THE ROLE OF EXTRINSIC AND INTRINSIC FACTORS ON THE DEPARTURE DECISIONS OF A LONG-DISTANCE MIGRATORY PASSERINE

EL PAPEL DE FACTORES EXTRÍNSECOS E INTRÍNSECOS EN LAS DECISIONES DE PARTIDA DE UN PÁJARO MIGRATORIO DE LARGA DISTANCIA

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SUMMARY.—Factors determining departure decisions of migrants from a stopover site can be extrinsic and/or intrinsic but the relative role of each of these factors on departure decisions is still poorly known. Date and wind should be the main factors determining departure decisions in a long-distance migrant, which is expected to minimise duration of migration. Date was considered as an intrinsic factor and wind as an extrinsic one. We analysed the capture-recapture data of a long-distance migrant European songbird, the sedge warbler *Acrocephalus schoenobaenus*, from a stopover site in northern Iberia during the autumn migration period to quantify the relative importance of several factors on emigration likelihood. Cormack-Jolly-Seber (CJS) models were used to estimate the emigration likelihood. From 107 models tested, only the model with an additive effect of date, tailwind assistance and population size substantially supported the data. As expected, sedge warblers were more likely to depart with high tailwind values and late in the season and, contrary to expectations, with decreasing sedge warbler abundance.

Key words: Cormack-Jolly-Seber models, date, density, departure decision, sedge warbler, tailwind assistance.

RESUMEN.—Los factores que determinan la decisión de abandonar un área de descanso durante el periodo de migración pueden ser extrínsecos y/o intrínsecos. En las aves que tienden a reducir el tiempo de la migración, tanto la fecha como la meteorología deberían ser los factores principales que determinan las decisiones de partir. Se analizaron datos de captura-recaptura de un migrador transahariano, el carricerín común *Acrocephalus schoenobaenus*, de un área de descanso en el norte de la península

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Ibérica durante el periodo de paso posnupcial para cuantificar la importancia relativa de diversos factores en la probabilidad de emigración. La probabilidad de partir se estimó con modelos Cormack-Jolly-Seber (CJS). De 107 modelos, solo uno tenía respaldo suficiente, de acuerdo al criterio AIC. Dicho modelo incluía el efecto aditivo de la fecha, viento y densidad de aves. Como se esperaba, los carricerines comunes tenían más probabilidad de partir con vientos de cola elevados y en fechas más tardías, siendo esta probabilidad más elevada para densidades bajas.

Palabras clave: asistencia con vientos de cola, carricerín común, decisión de partida, densidad, fecha, modelos de Cormack-Jolly-Seber.

INTRODUCTION

Migratory birds divide their journey into flight periods: when fuel stores are consumed, and stopovers: where fuel stores are replenished, mostly as fat but also as proteins (Klaassen et al., 1997; Salewski et al., 2009). As a result, most of the time spent by a bird during migration is spent at stopover sites (Newton, 2008). Thus, the duration of migration is normally determined by stopover duration, which in turn is conditioned by departure decisions (Schaub and Jenni, 2001a, 2001b). Consequently, factors affecting departure decisions from a stopover site are key elements of bird migration strategies (Alerstam and Lindström, 1990; Alerstam and Hedenström, 1998). Such parameters could be either extrinsic (environmental: such as meteorological conditions, competition, predators, food availability, etc.) or intrinsic (associated with individual internal elements, such as endogenous circannual rhythm, age, physiological status, fuel load, etc.) (Dänhart and Lindström, 2001; Bulyuk and Tsvey, 2006; Schaub et al., 2008).

Meteorological conditions, especially rain and wind, are considered to be amongst the most important extrinsic parameters (Richardson, 1978; Dänhart and Lindström, 2001; Erni *et al.*, 2002, 2005; Tsvey *et al.*, 2007). Tailwind is advantageous as it allows birds to cover longer distances with the same amount of fuel. Hence birds prefer to depart on nights or days when there is tailwind

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assistance (Åkesson and Hedenström, 2000; Dänhart and Lindström, 2001: Åkesson et al., 2002). Although wind characteristics on the ground are reported to influence departure decisions (Åkesson et al., 2001, 2002), the topography can modify such characteristics locally, generally affecting wind direction, but also wind velocity. In such a scenario, wind characteristics would be expected to vary with altitude and departure decisions would depend more on wind aloft (Schaub et al., 2004). Rain is another important environmental factor because it reduces visibility and wets plumage, hence increasing the costs of flight. Thus, birds avoid departing and flying on rainy nights or days (Schaub et al., 2004). Population size (density) of conspecifics at a stopover site is also an extrinsic factor that may condition departure decisions. High densities of conspecific birds at a stopover site, caused by date (migration peak) or by poor weather conditions (Erni et al., 2002; Ma et al., 2011), could force the departure of weaker birds as a consequence of intraspecific competition (Moore and Yong, 1991).

