptured at our study site, and only 13 out of 1045 (1.24%) birds initially marked at our study site were subsequently controlled at the ringing station. Moreover, in those birds staying at least one night, the probability of not observing a bird known to be present at the study site (estimated as the mean proportion of days with no observation of a given individual over the days of stopover) was 0.048 (0.013 SE) in spring ($n = 67$) and 0.030 (0.010 SE) in autumn ($n = 89$) (see Dierschke et al. 2005 for similar values). Thus, the vast majority of birds were faithful to the study site once settled, which is not unexpected given the large consumption of mealworms, and had high chances (> 0.95) of being resighted. The intensive observation sessions, the very high chances of resighting marked birds, and the peculiar habitat characteristics of the study site ensured that the bias in estimates of stopover duration and departures due to differential diurnal activity of fat and lean birds (Yong and Moore 1993, Titov 1999, but see Fusani et al. 2009) was likely to be small.

Weather variables

Weather data were recorded on the island of Ponza, ca 40 km NE of Ventotene, and were obtained from the website <www.wunderground.com> (accessed December 2007). We considered air temperature (°C, in centesimal scale), barometric pressure (mmHg), rainfall (cm d^{-1}) and wind speed (m s^{-1}) and direction (°). All variables were recorded at ground level (Åkesson and Hedenström 2000, Dänhardt and Lindström 2001, Tsvey et al. 2007, Åkesson et al. 2002, Navedo et al. 2010). Wind conditions were summarized as the tailwind and the crosswind component, according to the following formulas (from Åkesson and Hedenström 2000):

$$\text{tailwind component} = \omega[\cos(d - \alpha)]$$

$$\text{crosswind component} = |\omega\{\cos[(d + 90°) - \alpha]\}|$$

where ω = observed wind speed; α = observed wind direction; d = migration direction.

Migration directions were assumed to be 22.5° (NNE) in spring and 202.5° (SSW) in autumn. These values represent the estimated median migration directions over the central Mediterranean sea [see Pilastro et al. (1995) for spring migration and Spina and Volponi (2008) for both spring and autumn migration]. However, assuming a spring migration direction of 45° (NE) and an autumn migration direction of 225° (SW) (Casement 1966) did not qualitatively alter our conclusions (details not shown). Positive values of the tailwind component denote favourable tailwind conditions. The crosswind component was expressed as the module, so as to consider as equal the drift induced by lateral winds from both sides, in the absence of detailed information on the suitability of directional crosswinds at the study site (see also Saino et al. 2010a for a similar approach). High values of the crosswind component are assumed to denote unfavourable winds.

We considered weather values registered at 19:00 solar time (i.e. 1–2 h after sunset at the study site, depending on season) – except for rainfall, that was the total amount of rainfall of the day of interest – as these values were likely to be the closest to the timing of bulk evening departures of redstarts. Although departures of migrants at some stopover sites may take place throughout the night (Åkesson et al. 2001, Bolshakov et al. 2007, Schmaljohann et al. 2011), most departures take place soon after sunset and in the first hours of darkness (Gauthreaux 1971, Liechti and Bruderer 1995, Bulyuk and Tsvey 2006, Schmaljohann et al. 2007, see also Goymann et al. 2010 for a telemetry study of spring migrants on Ventotene).

An important assumption of our study is that wind conditions at the ground level, reflecting wind conditions actually perceived by birds while stopping over on the island, were positively correlated with wind conditions aloft. In fact, a positive correlation implies that migrants departing under perceived favourable ground winds have high chances of encountering favourable wind conditions also once reaching their cruising flight altitude. We thus obtained an estimate of the tailwind and crosswind components at 925 mbar (altitude interval 445–1134 m a.s.l., an average flight altitude of night migrants crossing ecological barriers; Fortin et al. 1999, Schmaljohann et al. 2009) based on NOAA-NCEP Reanalysis dataset <www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html> for each evening during the study periods (spring, $n = 30$ evenings; autumn, $n = 32$ evenings). In a linear model including NOAA evening tailwind as a dependent variable, and ground evening tailwind and season as predictors, ground tailwinds strongly and positively predicted high-altitude tailwinds ($F_{1,59} = 61.1$, $p < 0.001$; effect size: $r = 0.71$). The relationship did not differ between seasons, as the ground level tailwind × season interaction was not statistically significant ($F_{1,58} = 0.26$, $p = 0.61$), and was removed from the model. Results for crosswinds were similar, with ground crosswinds positively predicting high-altitude crosswinds ($F_{1,59} = 26.7$, $p < 0.001$; effect size: $r = 0.56$); also in this case, the ground crosswind × season interaction was not significant ($F_{1,58} = 1.96$, $p = 0.17$) and was removed from the model. Therefore, we conclude that ground winds may be used by migrants as a reliable cue to wind conditions they will encounter aloft (see also Schaub et al. 2004, Navedo et al. 2010, Schmaljohann et al. 2011). Moreover, though results were broadly similar, exploratory analyses revealed that high-altitude tail- and crosswinds were poorer predictors of redstart departure probabilities than those at ground level during autumn (spring departures were unaffected by either high-altitude or ground winds; details not shown for brevity).

