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Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: a multi-scale approach

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Abstract Many studies suggest that migratory birds are expected to travel more quickly during spring, when they are en route to the breeding grounds, in order to ensure a high-quality territory. Using data recorded by means of Global Positioning System satellite tags, we analysed at three temporal scales (hourly, daily and overall journey) seasonal differences in migratory performance of the booted eagle (*Aquila pennata*), a soaring raptor migrating between Europe and tropical Africa, taking into account environmental conditions such as wind, thermal uplift and day length. Unexpectedly, booted eagles showed higher travel rates (hourly speed, daily distance, overall migration speed and overall straightness) during autumn, even controlling for abiotic factors, probably thanks to higher hourly speeds, more straight routes and less non-travelling days during autumn. Tailwinds were the main environmental factor affecting daily distance. During spring, booted eagles migrated more quickly when flying over the Sahara desert. Our results raise new questions about which ecological and behavioural reasons promote such unexpected faster speeds in autumn and not during spring and how events occurring in very different regions can affect migratory performance, interacting with landscape characteristics, weather conditions and flight behaviour.

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Introduction

Comparing spring and autumn migration patterns is a useful tool to disentangle which ecological and behavioural correlates shape the departure timing of birds and their behaviour during the journey (Alerstam and Lindstrom 1990; McNamara et al. 1998; Nilsson et al. 2013). Selective pressures shaped by natural or sexual selection promote motivational asymmetries among the two migration seasons, due to the different migration goals (e.g. breeding vs. wintering). Birds are expected to migrate more quickly, thus minimising time rather than energy expenditure, when they are en route to the breeding grounds (Kokko 1999). Therefore, a time-selected (i.e. faster) migration would be expected in spring rather than in autumn (Alerstam 2006) and indeed this is what occurs in the majority of bird species tracked up to now (Nilsson et al. 2013).

An internal factor such as motivation interacts with diverse external factors (i.e. environmental conditions; Newton 2008). The effect of meteorological conditions on migration patterns has been studied extensively in the last decades at different temporal and spatial scales and with a wide arrange of different tools, such as field observations, radars and ringing (Newton 2008). From a natural selection perspective, it must be highlighted that a great proportion of annual mortality of adult birds takes place during migration (Sillett and Holmes 2002; Klaassen et al. 2014), and harsh weather conditions are supposed to be the main source of this mortality. Therefore, choosing optimal weather conditions is of paramount importance for migration success and fitness. The revolution in movement ecology research that took place in the last 20 years with the advent of satellite telemetry allowed researchers to measure with an unprecedented detail patterns such as

migration speed and its correlation with weather factors, especially on soaring birds, since they are large enough to carry satellite transmitters (Alerstam 2011). The migratory performance of soaring birds is strongly influenced by external factors such as landscape characteristics and meteorological conditions (Thorup et al. 2006; Klaassen et al. 2008; López-López et al. 2010; Borher et al. 2012; Mellone et al. 2012, 2013a). Landscape structure affects variation in migration speed, since some bird species fly slower in order to take advantage of foraging opportunities when moving over favourable habitats. Instead, when they have to overcome ecological barriers, such as deserts and sea surfaces, they increase their migration speed (Klaassen et al. 2008; Strandberg et al. 2009; López-López et al. 2010; Mellone et al. 2011, 2013a). However, due to their morphology, pure soaring migrants, such as eagles, vultures and buzzards probably store enough fat to reach their migratory goals without foraging en route (Smith et al. 1986; Alerstam and Hedenström 1998; Hake et al. 2003; Panuccio et al. 2006). Concerning meteorological conditions, wind assistance can be the single most important factor increasing the daily flight range (Liechti 2006, see also Mellone et al. 2012) irrespective of fuel expenditure (Alerstam 2003). Thereby, birds take advantage of winds to save both time and energy during migrations, although strong crosswinds can be very dangerous, especially when flying over ecological barriers (Klaassen et al. 2011). Thermal uplift can also boost migration speed (Borher et al. 2012), especially interacting with topography, since it has been shown that the same species can show diverse responses according to different orographic features (Mandel et al. 2011). Day length can enhance the migration speed of diurnal migrants, making larger the time window with optimal soaring conditions, but its effect has been little investigated and seems to be less important than other factors (Mellone et al. 2012).

