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Nocturnal bird migration in the Bay of Biscay as observed by a thermal-imaging camera

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ABSTRACT

Capsule: Bird migration was recorded by an infrared device at three sites in the southeastern Bay of Biscay, indicating seasonal east–west differences in migration flow.

Aims: The main aims of this study were to quantify and describe nocturnal migration dynamics in proximity of a sea barrier, and to assess seasonal and geographical drivers of migration patterns.

Methods: A thermal-imaging camera was used at two coastal study sites (Punta Galea, Cape Higuer) in spring and three study sites (coast: Punta Galea, Cape Higuer; inland: Iregua Valley) in autumn for four hours from sunset over 90 nights in 2014 and 2015.

Results: Migration was strong at both coastal sites in early spring. Autumn migration was weak at the western coast, but strong at the eastern coast and inland. Tailwind had no significant effect on migration intensity, but migration ceased during strong cross- or headwinds despite clear skies. The majority of the targets were passerines.

Conclusions: The patterns observed suggest spring migration occurs on a broader front, potentially involving sea crossing further to the west, while autumn migration concentrates more eastwards over land. In both seasons, there was no significant response to wind conditions.

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The East-Atlantic flyway represents one of the principal migration routes in Europe, comprising the Bay of Biscay as a geographical barrier for migratory landbirds. Few studies have been published concerning the role of the Bay of Biscay in bird migration. In their study on diurnal autumn migration through the Pyrenees, Lack & Lack (1953) observed great numbers of birds coming in from the Bay of Biscay as well as travelling along the coast and then continuing inland. They concluded that migration was proceeding on a broad front. In another study, which was based on passerines ringed at several coastal stopover sites along the Bay of Biscay, Arizaga *et al.* (2014) reported much weaker passage in spring compared to autumn. By contrast, a coastal operational radar located in the southeastern Bay of Biscay revealed high nocturnal activity in spring and low activity in autumn (Weisshaupt *et al.* 2014).

It is well known that variations in migration strategies found in short- and long-distance migrants cause changes in the spatial and seasonal flow of migration (Bruderer & Liechti 1999) resulting in different routes in spring and autumn (Klaassen *et al.* 2010, Agostini *et al.* 2012, Willemoes *et al.* 2014). For instance, in Iberia some migrants select more western (Atlantic)

flyways in autumn, but more eastern (Mediterranean) flyways in spring (Bairlein 2001).

Also prevailing seasonal meteorological conditions could have an impact on migratory routes, for example, when crossing geographical barriers (Thorup *et al.* 2003, 2006). Adverse weather, such as headwinds or precipitation, halt or delay the crossing of barriers, as it could entail excessive energy costs or increase mortality risk (Richardson 1978, Liechti & Bruderer 1998). Prevailing conditions over a given barrier could then eventually determine if migrants decide to cross or to make a detour. So basically, tailwinds (north- to north-easterly in autumn; south- to south-westerly in spring) both in autumn and spring would be expected to promote migration over the open sea of the Bay of Biscay. However, as the study region is characterized by a highly variable meteorological environment dominated by westerlies, the anticipated high numbers of autumn migrants would be faced with headwinds which might prevent them from flying over water. Interestingly, some studies suggest that birds also travel under suboptimal conditions, such as in headwinds or crosswinds, because waiting for optimal conditions would result in a major delay (Bruderer 1999, Karlsson

et al. 2011, Chapman *et al.* 2016). So, alternatively, it is also possible that tailwinds have a minor impact on migration intensity at the bay, given the overall challenging weather setting.

A large proportion of migratory movements occur at night (Alerstam 1990). Studying active nocturnal migration *per se* excludes certain sampling methods based on its very nature, such as ringing and visual counts. One available technique to study nocturnal activity is thermal-imaging (Liechti *et al.* 1995, Zehnder *et al.* 2001a, Gauthreaux & Livingston 2006). Such infrared devices are highly sensitive to even small temperature differences. Depending on the camera model and meteorological conditions, objects can be registered at distances of up to several kilometres (Liechti *et al.* 1995). General pros and cons of thermal-imaging are reviewed in McCafferty (2013). One of the advantages is that thermal-imaging allows us to obtain various migration parameters, such as migration intensity, direction and spatial arrangement of migrants (e.g. dense flocks vs. individuals). Flight altitudes can be estimated based on size classification of targets (Zehnder *et al.* 2001a). A further benefit is the ease of use and quick start-up of such cameras. Their relatively small size and weight permit swapping easily between study sites within a short time. A disadvantage is that thermal-imaging cameras alone cannot be used to identify species (Gauthreaux & Livingston 2006). However, it can be assumed that the major proportion of nocturnal migration concerns passerines migrating alone or in loose flocks, while larger flocks and many non-passerines (e.g. soaring species) tend to be more common on diurnal migration (Bruderer 1971, Alerstam 1990). Finally, as a consequence of temperature sensitivity, thermal-imaging devices strongly depend on thermally uniform environments for optimal data collection, such as completely clear or overcast skies, because thermal radiation from moving cloud layers could hamper the detection of birds (Zehnder *et al.* 2001a, Gauthreaux & Livingston 2006). Also humidity has been observed to affect thermal-imaging negatively.