Statistical analyses

We investigated whether stopover duration (in days) varied according to season, age of the birds (young or adult), capture date (expressed as the progressive day since the first day of trapping of each season, reflecting arrival date) and fat stores at arrival in a general linear model (GLM) with negative binomial error distribution and a log link function, where the first two variables were factors, whereas the other two were the covariates. In the initial model we also included all the two-way interactions between factors, and between factors and covariates. Non-significant interaction terms were dropped from the model at once. A similar model (with sex instead of age) was run to investigate sex differences in stopover duration of adult birds during spring migration only, because very few adult birds could be sexed during autumn (this analysis could not be performed in young birds because they cannot be reliably sexed in this species; see above). In these models, arrival date was included as a covariate to control for the confounding effects of the truncation of the observation period at the end of each season, because several birds were still staging on Ventotene on the day the observations were stopped (such individuals were excluded from these analyses). To overcome possible pitfalls associated with the estimation of stopover duration, and to assess the biological effect of arrival date (reflecting progress of season) on stopover decisions (review in Jenni and Schaub 2003), the same models were run while considering the probability of making a long stopover as a binary dependent variable (0 = birds leaving on the evening of the same day of arrival, 1 = birds staying at least until the day after arrival) in a logistic regression.

To analyse the effect of local weather on departure decisions, we adopted a dual approach. Firstly, through a logistic regression, we analysed the probability that a bird made only a short stopover at Ventotene, i.e. the probability that it departed on the evening of the same day of arrival, in relation to its fat score at arrival (the main determinant of stopover in both seasons, see Results) and to the weather conditions of the evening of the arrival day. The dichotomous dependent variable was coded as 0 (a bird that was observed again on the day after arrival) or 1 (a bird that departed on the evening of the same day of arrival). In these analyses, the effect of each weather variable was assessed separately, together with fat score and the interaction between the weather variable and fat score, because exploratory analyses suggested that testing the concomitant effects of weather variables resulted in unrealistic standard errors of parameter estimates, probably because of complex multicollinearity among variables (details not shown).

Secondly, for birds that were re-observed at the study site at least on the day after arrival, we investigated the independent and concomitant effect of weather variables on the probability of departing from the study site by running a random-effect pairwise logistic regression modelling the probability of correctly classifying the evening of departure (coded as 1) with respect to the evening prior to departure (coded as 0). In this analysis, we excluded birds that departed on the evening of the same day of capture, because we assumed that such birds were not on the island the day before capture and thus did not experience local weather conditions of the day before. This test differs from the previous one because it investigates whether individual birds are actually selecting favourable local weather conditions for tuning departure once a decision to stopover has been made, rather than reacting to the local weather conditions at arrival on the island. Weather variables were included as covariates (both separately and simultaneously), while a factor 'day of departure' (denoting a cluster of birds departing on the same evening) and a factor 'individual' (grouping each day of departure with the corresponding day before departure, nested within 'day of departure'), were included as random grouping variables. The structure of the random part of the model thus allowed for a pairwise design, whereby the effects of weather conditions of the day of departure of each individual were compared with those of the evening before departure, while simultaneously accounting for the non-independence of birds experiencing the same conditions on consecutive days.

Results of all logistic regression models are shown for spring and autumn separately, to facilitate the interpretation of the results. However, we also ran models including data for both seasons, where season was considered as a fixed factor, and tested the interaction terms between season and each weather variable to assess whether the effects of weather conditions on departure decisions differed between seasons.