Therefore, when studying seasonal differences in migration speed, taking into account all such exogenous agents is of the utmost importance, since a bird can behave with the aim to fly faster in a given season showing speed values still lower than in the other one because of less favourable environmental conditions (Nilsson et al. 2013), as for example, what occurs in the Egyptian vulture (*Neophron percnopterus*; Mellone et al. 2012; López-López 2014b).

The booted eagle (*Aquila pennata*) is a summer resident in Southern Europe, with the majority of individuals migrating to tropical Africa after the breeding season and concentrating at the Strait of Gibraltar and at the Bosphorus in order to cross the Mediterranean Sea (Cramp and Simmons 1980; Mellone et al. 2013b; Fig. 1). However, some individuals also winter in the Mediterranean basin (Martínez and Sánchez-Zapata 1999; Baghino et al. 2007). Radar studies indicate that this species, during migration over land, shows the typical flight behaviour of a soaring migrant resembling especially the honey buzzard (*Pernis apivorus*) and the Egyptian vulture (Spaar 1997).

Since thermals develop only over land, soaring birds like the booted eagle are usually reluctant to fly large distances over water bodies and hence they concentrate at narrow sea crossings (Kerlinger 1989; Bildstein 2006; Mellone et al. 2013b).

Here, we explored at multiple temporal scales (hourly, daily and overall journey; Fig. 2) the seasonal and regional (within and outside the Sahara desert) differences in travel patterns (speed, time budget and path straightness) of booted eagles migrating between their breeding areas in Spain and their African wintering grounds controlling for external factors such as meteorological conditions and day length. We investigated how seasonal and regional differences are affected by hourly flight speed and/or straightness, as well as by the time devoted to migration (measured as the number of travelling hours and the number of travelling/non-travelling days).

Materials and methods

Field procedures

Between 2011 and 2013, 12 breeding adult booted eagles were captured at several locations in Spain using a dho-gaza net placed close to active nests with fledglings and a live eagle owl (*Bubo bubo*) used as a decoy. All birds were equipped with 22 g Global Positioning System (GPS)-Argos satellite transmitters attached as backpacks, except for one individual with a GPS data-logger of the same weight (see details in Mellone et al. 2013b). All birds bred successfully after marking. Transmitters were programmed to collect GPS locations on an hourly basis from 06 a.m. to 20 p.m. (GMT) during migrations. Overall, we analysed data from nine individuals (three males and six females), accounting for 15 autumn and 10 spring journeys. We excluded from the analyses two birds that did not transmit data for at least a single journey, either due to a device failure or due to death, and also one bird that spent the winter in Spain.

