Opportunistic stopovers of Willow Warblers *Phylloscopus trochilus* in a reed bed area at the Bay of Biscay during autumn migration

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Rogalla S. & Arizaga J. 2018. Opportunistic stopovers of Willow Warblers *Phylloscopus trochilus* in a reed bed area at the Bay of Biscay during autumn migration. Ardea 106: 97–104. doi:10.5253/arde.v106i2.a1

During migration, birds often need to gain large fuel loads, especially if they must cross large geographic barriers with poor or absent fuelling opportunities. The Willow Warbler is a songbird associated with woodland that also opportunistically exploits other habitat types, such as reed beds, allowing it to fuel quickly. Reed beds along the coast of the Bay of Biscay constitute potentially targeted fuelling sites for birds moving from northern Europe to Africa in autumn. Using data obtained from a ringing station, we tested to what extent these coastal sites are opportunistically used by Willow Warblers. The study was carried out in a reed bed area at Txingudi marshlands, one of the main wetlands at the Bay of Biscay in northern Iberia. We found that when Willow Warblers were more abundant, that birds deposited fuel more quickly, and that annual mean fuel load was correlated with the number of captures, suggesting opportunistic stopover exploitation.

Key words: Atlantic flyway, fuel, northern Iberia, ringing, woodland passerines

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Stopovers play a critical role in bird migration, since birds use these sites to rest and/or refuel for the next flight bout (Alerstam & Lindström 1990). Moreover, most of the time spent during migration, and even most energy consumed during migration is at stopovers (Hedenström & Alerstam 1997). Detailed stopover studies are crucial to unravel bird migration strategies (Newton 2008, Chernetsov 2012). Within the Afro-European system of bird migration (Biebach 1990), Iberia plays a significant role as a target fuelling area during the autumn migration period. This is especially true for some migrants that need to gain large fuel reserves before crossing the sea between Iberia and Africa as well as the Sahara to arrive at their wintering sites in the sub-Saharan region (Tellería *et al.* 1999, Schaub & Jenni 2000, Andueza *et al.* 2014).

The Willow Warbler *Phylloscopus trochilus* is a widespread songbird breeding across much of the Palaearctic region, mostly within the temperate and boreal climatic zone (Cramp 1992). It overwinters from tropical to southern Africa (Cramp 1992), having one of the longest migratory flyways (up to 12,000 km or more) among European birds if distance is measured relative to body size (Alerstam 1993). Covering this distance requires sufficient fuelling, particularly before crossing geographic barriers, but the locations of potential key fuelling areas still remain poorly known. The Bay of Biscay is situated along a known migratory route for British and Western European migrant Willow Warblers that have to cross the sea between Europe and Africa, and the Sahara on route to their African winter quarters (Cramp 1992, Wernham *et al.* 2002).

Willow Warblers prefer open woodland habitats (Baker 1998), although during the non-breeding period they also inhabit other habitat types (Cramp 1992), such as reed beds (Arizaga *et al.* 2014a, b). They would thus benefit from reed patches rich in aphids *Hyalopterus* spp. (Cramp 1992), where they could quickly fuel, as in Sedge Warblers *Acrocephalus schoenobaenus* (Grandío 1998). This adaptation to a broad range of habitats may allow these birds to opportunistically exploit particular feeding resources, enabling them to fuel quickly during migration (Cramp 1992).

In this scenario, we predict that the number of Willow Warblers stopping over in reed bed areas along the coast of the Bay of Biscay will be correlated with foraging conditions (i.e. fuelling probability) in the reed beds, which likely varies from year to year. Variables such as the number of landed migrants (Arizaga *et al.* 2014a, b), fuel load and fuel deposition rate (Delingat *et al.* 2006) or stopover duration (Ktitorov *et al.* 2010) can be used as approximations for resource (e.g. food) availability, allowing us to obtain evidence of a possible opportunistic exploitation of a stopover site. We hypothesize that in years with higher values of these proxies for food availability we will find a proportionally higher number of Willow Warblers. Additionally, we hypothesize that in years in which Willow Warblers are more abundant, these birds show higher fuel loads, higher rates of fuel accumulation and longer stopover durations.