Statistical analyses were carried out by means of SAS 9.1.3 (PROC GENMOD and PROC GLIMMIX), SPSS 13.0 and StatXact 9.0. Since weather variables were not normally distributed in several subsets of data used in the analyses (details not shown for brevity), for simplicity we adopted non-parametric statistics throughout (results were qualitatively unchanged if parametric tests were adopted; details not shown for brevity). Sample sizes may vary slightly between different analyses because of missing data for some individuals.

Results

Factors affecting stopover duration

In both seasons, most birds made only a short stopover at the study site, departing on the evening of the day of arrival (stopover duration = 0 d; Fig. 2). In the negative binomial GLM of stopover duration (n = 261 individuals), all the two-way interaction terms between factors and between factors and covariates (see Statistical analyses) were non-significant (all $p > 0.12$, details not shown) and were dropped from the model. The simplified model revealed

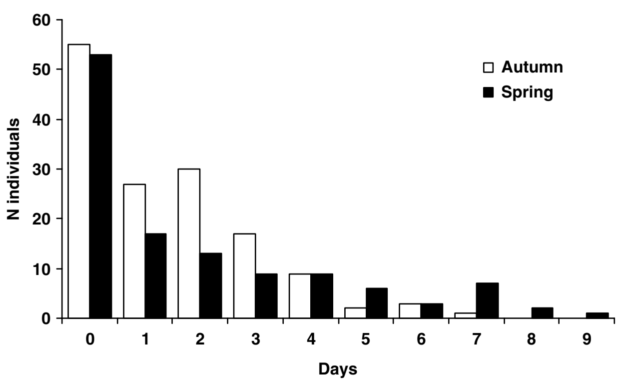

Figure 2. Frequency distribution of stopover duration of black redstarts at Ventotene during spring (n = 120) and autumn (n = 144) migration. A stopover duration of 0 d denotes individuals that were resighted after capture (Methods) but left the experimental stopover site on the evening of the same day of arrival.

that stopover duration did not differ between seasons, and was longer in birds with low fat stores (while controlling for first capture date; Methods) (Table 1). In addition, young birds stayed longer than adults [mean values estimated from the model: young 1.6 d (95% CL 1.4–1.9), adults 1.0 d (95% CL 0.7–1.4)] (Table 1). This age effect on stopover duration was not due to age differences in condition [mean fat score, young: 1.90 (0.07 SE), adults: 1.88 (0.17 SE); Mann–Whitney test, $z = 0.38$, $p = 0.71$]. During spring migration, we also investigated whether the patterns of stopover duration differed between adult males and females (Methods; $n = 37$ adults). After removing non-significant interactions (all $p > 0.16$, details not shown), no significant sex difference in stopover duration emerged ($\chi^2 = 2.83$, $p = 0.09$) (other model details not shown for brevity).

The same analyses were run while considering the probability of making a long stopover as a binary dependent variable instead of stopover duration (Statistical analyses; $n = 287$ individuals; sample size is larger than in the case of stopover duration because we included the additional birds that were still on the island at the end of the study periods, whose departure date and stopover duration could not be determined). After dropping non-significant interactions ($p > 0.10$) from the model, the only variable significantly predicting the probability of making a long stopover was fat score, with leaner birds having a greater probability of making a long stopover, and there were non-significant effects of age and season (Table 1; see also Table 2 for descriptive statistics of fat score), though young birds and autumn migrants showed a tendency towards a greater probability of making a long stopover (Table 1). When this model was run on adult males and females during spring migration ($n = 37$), after dropping the non-significant interaction terms (all $p > 0.17$), no significant sex difference in the probability of making a long stopover emerged ($\chi^2 = 0.34$, $p = 0.56$) (other model details not shown for brevity).

Effect of weather on departure decisions

Descriptive statistics of fat score and weather variables for birds departing on the evening of the same day of arrival and for those staying longer are shown in Table 2. Logistic regression analyses showed that both weather conditions and fat score affected the probability that a bird departed on the evening of the same day of arrival (Table 3). During both spring and autumn, when local weather conditions were favourable (strong tailwinds, weak crosswinds, low rainfall, high temperature, high pressure; Table 2), fat redstarts were highly likely to depart from the study site on the evening of the same day of arrival (Table 3). The interactions between fat score and weather variables were never statistically significant during both spring and autumn (all $p > 0.16$, details not shown), and were removed from the models. Some differences between seasons emerged, as the effects of crosswinds and temperature were apparently stronger in autumn than spring, while rainfall appeared more important in spring than autumn (Table 3). However, in models including data for both seasons, the interaction terms between each weather variable and season were never statistically significant (all $p > 0.18$, details not shown), thus suggesting that the effects of weather on the probability that a bird departed on the evening of the arrival day did not differ between seasons.