The aim of this study is to characterize and quantify nocturnal migration along the coast of the southeastern Bay of Biscay (northern Iberia) in order to (1) characterize migration phenology, (2) determine the potential impact of wind conditions on the spatial and temporal variations in migration intensity and (3) identify the main types of migrants passing, based on flight patterns, singly flying passerines or flocks.

Based on available data, we would expect to find broad-front migration in spring including sea crossing,

with comparable migration intensities and directions along the coast. In autumn, a more easterly concentration of migration is anticipated, with a pronounced coastal east-west gradient, with superior migration intensity in the innermost bay area and inland, and generally higher numbers of migrants compared to spring. Overall, wind assistance would be expected to favour migration, but it might play a secondary role based on the challenging nature of overall weather situations.

Methods

Data collection

A long-range thermal-imaging camera (LORIS, IRTV-445L, Inframetrics, Massachusetts, USA) was used with an opening angle of 1.45°. From direct comparisons with tracking radar it is known that the camera is able to detect small-sized passerines up to 3000 m above ground level in clear skies (Bruderer & Liechti 1994, Liechti *et al.* 1995).

Data were collected at three sites in northern Iberia: two on the Basque coast (Punta Galea, Bilbao 43°22'N 3°02'W; Cape Higuier, Hondarribia 43°23'N, 1°47'W) and one inland in the Iregua Valley, Ebro river basin, at Villoslada de Cameros (42°04'N 2°41'W) (Figure 1). The two coastal sites were selected to account for a possible east–west gradient in migration intensity, while the third site served as an inland reference point with a possible north–south gradient. The sampling was designed as follows: (1) in spring 2014, ten nights



Figure 1. Locations of the three sampling sites used to quantify bird migration across the Bay of Biscay: Punta Galea, Cape Higuier and Iregua Valley (Northern Spain).

were sampled each in March, April and May at Punta Galea (west); (2) in autumn 2014 (from August to October), 15 nights were sampled each at Punta Galea (west) and Cape Higuier (east) and ten nights in the Iregua Valley (inland); (3) in spring 2015, ten nights were sampled each at Punta Galea (west) and Cape Higuier (east) from March to April.

The number of sampling days was chosen to obtain a representative temporal coverage of migration at each site, switching between sites every second day if weather permitted. Sampling took place only on nights with no rain and with as clear skies as possible, to minimize a potential bias resulting from precipitation and cloud cover and to enhance detection of targets in the camera. The camera was positioned vertically and oriented to the north with the aid of a compass to facilitate posterior extraction of the migratory directions. Passing migrants were observed on a television screen and video-taped during 4 h from sunset. Subsequently, the videotapes were digitized for further analysis.

Meteorological data

Wind data for the three sampling sites were collected from the National Oceanic and Atmospheric Administration (n.d.), U.S. Department of Commerce. Particularly, both u and v wind components were used for pressure levels of 700, 850 and 925 mb, corresponding approximately to an altitude of 3250, 1500 and 775 m above sea level, respectively, at 18:00 and 00:00 h. The mean tailwind from 18:00 and 00:00 h was included as an additional variable accounting for possible fluctuations in wind parameters in the course of this six-hour interval. Based on the wind data, tailwind components were calculated as $V_w \cos(\phi_T - \phi_W)$, where V_w was the wind velocity, ϕ_T was the mean preferred track direction (in this case, 225° for the autumn migration period, and 45° for the spring migration period) and ϕ_W was the wind direction (Åkesson & Hedenström 2000).

Data analysis

Flight directions

For the extraction of flight directions the software Kinovea was used. All tracks were time stamped and classified by hour (hour 1–4, starting at sunset). All those targets which did not follow a straight trajectory (e.g. curves, sudden reversions) or which might have originated from bats or insects ('bubbles' as described in Zehnder *et al.* 2001a) were excluded. Flight tracks were analysed by means of the R package *circular* and

Oriana. Mean directions were calculated for each site and season. Following Zehnder *et al.* (2002a, 2002b), directions were classified as 'forward migration', if they fell within the site- and season-specific mean migration direction (mean direction $\pm 60^\circ$), or as 'reverse migration', if they fell within the range of directions $\pm 60^\circ$ around mean + 180°. A Rayleigh test was applied to test for the variance associated with the site- and season-specific circular distributions (uniform versus concentrated). A Watson–Williams test was used to test for variations in mean directions. Flight tracks were not corrected for possible wind drift.

