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USING CAPTURE-MARK-RECAPTURE MODELS TO ASSESS THE EFFECT OF AGE AND WEATHER ON LANDING DECISIONS OF SEDGE WARBLERS *ACROCEPHALUS SCHOENOBAENUS* DURING MIGRATION

EL USO DE MODELOS CAPTURA-MARCAJE-RECAPTURA PARA EL ESTUDIO DEL EFECTO DE LA EDAD Y LA METEOROLOGÍA EN LAS DECISIONES DE PARAR DEL CARRICERÍN COMÚN *ACROCEPHALUS SCHOENOBAENUS* DURANTE LA MIGRACIÓN

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SUMMARY.—Bird migration is usually performed in several consecutive flights, interrupted by stopovers when birds rest or replenish their fuel loads. As a result, migrants must decide when and where to land. Here, we studied the effects of meteorological conditions (wind and rain) and age (used here as a indicator of bird experience) on the probabilities of sedge warblers *Acrocephalus schoenobaenus* landing at a stopover site in northern Iberia. Data were collected over three consecutive years at a ringing station during the autumn migration period. We used reverse-time capture-mark-recapture models to estimate seniority, γ (i.e., the probability that an individual at time t was already present in the population at time t - 1), as an indicator of landing decisions, since 1- γ represents the probability of recording new individuals (i.e. recent landings). We ran 14 models with the above mentioned variables, four of which were best supported by the data. In these, only rain showed a significant positive effect on γ, indicating that birds of any age class avoid flying during rainfall and prefer to interrupt their migration. These results are similar to those obtained from an analysis of day-to-day variation in first captures that was used to validate the usefulness of capture-mark-recapture models. They suggest that CMR models can serve to study bird landing decisions during migration in some specific cases.

Key words: Cormack-Jolly-Seber models, northern Iberia, rain, seniority, stopover, Txingudi, wind.

RESUMEN.—Las aves realizan su migración en etapas alternativas de vuelos, interrumpidas por periodos de parada en áreas de descanso. Como consecuencia, las aves deben tomar decisiones sobre cuándo y dónde parar a lo largo de la migración. Hemos estudiado los efectos de las condiciones meteorológicas (lluvia y viento) y edad (como indicador de la experiencia de las aves) en las probabilidades

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de parar en el carricerín común *Acrocephalus schoenobaenus* en un área de descanso del norte de la península Ibérica. Los datos empleados fueron obtenidos en tres años consecutivos durante la migración postnupcial. Se aplicaron modelos de captura-recaptura para estimar el parámetro *seniority* (antigüedad), γ (probabilidad de que un individuo en la ocasión t estuviese presente en la población en la ocasión t-1), metodología nunca antes aplicada para analizar las decisiones de parar de aves migratorias. Se construyeron 14 modelos, cuatro de los cuales se adecuaron a nuestros datos. Sólo la lluvia mostró un efecto significativo. De acuerdo a lo esperado, la lluvia mostró un efecto positivo sobre γ, indicando que las aves tienden a interrumpir la migración bajo la lluvia. Estos resultados fueron similares a los obtenidos en un análisis de la variación en el número de primeras capturas, empleado para validar la metodología basada en modelos de captura-recaptura. Adicionalmente, se señalan los casos específicos en los que los modelos CMR pueden ser útiles para estudiar las decisiones de parar en áreas de descanso durante la migración.

Palabras clave: antigüedad, lluvia, modelos Cormack-Jolly-Seber, norte de Iberia, sitios de parada, Txingudi, viento.

Introduction

Migration is a highly energy-demanding process for birds, as it often involves flying over long distances, in some cases across inhospitable areas where fuelling is impossible or nearly impossible (Newton, 2008). Migration is usually performed in several consecutive flights, interrupted by stopover periods during which migrant birds replenish their fuel reserves, mainly stored as fat (Berthold, 2001). Birds have developed different migration strategies in order to optimise fuel and journey times during the migration period (Alerstam and Lindström, 1990). This involves continuous tactical decisions to land at particular stopover sites or to leave them (Chernetsov, 2012). In this scenario, knowing which factors determine both landing and departure decisions at stopover sites is key to understanding their migration strategies. The effects of factors such as meteorological conditions, fuel load, and date on departure decisions has been the object of numerous studies (i.e., Dänhart and Lindström, 2001; Dierschke and Delingat, 2001; Schaub *et al*., 2004; Tsvey *at al*., 2007; Schaub *et al*., 2008; Arizaga *et al*., 2011a), whereas less attention has been paid to factors affecting landing decisions (but see Barriocanal *et al*., 2002; Yaukey and Powel, 2008; Saino *et al*., 2010; Arizaga *et al*., 2011b).