Environmental variables

Both tailwinds and thermal uplift (the latter expressed as velocity of thermal convection ($w*$)), were computed using data from the NCEP/NCAR Reanalysis project, as provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA (http://www.cdc.noaa.gov), downloaded through the R package RNCEP (Kemp et al. 2012). Tailwind was calculated on the basis of U and V wind components following Thorup et al. (2003; see also, Mellone et al. 2012). Since booted eagles show a clear tendency to reach an intermediate goal area (the Strait of Gibraltar) during migration, two intended migration directions were used to calculate the tailwind component for each bird and season: the first one, towards the Strait of
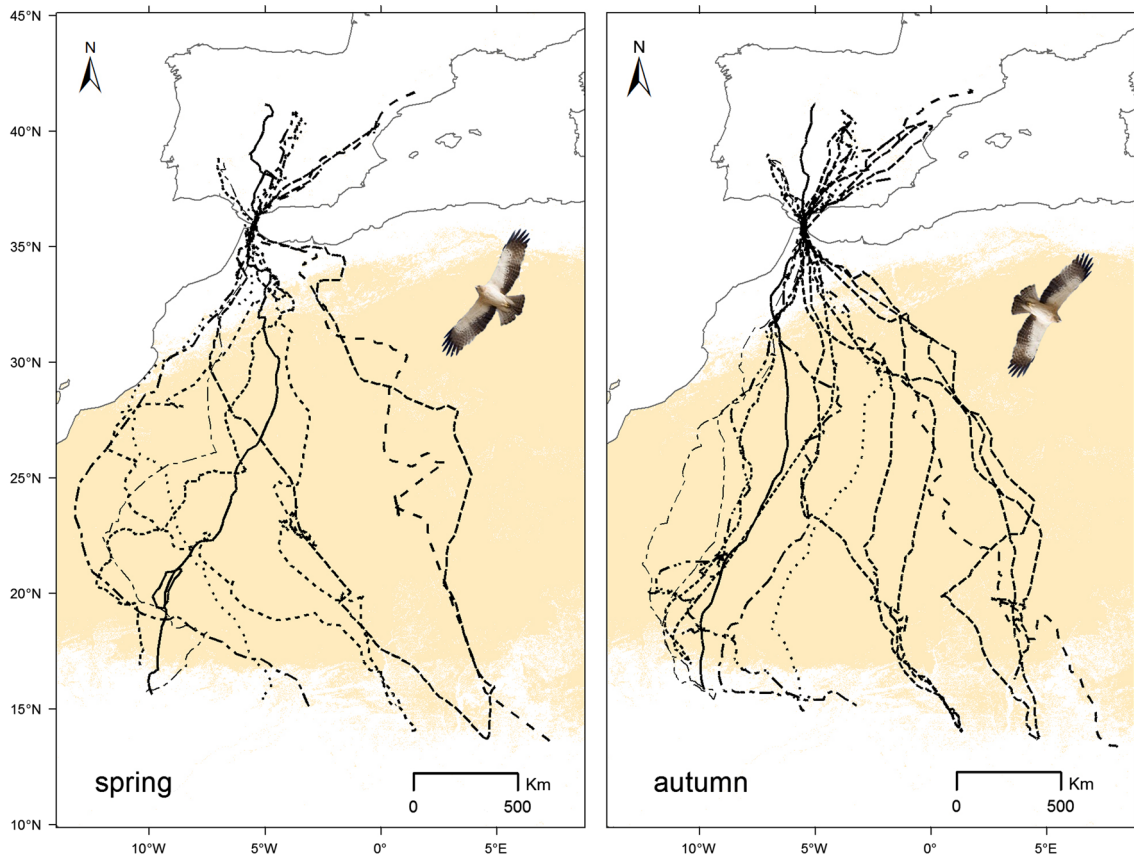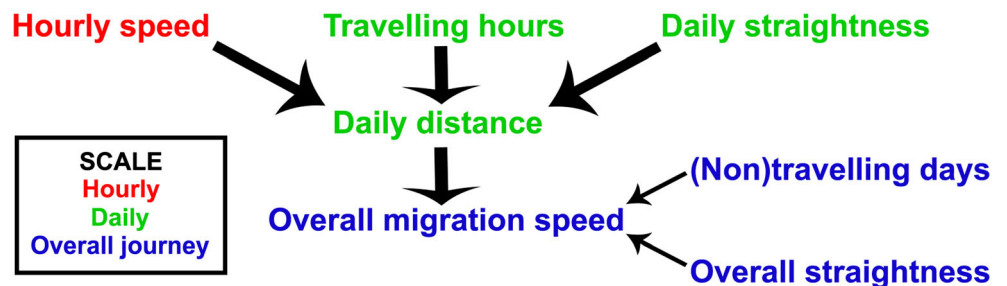
Fig. 1 Routes followed by nine booted eagles during spring and autumn migrations. Each type of line denotes a different individual. Desert areas according to the Global land Cover database are highlighted in yellow

Gibraltar, to compute tailwind data for the first part of each migration, and the second one towards the final goal (breeding or wintering area; see also, Klaassen et al. 2011), to compute tailwind data for the second part. Booted eagles are faithful to their nesting site and therefore we used always the same coordinates. Concerning wintering areas, we used the coordinates of the last point of autumn migration and the first one during spring migration. However, wintering areas are very distinctive and such points were always almost overlapping. Finally, migration departure and arrival were very easily defined on the basis of visual inspection of the tracks, since travel rates (speed and direction) change abruptly once each bird begin or finish the migratory journey.