Amongst intrinsic factors, age can play an important role in departure decisions from a stopover site (Woodrey, 2000). Adults have been reported to perform shorter stopovers than juveniles (Grandío, 1998, 1999; Rguibi-Idrissi *et al.*, 2003), partly because they often refuel more rapidly (Ellegren, 1991; Neto *et al.*, 2008). Accordingly, for birds arriving at the same time, adults would be expected to depart before juveniles. Fuel load can also determine the decision to depart from a stopover site. Although fuel load can be determined by several environmental factors, such as food availability and weather, (Bayly, 2007), it can be considered an intrinsic factor as it is associated with individual physiological status (Schaub *et al.*, 2008). Other things being equal, birds with higher fuel loads would be more likely to depart than those with low ones (Arizaga *et al.*, 2008).

Finally, timing of migration (date), although also associated with external cues such as food availability and fuelling rates at previous stopover sites, is also endogenously controlled, since the scheduling of the annual cycle of birds is mostly internally (genetically) determined (Berthold, 1996; Newton, 2008). Therefore, it can be considered as either an extrinsic or intrinsic factor. Here, we have included it as an intrinsic one, as a proxy of the circannual migrants' rhythm. The migrants' internal programme means that birds migrating later in the season are more time-stressed than those moving earlier (Bayly, 2006). Moreover, the longer the stay of a bird at a suitable stopover site with sufficient food the higher its fuel load and, as a consequence, the greater its departure probability (Yosef and Chernetsov, 2005).

So far, the effect of these factors on departure decisions has mostly been studied separately (Dierschke and Delingat, 2001; Bulyuk and Tsvey, 2006; Bolshakov et al., 2007; Arizaga et al., 2008). The development of more sophisticated model techniques for capture-recapture analyses (Schaub et al., 2001; Salewski et al., 2007, Arizaga et al., 2008; Schaub et al., 2008) allows the simultaneous analysis of the influence of all of these factors (Arizaga et al., 2011). Cormack-Jolly-Seber (CJS) models on capture-markrecapture data estimate survival (ϕ) and recapture (p) probabilities separately for open populations (Lebreton et al., 1992; Schaub et al., 2001). Assuming that the actual survival, ϕ , of a bird from one day to the next at a stopover site is almost 1, it might be assumed that ϕ in this type of study is the probability of remaining at that stopover site. The emigration likelihood, ε , is therefore 1- ϕ . Our aim was to determine the relevance of both extrinsic (wind, rain and sedge warbler density) and intrinsic parameters (date, age and fuel load) on the departure probabilities of a long-distance migratory passerine, using CJS models.

METHODS

The avian model chosen for this study was the sedge warbler Acrocephalus schoenobaenus. The sedge warbler is an abundant Palearctic songbird that breeds in most of central and northern Europe (Cramp, 1992) and winters in tropical Africa. During the autumn migration period it accumulates large fuel loads at suitable sites in Europe that offer a superabundant food supply, in particular the reed aphid Hyalopterus pruni, and then reaches its wintering areas south of the Sahara practically without refuelling (Bibby and Green, 1981; Schaub and Jenni, 2001a). As a typical warbler, it is a nocturnal migrant that initiates migratory flights around sunset (Moore, 1987; Åkesson et al., 1996).

Sampling site and field data

Sedge warblers were captured during the autumn migration period at Jaizubia, Txingudi marshlands, northern Iberia (43° 21' N 01° 49' W; 2 m above sea level). The sampling site is located in a tidal marsh with c. 25 ha of reedbeds *Phragmites australis*. Txingudi is situated in a geographical funnel, between the western border of the Pyrenees and the Bay of Biscay, so it is a major natural entry route for birds moving from northern Europe to Iberia and Africa during the autumn migration (Galarza and Tellería, 2003). This species did not breed in the area during the study period (Aierbe et al., 2001) so all captures were of migrants. Birds were captured in daily trapping sessions with mist nets (204 linear m) that were opened during a four-hour period starting at dawn, during three consecutive seasons (2007: 01-31 August; 2008 and 2009: 15 July-31 August). Each bird was individually identified with a numbered metallic ring, aged using wing feather abrasion (as first-year birds or adults, according to Svensson, 1998), weighed (± 0.1 g accuracy), and had its subcutaneous fat load determined (on a scale from 0 to 8, after Kaiser, 1993).