The analyses performed on birds that stopped over for at least one day gave a partially different picture. Descriptive statistics of weather variables on the evening of departure and on the evening before departure are reported in Table 4. The pairwise logistic regression analysis showed that no weather variable significantly predicted the probability of departure of redstarts from Ventotene during spring migration (Table 5). On the other hand, during autumn, redstarts departed from Ventotene with favourable winds (tailwinds, low crosswinds) and in days with low or no rainfall (Table 5). In univariate models including data for both seasons, the effects of tailwind and crosswind differed between seasons (tailwind × season, $t_{149} = 3.25$, $p = 0.001$; crosswind × season, $t_{149} = -2.48$, $p = 0.014$), whereas the effects of the other weather variables did not (all $t_{149} < |1.77|$, $p > 0.08$, details not shown for brevity).

Multiple regression models confirmed the results of univariate models, with the exception of the effect of crosswind, that became non-significant in the autumn model while controlling for the concomitant effects of the other weather variables (Table 5). In a multiple regression model including data for both seasons and the interaction terms between season and each weather variable, the effect of tailwind and rainfall differed between seasons (tailwind × season, $t_{141} = 4.01$, $p < 0.001$; rainfall × season, $t_{141} = 4.16$, $p = 0.043$), while the effects of the other weather variables did not (all $t_{141} < |1.71|$, $p > 0.19$, details not shown for brevity).

Table 1. Models of factors affecting a) stopover duration (negative binomial general linear model) and b) probability of making a long stopover (logistic regression; see Statistical analyses and Results for details) of black redstarts at Ventotene. Two-way interactions between factors and between factors and covariates were not significant in any case and were removed from the models.

Variable	χ^2	p	Estimate (SE)
a) Stopover duration (n = 261 individuals)			
Season	0.13	0.72	–
Age	5.05	0.025	–
Fat score	18.71	<0.001	−0.329 (0.076)
Capture date	15.92	<0.001	−0.042 (0.011)
b) Probability of making a long stopover (at least 1 d) (n = 287 individuals)			
Season	3.41	0.065	–
Age	2.75	0.097	–
Fat score	22.71	<0.001	−0.597 (0.132)
Capture date	0.32	0.57	−0.009 (0.017)

Table 2. Descriptive statistics [mean (SE; minimum to maximum)] of fat score and weather conditions on the evening of the day of arrival at Ventotene for black redstarts either departing on the same evening or staying at least one day (see Methods). Sample size for each group is 52 and 67 during spring, and 52 and 110 during autumn, respectively. Differences were tested by the Mann–Whitney test.

Weather variable	Departing on evening of arrival	Staying at least one day	z	p
Spring				
Fat score	2.17 (0.14; 0 to 4)	1.43 (0.13; 0 to 4)	3.65	<0.001
Tailwind	0.85 (0.38; −13.89 to 5.24)	−1.37 (0.74; −13.89 to 5.70)	1.71	0.09
Crosswind	1.20 (0.18; 0.00 to 4.75)	1.53 (0.29; 0.00 to 9.98)	0.66	0.51
Rainfall (cm d^{-1})	0.09 (0.03; 0.00 to 0.79)	0.23 (0.04; 0.00 to 1.09)	1.72	0.09
Temperature (10 × °C)	123.7 (1.3; 110 to 140)	124.6 (1.3; 90 to 140)	0.98	0.33
Pressure (mmHg)	1015.6 (0.9; 990 to 1023)	1010.4 (1.5; 986 to 1024)	1.84	0.07
Autumn				
Fat score	2.15 (0.12; 0 to 4)	1.63 (0.09; 0 to 4)	3.12	0.002
Tailwind	−0.14 (0.33; −9.50 to 3.80)	−1.51 (0.33; −9.50 to 3.80)	2.56	0.010
Crosswind	2.07 (0.18; 0.00 to 5.67)	3.22 (0.24; 0.00 to 8.75)	2.51	0.012
Rainfall (cm d^{-1})	0.05 (0.02; 0.00 to 0.71)	0.07 (0.02; 0.00 to 0.79)	0.11	0.92
Temperature (10 × °C)	162.5 (2.5; 130 to 190)	151.7 (1.6; 110 to 190)	3.49	<0.001
Pressure (mmHg)	1016.4 (0.5; 1004 to 1023)	1013.9 (0.6; 1001 to 1023)	2.38	0.017