METHODS

The main aim of this study is to determine to what extent Willow Warblers stopping over in reed beds along the coast of the Bay of Biscay exploit this habitat opportunistically. Therefore, we used data obtained in a reed bed area during eight consecutive years at Txingudi marshlands, one of the main wetlands of the Bay of Biscay in northern Iberia.

Study area and data collection

This study was carried out at the Jaizubia stream (43°21'N, 1°49'W, Txingudi marshlands, province of Gipuzkoa, northern Iberia). Birds were sampled in a tidal area dominated by reed beds *Phragmites australis*, surrounded by a mosaic of meadows, forests and shrubs and situated very close to the point where the Jaizubia stream meets the Bidasoa river mouth. The vegetation structure of the reed bed area did not vary significantly through the study period (Arizaga, pers. obs.).

The climate in the region is Atlantic, with mean annual temperatures of 14.5°C, and an average yearly precipitation of c. 1700 mm. The investigated area is situated in the south-eastern corner of the Bay of Biscay, west of the Pyrenees.

Willow warblers are not breeding in the area and, consequently, it can be assumed that all birds recorded in this study were true migrants coming from breeding sites located further north (Tellería *et al.* 1999).

Ringing data used in this study were compiled over a period of eight years (2007–2015), during the months of August and September. Birds were captured with mist nets, 204 linear meters positioned along two lines, placed always in the same site and opened daily during a period of 4 h starting at dawn. Mist nets remained closed on days of adverse weather conditions (e.g. heavy rains) and during high tides, so the number of sampling days varied annually. Due to logistic causes, in 2011 data were only collected until 15 September. Captured birds were ringed or the ring number was recorded, and we measured wing length (0.5 mm accuracy; method III in Svensson 1996) and body mass (0.1 g accuracy). Age data were not recorded consistently and therefore we did not consider this factor in our analysis.

A Willow Warbler is ringed in the Txingudi marshland to study its stopover behavior (18 August 2015).

Statistical analyses

To test whether the abundance of Willow Warblers varied annually, we used linear models with the number of captures per day as an object variable and year and the effect of day within a year as covariates (Figure S1). Additionally, we included rain in July as an index of dryness within the region since years with lower precipitation might force Willow Warblers to move to the reed bed areas because woodlands might be less suitable. Meteorological data was obtained from the meteorological station located at Lasarte (c. 20 km from Txingudi), provided by the Basque Agency for meteorology (EUSKALMET).

We assessed fuel load from the residual values obtained from a body mass to wing length linear regression model (Schulte-Hostedde *et al.* 2005). The regression line of body mass on wing length was described as body mass = 0.43 + 0.12 × wing length ($P < 0.001$, $n = 1636$). We used these residual values (hereafter, fuel load) as a dependent variable, and ran a Generalized Linear Model (GLM) with year and the date of the first capture event as covariates. Date was included in the model since it has been reported to affect fuel load of migrants during the course of migration at given stopover sites (e.g. Fransson 1998). In this case we used a linear-link function with Gaussian errors.

For the analyses on fuel deposition rate we only considered birds captured twice or more, at different days. In the case of repeated captures on a day we only used body mass of the first capture event in the day. For each bird, we calculated the difference in body mass between the last and the first capture event, divided by the number of days separating these two dates. Then we ran linear models on this dependent variable, with year, date and body mass at the first capture event as covariates. Owing to the low sample size in some years (Table 1), we excluded the data from the years 2008, 2013 and 2014 from this analysis (<10 recaptures).

To analyse the factors affecting departure decisions we used Cormack-Jolly-Seber (CJS) models. These models estimate survival (ϕ, probability that a bird captured at time t is still alive at $t+1$) and recapture probability (p, probability that a bird captured at t and still alive at $t+1$ is recaptured at $t+1$) separately (Lebreton *et al.* 1992). Assuming that mortality rate from one day to the next at a stopover site is negligible, we equate apparent local survival probability with the probability of remaining at that site (Schaub *et al.* 2001).