Nocturnal migrants normally fly during the hours of darkness and remain on the ground during the day, either just to rest and pass the time until night falls before continuing their migration, or to refuel (Delingat *et al*., 2006; Schmaljohann *et al*., 2007; Jenni-Eiermann *et al*., 2011; Chernetsov, 2012). However, adverse meteorological conditions, in particular headwinds and rain, have been reported to force birds to interrupt their migration, obliging them to land even at places considered to be suboptimal (Pyle *et al*., 1993; Barriocanal *et al*., 2002; Shamoun-Baranes *et al*., 2010; Arizaga *et al*., 2011b). By doing so, birds may avoid flying under bad conditions, thus saving energy and increasing their en route survival prospects. In contrast, both tailwinds and the lack of rain drive migrant birds to continue their migration at night and even permit them to look for optimal sites to land (Chernetsov, 2012). Therefore, it can be expected that headwinds and/or rain at night will force birds to land, increasing the number of migrant birds settled at a particular site in comparison to nights with tailwinds and/or no rain (e.g., Saino *et al*., 2010).

Bird experience, determined by age, has also been reported to affect stopover decisions during migration (Moore and Yong, 1991; Woodrey, 2000; Jakubas and Wojczulanis-Jakubas, 2010; Morganti *et al*., 2011), so it would be reasonable to expect an effect of age on landing decisions. Adults should be able to organise their stopover strategies in relation to the distribution of known favourable sites. In contrast, juveniles, i.e. first-year birds, may lack the experience to identify these favourable sites as efficiently as adults, and, may therefore be more likely to stop at sub-optimal stopover sites, irrespective of other potential influences such as meteorological conditions.

In small passerine birds, landing decisions in relation to meteorological conditions, for example, have traditionally been studied using daily changes in the number of captures (Saino *et al*., 2010; Arizaga *et al*., 2011b) or, more rarely, using tall mist nets to catch the birds as they land (Bolshakov *et al*., 2003a, b). Both approaches work at the individual level, allowing more accurate analyses than would be obtained using a population approach. However, the first method involves an inherent bias associated with the fact that the first capture event of a bird at a stopover site does not always occur on the first day of its stay (Schaub *et al*., 2001). Tall mist nets solve this problem but require a huge, even disproportionate, sampling effort (Bolshakov *et al*., 2003a, b). Cormack-Jolly-Seber (CJS) models (or, in a broader context, capture-mark-recapture models, CMR) work at a population level. Hence they estimate stopover duration rather than calculating a mean from individual stopover durations. CMR models have been commonly used for the study of departure decisions in migrants and stopover duration (e.g. Schaub *et al*., 2001; Schaub *et al*., 2004; Arizaga *et al*., 2011a) but not to analyse which factors influence landing decisions (but see Schaub *et al*., 1999).

The aim of this work was to determine the influence of meteorological conditions and age on landing decisions at a stopover site of a long-distance, nocturnal migrant passerine, using CMR models. We expected that rain and headwinds would increase landing probabilities for both adults and juveniles. In addition, juveniles were expected to show higher landing probabilities than adults under good weather conditions at our study site.

Methods

Study species

The sedge warbler *Acrocephalus schoenobaenus* is a long-distance migratory songbird that breeds in most of Europe, excluding the circum-Mediterranean region and the northernmost boreal region (Cramp, 1992). It overwinters in tropical Africa (Cramp, 1992). Many sedge warblers breeding in central-western Europe cross Iberia during the autumn migration period. As is the case with many other insect-eating passerines in Europe, the sedge warbler is a nocturnal migrant (Åkesson *et al*., 2002). During migration, West European populations of this species have been reported to depend on the superabundance of plum aphids *Hyalopterus pruni* mainly in northwestern France and Britain to gain the necessary fuel to reach tropical Africa. More southern sites, such as Iberia, serve more as resting places than for refuelling (Bibby and Green, 1981; Grandío, 1998; Schaub and Jenni, 2000a, b; Wernham *et al*., 2002).

Sampling site and data collection

Sedge warblers were captured with mist nets during the 2009-2011 autumn migration seasons at the Jaizubia stream in the Txingudi marshlands, Gipuzkoa, northern Spain (43º 21´ N 01º 49´ W). The sampling site is a *c*. 25 ha tidal marsh with abundant reed beds of *Phragmites australis*, where migrant birds, especially wetland-associated species, are common during migration periods (Mendiburu *et al*., 2009). On average (mean ± SE), 50.3 ± 11.0 different species and 2921.3 ± 968.6 migrating individuals were captured during the 2009-2011 autumn migration seasons. The sedge warbler does not breed in the study area (Aierbe *et al*., 2001) so all captured individuals were on migration.