Flight altitude

Targets were assigned to seven size categories, corresponding to flight altitudes from 0.3 km (Class 7) to 2.1 km (Class 1) (*sensu* Zehnder *et al.* 2001a). However, the camera could detect birds at higher levels of up to at least 3 km (Liechti *et al.* 1995). Therefore the scale of the size categories is only to be considered an approximation, reflecting mainly altitudinal distribution rather than exact flight altitude levels. Gauthreaux & Livingston (2006) criticized the use of thermal-imaging as a stand-alone method, pointing out the potential errors when dealing with differently sized birds and any resulting effect on flight altitude estimation. However, the camera used in this study was tested and calibrated previously by tracking radar by Liechti *et al.* (1995), and findings indicated size bias in nocturnal songbirds was negligible.

Migration intensity

The migration traffic rates (MTR) were computed to account for the conical sampling in which the surveyed volume increases with distance of the target to the recording device (Lowery 1951). The MTR represents the number of birds passing a line of one kilometre perpendicular to the flight direction in one hour (birds * km⁻¹ * h⁻¹). For each site the mean MTRs were calculated per night, month and season (for details see Zehnder *et al.* 2001a). The effect of factors potentially driving migration intensity was tested by generalized linear models in the program R (R Development Core Team 2008). The analyses were conducted with three separate data sets: (1) Punta Galea (west) in spring 2014, (2) Punta Galea (west) and Cape Higuier (east) in autumn 2014 and spring 2015 and (3) Punta Galea (west), Cape Higuier (east) and Iregua Valley (inland) in autumn 2014. The purpose of conducting three separate analyses was to better disentangle seasonal and geographical patterns. Log-transformed (log transformation plus 1 to account for 0 values) hourly MTR values were set as the

response variable and the independent explanatory variables were: site (only in analyses 2 and 3), hour, month (only analysis 1), season (only analysis 2) and tailwind components. Site, hour, month and season were included as discrete control factors, while tailwind components were included as linear (quantitative) variables. The tested models included all combinations of one of the six tailwind variables (for three heights and two instants of time, see above) and the other variables, as well as double interactions, though not the full model because of the many types of tailwind variables and potential confounding effects.

All models were ranked according to their small sample size corrected Akaike values (AICc) by means of the function *model selection* of the R package *MASS* and *MuMIn* (Burnham & Anderson 1998, Johnson & Omland 2004). Models differing by less than 2 AICc values were assumed to support the data equally well. *B*-parameters with $P > 0.05$ were considered to be non-significant.

Results

Overall, 11 804 bird tracks from 420 h of video recordings were included in the analysis: 6144 tracks for Punta Galea (west) (4249 in spring 2014, 292 in autumn 2014, 1603 in spring 2015), 4657 for Cape Higuier (east) (2217 in autumn 2014, 2440 in spring 2015) and 1003 for the Iregua Valley (inland) in autumn 2014. Overall, 698 tracks were excluded from analysis, that is, 116, 542 and 40 in spring 2014, autumn 2014 and spring 2015, respectively, which belonged to potential insects or other objects, or tracks without a clear heading (e.g. curves or reversion). Only 0.6% of all the flight tracks belonged to visually distinct flocks of 2–15 individuals.

Flight directions

The Rayleigh test showed that circular data in each season and site were not uniformly distributed, but exhibited a preferential migratory direction ($P < 0.001$). Overall, flight directions tended to be more concentrated in spring than in autumn. The mean percentage of tracks falling within $\pm 60^\circ$ around the mean site- and season-specific directions was 95.8% in spring (Table 1). Overall, tracks were more unidirectional in the three highest levels, that is Classes 1–3, than in lower levels. Mean directions in the three upper height levels concentrated within $\pm 10^\circ$ around the seasonal mean, while in the lower levels mean values deviated between 2° and 144° (online Supplementary Appendix 1). Reverse migration

Table 1. Mean (\pm se) migratory direction by site and season. Forward migration is defined as being within 60° of mean directions; reverse migration is defined as being within 60° of the opposite to mean directions.

