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# Evaluation of the use of the Atlantic flyway in northern France and the Bay of Biscay by a reedbed specialist bird during the autumn migration

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**ABSTRACT**
**Capsule:** Sedge Warblers *Acrocephalus schoenobaenus* that stopover along the Atlantic flyway refuelled at varying rates, depending on age, initial body condition and latitude; refuelling rates were poorly structured among sites, suggesting a broad capacity of birds to exploit various wetlands during stopover.
**Aims:** To test how Sedge Warblers accumulate fuel during stopovers in a major migratory corridor along coastal Atlantic wetlands, from northern France to the Bay of Biscay in Spain, and to identify factors affecting the fuel deposition rate (FDR).
**Methods:** We analysed 7,149 records of Sedge Warblers captured at least twice within the same site and year, collected over 32 years across 28 wetlands. We used linear mixed models to test the effect of age, initial body mass, date, latitude and habitat structure on FDR. Additionally, we modelled initial body mass as a response variable to examine large-scale variation in the arrival condition of birds, with age, date, latitude and habitat features as predictors.
**Results:** The fuel deposition rate declined with increasing initial body mass. The effect of latitude varied with age: for yearlings, refuelling rates increased from north to south, while adults showed relatively constant rates along the flyway. Initial body mass was higher in birds captured later in the season and in those using landscapes with smaller and more fragmented wetlands, but decreased with latitude. Habitat metrics had limited explanatory power.
**Conclusion:** Sedge Warblers appeared to refuel opportunistically throughout the extensive network of wetlands that spans the Atlantic flyway. This finding reinforces the importance of preserving habitat connectivity along migratory routes and supports a landscape-scale conservation approach that integrates ecological functionality and behavioural flexibility.

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During migration, birds need to stopover in suitable habitat to accumulate fuel for subsequent flights (Berthold 2001, Newton 2008). Fuel accumulation is therefore critical for migratory birds, and the factors influencing this process play a key role in shaping their migration strategies (Alerstam & Lindström 1990). Avian migrants with highly specific ecological requirements, which are restricted to particular habitats or dependent on a few key trophic resources, often rely on a narrow spectrum of stopover sites to refuel (Greenberg & Marra 2005). This phenomenon is relatively frequent in long-distance migrants, including several water bird species (Piersma *et al.* 2005, Navedo *et al.* 2007, Tang *et al.* 2023) and passerines (Biebach 1990, Schaub & Jenni 2000, Fransson *et al.* 2006, Lemke *et al.* 2013, Ouwehand & Both 2016), whereas it is much less common in short-distance migrants, which tend to migrate across broader fronts and can stopover wherever suitable terrestrial habitats are found (Catry *et al.* 2004).

Compared to sites where birds land and stay for (normally) short periods without refuelling, Warnock (2010) defined a 'true' stopover as a site where birds stay for a relatively long period and consistently gain

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enough fuel to undertake a very long flight (Battley *et al.* 2012) or complete a series of subsequent flights without needing to refuel (Schmaljohann *et al.* 2007). The migration strategies of European passerines travelling from Europe to Africa, particularly their stopover behaviour and fuel accumulation before crossing the Sahara, remain an active field of research due to their ecological, evolutionary and conservation significance (Schmaljohann *et al.* 2022, Fattorini *et al.* 2023). Theoretically, fuel load is proportional to the extent of the geographical barrier to be crossed (Rubolini *et al.* 2002), particularly because massive fuel loading incurs an energetic cost (fuel transportation) and increases the risk of predation (Alerstam & Lindström 1990, Klaassen & Lindström 1996, Kullberg *et al.* 1996).

For many long-distance migratory songbirds, the Sahara Desert is considered the primary ecological barrier on the route to their wintering grounds in the Sahelian belt and/or southern Africa (Zwarts *et al.* 2009, Franks *et al.* 2022). To minimize energy loss and survival costs, long-distance migrants must balance the use of highly productive sites, where refuelling conditions are favourable but may deteriorate from north to south in autumn due to summer droughts around the Mediterranean, with the need to avoid excessive fuel loads during subsequent flights. The existence of this latitudinal trade-off for massive fuel loading before the Sahara is still a subject of debate, varying substantially between species (Biebach 1990), and requires further research.