Finally, we compared the variances in weather conditions (by means of the non-parametric Conover test; Conover 1999) at departure of birds leaving on the evening of the day of arrival with those of birds staying longer (see Tsvey et al. 2007 for a similar approach), and found that they were similar between birds making short and long stopovers during both seasons (Table 6), with few exceptions (crosswinds during both seasons, temperature in spring and air pressure in autumn) when variances were significantly larger for birds staying longer compared to those making short stopovers. Air temperature at departure was higher for birds making short stopovers in both seasons, while there were no significant differences according to stopover duration for the other variables (Table 6). Importantly, we can rule out that these patterns originated from differences in departure dates (Mann–Whitney test, spring: $z = 1.26$, $p = 0.20$; autumn: $z = 0.07$, $p = 0.94$) or in variances of departure dates between long- and short-staying birds (Conover test, spring: $z = 0.30$, $p = 0.76$; autumn: $z = 0.52$, $p = 0.60$). Hence, birds making long stopovers departed under cooler and more variable weather conditions compared to those making a short stopover.

Sex and age differences in weather conditions at departure

We investigated whether weather conditions on the evening of departure differed between adult birds of the two sexes during spring migration, and between young and adult birds during both spring and autumn migration. Since this analysis involved only a comparison of weather conditions on the evening of departure, we included also the birds that departed on the evening of the day of arrival. The analysis of sex difference involved 37 individuals (22 males and 15 females). Weather conditions at departure did not differ between males and females (Mann–Whitney test, all $z < |0.89|$, p always > 0.49; details not shown for brevity), with the exception of tailwind assistance, that was significantly lower for males than for females ($z = 2.27$, $p = 0.024$; Fig. 3a). Specifically, tailwind assistance was not significantly different from 0 in males (Wilcoxon one-sample test, $z = 0.98$, $p = 0.33$), whereas it was significantly larger than 0 in females ($z = 2.90$, $p = 0.004$). Neither date of departure nor fat score at arrival differed between the sexes (Mann–Whitney test, $z = 0.95$, $p = 0.35$ and $z = 0.52$, $p = 0.61$, respectively).

The analyses of age differences involved 118 individuals during spring (81 young and 37 adults) and 136 individuals during autumn (122 young and 14 adults). In spring, young departed under less favourable tailwinds than adults ($z = 2.34$, $p = 0.019$; Fig. 3b). Tailwind assistance was not significantly different from 0 in young birds, whereas it was significantly larger than 0 in adults (Wilcoxon one-sample test; young: $z = 1.15$, $p = 0.25$, adults: $z = 2.84$, $p = 0.004$). There were no age differences in all the other weather variables during both seasons (Mann–Whitney test, all

Table 3. Simple logistic regression analyses of the effect of different weather variables and fat score on the likelihood that a black redstart departed from Ventotene on the evening of the same day of arrival (i.e. made a short stopover on the island). The effect of fat score was positive and statistically significant in all 10 regression models (details not shown for brevity; spring, all $p < 0.005$; autumn, all $p < 0.008$). The interaction terms between fat score and weather variables were never statistically significant in both spring and autumn models (all $p > 0.16$, details not shown). Moreover, in models including data for both seasons, the interaction terms between season and each weather variable were never statistically significant (all $p > 0.18$, details not shown).

	Spring (n = 119)			Autumn (n = 162)		
	Estimate (SE)	χ^2	p	Estimate (SE)	χ^2	p
Tailwind	0.106 (0.049)	5.60	0.018	0.162 (0.064)	7.37	0.007
Crosswind	−0.160 (0.112)	2.15	0.14	−0.307 (0.111)	11.08	0.001
Rainfall	−1.329 (0.705)	4.00	0.045	−1.291 (1.182)	1.34	0.25
Temperature	0.001 (0.019)	0.00	0.95	0.030 (0.010)	9.21	0.002
Pressure	0.060 (0.023)	8.25	0.004	0.103 (0.037)	8.91	0.003

Table 4. Descriptive statistics [mean (SE)] of weather conditions on the evening of departure of black redstarts from Ventotene compared to weather conditions of the evening prior to departure for birds stopping over at Ventotene at least one day. Differences in mean values were tested by the Wilcoxon matched-samples test.