| Site/Season | Mean \pm se direction | % forward migration | % reverse migration |
|------------------------|-------------------------|---------------------|---------------------|
| Punta Galea (west) | | | |
| Spring 2014 | 47.9° \pm 0.5° | 95.2 | 1.6 |
| Autumn 2014 | 251.6° \pm 4.7° | 63.6 | 19.9 |
| Spring 2015 | 45.9° \pm 0.7° | 96.3 | 0.7 |
| Cape Higuier (east) | | | |
| Spring 2015 | 61.1° \pm 0.6° | 95.9 | 1.6 |
| Autumn 2014 | 255.7° \pm 1.2° | 78.6 | 9.5 |
| Iregua Valley (inland) | | | |
| Autumn 2014 | 220.6° \pm 1.4° | 85.6 | 7.4 |

occurred overall less frequently in spring (<2% of tracks) than in autumn (7.4–19.9% of tracks). The highest nightly MTR of reverse migration occurred at Cape Higuier (east) in October 2014, with 303 birds \cdot km⁻¹ \cdot h⁻¹ moving NE. A chi-square test showed no significant differences in the proportion of forward and reverse migration between Punta Galea (west) and Cape Higuier (east) in spring ($\chi^2 = 3.62$, $P > 0.05$) or between spring 2014 and spring 2015 at Punta Galea (west) ($\chi^2 = 4.64$, $P > 0.05$). The proportion of reverse and forward migration between sites differed significantly in autumn (Punta Galea [west] and Cape Higuier [east] $\chi^2 = 9.35$; Punta Galea [west] and Iregua Valley [inland] $\chi^2 = 20.05$; Iregua Valley [inland] and Cape Higuier [east] $\chi^2 = 8.03$; $P > 0.05$), with the highest rate of reverse migration at the western coastal site (Punta Galea) and lowest at the inland site (Iregua Valley).

Mean directions between the two coastal sites differed significantly in spring ($F_{1, 4041} = 270.9$, $P < 0.001$; online Supplementary Appendix 1), pointing more eastwards in the east, compared to more northern directions in the west. In autumn, there were also significant differences between each coastal site and the Iregua Valley (inland) (Iregua Valley [inland] and Punta Galea [west], $F_{1, 1292} = 63.811$, $P < 0.001$; Iregua Valley [inland] and Cape Higuier [east], $F_{1, 3219} = 323.89$, $P < 0.001$) which showed more southward directions, but not between the two coastal sites ($F_{1, 2507} = 1.033$, $P = 0.3$) (online Supplementary Appendix 1).

Flight altitude

Most (80–100%) of the tracks concentrated at high altitude in Classes 1 and 2 (corresponding to an estimated altitude of 2.1 and 1.9 km, respectively), with only marginal activity in the lower levels (classes 3–7;

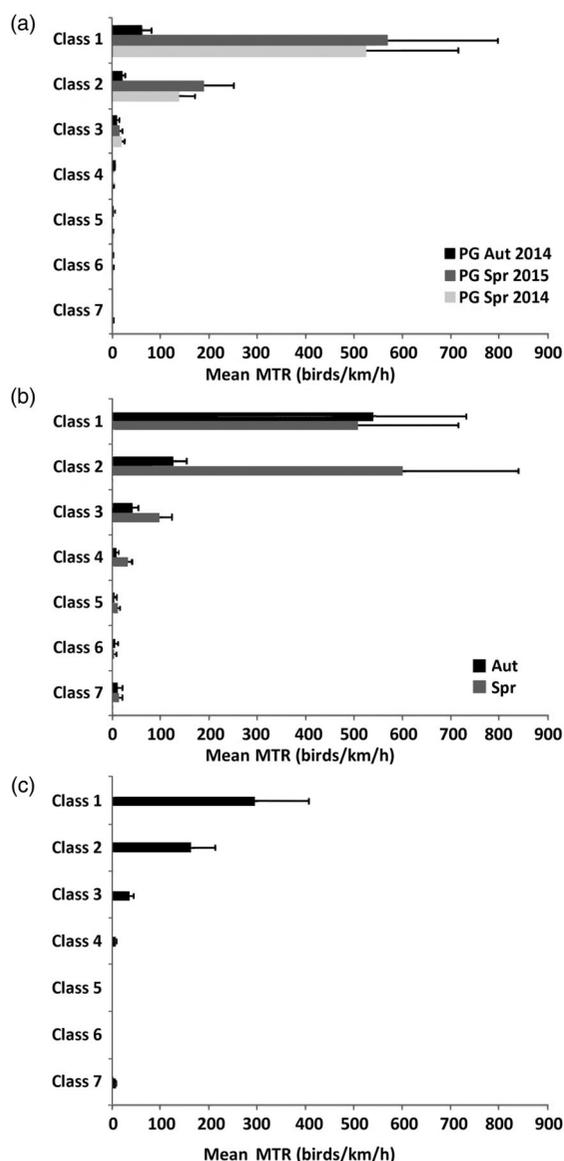


Figure 2. Migration altitudes in relation to the site and season determined by means of a thermal-imaging camera operating during a period of 4 h from sunset (a) Punta Galea (west); (b) Cape Higuier (east) and (c) Iregua Valley (inland).