The Sedge Warbler *Acrocephalus schoenobaenus* is an insect-eating songbird that breeds in western and central Europe, and winters in the large sub-Saharan wetlands of western and central Africa (Cramp 1992). During migration, the species has a very high dependence on reed-associated aphids (*Hyalopterus* spp.) to refuel (Bibby & Green 1981, Koskimies & Saurola 1985, Chernetsov & Manukyan 2000), and it has been extensively studied for its ability to accumulate fuel reserves at a remarkably high rate (up to >1 g per day; e.g. Grandío 1998) in preparation for long migratory flights (Bibby & Green 1981, Schaub & Jenni 2000).

The fuel deposition rate is a key factor for understanding migratory strategies, as it influences stopover duration, departure decisions, and ultimately, the success of migration (Alerstam & Lindström 1990, Schaub & Jenni 2001). The concentration of huge numbers of Sedge Warblers in north-western France (Caillat *et al.* 2005) has long been hypothetically linked to the high fuelling opportunities of the wetlands of this region (Bibby & Green 1981). In theory, Sedge Warblers could gain enough fuel in this region of France to reach the southern border of the Sahara Desert without needing additional refuelling (Biebach 1990). However, Grandío (1998) showed that Sedge Warblers also reached very high refuelling rates at sites located further south, in north-western Spain, suggesting that substantial fuel accumulation was not exclusive to the north-western French wetlands.

The Atlantic region spanning the coast of France and northern Spain represents a critical migratory corridor for Sedge Warblers; however, the extent to which it supports high fuel accumulation, and whether some sites serve as true stopovers rather than emergency or transient staging points, remains poorly understood (Arizaga et al. 2014). Investigating spatial variation in fuel deposition rate among coastal wetlands along this route may shed light on the habitat quality and the role these sites play in the broader migratory network.

To determine whether maximal fuel accumulation in the Sedge Warbler, a foraging specialist, is restricted to specific regions along its flyway, or can also occur wherever suitable conditions are available depending on spatial context and habitat structure, we analysed 7,149 individuals captured at least twice within the same site and year, over a 32-year period across wetlands distributed from northern France to the Bay of Biscay in Spain. In particular, we tested the hypothesis that fuel deposition rate varies significantly between different wetland sites, in relation to habitat quality proxies (total wetland surface and spatial configuration) and controlling for other factors (including initial body mass, age, site and latitude). By integrating field-based measurements of fuel deposition rate with environmental data, this study aimed to improve our understanding of stopover ecology and how migratory strategies of the Sedge Warbler are spatially structured.

## Methods

### *Sampling area and data collection*

This study was carried out using data collected during 1984–2015 during the autumn migration period (August) at 28 sampling sites distributed from north-western France to north-western Spain (Fig. 1; data: Dehorter & CRBPO 2016). These sites were grouped into 16 wetland complexes (see Appendix 1 in supplementary material).

Sedge Warblers at each site were captured with mist nets placed within or near reedbeds. Depending on the site and year, daily sampling effort lasted 4–6 h starting at dawn. Once captured, birds were either ringed (with an official metal ring bearing a unique number) or

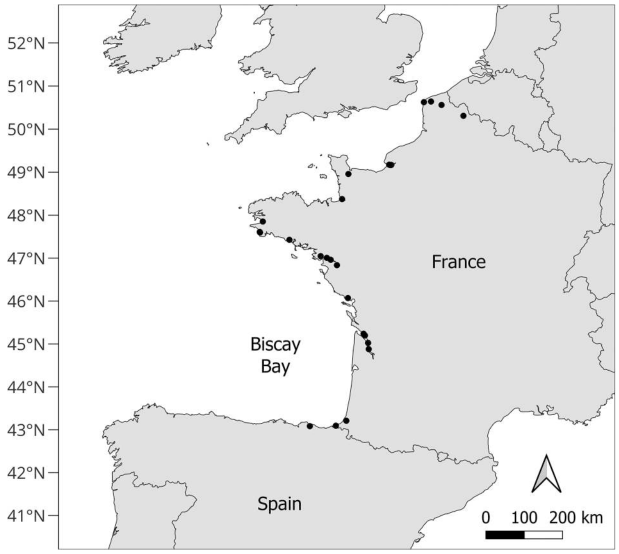


**Figure 1.** Locations of the 28 wetlands with at least 10 capture–recapture records of Sedge Warblers within the same year, used to calculate fuel deposition rate during the post-breeding migration (August) along the western coasts of France and northern Spain.

identified from their ring (recaptures), aged as first-year or adult (following Cramp 1992), and measured for wing length (to 0.5 mm) and body mass (to 0.1 g). Because the exact capture time was unavailable for most sites, this information could not be considered when calculating the interval between captures. Consequently, the fuel deposition rate (FDR) was estimated as the average daily gain in body mass (g/day), based on the difference in body mass and the number of days between captures, assuming full-day intervals.