Thermal uplift (w^*; Borher et al. 2012) was calculated using sensible heat net flux and temperature data from the NCEP/NCAR Reanalysis project, according to the formula $w^* = (gH/t)^{1/3}$, where g is the gravitational acceleration (=9.81), H is the sensible heat net flux and t is the temperature gradient (°C/100 m) calculated following Chevallier et al. (2010), using data at pressure levels of 1000, 925, 850 and 700 mb. Day length was expressed as that one experienced by each individual throughout a given day (i.e. the time difference between sunset at the roosting site and sunrise at the departure one), calculated following the formulae provided by NOAA (http://www.ecy.wa.gov/programs/eap/models.html; Mellone et al. 2012).

Fig. 2 Plot diagram of migration patterns across three time scales

Data selection and time scale

We analysed migration patterns at three scales: (1) overall journey, (2) daily scale and (3) hourly scale (Fig. 2).

Concerning the overall journey scale, we computed the following parameters: (i) migration speed (the linear distance between the nest and the wintering area divided by migration duration in days), (ii) number of 'non-travelling days', i.e. days with daily distance <50 km or with direction opposite to the general migration direction and (iii) straightness index computed as the ratio between the linear distance and the cumulative distance covered by the birds, using only a single location, the roosting one, per day (Benhamou 2004; Mellone et al. 2013a). Means are given with standard deviations throughout the paper.

At the daily scale, we calculated the daily distance as the distance between consecutive roosting sites and used it as dependent variable in our analyses. No case of nocturnal migration was recorded. Non-travelling days were excluded from the analyses. We also excluded the last day prior to the arrival to the wintering or breeding area in order to include only days during which we assumed that eagles tried to maximise the daily distance. For a sub-set of days when the transmitter worked continuously (i.e. one location was recorded for every hour during the whole daily-working period of the transmitter), we also computed the total number of travelling hours (i.e. hourly segments with speed >5 km/h; Strandberg et al. 2009) and the daily straightness (S.I.), defined as the ratio between the daily distance (linear distance between roosting sites) and the actual distance travelled (calculated as the sum of all 1-h segments within that day).

Finally, at the hourly scale, we computed ground speeds using the distance covered during 1-h travelling segments (>5 km/h) belonging to travelling days.

At the daily and the hourly scale each segment was considered as being inside or outside the desert (binary variable 'region') according to the latitude of its daily departure site, using a threshold of 31° N (Mellone et al. 2012), i.e. data between the breeding site and 31° N is considered as 'non-desert', while data between 31° N and the wintering site as 'desert'.

Statistical analysis

For all temporal scales, to analyse migration speeds, straightness and migration distances, we used linear mixed models (LMM); while to analyse travelling and non-travelling hours and days (count data), we applied generalised linear mixed models (GLMM) with Poisson error distribution and log-link function. In all models, bird identity was included as a random intercept.

We followed a top-down strategy for model selection; first, we found the optimal structure of the random part of the model, and then of the fixed one (Zuur et al. 2009). Random effects were examined considering models with a random intercept and models with a random intercept and random slope, with respect to all predictors for each individual. Small inter-individual variation was found in all cases. Models with random intercept and random intercept and slope did not differ significantly, setting that with bird identity as the random intercept as the most parsimonious model. Afterwards, we found the optimal structure of the fixed component following a stepwise model simplification. Data was log-transformed when required to account for normality and homoscedasticity, and the distribution of model residuals was examined to ensure the correct model choice. This procedure was followed for all models performed at each temporal scale (i.e. hourly, daily and overall). Statistical analyses were made with R software version 2.15.1 (2012, R Development Core Team, Vienna, Austria). LMM were performed with the 'nlme' package and GLMM with the 'lme4' package. For mixed models, we used the Kenward-Roger method to estimate degrees of freedom. Tukey's pairwise comparisons with 95 % confidence level were conducted with the 'multcomp' package.