Figure 2). Overall, tracks were more unidirectional at the three highest levels (classes 1–3), than at lower levels.

Migration intensity

The general migration pattern observed during each four-hour sampling was unimodal, with an activity peak either during the second or third hour after sunset (Figure 3). Migration intensity varied considerably between nights. Hourly MTRs ranged from 0 to 6713 birds * km⁻¹ * h⁻¹ and nightly mean MTRs from 0 to 5290 birds * km⁻¹ * h⁻¹ with only a small proportion of high-traffic nights of more than

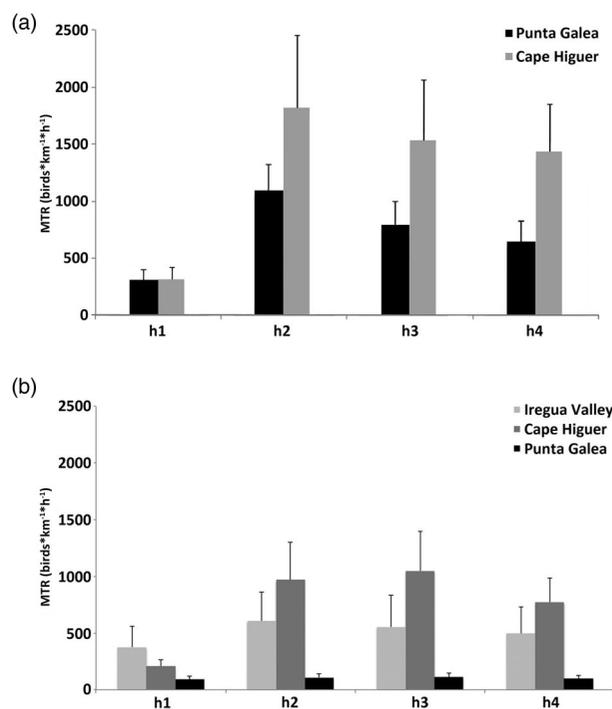


Figure 3. Mean (\pm se) hourly migration intensity in relation to site and season (a) spring and (b) autumn. Years have been pooled for the analysis.

3000 birds * km⁻¹ * h⁻¹ (Supplementary Appendix 2). At Punta Galea (west) in spring 2014, migration intensity declined steeply from a monthly mean of 1458 birds * km⁻¹ * h⁻¹ in March to 483 birds * km⁻¹ * h⁻¹ in April and finally 53 birds * km⁻¹ * h⁻¹ in May. At Cape Higuier (east) a similar, though less pronounced tendency could be observed with 1461 birds * km⁻¹ * h⁻¹ in March and 995 birds * km⁻¹ * h⁻¹ in April. In autumn, August was the month of least activity at all sites. September was the peak month at Cape Higuier (east) (996 birds * km⁻¹ * h⁻¹) and in the Iregua Valley (inland) (623 birds * km⁻¹ * h⁻¹), while Punta Galea (west) exhibited a small peak in October (128 birds * km⁻¹ * h⁻¹).

For Punta Galea (west) in spring 2014, only one model fitted the data better than the rest (Table 2). This model showed that MTR varied between months and between the four hours from sunset. The analysis of *B*-parameters revealed that the MTR peaked in the second hour after sunset and reached its highest values in March (Table 3, Figure 4).

The comparison between Cape Higuier (east) and Punta Galea (west) in autumn and spring showed a significant effect of site and season on MTR (Table 4). The interaction between site and season was not significant (Table 5), but migration intensity in autumn was significantly lower than in spring, and higher at Cape Higuier (east) than at Punta Galea (west) (Table 5).

Table 2. Rank of the model with lowest AIC and the null model (birds~1) used to identify the variables determining the intensity of nocturnal bird migration at Punta Galea (west) during spring 2014. Other candidate models were ranked within a position of >2 AICc values from the best model. Abbreviations: AICc, small sample sizes-corrected Akaike values; Δ AICc, difference in AICc values in relation to the top model.

| Models | AICc | Δ AICc | AICc weight | Number of parameters |
|-----------------|-------|---------------|-------------|----------------------|
| 1. Month + Hour | 271.8 | 0.0 | 0.99 | 7 |
| 2. Null | 335.2 | 63.3 | 0.00 | 1 |

Table 3. B-parameter estimates obtained from the model with lowest AIC of Table 2.

| Parameters | B | se (B) | P |
|--------------------------|-------|--------|--------|
| (Intercept) | +2.16 | 0.17 | <0.001 |
| Month: Apr. ^a | -0.30 | 0.17 | 0.086 |
| Month: May ^a | -1.37 | 0.17 | <0.001 |
| Hour 2 ^b | +1.00 | 0.20 | <0.001 |
| Hour 3 ^b | +0.65 | 0.20 | 0.001 |
| Hour 4 ^b | +0.55 | 0.20 | 0.007 |

Note: Hour 1, 2, 3 and 4 refer to hours after sunset; Hour 1 = first hour from sunset.