The sampling period each year lasted from 15 July to 30 October, although here we have only used the data obtained in August, the peak month for sedge warblers at this sampling site, according to our own ringing results. Sampling was carried out daily during a four-hour period starting at dawn. Overall, we used 204 metres of mist nets, placed at fixed sites across the reed bed. Once captured, each bird was individually ringed (or any existing ring was read) and aged as an adult or first-year following Svensson (1992). Birds were not retained for longer than 90 minutes, usually less than an hour.

Meteorological data

Sedge warblers depart from their stopover sites around sunset, as do most nocturnal migrants (Moore, 1987; Zehnder *et al*., 2001; Åkesson *et al*., 2002). We considered meteorological data (wind and rain) during an eight-hour period starting at dusk, which varied across the season from 22:00 to 06:00 and 21:00 to 05:00 hrs. Meteorological data were obtained from the nearest meteorological station, at the top of the Jaizkibel mountain (525 m a.s.l.), 3.5 km from the ringing site. Wind velocity and direction measurements, available every ten minutes, were averaged for the eight-hour period. The tailwind component, *b*, was calculated according to Åkesson and Hedenström (2000):

$$b = V \times \cos [\alpha_T - (180 + \alpha_W)]$$

where V is wind velocity (m/s), α_T is the expected departure/migration direction from Jaizubia for the studied species (225°; Arizaga *et al*., 2011b; Andueza *et al*., 2013a), and α_W is the wind direction (0° = north). High positive values of b indicate a strong tailwind and high negative values correspond to a strong headwind. Precipitation values were transformed into a binary variable ("rain", "no rain"), considering rainy nights to be those with accumulated precipitation values ≥ 2mm over the eight-hour period (Schaub *et al*., 2004).

CMR models

Capture-mark-recapture (CMR) data were analysed with reverse-time capture-recapture models (Pradel, 1996), using MARK software (White and Burnham, 1999). CMR models have been largely used in survival analyses as they allow estimating survival (ϕ) and recapture (p) probabilities separately, and specifically reverse-time models can be used to study population recruitment (Pradel, 1996). In this approach the parameter estimated is seniority (γ), which can be defined as the probability that an individual at time t was already present in the population at time t-1. In our study it can be considered as the probability of being at the site during the previous capture event. Hence 1-γ can be seen as the probability of a bird landing at our sampling stopover site after the previous capture event.

Before modelling landing probabilities, we explored the fit of our data to the assumptions of CJS models (no transients, no trap dependence) with a goodness-of-fit (GOF) test performed with the U-CARE program (Choquet *et al*., 2001). Our data met the CJS assumptions (global GOF test: χ^2 = 185.9, P = 0.99; test 3SR to detect transients: $z = 0.74$, $P = 0.46$; test 2CT to detect trap dependence: $z = 1.12$, $P = 0.26$).

We created a matrix with the individual capture histories of sedge warblers, containing 889 rows (individuals) and 90 columns (trapping sessions). We pooled the data from 1-31 August 2009-2011 longitudinally in the matrix (columns), removing days with no captures and indicating the time elapsed between capture days. The values of γ and *p* from the last day of one year to the first day of the next year were fixed at zero. Before

TABLE 1

CMR models used to study landing probabilities in relation to rain, wind and age. Basic models, assuming either constant or time-dependent γ and *p*, were run before modeling γ in relation to different variables (Alternative models). Abbreviations: γ: seniority; *p*: recapture probability; AICc: corrected Akaike's Information Criterion; ΔAICc: difference in AIC values of each model from the first one; +: additive models; ×: models considering interaction between variables.
[Modelos CMR empleados para estudiar las probabilidades de parar en relación a la lluvia, viento y edad. Los modelos básicos, en los que γ y p se consideran constantes o variables en el tiempo, se corrieron antes de modelar γ en relación a diferentes variables (modelos alternativos). Abreviaturas: γ: antigüedad; p: probabilidad de recaptura; AICc: Akaike's Information Criterion corregido; ΔAICc: diferencia en los valores AIC de cada modelo respecto al primero; +: modelos aditivos; ×: modelos con interacción entre variables.]