Overall journey scale

We checked for seasonal and sex differences with respect to overall migration speed, number of non-travelling days and overall straightness by running three different models (one for each dependent variable) with season, sex and their interaction as fixed factors and bird identity as a random factor. Only statistically significant variables ($p<0.05$) are shown in the article. Further, we tested the effect of straightness and non-travelling days on migration speed using two additional LMMs.

Daily scale

To explore daily distance variation between the four possible combinations of season and region (spring and autumn inside and outside the desert), we performed a LMM with a four-level categorical variable as a fixed factor and bird identity as a random factor, followed by a Tukey's post-hoc test. Then, to analyse the effect of season (spring/autumn), region (inside/outside the desert), bird's sex (male/female) and abiotic variables (tailwind, day length and $w*$; including interactions with season), on daily distance, we followed a backward stepwise selection analysis, identifying the most parsimonious combination of explanatory variables, based on stepwise model simplification. We found the optimal structure of the random component (including the random intercept and random

intercept and slope) with the 'beyond optimal model' (Zuur et al. 2009), using AIC as the selection tool to find the optimal model. Following an inspection of model residuals and considering dispersion, we chose linear mixed models as the most appropriate.

We used also a LMM to test for seasonal differences in daily straightness. For travelling hours (count data), we used GLMM considering a Poisson error distribution and a log-link function.

Finally, seasonal and regional differences among abiotic variables were analysed, exploring variation among four categories (spring and autumn inside and outside the desert), followed by a Tukey's post-hoc test.

Hourly scale

To explore hourly speed variation between the four possible seasonal and regional combinations (spring and autumn inside and outside the desert), we performed a LMM with a four-level categorical variable as a fixed factor and bird identity as a random factor, followed by a Tukey's post-hoc test.

Results

Overall journey scale

Considering the whole journey (sample sizes: autumn=15, spring=10), there were significant seasonal differences but not sex ones in all three parameters (Table 1). Migration speed was faster in autumn than in spring (106.5±34.5 km/day in spring vs. 146.8±46.7 in autumn); migration routes were straighter during autumn (straightness index=0.76±0.13 in spring vs. 0.85±0.09 in autumn); and non-travelling days were less frequent in autumn (10±6 days in spring vs. 6±8 in autumn). Migration speed was positively correlated with straightness (t=4.6, p=0.0001, n=25) and negatively with the number of non-travelling days (t=−7.72, p<0.0001, n=25).

Table 1 Final LMMs showing the effect of season on three different variables at the overall journey scale; t values are given for speed and straightness (LMM, Gaussian error distribution) and z values for non-travelling days (GLMM with Poisson error distribution and log-link function)

Dependent variable	Estimate	SE	t/z	P value
Speed	41.63	13.14	3.17	0.001
Straightness	0.1	0.04	2.27	0.02
Non-travelling days	−0.58	0.15	−3.67	0.0001

Daily scale

The LMM exploring variation in daily distance among seasons and regions yielded significant results ($F_{3,\ 369}$=55.86, p<0.0001), with daily distance showing the lowest values in 'spring outside the desert', which significantly differed from the other three categories, as shown by the Tukey's post-hoc comparison test (Table 3).

The final LMM testing the effect of environmental factors on daily distance included season, region, tailwind and thermal uplift (Table 2), with booted eagles travelling faster during autumn and inside the desert (see also mean values in Table 3), favoured by tailwinds and thermal uplift. All tested interactions, and the variables sex and day length, were not significant.

With regards to abiotic variables, there were no differences among the four categories of tailwind ($F_{3,\ 377}$=1.78; p=0.15). Instead, significant differences occurred for thermal uplift ($F_{3,\ 377}$=55.86; p<0.0001) and day length ($F_{3,\ 377}$=49.98; p<0.0001). In particular, the best thermal values occurred in autumn outside the desert and in spring inside it (Table 3).

Within the subsample of travelling days when hourly data were available (n=160), there were no seasonal differences for both travelling hours (7.6±1.5 h in spring vs. 8.0±1.5 h in autumn; z=1.83; p=0.33) and daily straightness (S.I.=0.9± 0.08 in spring vs. 0.899±0.08 in autumn; t=0.81; p=0.42).