Meteorological data

Meteorological data were obtained from Jaizkibel Meteorological Station (525 m above sea level), the closest station to the sampling site (3.5 km). Since sedge warblers are nocturnal migrants, meteorological conditions around sunset were considered (four hours before and four hours after sunset). Most birds start migratory flights within this time window (Åkesson et al., 2001, 2002). Precipitation was considered as 'rain', for values ≥ 2 mm within the eight- hour period, or 'no rain' for values < 2 mm (Schaub et al., 2004). Wind velocity (m/s) and direction (measured as the angle relative to), were available every ten minutes from the station and were averaged for the eight-hour period. The tailwind component, b, was estimated as: $b = V \times \cos \left[\alpha_{\rm T} - (180 + \alpha_{\rm W}) \right]$, where V is wind velocity (m/s), α_T is the bearing on which the sedge warblers depart from Jaizubia, and α_w is the wind direction angle. α_T was assumed to be 225°, according to data from sedge warblers ringed at Jaizubia and recaptured along a south-west axis from Jaizubia (J. Arizaga, unpubl. data). High

positive values of b indicate a strong tailwind and high negative values correspond to a strong headwind.

Statistical analyses

Data were analysed with Cormack-Jolly-Seber (CJS) models, for which MARK software (White and Burnham, 1999) was used. Before starting to select models, we explored the fit of the data to CJS assumptions (no transients, no trap dependence) with a goodness-of-fit (GOF) test. The GOF test on a CJS model where both ε (that is 1- ϕ) and p (emigration and recapture likelihood, respectively) were time-dependent [$\varepsilon(t) p(t)$], as other fitted models were nested within this starting one, was carried out using U-CARE software (Choquet et al., 2001). Neither the global GOF test (χ^2_{323} = 223.32, P = 0.99), nor the specific test 3SR to detect transients (z = 0.92, P = 0.36), nor the test 2CT to detect trap dependence (z = -1.84, P = 0.07), were significant. Thus, the best model from which to start to model emigration likelihood was the one in which both ε and p were time-dependent [$\varepsilon(t) p(t)$].

The capture history of sedge warblers captured more than once within a season was divided into individual histories using the capture occasions. Hence, for these birds the first capture event of each individual history was the last recapture of the previous history, except in the case of the last history which contained only the last recapture (i.e. a capture history with an initial capture and two recapture events '1001010' would be split into three histories: '1001000 -1;', '0001010 -1;', '0000010 1;'). In MARK the term '-1' indicates that this bird was 'removed' from the data set after the last capture. The reasoning behind this was that, if a bird was recaptured, ϕ between the first and second captures was 1 (no departure), and what we were interested in was estimating the departure probability after the last recapture. Capture days were introduced longitudinally in the matrix (from 01 August 2007 to 31 August 2009). ϕ was fixed as 0 between the last day of capture of one year and the first day of capture of the next consecutive year. Days with 0 captures were removed and we specified the number of days between capture occasions. We obtained a matrix with 121 columns (sampling days with captures) and 1,640 rows (capture histories).

The date of the first capture in a season and the number of days stay before the last recapture were introduced as individual covariates. For birds captured once, we assigned 1 day of stay; for recaptured birds the number of days stay for each divided capture history was the number of days since the first capture. Fuel and age were considered as groups. Two age classes were considered: first-year birds and adults. As an indicator of fuel load we used fat scores according to Kaiser, transformed into an ordinal qualitative variable: low (from 0 to 2), medium (2.5)to 5) and high (5.5 to 8). From the combination of age and fuel we obtained six groups. Meteorological data and population size are daily variables and not characteristics of each bird, and hence they were not included in the matrix but were introduced during MARK analysis. The number of captures per 100 metres of mist net per day was used as an index of sedge warbler abundance (or density).