Model	AICc	ΔAICc	AICc Weight	No. Parameters
Starting Models				
1. γ(.), *p*(.)	3300.813	0	0.783	2
2. γ(t), *p*(.)	3303.383	2.57	0.217	88
3. γ(.), *p*(t)	3315.552	14.739	< 0.001	88
4. γ(t), *p*(t)	3389.411	88.598	< 0.001	166
Alternative Models (with constant *p*)				
1. γ(rain×wind), *p*(.)	3250.613	0.000	0.302	5
2. γ(age+rain), *p*(.)	3251.029	0.417	0.245	4
3. γ(rain), *p*(.)	3252.194	1.582	0.137	3
4. γ(age+rain+wind), *p*(.)	3252.216	1.603	0.136	5
5. γ(age×rain)	3252.756	2.143	0.103	5
6. γ(rain+wind)	3253.353	2.740	0.077	4
7. γ(age×wind)	3268.364	17.752	< 0.001	5
8. γ(age+wind)	3268.860	18.247	< 0.001	4
9. γ(wind), *p*(.)	3270.540	19.927	< 0.001	3
10. γ(age), *p*(.)	3298.662	48.050	< 0.001	3

modelling seniority in relation to different variables, we ran basic models on γ and p assuming either constant or time-dependent parameters. Values of p were observed to fit the data better when constant (table 1), so were fixed to be constant when we ran most γ complex models that included the following variables: age (as a binary variable: first-year birds/adults), rain (transformed into a binary variable: rain or no rain, associated with the date) and tailwind assistance, b (as a linear variable, associated with the date). The meteorological conditions (wind and rain) considered refer to those existing during the night previous to the capture day (morning). We considered a constant p in all these models since the model with a constant p fitted the data better than the models considering a time-dependent p. Due to sample size constraints we tested the effects of these variables using additive models of up to 3 variables, as well as interaction models of up to 2 variables. The logit-link function was used in all the models.

We used Akaike's Information Criterion corrected for small sample sizes (AICc) to rank the models and identify the one (or ones) that best fitted the data (Burnham and Anderson, 1998). Models were considered to be significantly different if they showed an AICc difference < 2 (Burnham and Anderson, 1998). In a given model, the effect of a variable was considered to be significant if the 95% confidence interval of the corresponding model parameter (B parameter) did not include "zero".

Analyses of changes in bird abundance

To support the utility of CMR models, we compared the results obtained from CMR models with those obtained after studying the day-to-day variations in the numbers of first captures. For that, we compared the change in numbers of first captures of each day (t) in relation to the previous sampling day ($N_t - N_{t-1}$) (as in Saino *et al*., 2010), for (1) days (nights) with and with no rain, and (2) with tailwinds and headwinds (tailwind, $b > 0$; headwind, $b < 0$). For such comparisons we ran non-parametric U tests since this variable and its residual values did not follow a normal distribution. By using daily changes instead of absolute numbers of captures the possible date effect was omitted, because the number of captured birds tends to change as migration progresses depending on the timing of passage of different waves of migrants (Saino *et al*., 2010).

Results

Overall, 889 different sedge warblers were captured at Jaizubia during the sampling periods (1-31 August) of 2009-2011 (fig. 1, table 2). Of these, 301 individuals were recaptured at least once within the same season. Rain (≥ 2mm) was registered on 15.2% of the nights and tailwinds were dominant (66.7% of nights) over headwinds (33.3%; $\chi^2 = 8.170$, $P < 0.001$) (table 2, fig. 2).

Overall, 14 CMR models were tested (table 1). Four models were clearly better supported by the data than the remainder (table 1). Among the variables included in these models, age did not have a significant effect according to the B parameters (table 3). Model 1 (table 1) included the interaction effect of wind and rain (table 3), so birds were more likely to land on rainy nights with headwinds than on dry nights with tailwinds. However, after model averaging (we averaged β from the entire model set according to the models AICc weights, setting $\beta = 0$ in models without the corresponding variable, and then calculated γ for different values of the variables from the averaged equation), only rain showed a significant effect (fig. 3). Thus, sedge warblers were more likely to land on rainy nights (fig. 3). In addition, CMR models

TABLE 2

Numbers of sampling days (zero capture days in parentheses), number of captures (first-year birds/adults in parentheses; within-season recaptures are excluded), number of nights with rain (≥ 2mm for a period of 8 hours starting at dusk), and number of nights with a tailwind/headwind during 1-31 August 2009-2011. *[Número de días de muestreo (número de días sin capturas entre paréntesis), número de capturas (jóvenes/adultos ente paréntesis; sólo se considera una captura por ave, excluyendo las recapturas intra-anuales), número de noches lluviosas (≥ 2mm durante un periodo de 8 h desde el atardecer), y número de noches con vientos de cola/cara desde el 1 al 31 de agosto 2009-2011.]*

	Sampling days	Captures	Nights with rain	Nights with tail-/headwind
2009	31 (2)	382 (270/112)	6	23/8
2010	31 (0)	350 (225/125)	4	21/10
2011	30 (1)	157 (96/61)	4	17/13
Total	92 (3)	889 (591/298)	14	61/31

showed that first-captures are not always birds that have just arrived, because γ was not zero (fig. 3).