### Environmental data collection

To test for the effect of habitat-related environmental traits on fuel deposition rate at each wetland site, we used the Corine Land Cover (CLC) v. 18.5 (accessed in February 2016) European seamless vector database. Although wetland characteristics may have changed over time, we consider the CLC 2016 data to reasonably represent the state of the wetlands studied during the study period. This assumption is supported by the general stability of most of the wetlands included in our sampling area, as highlighted by the previous studies (Ximenès *et al.* 2007, Genty 2012). While minor local changes may have occurred in some wetland types, these were considered unlikely to significantly affect the results of our study.

More particularly, we calculated different variables within buffers of a 20-km radius from the centre (centroid) of each sampling location. We selected four types of wetlands likely to constitute favourable migratory stopovers for the Sedge Warbler: inland marshes and lagoons, peat bogs, intertidal marshes and salines (CLC codes 411, 412, 421 and 422). The following habitat-related variables were then calculated: (1) relative wetland surface (WET) as the percentage of area covered by each sampled wetland within the buffer; (2) largest patch index (LPI) as the percentage of area occupied by the largest wetland patch within the 20 km buffer; (3) patch density (PDE) as the number of wetland patches within the buffer; (4) landscape division index (LDI) as the probability that two randomly chosen wetland pixels are not situated in the same patch; (5) shortest (Euclidean) distance (NND) as the distance between the nearest wetland patches and (6) aggregation index (AIN) as the frequency with which different pairs of wetland patches appeared side-by-side on the map. All metrics were calculated using FRAGSTATS 4.2 (McGarigal *et al.* 2012). These six metrics were subsequently included in a principal component analysis (PCA, see below).

### Statistical approach

From body mass data of aged individuals captured at least twice within the same site and year, we computed the individual fuel deposition rate (*fdr*, in g/day). The *fdr* variable is defined as $(mass_2\text{-}mass_1)/(date_2\text{-}date_1)$, where *mass* is the body mass, *date* is the calendar date, and 1 and 2 correspond respectively to the first and last captures of each individual in a site and year. To discard stress-induced body mass losses subsequent to the initial capture, all birds recaptured the following day were removed from the data set to be analysed (e.g. Ellegren 1991, Schmaljohann & Eikenaar 2017). Datasets of a sample size <10 individuals for a given site-year were removed. Overall, from an original sample size of 10,225 cases, we retained a sample of 7,149 cases after applying these two filters.

Before building a model, we gathered the six habitat-related variables (20 km buffer) in a PCA using the *R* ‘ade4’ package (Dray & Dufour 2007, R Core Team 2023). This was done to reduce possible over-parameterization and multicollinearity between these habitat-related variables. The two uncorrelated principal components with eigenvalues >1 (PC1 and PC2; Table 1) were retained for subsequent analyses. PC1 was strongly and negatively associated with WET and LPI (i.e. the relative area and spatial dominance of wetland patches within the 20 km buffer), and positively correlated with LDI, which reflects landscape division (i.e. lower spatial cohesion when

**Table 1.** Factor loadings, eigenvalue and the percentage of explained variance obtained for the components 1 and 2 (PC1, PC2) from a principal component analysis on six habitat-related variables of those wetlands where Sedge Warblers were ringed during the autumn migration period from northern France to the Bay of Biscay in Spain. WET = relative wetland surface, LPI = percentage of area occupied by the largest wetland patch, PDE = wetland patch density, LDI = landscape division index, NND = shortest (Euclidean) distance between nearest wetland patches, AIN = aggregation index (see Methods for details).

| Variables | PC1 | PC2 |
|---|---|---|
| WET | −0.51 | −0.03 |
| LPI | −0.51 | −0.08 |
| PDE | −0.35 | +0.44 |
| LDI | +0.49 | −0.05 |
| NND | +0.06 | −0.74 |
| AIN | −0.33 | −0.51 |
| Eigenvalue | 3.78 | 1.40 |
| Explained variance (%) | 63.0 | 23.5 |

high). PC2 was highly and negatively associated with both NND and AIN, and positively with PDE, thereby defining a fragmentation gradient characterized by higher patch density, shorter inter-patch distances, and lower aggregation.