In order to model emigration likelihood, covariates were incorporated into the models and we tested different combinations of these, including additive effects and interactions, using the logit-link function, $logit(\phi) = B_0 + B$ (covariate). The most complex models included the additive effects of three variables. Interactions between models were not considered due to sample size constraints. Akaike's Information Criterion (AICc) was used to rank and choose the best models fitting to the data (Burnham and Anderson, 1998). Two models were considered to have

the same support if the difference between their AICc values was less than 2 (Burnham and Anderson, 1998). For a given model, the effect of a variable was considered to be significant if the 95% confidence interval (CI 95%) of its *B* parameter did not include 0 within its limits. The AICc weight of a model could be read as the probability of the model to rank best given the data. The sum of the weights of all models including a variable can be used as an indicator of the importance of this variable as a predictor (Burnham and Anderson, 1998). We also ran analyses of deviance (ANODEV) to test the effect of covariates (Grosbois et al., 2008). Mean values are given \pm SE.

RESULTS

Captures and meteorological data

Overall 1,145 sedge warblers were captured, 346 of which were recaptured at least once within the season: 72.9% of captures were first-year birds and 27.1% were adults. The proportion of each age class did not differ between years ($\chi^2_2 = 2.08$, P = 0.35).

The abundance of sedge warblers (number of captures per 100 m of net per day) ranged from 3.42 ± 0.27 (2008) to 9.35 ± 1.13 (2007) (mean 6.90 ± 0.50). The mean number of captures per unit effort differed between years ($F_{2,120} = 18.95$, P < 0.001), 2008 being the year with the lowest number of captures per unit effort (fig. 1).

Mean tailwind values ranged from 0.37 ± 0.51 m/s (2007) to 1.03 ± 0.39 m/s (2009), without significant differences between years ($F_{2,120} = 0.57$, P = 0.57; mean: 0.3 ± 0.24). There were more days with tailwind (66.1%) than with headwind (33.9%; $\chi_1^2 = 12.57$, P < 0.001; fig. 2), without significant differences in that proportion between years ($\chi_2^2 = 2.99$, P = 0.22). It rained on 13 days (10.7%) overall during the three year study period.



FIG. 1.—Index of abundance (used to assess population size) of sedge warblers *Acrocephalus* schoenobaenus at Jaizubia. All captures refer to a four-hour sampling period starting at dawn. Asterisks (*) indicate no-sampling days (sampling suspended, normally due to poor meteorological conditions). In 2007, the sampling period started on 01 August.

[Índice de abundancia (empleado como indicador del tamaño poblacional) de carricerines comunes Acrocephalus schoenobaenus en Jaizubia. Todas las capturas comprenden muestreos de 4 horas desde el amanecer. Los asteriscos (*) indican días sin muestreos (suspendidos, normalmente debido a condiciones meteorológicas adversas). En 2007, el periodo de muestreo comenzó el 01 de Agosto.]

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FIG. 2.—Mean tailwind values (m/s) at Jaizubia during the sampling period in 2007, 2008 and 2009 around sunset (sunset ± 4 h). Asterisks (*) indicate no-sampling days (sampling suspended, normally due to poor meteorological conditions). In 2007, the sampling period started on 01 August.

[Valores promedio del componente de cola (m/s) en Jaizubia durante el periodo de muestreo de 2007, 2008 y 2009 alrededor de la puesta de sol (puesta de sol ± 4 h). Los asteriscos (*) indican días sin muestreos (suspendidos, normalmente debido a condiciones meteorológicas adversas). En 2007, el periodo de muestreo comenzó el 1 de Agosto.] The mean tailwind value under rainy conditions was -1.59 ± 0.55 m/s, whereas on nights without precipitation it was 1.01 ± 0.25 m/s ($t_{120} = 3.45$, P = 0.001).

Modelling departure probabilities

From 107 models tested, only one model had substantial support (Model 1), showing an AICc difference > 2 with the second best model (table 1). Furthermore, Model 1 showed an AICc weight ten times greater than Model 2 (table 1), so model-averaging was unnecessary. Thus, Model 1 supported a significant, additive effect of date, wind and sedge warbler abundance on ε . The *B* parameters of this model were significant for all variables (table 2). In particular, ε values were higher with increasing tailwind values, decreasing bird abundance and proximity to the end of the season (fig. 3). ANODEV analyses showed a significant effect of wind ($F_{1,121} = 3.950$, P = 0.049) and bird abundance ($F_{1,121} = 9.582$, P = 0.003), but not of date ($F_{1,121} = 2.639$, P = 0.107).