Weather variable	Evening prior to departure	Evening of departure	z	p
Spring (n = 67)				
Tailwind	0.13 (0.52)	0.24 (0.36)	0.68	0.50
Crosswind	2.10 (0.31)	2.03 (0.31)	0.98	0.33
Rainfall (cm d^{-1})	0.20 (0.04)	0.12 (0.04)	1.90	0.06
Temperature (10 × °C)	118.4 (1.6)	118.2 (1.8)	−0.08	0.94
Pressure (mm Hg)	1010.7 (1.4)	1012.4 (1.3)	−2.99	0.003
Autumn (n = 84)				
Tailwind	−2.69 (0.32)	−0.78 (0.26)	−4.21	<0.001
Crosswind	3.85 (0.35)	2.19 (0.21)	3.60	<0.001
Rainfall (cm d^{-1})	0.10 (0.03)	0.03 (0.01)	2.88	0.004
Temperature (10 × °C)	147.3 (2.4)	151.2 (2.2)	−1.88	0.06
Pressure (mm Hg)	1013.8 (0.8)	1015.2 (0.6)	−2.09	0.003

$z < |1.37|$, p always > 0.17), as well as in date of departure and fat score (all $z < |1.59|$, p always > 0.11; details not shown for brevity).

Discussion

In this study, we tackled the issue of the effect of local weather conditions on stopover and departure decisions of a short-distance migrant passerine bird, the black redstart, on a Mediterranean island during both spring (pre-breeding) migration, after extensive non-stop sea crossing, and autumn (post-breeding) migration, just prior to ecological barrier crossing. Moreover, we investigated the effects of fat stores at arrival at the study site, where food was provided continuously, on stopover decisions.

Effects of fat stores and weather on stopover and departure decisions

First, we found that fat stores not only had a major effect on the decision to stopover, but also modulated the duration of stay of birds that did not leave on the evening of the arrival day (Table 1). This was the case during both spring and autumn migration. This finding is in line with most previous knowledge of stopover behaviour, although the generality of an effect of fat stores on stopover duration has been questioned (Salewski and Schaub 2007; review in Jenni and Schaub 2003). However, discrepancies between studies may be due to differences in field protocols (we provided food to standardize stopover site quality, whereas this was not the case in other studies) or location of study, since an effect of fat stores on departure decisions is more likely to emerge before or soon after ecological barrier crossing, like in our case, rather than on mainland stopover sites, where opportunities to refuel are greater (Jenni and Schaub 2003, Tsvey et al. 2007).

On the whole, our analyses showed that departure decisions were affected by local weather, independently of fat stores at arrival: birds left Ventotene under favourable weather conditions, as gauged by tailwinds, low cross-winds, low rain, high temperatures, and high barometric pressure.

Specifically, during both seasons, weather conditions at arrival (especially tailwinds and air pressure levels) significantly predicted the likelihood that a bird departed from Ventotene on the evening of the arrival day (Table 3), and the effects of weather variables did not differ between seasons. However, the selectivity of local weather conditions

Table 5. Simple and multiple pairwise logistic regression models of the effects of weather variables on the probability of correctly classifying the evening of departure (coded as 1) with respect to the evening prior to departure (coded as 0) of black redstarts stopping over at Ventotene at least one day. Degrees of freedom are as follows: spring migration, simple regressions: 66; multiple regression: 62; autumn migration, simple regressions: 83; multiple regression: 79. See Results for details of tests of interaction terms between season and weather variables.

	Simple regression			Multiple regression		
	Estimate (SE)	t	p	Estimate (SE)	t	p
Spring						
Tailwind	0.008 (0.047)	0.17	0.86	−0.047 (0.066)	−0.72	0.48
Crosswind	−0.011 (0.068)	−0.15	0.88	0.020 (0.084)	0.24	0.81
Rainfall	−0.692 (0.537)	−1.29	0.20	−0.428 (0.683)	−0.63	0.53
Temperature	0.038 (0.124)	0.31	0.76	−0.022 (0.020)	−1.07	0.29
Pressure	0.014 (0.016)	0.87	0.39	0.038 (0.038)	1.00	0.32
Autumn						
Tailwind	0.267 (0.064)	4.17	<0.001	0.435 (0.099)	4.39	<0.001
Crosswind	−0.243 (0.064)	−3.77	<0.001	−0.110 (0.101)	−1.09	0.28
Rainfall	−3.327 (1.389)	−2.39	0.019	−4.404 (1.786)	−2.47	0.016
Temperature	0.009 (0.007)	1.21	0.23	−0.022 (0.015)	−1.48	0.14
Pressure	0.035 (0.025)	1.43	0.16	−0.037 (0.049)	−0.75	0.45