Overall, we obtained a matrix of 1636 rows (individuals) by 61 columns (days from August to September). From these 1636 birds, 156 (nearly 10%) were recaptured once or more within the same year. A goodness of fit (GOF) test was done to find out whether the data fitted well to CJS assumptions (Choquet *et al.* 2009). The overall GOF test on a CJS model, where both ϕ and p varied with time [$\phi(t)$ $p(t)$], was run with the U-CARE software (Choquet *et al.* 2009), allowing us to identify a basic model that fits the data and which could then be improved to start model selection. The

Mist-netting in a reed bed in the Txingudi marshlands, northern Iberia (18 August 2015).

global GOF test for the data set was not significant (χ^2_{117} = 45.574, P = 0.999), and neither was the specific test to detect transients (Z = 1.306, P = 0.192) or trap-dependence (Z = 0.251, P = 0.802). Thus, [$\phi(t)$ $p(t)$] was the basic model used to select other models. Apart from assuming either constant or time-dependence on ϕ or p, we tested for the effect of year and fuel load on ϕ. A possible effect of year on p was tested too. CJS models were run using the logit-link function for the parameters. Corrected Akaike values (AICc) were used for ranking the fit of models to the data (Burnham & Anderson 1998). Models with a ΔAICc < 2 were considered to fit the data, and those with a difference > 2 were considered to fit the data insufficiently. Because models with additional unsupported parameters are likely within 2 AICc units and were non-competitive unless the extra parameter leads to a reduction in AICc (Arnold 2010), we analysed the parameter estimates (b) of all models having an ΔAICc < 2 from the best-supported one in order to see if the parameters affected ϕ. Parameters with a 95%-CI including zero were considered non-significant (Taylor *et al.* 2004). Finally, we calculated model-averaged parameters using both the top and the subset of models with a ΔAICc < 2 in relation to the top one (Burnham & Anderson 1998).

The statistical analyses were run with the programs R v. 3.0.2 (R Core Team 2014) and MARK (White & Burnham 1999).

Table 1. Number of individual Willow Warblers captured each year (from August to September), proportion of within-year recaptures (each bird considered only once), and number of sampling days per year at Jaizubia marshes. We only show birds with recorded wing length and body mass.

Year	Captures	Recaptures (%)	Sampling days
2007	218	7.8	60
2008	71	0.0	61
2009	423	14.2	60
2010	235	8.1	57
2011	259	9.7	42
2012	140	7.9	54
2013	51	2.0	55
2014	49	6.1	57
2015	190	10.5	48

Table 2. Results of the linear models testing for the influence of the effect of date, total precipitation in July and year on the daily total number of captures of Willow Warblers (each bird considered only once per day).

Model	b	SE	P	r
Date	–0.183	0.028	<0.001	0.347
Precipitation	0.014	0.014	0.322	0.055
Year	–0.293	0.188	0.119	0.087
Date + Precipitation + Year				**0.366**
Date	–0.184	0.028	<0.001	
Precipitation	0.011	0.014	0.417	
Year	–0.413	0.185	0.026	