Days with a high number of first captures occurred after rainy nights (Mann-Whitney U = 310.50, P = 0.010), whereas wind conditions did not affect the change in numbers of first captures (Mann-Whitney U = 919.50, P = 0.830) (fig. 4).

DISCUSSION

We studied the landing decision of the sedge warbler, a long-distance migratory European passerine, according to meteorological conditions (wind and rain) and age: taken as an indicator of experience, using CMR models, a methodological approach rarely used to address this question (Schaub *et al*., 1999).

We found that the proportion of newly landed birds in the population was higher after rainy nights than after dry nights. This result agrees with the expectation that migrants decide to interrupt their migration under rainy conditions (Pyle *et al*., 1993; Barriocanal *et al*., 2002; Yaukey and Powel, 2008; Arizaga *et al*., 2011b). Rain has a negative effect on flying performance, because it reduces visibility, hence causing disorientation, and it also wets plumage, hence increasing the costs of flight and making migrants lose heat rapidly (Newton, 2007). We found the same result when data on change in numbers of first captures from one day to the next were analysed, thus validating what we obtained from CMR models. In particular, we registered an increasing number of first captures after nights with rain, indicating that rain forced migrating birds to land.

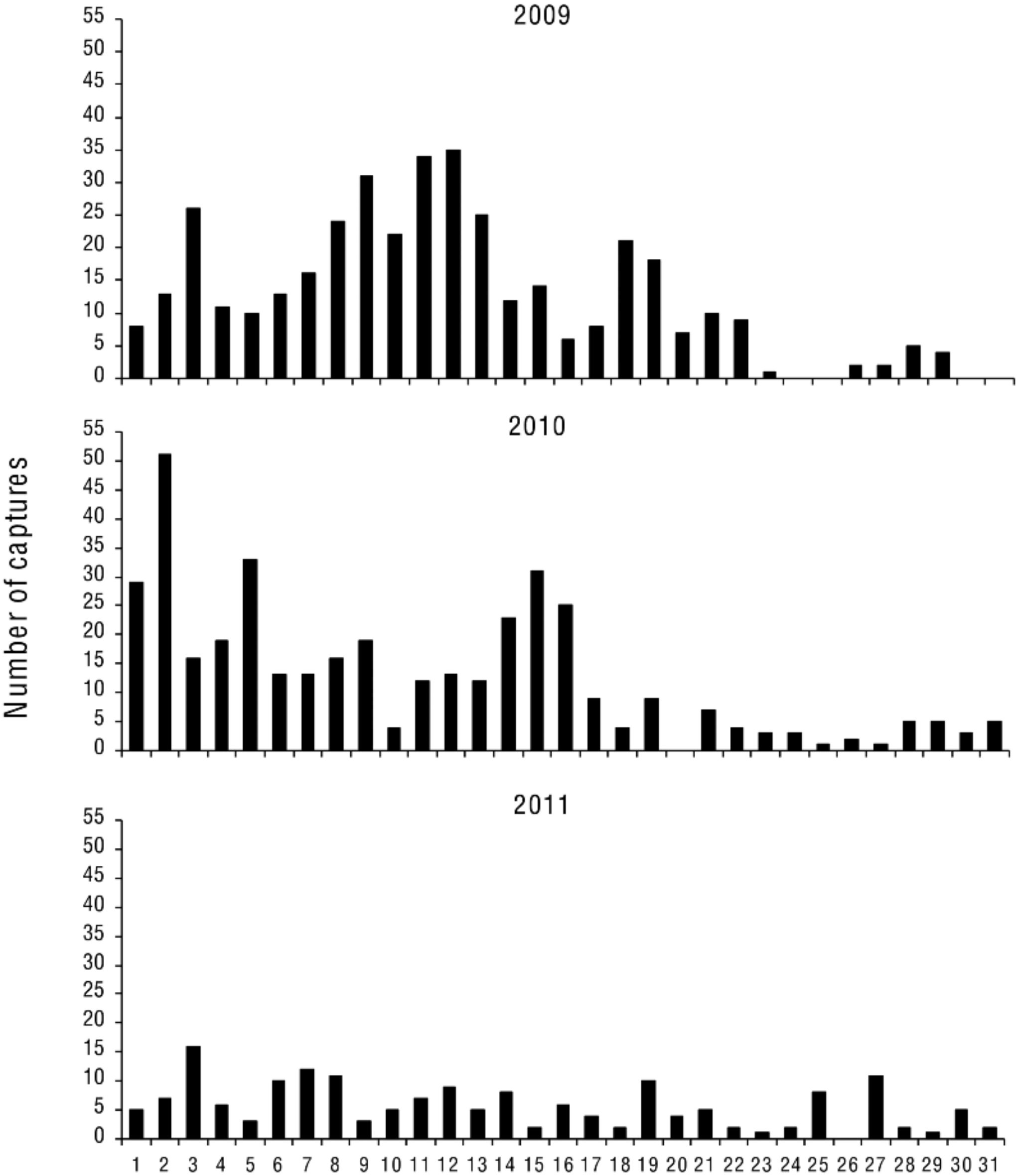

FIG. 1—Daily totals of sedge warblers captures, August 2009-2011.
[Número de capturas diarias de carricerines comunes durante agosto de 2009-2011.]

Saino *et al*. (2010) detected a negative effect of tailwind on the presence of migrants on small Mediterranean islands, showing that migrants moving through the Mediterranean continued flying under favourable winds. One of our best models showed a similar wind effect, as sedge warblers were less likely to land under tailwinds, especially on nights with no rain. However, the average effect of wind on landing decisions was not significant. Wind

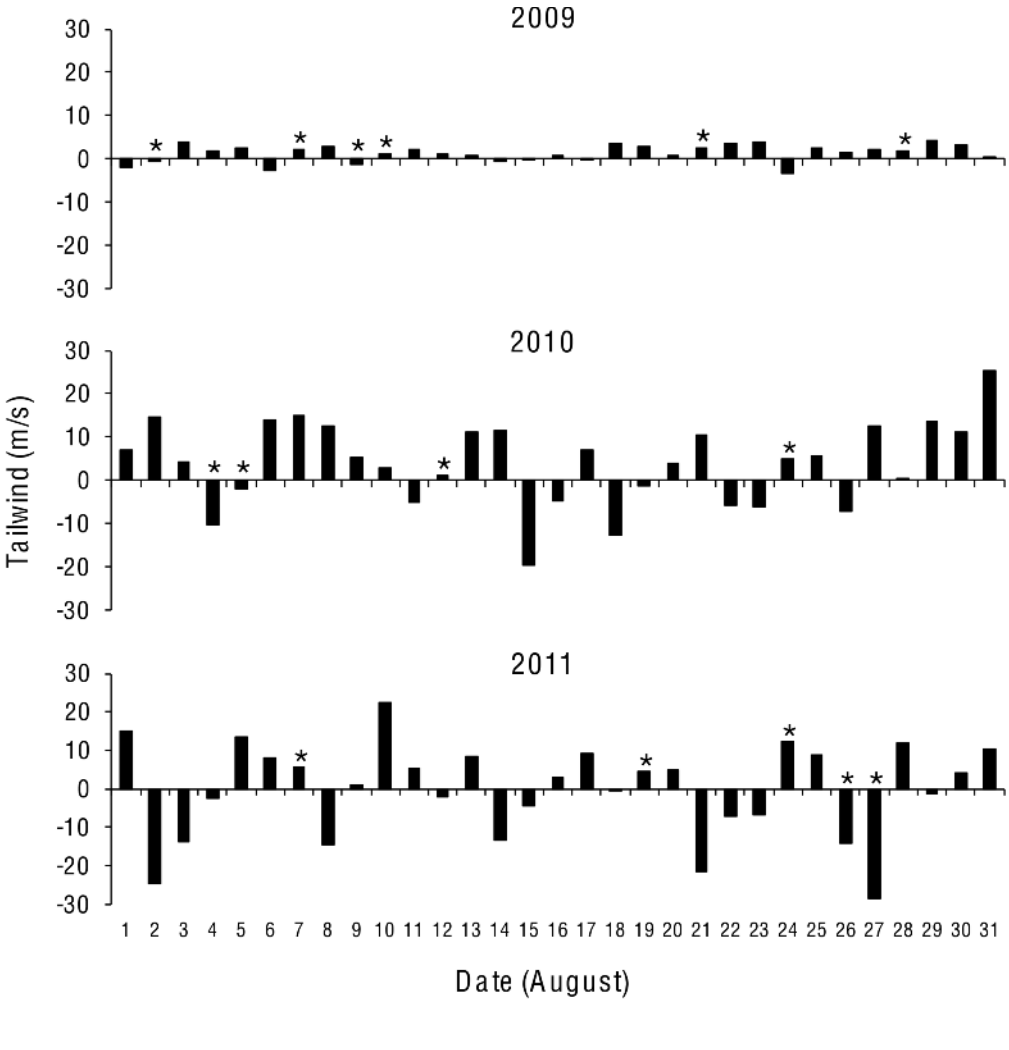

FIG. 2—Daily tailwind component (*b*) values during an 8 hour period, starting at dusk, August 2009-2011. * indicates accumulated rain > 2mm for the same period; ♦ indicates days without sedge warblers captures.