Hourly scale

At the hourly scale, significant differences in ground speed were confirmed by a LMM exploring variation in ground speed across four subsets of data (i.e. spring and autumn outside and within the desert; $F_{3,\ 2073}$=16.53; p<0.0001). Tukey post-hoc tests revealed that there were significant differences in the three pairwise comparisons including speed values from spring outside the desert (all p<0.001), being significantly lower than in the remaining three categories, in agreement with the analyses at the daily scale (Table 3). Although anecdotal, it is remarkable that the highest value of ground speed was 88 km/h (bird no. 68456) and was detected on a 4-h interval of a day with strong tailwind support in the desert during spring (9.6 m/s).

Table 2 Final LMM with daily distance as dependent variable

Explanatory variable	Estimate	SE	t	P value
(Intercept)	4.72	0.09	54.01	<0.0001
Season	0.21	0.04	4.79	<0.0001
Region	0.21	0.04	4.67	<0.0001
Tailwind	0.04	0.01	7.14	<0.0001
w*	0.00	0.00	3.35	0.0008

w* is a measure of thermal uplift, see the text for more details

Table 3 Average values (standard deviation in brackets) of different variables used for the analyses according to region and season categories

Category	Daily scale				Hourly scale		
	n	Daily distance	Tailwind (m/s)	$w*$	Day length (min)	n	Hourly speed
Autumn non-desert	69	193.2 (59.0)	−0.3 (2.3)	1179.6 (393.3)	761.7 (41.2)	433	26.2 (11.7)
Autumn desert	135	208.8 (87.4)	0.1 (3)	694.6 (234.1)	729.5 (22.8)	787	27.7 (13.8)
Spring desert	113	202.6 (85.1)	0.7 (4.4)	1173.6 (426.5)	719.6 (16.2)	558	26.4 (12.7)
Spring non-desert	64	145.3 (71.7)	0.7 (3.6)	706.2 (409.3)	752.2 (23)	306	21.5 (11.2)

$w*$ is a measure of thermal uplift, see the text for more details

Discussion

Competition for breeding resources has been suggested to be the main factor driving faster migration speed and time minimization during spring (Kokko 1999), and indeed this is the rule in many species (Nilsson et al. 2013). Hypothetically, faster migration during autumn might be promoted by competition for better winter territories (Greenberg 1986; Leisler 1990), albeit such a relationship has never been confirmed (but see, Higuchi et al. 2005; Agostini and Mellone 2007; Yamaguchi et al. 2008). Unexpectedly, booted eagles migrated more quickly during autumn than during spring, minimising time during autumn, even controlling for environmental conditions. This result was also confirmed by the analyses at different temporal scales, including the hourly scale, with faster ground speeds during autumn. In addition, overall straightness showed that routes were more linear in autumn than in spring.

Overall migration speed is shaped by the proportion of days allocated to travelling or to stopover (including non-travelling days during which fuel deposition does not take place), by daily flight range and by straightness. The higher the proportion of days devoted to travelling and their daily distance, the lower the migration duration will result. Furthermore, within a travelling day, the daily distance may be 'dissected' identifying three factors that act independently of each other, namely hourly ground speed, straightness and flight duration (number of travelling hours; Fig. 2). In our case, we found seasonal differences in the first parameter, since booted eagles showed higher hourly ground speed during autumn. Therefore, it seems that the overall shorter migration duration during autumn is mainly a result of such higher flight speeds, which enhance the daily distance, together with higher overall straightness and also by a lower amount of non-travelling days. Among abiotic factors, according to the LMM tailwind is the most important agent that increases the daily flight range, in agreement with previous results from other species migrating in the same regions (Mellone et al. 2012), although also thermal uplift proved to be statistically significant. Unlike other species wintering in the Sahel that are more nomadic such as Egyptian vultures and Montagu's harriers