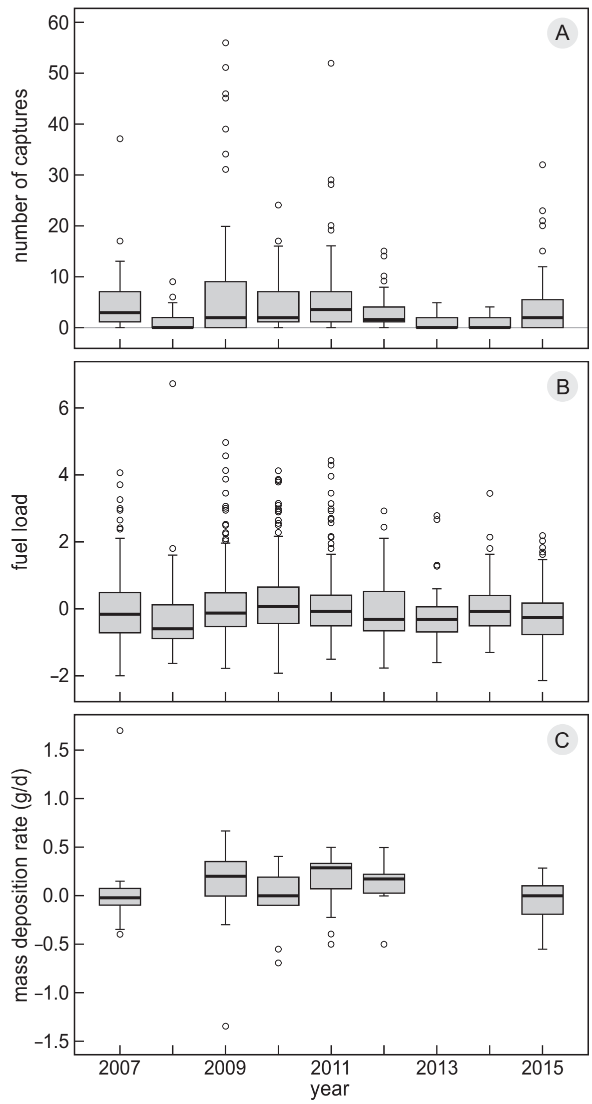

Figure 1. Yearly variation in (A) daily mean number of captures of Willow Warblers caught at Jaizubia (each bird has been considered only once per day), or in (B) mean fuel load (each bird has been considered only once per year; first capture event), or in (C) mass deposition rate of recaptured Willow Warblers at Jaizubia (in this case no data for 2008, 2013 and 2014).

RESULTS

We obtained complete data on birds with both their wing and body mass measured, from 1636 Willow Warblers of which 156 were recaptured once or more (Table 1). The number of captures of Willow Warblers was negatively correlated with the effect of date and also varied annually (Table 2). Mean number of captures per day in 2008, 2012, 2013 and 2014 were below the mean observed in 2007 (Figure 1A). There was no evidence for a correlation between the number of captures and yearly precipitation (Table 2).

Mean initial body mass of Willow Warblers was 8.6 ± 1.0 g. We found a significant effect of year on fuel load (Table 3). Although Willow Warblers were more fuel loaded than the mean in 2010, but less fuel loaded than the mean in 2013 (Figure 1B), the difference was marginal. Thus, the mean fuel load of the birds can be considered to be constant throughout the study period (or too variable to detect significant differences). Additionally, we observed higher numbers of captures of Willow Warblers at Jaizubia in those years in which the species tended to be more fuel loaded ($r = 0.05$, $P = 0.040$; Figure 2A).

Table 3. Parameter estimates of a GLM used to test for the influence of migration date and year on fuel load of Willow Warblers stopping over at the Jaizubia marshes during the autumn migration period ($r = 0.09$).

Factor	*b*	SE	*P*
Date	–1.496	1.329	0.260
Year	–0.045	0.020	0.025
Date × Year	0.001	0.001	0.262

The mean mass gain per day was 0.1 ± 0.3 g/d and did not vary significantly between years (Year: $F_5 = 2.020$, $P = 0.079$; Date: $F_1 = 2.019$, $P = 0.158$; Mass: $F_1 = 11.225$, $P = 0.001$; Figure 1B). We found that date and body mass at first capture in recaptured Willow Warblers were negatively correlated with mass deposition rate (Table 4). The annual number of captures tended to be positively correlated with the mean mass deposition rate of each year, although the difference was not significant ($r = 0.54$, $P = 0.266$; Figure 2B).

Overall, two out of 14 CJS tested models showed substantial support (AICc difference with the third model > 2; Table 5). Both the first and second model showed an effect of year on ϕ, whereby the second model also considered an additive effect of fuel on ϕ. Model-averaged values of ϕ showed that apparent

Table 4. Results of the linear models testing for the effects of date, body mass at first capture event, and year on mass deposition rate in recaptured Willow Warblers ($n = 152$). Years 2008, 2013 and 2014 were excluded from this analysis due to the absence (2008) or low number of recaptures.