TABLE 1

Emigration models of sedge warblers *Acrocephalus schoenobaenus* from a stopover site during the autumn migration period in northern Iberia. We show the emigration likelihood, ε ; Corrected Akaike's Information Criterion (AICc); difference in AIC values of each model with the first one; AICc weights, number of parameters and deviance. Only the best ten out of 107 models run are shown. Variables: tailwind values (wind), date of passage (date), index of sedge warbler abundance (abun), age, fuel load (fuel), and minimum stopover duration before the first capture event (days).

[Modelos sobre la probabilidad de partida (ε) del carricerín común Acrocephalus schoenobaenus de un área de descanso en el norte de la península Ibérica durante la migración otoñal. Se muestran para cada modelo los valores del criterio de información Akaike corregido (AICc); la diferencia entre valores AICc respecto al primer modelo; los pesos AICc; número de parámetros y desviación. Sólo se muestran los 10 mejores modelos de 107. Variables: valores del componente de cola (wind), fecha de pasada (date), índice de abundancia de carricerines comunes (abun), edad (age), carga de fuel (fuel) y tiempo mínimo de estancia antes de la primera captura (days).]

Model	AICc	ΔAICc	AICc Weight	N°. Parameters	Deviance
1. ε [wind + date + abun], p	4031.431	0.000	0.628	5	4021.394
2. ε [date × abun], <i>p</i>	4036.101	4.670	0.061	5	4026.064
3. ε [date + abun], <i>p</i>	4037.285	5.854	0.034	4	4029.260
4. ε [age + fuel + date + days], p	4037.387	5.957	0.032	9	4019.277
5. ε [age + fuel + days], p	4037.462	6.031	0.031	8	4021.373
6. ε [age+fuel], p	4038.238	6.807	0.021	7	4024.169
7. ε [wind × abun], p	4038.388	6.957	0.019	5	4028.351
8. ε [days+date+abun], p	4038.397	6.966	0.019	5	4028.360
9. ε [age+abun+date], p	4038.492	7.062	0.018	5	4028.456
10. ε [fuel+date+days], p	4038.745	7.314	0.016	6	4026.694

TABLE 2

Parameters	Beta	SE	95% IC		
			Lower	Upper	
Wind	0.109	0.042	0.027	0.192	
Date	0.018	0.005	0.008	0.029	
Pop. size	-0.049	0.013	-0.074	-0.024	

Standardized *B*-parameters (\pm SE and the 95% interval of confidence) of model 1 from table 1. [*B*-parámetros estandarizados (\pm ES y el intervalo de confianza al 95%) del modelo 1 de la tabla 1.]

The importance of date, wind and population size on the departure decisions of sedge warblers is also evident when considering the sum of AICc weights of models including these variables (date: 0.847; population size: 0.819; wind: 0.646). The remaining variables had much lower weights (days: 0.135; fuel: 0.054; age: 0.025; rain: 0.018).

DISCUSSION

Our results indicate that the departure decisions of sedge warblers from a stopover site in northern Iberia during the autumn migration seemed to be determined by both extrinsic variables (wind, abundance of conspecifics) and intrinsic variables (date: used here as a proxy of the circannual rhythm). The most important variables determining departure decisions were date and sedge warbler abundance, according to their models' AICc sums, followed by wind.

Emigration likelihood would be expected to increase with increasing bird densities at a stopover site, owing to intraspecific competition. However, we detected the opposite relationship, since departure probability increased when population size was low. A number of possible explanations may explain our results: (1) Sedge warblers depend on a superabundance of reed aphids to accumulate sufficient fuel (Bibby and Green, 1981; Grandío, 1998). If food availability is insufficient to allow birds to accumulate large fuel loads, newly arriving birds ought to depart from the site shortly after arrival and search for more suitable sites where they can gain sufficient fuel (Alerstam and Lindström, 1990). Hence, low densities of sedge warblers could be used by newly arriving birds as an indicator of poor foraging conditions. (2) Migrants can experience lower rates of fuel accumulation if they have to watch for potential predators (Lind, 2004; Bayly, 2006). So, high densities of conspecifics would allow sedge warblers to reduce their vigilance and therefore experience higher refuelling rates (Fransson and Weber, 1997; Bayly, 2006). (3) Later in the season, the decline in population size (fig. 1) coincides with the period when birds were more likely to depart, meaning that bird abundance and departure probability may not be independent.