Table 6. Descriptive statistics [mean (SD)] of weather conditions on the evening of departure for black redstarts making a short stopover (departing on the evening of the day of arrival) and those staying longer (staying at least one day). Sample size for each group is 52 and 67 during spring, and 52 and 84 during autumn, respectively. Differences in mean values were tested by the Mann–Whitney test, whereas differences in variances were tested by the Conover test (Conover 1999).

Weather variable	Short stopover	Long stopover	Mann–Whitney z	Mann–Whitney p	Conover z	Conover p
Spring						
Tailwind	0.85 (2.72)	0.24 (2.96)	−1.35	0.18	−1.86	0.06
Crosswind	1.20 (1.31)	2.03 (2.55)	1.00	0.32	−5.01	<0.001
Rainfall (cm d^{-1})	0.09 (0.23)	0.12 (0.30)	0.05	0.96	−5.33	<0.001
Temperature (10 × °C)	123.7 (9.3)	118.2 (14.5)	−1.94	0.053	−3.35	0.001
Pressure (mm Hg)	1015.6 (6.7)	1012.4 (10.5)	−1.07	0.29	−3.26	0.001
Autumn						
Tailwind	−0.14 (2.39)	−0.78 (2.36)	1.64	0.10	−1.17	0.24
Crosswind	2.07 (1.33)	2.19 (1.89)	1.14	0.26	−1.59	0.11
Rainfall (cm d^{-1})	0.05 (0.12)	0.03 (0.09)	−1.60	0.11	6.27	<0.001
Temperature (10 × °C)	162.5 (17.8)	151.2 (20.4)	−3.29	0.001	−0.24	0.81
Pressure (mm Hg)	1016.4 (3.9)	1015.2 (5.4)	−0.50	0.62	−3.16	0.002

in birds stopping over at Ventotene for at least 1 day differed between seasons. In these analyses, no weather variable significantly predicted departures during spring, whereas favourable tailwinds, low crosswinds and low rainfall predicted departures in autumn (Table 5). Importantly, the effects of tailwind and rainfall on the probability of departure were stronger in autumn than spring.

A difference between seasons in the effects of local weather on departure decisions may have several non-mutually exclusive causes. First, it may be caused by a different distance to be covered before reaching the next suitable stopover site in either season. In fact, migrating redstarts departing from Ventotene have to cross a wider stretch of sea in autumn (ca 300–600 km) than in spring (ca 50 km), implying that favourable weather may be more important for tuning departure decisions in autumn. Alternatively, average weather conditions may be more favourable in spring than in autumn (Kemp et al. 2010), leading redstarts to be less selective of generally favourable weather for tuning departures. However, weather conditions did not differ between spring and autumn (Mann–Whitney test, all $p > 0.11$), with the exception of the tailwind component, that was on average more favourable (more positive values) in spring than in autumn ($p = 0.032$), and temperature, that was lower in spring than in autumn ($p < 0.001$). The latter findings thus leave open the possibility that between-season differences in average weather conditions contribute to the observed patterns. Moreover, spatio-temporal endogenous programmes (sensu Gwinner 1996) may differently affect the stopover behaviour of redstarts during spring and autumn. Such an explanation implies that the relative importance of spatio-temporal programmes vs environmental cues in modulating stopover decisions in either season differ.

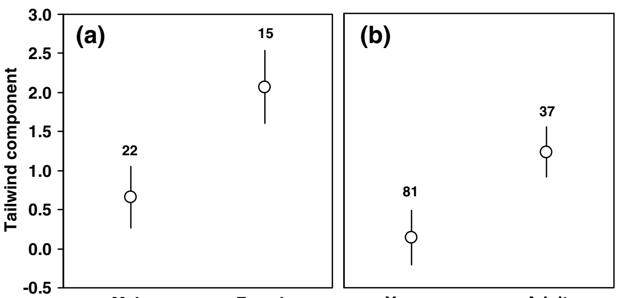

Figure 3. Mean (SE) tailwind component at departure from Ventotene during spring migration for adult males vs females, and for adult vs young birds. Numbers above bars indicate sample size.