Model	*b*	SE	*P*	*r*
Year	–0.013	0.011	0.215	0.101
Date + Mass				0.292
Date	–0.005	0.003	0.052	
Mass	–0.078	0.025	0.002	
Year + Date + Mass				**0.328**
Year	–0.020	0.011	0.056	
Date	–0.006	0.003	0.022	
Mass	–0.082	0.024	0.001	

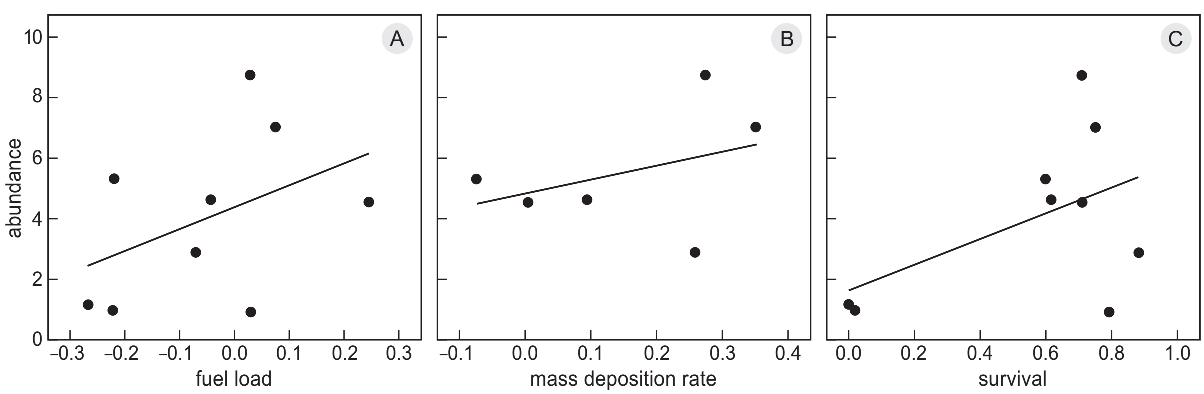

Figure 2. Regression lines of the mean annual number of captures in relation to the mean annual values of (A) fuel load, (B) mass deposition rate, and (C) survival of Willow Warblers stopping over at a reed bed area in northern Iberia during the autumn migration period from 2007 to 2015.

survival did not vary substantially among years (overlapping 95% confidence intervals; Figure 3), except for 2008 and 2013. The extremely low values for these years may indeed reveal insufficient data for proper apparent survival estimation (Table 1, but see Figure 2C). Fuel load tended to have a slight negative effect on ϕ (Figure 4), indicating that more fuel loaded Willow Warblers tended to leave the marsh sooner than lean Willow Warblers. Averaged *p*-values ranged from 0.011 (SE = 0.005, in 2012) to 0.074 (SE = 0.025, in 2015; years 2008 and 2013 excluded due to the very low number of recaptures).

DISCUSSION

The number of Willow Warblers caught in a reed bed area in northern Iberia varied annually and might be associated with altering foraging conditions on a local scale (Grandío 1998). For instance, in years with fewer captures, mean fuel load of Willow Warblers tended to be smaller, and when few birds were recaptured, estimating fuel deposition rate or apparent local survival was even no longer possible. Taken together, these results support our hypothesis of an opportunistic exploitation of the reed bed area at our study area.

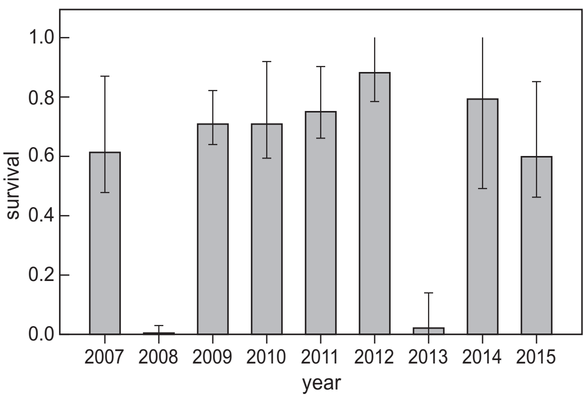

Figure 3. Mean (±95% confidence intervals) daily survival value of Willow Warblers stopping-over in a reed bed area in northern Iberia. Values were obtained after averaging the first two models of Table 5. Estimates from 2008 and 2013 were based on insufficient data for proper survival estimation.