We fitted linear mixed models (LMMs) to explain the variation in fuel deposition rate, with the following fixed effects: age (as a factor: first-year versus adult), initial body mass (mass recorded at first capture), date (with 1 August coded as date 1), PC1, PC2 and latitude (expressed in degrees, EPSG: 4326 – WGS 84). PC1, PC2 and latitude were entered simultaneously, so their coefficients represented partial effects (associations conditional on the other predictors). This reduced potential confounding between geographic and habitat gradients, although strong collinearity could still inflate standard errors. Site nested within year was included as a random effect (notation: 1|site:year). We tested two-way interactions between age and each of the following covariates: initial body mass, date and latitude, to account for potential differences in the fuelling strategies of first-year birds compared to adults. In addition, we evaluated alternative models including quadratic effects of initial body mass and/or date, to test for potential non-linear relationships, such as variation in fuel deposition rate at extreme values of body condition or migration timing.

Using the 'lme4' package in the program R (Bates *et al.* 2014), we first constructed four candidate models: (1) with only linear effects; (2) with a quadratic effect of initial body mass; (3) with a quadratic effect of date; and (4) with quadratic effects of initial body mass and date. We compared the model fit using Akaike information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). All models including a quadratic effect of body mass and/or date were less supported (ΔAICc > 2) than the model with untransformed terms (AICc = 3758.8). Therefore, we ran this last model with untransformed terms using the 'dredge' function of the 'MuMIn' package to perform a model selection procedure based on AICc values (Barton 2014), evaluating the fit of all candidate nested models, including the null model.

Additionally, because initial body mass at capture may reflect how geography influences the state in which migrants reach stopover sites, we conducted a complementary analysis on fuelling patterns and fuel load in Sedge Warblers across the studied region. We thus repeated the modelling using initial body mass as the response variable, including age, latitude, date, PC1 and PC2 as fixed effects. We also included two-way interactions between age and both date and latitude, because age classes may differ in their fuelling patterns across the flyway and the season (Chernetsov 2012). As before, model selection was performed using the 'dredge' function applied to a saturated model including all fixed effects and specified two-way interactions. Model averaging was conducted when more than a single model was found to fit to the data equally well (ΔAICc < 2). In this case, parameter estimates from all models with ΔAICc < 2 were averaged using the MuMIn package (Barton 2014).

## Results

Our sample for analysis included data from 7,149 birds, captured across 28 localities (see Appendix 1 in supplementary material). The top-ranked model, which included age, latitude and initial body mass (measured at first capture) as predictors of fuel deposition rate, provided the best fit to the data (Tables 2 and 3). The next-ranked model, which additionally included PC2, was much less supported (ΔAICc = 3.70; Table 2). Examination of the beta estimates of the best model (Table 3) showed that the

**Table 2.** Ranking of the first two top-ranked models, together with the full (saturated) and null models, used to test for the effect of the age, initial body mass (at first capture event), date, PC1, PC2 and latitude on the fuel deposition rate. All models included site-year as a random factor. AICc = small sample sizes-corrected Akaike values; ΔAICc = difference relative to the top model; df = degrees of freedom.

| Models | AICc | ΔAICc | df |
|---|---|---|---|
| Age × latitude + initial body mass | 3,708.9 | 0.0 | 7 |
| Age × latitude + initial body mass + PC2 | 3,712.6 | 3.7 | 8 |
| Full: age × latitude + age × initial body mass + age × date + PC1 + PC2 | 3,758.8 | 49.9 | 12 |
| Null (with only a random term) | 4,003.0 | 294.1 | 3 |

**Table 3.** Beta-parameter estimates obtained from the top-ranked model shown in Table 2, used to test for the effect of a number of factors on the fuel deposition rate of Sedge Warblers stopping over at wetland sites along the Atlantic European coast from northern France to the Bay of Biscay in Spain.

| Explanatory variables | Beta | SE (Beta) | *P* |
|---|---|---|---|
| Intercept | +2.032 | 0.266 | <0.001 |
| Initial body mass | −0.046 | 0.002 | <0.001 |
| Age (adults)[1] | −1.150 | 0.295 | <0.001 |
| Latitude | −0.030 | 0.006 | <0.001 |
| Age (adults) × latitude | +0.028 | 0.006 | <0.001 |

[1]Reference category (Beta = 0): first-year birds.