^aReference values ($B = 0$): Month = Mar.

^bReference values ($B = 0$).

Autumn analysis of the three sampling sites also yielded two models which fitted the data better than the rest (Table 6). These models included the interaction between site and tailwind at 775 and 1500 m above ground level, respectively, at 18:00 h. However, in model averaging, only the site variable was significant (Table 7).

Discussion

This is the first thermal-imaging study to determine nocturnal bird migration phenology at the Bay of Biscay. Migration altitude, direction and intensity at

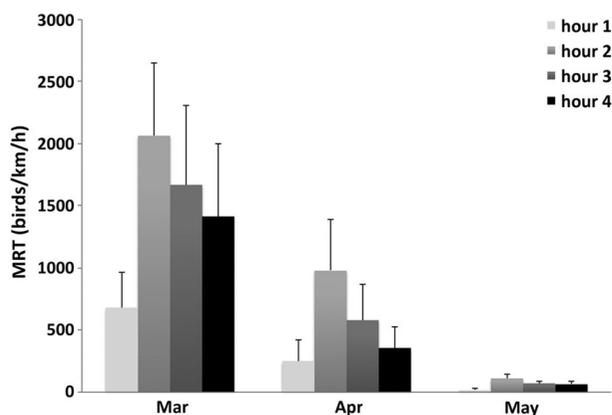


Figure 4. Mean (\pm se) migration intensity by month at Punta Galea (west) during spring 2014.

Table 4. Rank of the model with lowest AIC and the null model to identify the variables determining the intensity of nocturnal bird migration at Punta Galea (west) and Cape Higer (east) in autumn 2014 and spring 2015. Other candidate models were ranked within a position of >2 AICc values from the best model.

| Models | AICc | Δ AICc | AICc weight | Number of parameters |
|-------------------------|-------|---------------|-------------|----------------------|
| 1. Site \times Season | 550.4 | 0.0 | 0.52 | 5 |
| 2. Site + Season | 551.8 | 1.3 | 0.27 | 4 |
| 3. Null | 587.0 | 36.6 | 0.00 | 1 |

Table 5. B-parameter estimates obtained from model averaging of the models 1 and 2 of Table 4.

| Parameters | B | se (B) | P |
|--------------------------------------|-------|--------|--------|
| (Intercept) | +2.06 | 0.16 | <0.001 |
| Season: Autumn ^a | -0.55 | 0.21 | 0.010 |
| Site: Cape Higer (east) ^b | +0.59 | 0.24 | 0.012 |
| Season \times Site | +0.33 | 0.32 | 0.308 |

^aReference values ($B = 0$): Season: Spring.

^bReference values ($B = 0$): Site: Punta Galea (west).

three sites within the East-Atlantic flyway, exhibited large inter-night fluctuations, but also spatio-temporal variation in relation to the site and season. The majority of registered tracks stemmed from single flying birds, indicating a predominance of passerines, as found in other regions (Bruderer 1971, Alerstam 1990). The small fraction of birds in compact flocks or line formations probably can be ascribed to waterfowl or waders, based on findings from a parallel moonwatching study (Weissaupt *et al.* 2016).

Even though clear skies were preferably selected for sampling, interference from small-scale and large-scale weather changes still occurred given the highly variable meteorological conditions in the study area. In connection with this, a detection bias cannot be excluded through cloud layers and/or wind conditions, which might have prompted the birds to fly at higher/lower altitudes within or beyond the scope of the camera. However, this effect, if any, would be expected to affect all sites more or less equally in each season and thus the fluctuations cannot be solely attributed to weather, but do actually reflect variable numbers of migrants.