Date was positively correlated with emigration likelihood and, under the same wind conditions, birds arriving later in the season had higher departure probabilities, especially when favourable tailwinds occurred (fig. 3). This result agrees with the idea that sedge





FIG. 3.—Estimated emigration probability in relation to tailwind values, population size (number of sedge warblers standardized for 4 h and 100 m of mist nets) and date, based on model 1 from table 1. [Probabilidad de partida estimada en relación al componente de cola, tamaño poblacional (número de carricerines comunes estandarizado para 4 h y 100 m de red), y fecha, basada en el modelo 1 de la tabla 1.]

warblers are under more time-related pressure to reach their wintering areas as the season progresses (Bayly, 2006, 2007). However, our results also support alternative hypotheses. Sedge warblers may depart more quickly later in the season due to extrinsic factors, such as seasonal food depletion at stopovers (Grandio, 1999), or they may have already accumulated fuel at more northern sites and hence were just passing through our site.

As expected, sedge warblers tended to depart on nights with tailwinds, thereby agreeing with previous studies (Weber et al., 1998; Åkesson and Hedenström, 2000; Dänhart and Lindström, 2001; Åkesson et al., 2002; Erni et al., 2002, 2005) and indicating that departure decisions are highly governed by meteorological conditions. Our sampling site, Jaizubia, was located 2 m above sea level whilst the meteorological station was at 525 m, on the top of a coastal mountain (Jaizkibel), so it is unclear whether the meteorological data used is representative of the wind aloft itself or whether it was used as a ground clue by migrants to decide on departure. Tail winds aloft allow birds to maximise the distance of flight and save time and energy. Weber et al. (1998) introduced wind as an additional factor in time-minimising models and they assumed that migrants are not sensitive to wind conditions until they are ready to depart. Furthermore, such models show that, if suboptimal weather conditions prevail for a long time period, birds will leave a stopover site independently of wind conditions. However, our results suggest that: 1) both birds with high fuel loads and birds that stayed in the area for long periods, as well as 2) birds with low fuel loads, left the area under favourable wind conditions. In this line of reasoning, neither fuel load nor days of stay showed a significant effect on emigration likelihood as would have been expected. This suggests that wind conditions were considered by migrants independently of their fuel loads and length of stay at this site. Sedge warblers have recently been reported to carry out two different fuelling behaviours (Bayly, 2007): (1) stopping over for a few days and accumulating a small amount of fuel, or (2) stopping over for longer periods and accumulating sufficient reserves to reach tropical Africa directly without needing to refuel. This behaviour is compatible with our results and, consequently, when favourable wind conditions occur, these may be considered opportune both by birds that have large fat reserves and those with small fat reserves. Moreover, Jaizubia is located in northern Spain, so birds that depart with insufficient fat loads to cross the Sahara can find suitable places to refuel later, before facing that barrier.

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Rain, contrary to expectations, did not show an important effect on departure decisions. In fact, rain was the variable with the lowest value of \sum AIC Weight in the models where it was included. Rain has been reported to have an important influence on the probability of leaving a stopover site since it wets plumage, hence making flight more difficult and increasing energy demands. It also decreases visibility, which makes disorientation more likely and, in general, causes higher mortality associated with migration (Dänhart and Lindström, 2001; Schaub et al., 2004). Our results may be explained by the low number of days with rain around the sunset period considered in this study (13 rainy nights only). Ten of these rainy nights coincided with headwinds; thus, although these two meteorological conditions may not be completely independent, the masking effect in our results is probably weak, given the low number of rainy nights in relation to those with headwind values. Hence, the existence of a wind effect independent of rain in explaining departure from a stopover cannot be fully rejected.

In conclusion, the departure decisions of sedge warblers from a stopover site in

northern Iberia were influenced mainly by extrinsic parameters. However, the relative importance of each of these parameters may differ between sites because birds can consider or give priority to different factors depending on such aspects as whether or not there is a geographical barrier nearby. Fuel load was not included in our models but sedge warblers may take this factor into account if they are departing from southern Iberia to cross a large area (of the Atlantic and the Sahara), with practically no possibilities of refuelling before reaching their wintering areas in tropical Africa.

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