*[Valores diarios del componente de cola (b) durante un periodo de 8 horas desde el atardecer para agosto de 2009-2011. * indica valores acumulados de lluvia > 2mm durante el mismo periodo; ♦ indica días sin capturas de carricerines comunes.]*

TABLE 3

β-parameters values, SE and 95% CI of each variable included in the best models according to table 1. Variables are significant if their 95% CI do not span the zero value.
[Parámetros β, SE y IC 95% para cada variable incluida en los mejores modelos de la tabla 1. Las variables son significativas si su IC 95% no incluye el 0.]

			95% CI	
	β	SE(B)	Lower	Upper
Model 1				
wind	0.058	0.035	-0.01	0.125
rain	-1.472	0.311	-2.081	-0.863
rain×wind	-0.128	0.051	-0.227	-0.029
Model 2				
age	0.246	0.137	-0.022	0.514
rain	-1.256	0.257	-1.759	-0.754
Model 3				
rain	-1.278	0.257	-1.781	-0.775
Model 4				
age	0.248	0.138	-0.023	0.519
wind	-0.036	0.034	-0.103	0.03
rain	-1.444	0.332	-2.095	-0.792

is known to determine departure decisions (Weber *et al*., 1998; Åkesson and Hedenström, 2000; Dänhardt and Lindström, 2001; Åkesson *et al*., 2002; Arizaga *et al*., 2011a; Andueza *et al*., 2013b) and if tailwinds are predominant, as in this study (fig. 2), waiting for favourable wind conditions would be preferable as the waiting period may be short (Bulyuk and Tsvey, 2013). However, once in flight, the effect of wind conditions on landing could be different, depending on whether migrants are crossing land or large open water areas, such as the sea. For migrants that minimise the duration of migration (i.e. time-minimisers; Alerstam and Lindström, 1990), possibly including the sedge warbler (Bayly, 2007), it is disadvantageous to interrupt migration in the event of headwinds, especially when tailwinds may soon blow (fig. 2). In the proximity of departure sites, flying into headwinds could be preferable to stopping over (Erni *et al*., 2002).

Finally, we detected no differences in the effect of rain and wind in the landing behaviour between first-year birds and adults. Biometric differences between juveniles and adults, in particular in wing morphology (Lockwood

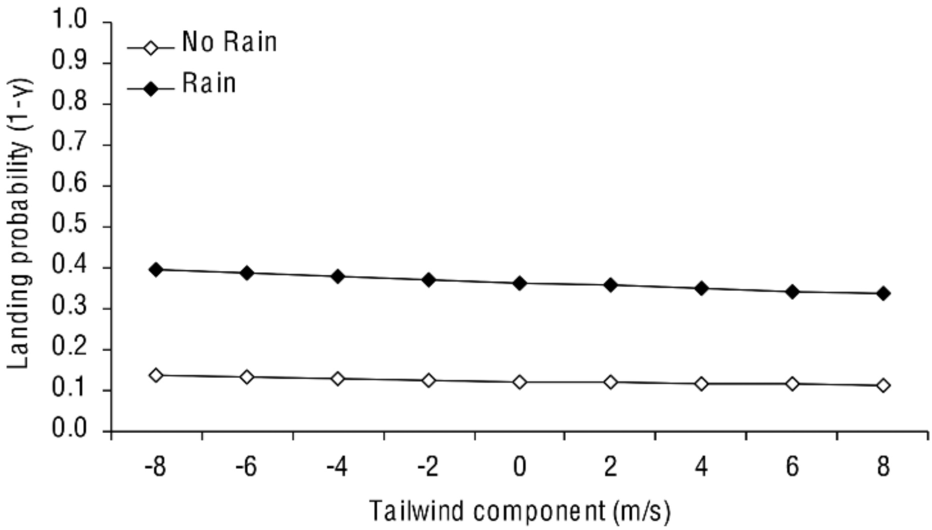

FIG. 3.—Landing probabilities (1-γ) under rainy and dry conditions at night for increasing tailwind component values, resulting from averaging the ten alternative models from table 1 according to their AICc weights.
[Probabilidades de parar (1-γ) bajo condiciones de lluvia y no lluvia durante la noche para valores crecientes del componente de cola, resultantes de promediar según sus pesos AICc los 10 modelos alternativos de la tabla 1.]

et al., 1998; Pérez-Tris and Tellería, 2001; De Neve *et al.*, 2010), could make juveniles more vulnerable to adverse weather conditions (Saino *et al.*, 2010). However, sedge warblers passing through Iberia do not present age-related wing morphology differences (M. Andueza, pers. obs.), and, as a result, no differences in flight efficiency would occur between age categories.