Table 6. Rank of the models with Δ AICc <2 and the null model to identify the variables determining the intensity of nocturnal bird migration at Punta Galea (west), Higher Cape and Iregua Valley (inland) in autumn 2014. Tailwind refers to values at 775 and 1500 m above sea level at 18:00 h.

| Models | AICc | Δ AICc | AICc weight | Number of parameters |
|--------------------------------|-------|---------------|-------------|----------------------|
| 1. Site \times Tailwind 775 | 411.7 | 0 | 0.53 | 7 |
| 2. Site \times Tailwind 1500 | 413.1 | 1.4 | 0.27 | 7 |
| 3. Null | 451.5 | 39.8 | 0.00 | 1 |

Table 7. *B*-parameter estimates obtained from the model averaging of the models 1 and 2 of Table 6. Tailwind refers to values at 775 and 1500 m above sea level at 18:00 h.

| Parameters | <i>B</i> | se (<i>B</i>) | <i>P</i> |
|---|----------|-----------------|----------|
| (Intercept) | +1.46 | 0.11 | <0.001 |
| Site: Cape Higuier (east) ^a | +1.14 | 0.18 | <0.001 |
| Site: Iregua Valley (inland) ^a | +0.68 | 0.21 | 0.001 |
| Tailwind 775 | -0.01 | 0.02 | 0.67 |
| Cape Higuier (east) × Tailwind 775 | +0.05 | 0.05 | 0.29 |
| Iregua Valley (inland) × Tailwind 775 | +0.09 | 0.08 | 0.22 |
| Tailwind 1500 | +0.00 | 0.01 | 0.86 |
| Cape Higuier (east) × Tailwind 1500 | +0.02 | 0.03 | 0.56 |
| Iregua Valley (inland) × Tailwind 1500 | +0.04 | 0.05 | 0.51 |

^aReference values (*B* = 0): Site: Punta Galea (west).

Flight directions and altitude

Mean directions in both spring and autumn were in line with the main migratory axis (northeast in spring, southwest in autumn) through western Europe (Zink 1970, Hilgerloh 1989, Trösch *et al.* 2005). The significant statistical difference between the two coastal sites Punta Galea (west) and Cape Higuier (east) in spring remains unclear. It could be due to a possible divide in migration flow between birds of more western versus eastern breeding grounds or an influence of topography at a local scale. Interestingly, however, we did not detect any significant difference between the two coastal sites in autumn, but only between the coastal sites and the inland site (Iregua Valley). This difference suggests a shift to a more southern direction towards the interior of Iberia compared to the coast, which might be the beginning of the ‘zugknick’: a pronounced migratory directional shift southwards found in various species in southwestern Europe (Gwinner & Wiltschko 1978, Beck 1984, Hilgerloh 1985, Liechti *et al.* 2012). This scenario would also be supported by the low MTR values at the western site and more similar MTRs between the eastern and the inland site. Alternatively, it could be argued that birds simply followed the direction of the valley in which sampling took place. However, this conclusion seems less likely given the complex topography of the mountainous area with short, rather high valleys of varying alignments, surrounded by the extensive Ebro valley. Furthermore, on a more local scale, the valley in question extends on a more southerly axis of 190–205°, compared to the mean migration direction of 220.6° (± 1.4°).

Flight directions were highly unidirectional in spring with only a negligible proportion of reverse migration (<2%). In contrast, autumn showed a significantly higher scattering with the highest rate of reverse migration at Punta Galea (west) (approximately 20%). It is unlikely that this pattern was due to weather

conditions only because abrupt weather changes occur both in autumn and spring. A plausible explanation would be the higher proportion of juvenile birds in autumn (Zehntindjiev & Liechti 2003, Nilsson *et al.* 2014).

Considering the seasonal patterns and the geographical setting, the mean migration direction suggests movement on a broader front, including sea crossing in spring. In principle, the mean direction can be interpreted in two ways: (1) migrants follow the coast and do not cross the open sea of the bay, as directions at Punta Galea (west) coincided well with the coastline both in spring and autumn or (2) the parallel direction is by chance and birds fly well out across the sea at Punta Galea (west). The actual strategy could be a combination of the two hypotheses. While passing the study site, birds still follow the coastline until reaching the northernmost point and then fly out to the sea. This interpretation is supported by both the seasonal patterns and the mean direction at Punta Galea (west) in spring pointing to the region of Bordeaux, France. Such a trajectory would coincide with a direct distance of approximately 250 km which could be covered by a songbird in a single non-stop flight (Bruderer & Boldt 2001). Taking into account the observed southern directions at the autumn inland site, it seems reasonable to conclude that birds would perceive the western site as an unnecessary detour when heading south over land in autumn, but not in the face of the time pressure in spring.

Another indicator of sea crossing is the predominance of high flight altitude, as reported in this study, while low nocturnal altitudes are associated with coasting or landing (Bruderer & Liechti 1998, Nilsson *et al.* 2014). Studies in other coastal areas, such as in southern Scandinavia, found a similar pattern (Zehnder *et al.* 2001a, Nilsson *et al.* 2014). The mountainous region around the Iregua Valley (inland) with peaks of about 2000 m above sea level could account for a similar effect. Zehnder *et al.* (2001b) reported flight altitudes of less than 3500 m in the Alps, stating that birds avoid climbing/descending flights between valleys and mountains by choosing high flight altitudes in mountains. More research is needed to answer this question conclusively.