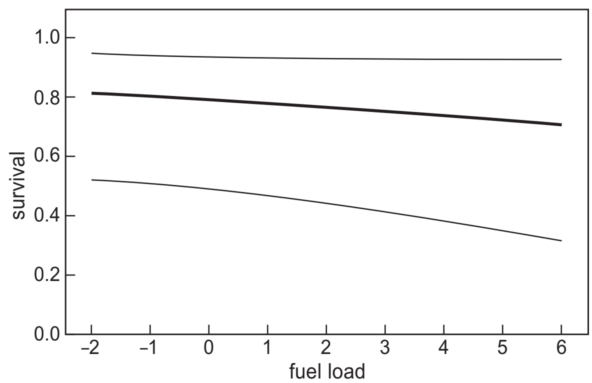

Figure 4. Apparent daily survival value (±95% confidence interval) of Willow Warblers stopping over at a reed bed area in northern Iberia in relation to their fuel load (residual mass in relation to wing length). Estimates obtained from the second model in Table 5 (year 2015).

Table 5. CJS models used to test for the effect of year and fuel on emigration probability of Willow Warblers stopping over in a reed bed area in northern Iberia during the autumn migration period from 2007 to 2015. AICc: small sample sizes-corrected Akaike values; ΔAICc: difference between the models' AICc values with the top model; np: number of parameters; year: effect of year on apparent survival (ϕ: here, probability that a bird caught on the day t is present in the area on the day $t+1$) or recapture probability (p: probability that a bird captured in t and still alive in $t+1$ is recaptured in $t+1$); fuel: effect of fuel on ϕ; t: time-dependence. We tested for both additive (+) or interaction (×) models.

Models	**AICc**	**ΔAICc**	**AICc weight**	**np**	**Deviance**
ϕ(year), p(year)	1799.777	0.000	0.580	18	1763.394
ϕ(year+fuel), p(year)	1800.834	1.057	0.342	19	1762.408
ϕ, p(year)	1805.385	5.608	0.035	10	1785.262
ϕ(year), p	1806.627	6.850	0.019	10	1786.504
ϕ(fuel), p(year)	1807.149	7.372	0.015	11	1785.002
ϕ(year+fuel), p	1808.101	8.324	0.009	11	1785.954
ϕ(year×fuel), p(year)	1820.308	20.531	0.000	28	1763.394
ϕ(year×fuel), p	1820.383	20.606	0.000	20	1779.912
ϕ, p	1820.481	20.704	0.000	2	1816.474
ϕ(fuel), p	1822.364	22.587	0.000	3	1816.351
ϕ(t), p(t)	1914.649	114.872	0.000	119	1659.709

CJS models revealed annual variations in apparent survival, although this was mainly due to two years: 2008 and 2013. However, these two years had few captures and no (2008) or a too low proportion (2%) of recaptures (2013). In consequence, 2008 and 2013 were years with few birds and, probably, a very high proportion of transients (birds that stayed in the area for less than 24 h). It is noteworthy that in 2008 and 2013, two years with lower numbers of captures, the species had a low mean fuel load. This further supports our hypothesized opportunistic use of the reed bed.