(*Circus pygargus*; López-López et al. 2013; Trierweiler et al. 2013), booted eagles winter territories seem to be well constrained (Mellone et al. 2013b, authors unpublished data). Hence, it would be interesting to verify by field observations if they actively defend these territories, which could lead eagles to migrate more quickly during autumn. This could confirm a time-minimization strategy mediated trough competition for better winter territories operating during this season. An alternative hypothesis could be that resources in the wintering grounds decrease abruptly and therefore booted eagles are forced to begin the migration sooner and migrate slowly in order to arrive to the breeding grounds not too early, especially in the case of individuals breeding in the central mountains of Spain, where optimal conditions are more delayed. Furthermore, booted eagles may be selected to migrate at a slower pace during spring, discarding a sprint strategy, in order to be able to start reproduction without the need of replenish quickly their energy reserves upon arrival at breeding areas (Alerstam 2006; see also, Sirot and Touzalin 2014). By doing this, booted eagles could be even in better condition to ensure and defend a good site for reproduction after arrival at their breeding areas. In this scenario, it is interesting to note that according to our data booted eagles occupy their breeding territories as soon as they arrive to Spain. Instead, a similar trans-Saharan migratory raptor like the Egyptian vulture does not occupy its breeding territories just after arrival (López-López et al. 2013, 2014b) although it shows higher speeds during spring over the Sahara desert (when controlling for wind conditions, see Mellone et al. 2012). Interestingly, unlike booted eagles, Egyptian vultures replenish their energy reserves after their arrival to breeding grounds, using staging areas far away from their breeding sites before the onset of breeding activities (García-Ripollés et al. 2010; López-López et al. 2014a, b).

Regional differences in speed (at both hourly and daily temporal scale) were absent during autumn but not during spring. Overall, it seems that differences in speeds are mainly due to the slow speeds recorded during spring outside the desert, in the last step of the migration journey, both at the daily and the hourly scale. On the contrary, during autumn, no regional differences occurred: perhaps booted eagles maintain

the same high speed as outside the desert, even if the thermal uplift is not as favourable (see Table 3), in order to overcome the ecological barrier as early as possible and complete soon the last leg of autumn migration, also to occupy immediately the winter territories (see above). Instead, during the last leg of spring migration, outside the desert, thermal uplift values are as low as in autumn within the desert (ca. 700; see Table 3), but the habitat is more favourable and therefore the eagles have less pressure to migrate quickly. Unlike raptors using powered flight, such as the Osprey *Pandion haliaetus* or the Eleonora's falcon *Falco eleonorae* (Klaassen et al. 2008; Mellone et al. 2013a), booted eagles are expected to fast during migration, relying only on fuel reserves accumulated before and thus, with no need to forage. Despite their fasting behaviour during migration, stopping involuntarily for many days in an unfavourable habitat could have serious consequences for fitness (Strandberg et al. 2010). Another soaring and fasting migrant, the Honey buzzard, also increases its speed during desert crossing, but there are only autumn data in this respect (Hake et al. 2003).

It is highly likely that non-travelling days occurring in the desert and close to the Strait of Gibraltar were caused by bad weather conditions (Mellone et al. 2013b). On the other hand, is difficult to confirm whether non-travelling days recorded in non-desert areas far from the Strait of Gibraltar were used for fuel deposition. Hunting behaviour during migration has been investigated in satellite-tracked Ospreys, which only feeds on lakes (Klaassen et al. 2008) but, since booted eagles can forage in a high variety of habitats (Cramp and Simmons 1980), our satellite tracking data do not allow confirming foraging activities. A likely exception, although not supported by visual confirmation of its behaviour, would be the case of one individual (no. 91724211) that stopped for several weeks (27 days in autumn, 17 in spring) during both migrations in the same restricted area, located ca. 250 km south of the Strait of Gibraltar in an apparently suitable habitat for foraging.

In conclusion, here we have shown how the migration patterns of a long-distance migrant can be shaped by the interaction of landscape characteristics, weather conditions and flight behaviour. Our results clearly show that the booted eagles migrate faster during autumn than during spring and opens new questions about which behavioural and ecological aspects promote such unexpected behavioural pattern. Further information is needed, especially from other species/ populations that breed in Mediterranean environments and that therefore experience a window of optimal breeding conditions longer than species breeding at more northern latitudes. Perhaps these birds experience a lower selective pressure than birds breeding at northern latitudes to reach the breeding areas as early as possible (see also, Panuccio et al. 2014).

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