Migration intensity

The overall migration intensity peaked during the second or third hour after sunset, independently of the site and season. This is in agreement with findings from earlier studies (Alerstam 1976, Dolnik 1990, Bruderer 1997), and has been linked to the main take-off period in the first hour after sunset. Local radar

data (Weisshaupt *et al.* 2014) showed a similar pattern, with bird migration extending 1–2 h after sunset across the entire height profile (i.e. to be interpreted as a peak) and then signals continued (or were absent) in a slightly narrower, but uniform altitudinal extension, throughout the night. Therefore, the low autumnal intensity observed at Punta Galea (west) in the first half of the night cannot be explained by the hypothesis that migrants potentially crossing the sea have not reached the area yet, even though such a pattern would remain unappreciated in measurements during the first four hours after sunset. It rather reflects actual absence of migration in the area. It seems more reasonable that spring migration occurs on a broad front, while autumn migration is concentrated more eastwards with migrants entering Iberia over the continent and potentially avoiding sea crossing. This explanation would be also supported by the observed steep east-west decrease of MTRs between the two coastal sites Punta Galea (west) and Cape Higuier (east) as well as findings based on ring-recovery analyses for northern Iberia (Galarza & Tellería 2003). Diverging spring and autumn migration routes have been shown for various species (Klaassen *et al.* 2010, Willemoes *et al.* 2014) and have been attributed to greater time pressure to reach the breeding grounds in spring (Kokko 1999). Concentration over land in autumn could be also explained by a higher proportion of juvenile birds choosing a safer route.

At the two coastal sampling sites the migration intensity in spring was characterized by several extreme migration events (nightly MTR between 3500 and 6000 birds * km⁻¹ * h⁻¹) alternating with nights of low and medium migration intensities (0–1500 birds * km⁻¹ * h⁻¹). A bias on intensities is possible given that only one camera was available and no simultaneous measurements were possible. However, it can be assumed that all sites underlie the same probability of missing low or high intensities based on the study design (sampling intervals of 1–3 days per site), so the bias is expected to be negligible. The inter- and intraseasonal decrease at Punta Galea (west) fits with radar findings obtained by Weisshaupt *et al.* (2014) at the same site. Spring MTRs from Punta Galea (west) (1458 birds * km⁻¹ * h⁻¹ in 2014; 778 birds * km⁻¹ * h⁻¹ in 2015) indicate that data from one season may be insufficient to properly reflect the typical numbers of a site. External drivers, such as weather conditions, can probably have a strong impact on migration dynamics. February 2015 brought severe winter weather with snow down to the coastline and low temperatures prevailing until March. Furthermore, there were long periods of northerly and partially easterly winds. So it

cannot be ruled out that these adverse large-scale weather conditions possibly influenced the observed lower migration intensity at Punta Galea (west) compared to the previous year.

Overall, however, a decreasing number of migrants in the course of spring is in accordance with the idea that spring migration in this region is mainly shaped by short-distance migrants, probably overwintering in Iberia or northern Africa, rather than long-distance migrants spending the winter in tropical Africa (*sensu* Finlayson 1992). This interpretation is also compatible with the fact that Eurasian Reed Warblers *Acrocephalus scirpaceus*, a long-distance migrant captured in the study region, were caught in very low numbers during ringing campaigns on the Basque coast in spring (Arizaga *et al.* 2014).

Interestingly, tailwind did not have any significant effect on migration intensity. Despite that result, however, migration in spring ceased completely during strong easterly or northerly winds (i.e. direct or lateral headwinds) even though skies were clear. Thus, migrants may not show a clear preference for one particular wind direction, but simply for winds that would offer some tailwind component, and which may remain unappreciated in some of the analyses because of the wide range of wind directions (Nisbet & Drury 1967, Steidinger 1972).

Conclusions

In conclusion, thermal-imaging provided novel insights on nocturnal migration phenology at the southeastern coast of the Bay of Biscay, complementing previous data from diurnal studies. Flight directions, altitudes, as well as seasonal and geographical variations in migration intensity, indicate that spring migration occurs on a broader front than autumn migration, potentially involving sea crossing. In autumn, there is a pronounced east–west gradient, indicating a more eastern migration flow. Tailwind assistance did not have any significant impact on the spatial and temporal variation of migration. The majority of the tracks originated from single flying birds, indicating a predominance of passerines.

It would be interesting to further investigate the observed patterns based on simultaneous data from long-range remote sensing technology, such as weather radar, to improve our understanding of migratory dynamics and patterns on a larger geographical scale.

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