Although one of our best fitting models showed that fuel load positively influenced the departure decision, we found that this effect was very weak and statistically marginally significant (Figure 5). This result is partly consistent with that reported for a population of Willow Warblers stopping over at an island in Germany (Schaub *et al.* 2008). In this case actual fuel load did not have an impact on departure decisions. While some studies have reported an effect of fuel load on emigration decision (Biebach *et al.* 1986, Loria & Moore 1990, Dierschke & Delingat 2001, Arizaga *et al.* 2011), other studies found no such relationship (Ellegren 1991, Morris 1996). The decision to depart in Willow Warblers crossing continental areas, as in other passerine birds, is probably not or only marginally shaped by actual fuel stores, while other parameters, such as fuel deposition rate, seem to be much more decisive (Schaub *et al.* 2008). Future research should test to what extent fuel stores may affect the decision to depart of Willow Warblers facing ecological barriers, such as the Sahara.

In conclusion, we found that local Willow Warbler numbers in a reed bed area in northern Iberia were associated with fuel load and, to some extent (although not proven due to sample size constraints), fuel deposition rate. This suggests that the reed bed was used opportunistically, with the species exploiting the area when local foraging conditions were sufficient.

ACKNOWLEDGEMENTS

This research was partly funded by the Basque Government and the Gipuzkoa Administration. We thank the people who assisted during the ringing sessions. Ringing activity was authorized by the Gipuzkoa Administration. Dr. R.H.G. Klaassen, two anonymous reviewers and Dr. P. Wiersma provided valuable comments that helped us to improve an earlier version of this work.

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SAMENVATTING

Wanneer vogels trekken, moeten ze vaak een grote energievoorraad aanleggen, vooral als ze grote geografische barrières moeten overbruggen met weinig of geen mogelijkheden om bij te tanken. De Fitis *Phylloscopus trochilus* is een zangvogel die geassocieerd wordt met bossen en struiken, maar die heel opportunistisch ook andere habitattypen exploreert, zoals rietvelden, om snel energie te vergaren. Rietvelden langs de kust van de Golf van Biskaje in het noorden van het Iberisch Schiereiland vormen potentiële foerageerplaatsen voor vogels die in de herfst van Noord-Europa naar Afrika trekken. Aan de hand van gegevens verzameld op een vogelringstation, hebben we onderzocht in welke mate deze kustgebieden op opportunistische wijze worden gebruikt door Fitissen. Het onderzoek werd uitgevoerd in een gebied met rietvelden in het moerasgebied Txingudi, een van de belangrijkste wetlands langs de Golf van Biskaje. Uit onze analyse blijkt dat de Fitissen sneller hun energievoorraad aanvulden als de vogels talrijk waren en dat de jaarlijkse gemiddelde energievoorraad die de vogels aanlegden, correleerde met het aantal vangsten. Dit wijst op een opportunistisch gebruik van deze wetlands door Fitissen tijdens de najaarstrek.zuidelijk gelegen broedgebieden.

Corresponding editor: Raymond Klaassen
Received 10 February 2016; accepted 18 March 2018

SUPPLEMENTARY MATERIAL

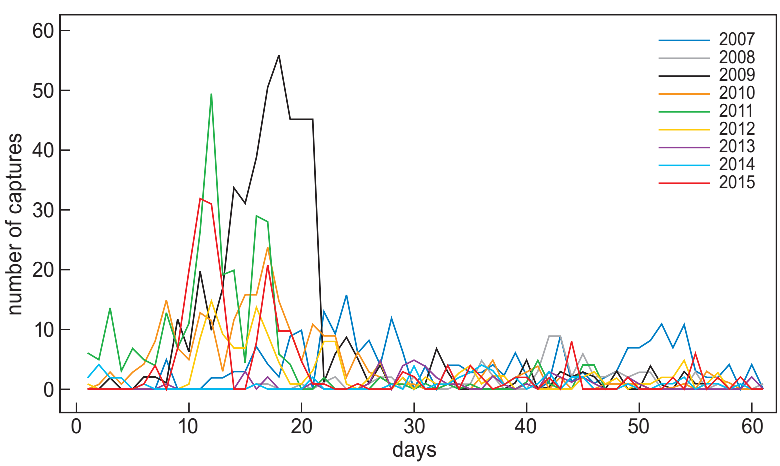

Figure S1. Daily number of captures of Willow Warblers throughout the study period per year. Date 0 corresponds to 1 August.