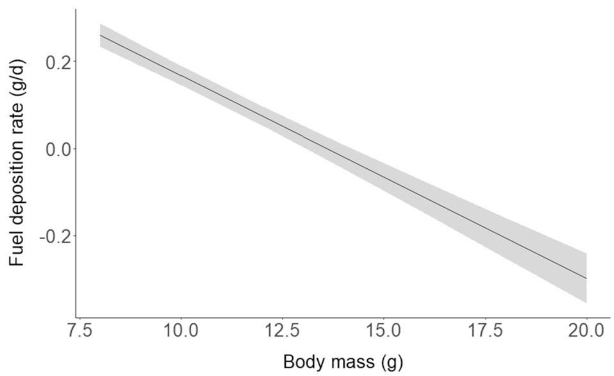


**Figure 2.** Predicted effect (±95% confidence interval) of initial body mass at first capture on fuel deposition rate according to the top-ranked model from Table 2.

fuel deposition rate decreased with increasing initial body mass (−0.046 g/day per g, Figure 2). The model also revealed a significant age × latitude interaction (Table 3): refuelling rates declined with latitude in first-year birds, whereas in adults the slope was close to zero, indicating relatively stable rates across the flyway (Table 3; Figure 3). The negative coefficient for the main effect of age (Table 3) should not be

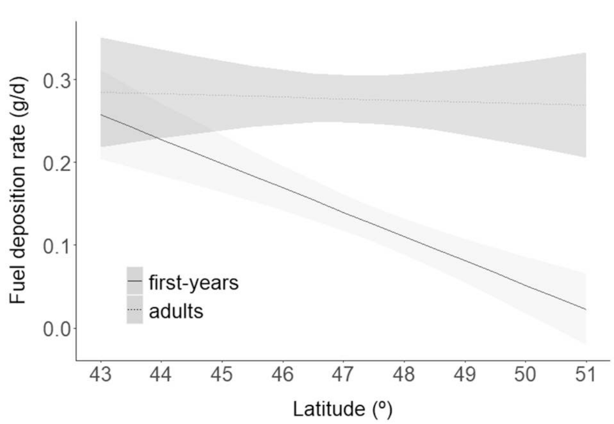


**Figure 3.** Predicted effect (± 95% confidence interval) of latitude on fuel deposition rate in relation to age, according to the top-ranked model from Table 2.

**Table 4.** Ranking of the four top-ranked models, together with the full (saturated) and null models, used to test for the effect of the age, date, PC1, PC2 and latitude on initial body mass (measured at first capture event of each bird). All models included site-year as a random factor. AICc = small sample sizes-corrected Akaike values, ΔAICc = difference relative to the top model, df = degrees of freedom.

| Models | AICc | ΔAICc | df |
|---|---|---|---|
| Age + date + latitude | 23478.7 | 0.0 | 6 |
| Age + date | 23479.6 | 0.9 | 5 |
| Age + date + latitude + PC1 | 23480.6 | 1.9 | 7 |
| Age + date + PC1 | 23481.5 | 2.8 | 6 |
| Full: Age + date + latitude + PC1 + PC2 | 23502.1 | 23.4 | 10 |
| Null | 24062.3 | 583.6 | 3 |

**Table 5.** Beta-parameter estimates obtained after a model averaging procedure based on the top-ranked models (ΔAICc < 2) shown in Table 4, used to test for the effect of a number of factors on initial body mass of Sedge Warblers stopping over at wetland sites along the Atlantic European coast from northern France to the Bay of Biscay in Spain.

| Explanatory variables | Beta | SE (Beta) | *P* |
|---|---|---|---|
| Age (adults)[a] | +1.10 | 0.05 | < 0.001 |
| Date | +0.010 | 0.002 | < 0.001 |
| Latitude | −0.06 | 0.02 | 0.002 |
| PC1 | +0.06 | 0.02 | 0.018 |

[a]Reference category (Beta = 0): first-year birds.

interpreted in isolation, as it does not represent an overall difference across the flyway but is conditional on the centred value of latitude. Overall, the model explained 16.2% of the variance in fuel deposition rate (conditional $R^2$), with 5.8% attributed to the fixed effects alone (marginal $R^2$).