In this work we studied landing decisions at a single sampling site, Jaizubia, which can be considered a suboptimal fuelling site for sedge warblers (Bibby and Green, 1981; Grandío, 1998; Schaub and Jenni, 2000a, b; Wernham *et al.*, 2002). Hence, our stopover site is likely to be used more as an emergency or secondary stopover site than as a targetted destination, given that sedge warblers were found to leave Jaizubia under good weather conditions independently of their fuel loads (Andueza *et al.*, 2013b). Our results refer to the influence of rain, wind and age on the interruption of nocturnal migration at a particular suboptimal stopover site, so whether the relative role of such factors varies along the route or depending on the stopover quality of sites (Dierschke and Delingat, 2001; Schaub *et al.*, 2008), needs further research.

CMR models turned out to be useful for analysing the influence of weather on landing decisions of migrants, particularly in relation to small passerine birds captured abundantly at a stopover site, since our modelling results were consistent with those obtained from a simple analysis on changes in bird abundance. Also, in agreement with previous work (Schaub *et al.*, 2001), we have shown that migrants at our site were not necessarily newly-arrived birds on first capture. Thus, CMR models provide more accurate results than analyses of changes in bird abundance since capture probabilities, and hence birds which are present in the area but are not seen, are taken into account. Also, in contrast to the classic approach, whose results are more limited, CMR allows quantifying the effect of the studied factors at a population level in the form of landing probabilities, as well as inferring the relative importance of such factors.

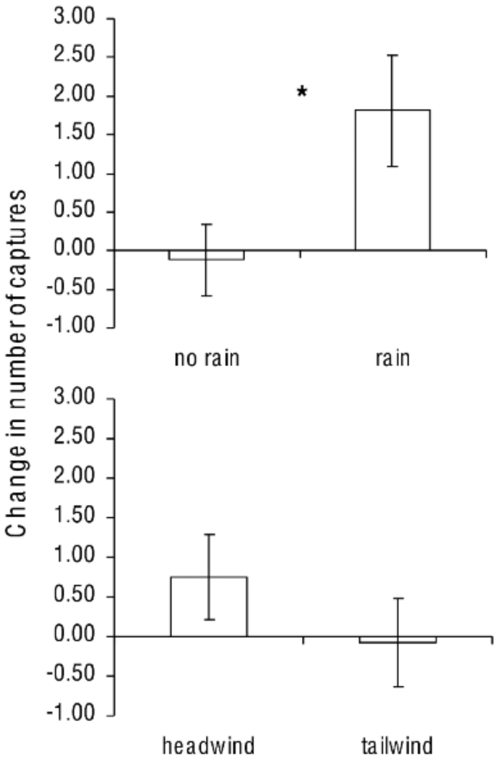

FIG. 4.—Changes in numbers of first captures from one day to the previous one (median values ± interquartile ranges) in relation to rain (rainy nights n = 15; dry nights n = 78) and wind conditions (tailwind nights n = 62; headwind nights n = 31) during the nights preceding capture days. * indicates significant differences (P < 0.05).
[Cambio en el número de primeras capturas de un día para otro (se muestra la mediana ± rango intercuartil) según las condiciones de lluvia (noches lluviosas n *= 15; noches no lluviosas* n *= 78) y de viento (noches con vientos de cola* n *= 62; noches con vientos de cara* n *= 31). * indica diferencias significativas (P < 0,05).]*

However, this methodology could only be used to study landing probabilities in certain cases. In particular, CMR models are appropriate to study the factors that interrupt nocturnal migration, under which conditions birds arrive, such as adverse weather conditions. This is especially the case at suboptimal stopover sites where migrants would not otherwise have stopped. However, the method may not be suitable for studying the factors that determine the selection of stopover sites, i.e. inferring the landing probabilities of birds approaching a stopover site in relation to certain factors, which can be highly influenced by habitat availability and individual energy reserves. As a result, the use of CMR models may not be appropriate for analysing the effects of several other factors on landing probabilities, such as fuel load or conspecific abundance. Studying landing probabilities in relation to, for example, sedge warbler abundance at a site using this methodology may result in trivial conclusions unrelated to actual nocturnal movements, as landing probabilities are highly dependent on passage intensity: after nights when many sedge warblers have landed, their numbers increase at a site, thus resulting in higher γ values for increasing sedge warbler abundance. In conclusion, despite the limitations of CMR models for studying landing decisions, they can be a suitable methodology for studying situations in which alternative biological or ecological determinants may be excluded *a priori*.

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