Interestingly, we also found that variances in weather conditions differed between birds making short and long stopovers, with long-staying birds departing under a wider range of conditions than short-stayers (with the only exception of autumn rainfall, where the opposite was the case). This finding is at odd with previous studies documenting larger variances in weather conditions at departure in short- vs long-stayers (Dierschke and Delingat 2001, Tsvey et al. 2007). The reason for this discrepancy is unclear, but may be related to differences in sampling protocols, because, differently from this study, previous studies did not alter stopover site quality. In our study, long-stayers had low fat stores, whereas short-stayers had high fat stores, as observed also in other species at Ventotene (Goymann et al. 2010, Tenan and Spina 2010). It is thus possible that low fat individuals refuelled at the study site and then departed once reaching a threshold body condition that may partly offset weather effects on departure decisions, resulting in greater variability in weather conditions at departure of long-staying birds. This view is supported by the observation that long-stayers also departed with lower temperatures (i.e. worse weather conditions) than short-stayers, especially in autumn (Table 6), and would be consistent with early studies suggesting that the threshold for the initiation of migratory flights is lowered after long periods of rest (Rudebeck 1950, Hinde 1951, both cited in Alerstam 1979), as well as with theoretical predictions suggesting that the tendency to depart with suboptimal wind conditions might be higher as time spent on stopover and fuel load increase (Liechti and Bruderer 1998, Weber et al. 1998).

Sex and age differences in weather conditions at departure

Our study highlighted a novel difference in the response to weather conditions at departure between males and females. During spring migration (too few data were available for autumn), females departed with favourable tailwinds, whereas males did not rely on wind assistance when deciding to leave the study site, implying that migration schedules of spring migrating male black redstart may be less constrained by environmental variability than those of females. This finding was not confounded by sex differences in phenology or condition at arrival. Although no sex differences in stopover duration or stopover probability emerged at our study site (Coppack and Pulido 2009), the observed lower selectivity of favourable wind conditions by males may promote protandry. For example, if males and females depart simultaneously from the wintering areas, males may arrive to their goal areas earlier than females because they do not need to wait for favourable weather to leave a stopover site, though they may spend more energy per distance unit by flying with less favourable winds. An earlier arrival to breeding territories is expected to result in greater fitness payoffs, as documented in this (Landmann and Kollinsky 1995) and other bird species (Kokko 1999), but possibly at the cost of increased energy expenditure during migratory flights.

Adult and young birds also showed intriguing differences in their response to wind conditions at departure, because during spring young left the island with no wind assistance, whereas adults selected favourable tailwinds. Also in this case, there were no confounding effects of age differences in phenology or condition at arrival. Thus, the decision to leave a stopover site may be affected to some extent by individual age. An inability to select the best weather condition in the young, coupled with a lower foraging and flight efficiency as compared to adults, and a lower social rank (Moore et al. 2003), may further increase their risk of death during migration (Strandberg et al. 2009), and may contribute to originate the generally higher annual mortality observed among young vs adult migratory birds (Newton 2008), as well as the age differences in stopover duration, with young birds staying longer than adults, observed in this study. A possibility is indeed that the cohort of young birds include a larger fraction of low-quality individuals than the adult cohort, since selection has had the time to act for a longer time on adult compared to young individuals. At least in passerines, which may suffer from wind displacement due to their low body mass (Alerstam 1979), the ability to select the best weather conditions (especially favourable tailwinds and weak or no crosswinds) for tuning departure decisions in order to increase the chances of safely reaching the next suitable stopover site may be crucial in determining the success of migratory flights (Liechti and Bruderer 1998, Erni et al. 2005).

In conclusion, departure decisions of black redstarts migrating through the Mediterranean Sea were differently affected by weather conditions during spring and autumn. Wind conditions, especially favourable tailwinds, were likely the most important determinants of departure decisions, although other weather variables (rainfall, temperature, air pressure) significantly predicted departures. Moreover, birds of different sex and age classes may be differentially sensitive to weather in tuning their departure decisions, as spring migrating males left the stopover site under less favourable weather than females, and young departed under less favourable wind than adults. The latter findings may have broader implications for our understanding of sex differences in migration schedules (i.e. protandry) during spring migration as well as for explaining the lower annual survival of young vs adult migratory birds.

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