In the complementary analysis of initial body mass, three models provided an equivalent fit to the data (ΔAICc < 2; Table 4). The averaged model revealed that initial body mass increased with age, date and PC1, but decreased with latitude. None of the tested interactions were significant (Table 5), i.e. interaction terms were not retained in the top models with ΔAICc < 2.

## Discussion

Ringing stations with constant effort can provide valuable information for large-scale studies of stopover ecology. In this context, our work represents the first study to use the network of ringing stations operating during the migration period along the Atlantic flyway in France and Spain to disentangle the respective effects of geography, habitat and individual traits on the fuel deposition rate of a foraging specialist landbird.

Among first-year Sedge Warblers, the fuel deposition rate increased gradually with decreasing latitude (i.e.

from north to south), indicating that the birds do not rely exclusively on a few discrete high-quality stopover sites, but instead exploit a broad range of wetlands distributed along the flyway. This implies that specialist migratory passerines may benefit from a gradient of suitable stopover conditions rather than depending solely on isolated high-quality sites. The absence of a significant effect of surrounding landscape structure (as summarized by the principal components of habitat configuration metrics) shows that habitat structure had limited explanatory power in our models, suggesting that local-scale factors, such as water level, aphid phenology and prey abundance, may be more decisive for fuelling than broader-scale landscape composition (Grandío 1998), although other environmental or behavioural factors may also contribute. Future analyses that include additional variables should help to better identify the factors potentially driving the large proportion of variance not explained by the models fitted in this study.

From a conservation standpoint, our results suggest that the Atlantic region of south-western Europe acts as a continuous and functional ecological corridor for Sedge Warblers during their autumn migration. Therefore, maintaining connectivity among these wetlands is as important as protecting specific sites, since their functionality seems to depend more on the network of available stopovers than on the outstanding quality of any single site. Although a preference for refuelling in northern France has been suggested (Bibby & Green 1981), our results highlight that wetland sites in southern France and along the northern coast of Spain may also play a relevant role, by offering suitable refuelling conditions for individuals that may not have accumulated sufficient fuel further north.

Fuel deposition rate was influenced by a significant age × latitude interaction. In first-year birds, FDR increased gradually with decreasing latitude (i.e. from north to south), whereas adults maintained high and relatively stable refuelling rates across the flyway. While previous studies have often reported higher FDR in adults for various passerines (Grandío & Belzunce 1987, Woodrey 2000, Heise & Moore 2003, Choi *et al.* 2009, Schmaljohann *et al.* 2018), potentially reflecting greater foraging efficiency or social dominance (Newton 2008), our results suggest that such patterns may depend on latitude. In southern regions, first-year birds may thus display stronger latitudinal sensitivity, suggesting a greater dependence on favourable local conditions during stopovers.

Individuals with greater initial body mass exhibited lower fuel deposition rates than leaner individuals, indicating that part of the variation in refuelling performance was associated with body condition at arrival (Maitav & Izhaki 1994, Schaub & Jenni 2001). This could reflect different stopover strategies: heavy Sedge Warblers may have already accumulated fuel at the current site (i.e. being captured at the end of their stopover) or at a previous site and had landed for reasons unrelated to refuelling (Schmaljohann & Eikenaar 2017). In both cases, such individuals are likely to display reduced fuel deposition rates, either because they are approaching their physiological limit for energy storage, or because they have already initiated pre-migratory digestive tract organ reduction (thus reducing their foraging capacity, Berthold 2001).

Initial body mass increased with age and date, suggesting that older individuals and those captured later in the season generally carried more fuel. This pattern may reflect a combination of greater foraging efficiency in adults and seasonal trends in pre-migratory fattening, although it is worth noting that date had no significant effect on fuel deposition rate itself. Initial body mass was also greater in landscapes characterized by smaller and more fragmented wetlands (high PC1 values, reflecting low wetland extent and dominance but high landscape division). While landscape structure had no significant effect on fuel deposition rate itself, this association with initial body mass does not necessarily imply that smaller wetlands promote fuelling, but rather that birds arriving in such landscapes may already carry larger fuel loads, potentially accumulated at previous sites. Moreover, body mass decreased towards higher latitudes (i.e. northward), consistent with the latitudinal gradient observed for fuel deposition rate. Together, these findings suggest that individuals captured in the southern part of the flyway may already carry substantial fuel loads, whereas leaner birds at higher latitudes are likely to continue southward in search of further fuelling opportunities. This reinforces the functional importance of wetlands throughout the Atlantic flyway, rather than exclusively highlighting those situated in northern and north-western France.

In conclusion, Sedge Warblers appear to rely on the extensive network of wetlands spanning northern France and the Bay of Biscay, which offers broadly suitable stopover opportunities, rather than depending exclusively on a few discrete, high-quality sites. The observed interplay between fuel deposition rate, initial body mass, age and latitude suggests that stopover behaviour reflects both environmental context and individual condition, with first-year birds appearing particularly sensitive to geographic variation in refuelling opportunities. Although our data do not permit inference about long-term evolutionary adaptations, they highlight the importance of maintaining habitat connectivity along migratory routes and support the need for a landscape-scale conservation strategy that integrates both ecological functionality and behavioural adaptability.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Appendix 1. Wetlands with a sample size ≥10 capture–recapture data of Sedge Warblers within the same year for which the fuel deposition rate was calculated during the post-breeding migration period (August) along the French and Spanish western coasts.

| Wetland complex | Station code | Coordinates (lat., lon.) | Wetland area within 20 km buffer ($km^2$) | Sample size | Sampling years |
|---|---|---|---|---|---|
| Adour | ADOU | 43.4648, −1.4708 | 5.28 | 27 | 2009–2011 |
| Aiguillon | AIGU | 46.3495, −1.3369 | 35.05 | 80 | 2004, 2005, 2009, 2013 |
| Audierne | AUD1 | 47.9085, −4.3709 | 5.60 | 155 | 1993, 1994, 1996–1998, 2003, 2006, 2012 |
| | AUD2 | 47.8958, −4.3618 | 5.60 | 2292 | 1988–1997, 1999–2014 |
| Brière | BRI3 | 47.3453, −2.2496 | 141.68 | 7 | 2010 |
| Douarnenez | DOUA | 48.1544, −4.2700 | 3.32 | 88 | 2007, 2008, 2010, 2013, 2014 |
| Gironde | CON1 | 49.2653, −1.2250 | 18.59 | 427 | 2011–2014 |
| | GIR1 | 45.4794, −0.8184 | 16.18 | 97 | 2011, 2012 |
| | GIR2 | 45.1368, −0.6814 | 26.93 | 41 | 2009 |
| | GIR3 | 45.2830, −0.6971 | 32.03 | 81 | 2010–2014 |
| | GIR4 | 45.5016, −0.8398 | 19.47 | 77 | 1984, 1990, 1991, 2000, 2010, 2012 |
| | GIR5 | 45.4606, −0.7961 | 15.74 | 39 | 1998, 2000, 2004 |
| Grand-Lieu | GRA2 | 47.1272, −1.6919 | 28.47 | 75 | 2006, 2007 |
| Loire | LOI1 | 47.3032, −2.0366 | 98.87 | 1112 | 2003–2006, 2008–2014 |
| | LOI2 | 47.2569, −1.9049 | 29.94 | 698 | 1997, 2001–2004, 2007–2014 |
| St. Michel | MICH | 48.6791, −1.4700 | 39.42 | 249 | 2000–2003, 2011, 2013, 2014 |
| Morbihan | MOR1 | 47.7312, −3.3335 | 7.83 | 15 | 2008 |
| Nord | NORD | 50.4889, 3.0593 | 4.22 | 25 | 2009, 2010 |
| Côte d'Opale | OPA1 | 50.8797, 1.9057 | 9.16 | 85 | 2009–2011, 2013 |
| | OPA2 | 50.7819, 2.2860 | 4.83 | 87 | 2000, 2001, 2012–2014 |
| | OPA3 | 50.8750, 1.6416 | 4.4 | 43 | 2009, 2011 |
| Seine | SEI1 | 49.4450, 0.3283 | 17.46 | 219 | 2007–2009 |
| | SEI2 | 49.4442, 0.3119 | 17.46 | 42 | 2009, 2011, 2014 |
| | SEI3 | 49.4443, 0.2937 | 17.46 | 512 | 2003, 2007, 2008, 2010–2014 |
| | SEI4 | 49.4520, 0.2513 | 17.45 | 17 | 2008 |
| | SEI5 | 49.4482, 0.2684 | 17.46 | 13 | 2005 |
| Txingudi | TXIN | 43.3515, −1.8115 | 0.57 | 487 | 2007–2015 |
| Urdaibai | URD1 | 43.3470, −2.6500 | 4.80 | 59 | 2011–2013 |